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RECENT AND FOSSIL VIVIPARIDAE.

A STUDY IN DISTRIBUTION, EVOLUTION AND PALAEOGEOGRAPHY.

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(Plate XIX.)

CONTENTS.

1. INTRODUCTION.

The following paper does not presume to be a monograph or a systematic revision of the recent and fossil Viviparidae, but is the result of my examination of extensive collections of the family and a careful scrutiny of the literature on the subject. The work was started in connection with my studies on the development and formation of the sculpture on the shells of the different members of the family. On working through the literature on the subject it was found that the question of the nomenclature of the species of this family was greatly confused, and that no attempt had hitherto been made to classify into groups, genera or subgenera, the species which have similar types of shells and which are evidently related to one another. Further, no author has so far considered the relationships of the recent and the fossil species of the family, and I have not found any account of the evolution and distribution of the family as a whole.

While working on the distribution of the family I was greatly struck by its peculiar and restricted distribution, and the relationships of the various members found in different parts of the world. It was not, however, till the sketch-map illustrating the distribution of the family was prepared at the suggestion of Professor J. H. Ashworth, that the full significance of the facts about the distribution of the family became clear, and it was considered of sufficient importance to go further into details.

The latest monograph on the recent species of the family was completed by Kobelt [1] in 1909, but this work, though based on extensive collections, most of which I have also been able to examine, and copiously illustrated, is very faulty and difficult to use. The author devoted himself mainly to the description of the species of the Old World, but did not consider the relationships of the forms found in different areas, and paid no attention to the question of the distribution of the family as a whole. In the case of the Palaearctic species he casually referred to the distribution of the recent species and their relationship to the ancestral fossil species, but he did not deal with the subject in any detail. In the following account the recent species are treated in accordance with the countries, rather than the zoo-geographical regions, in which they are found. The justification for this course will be clear from my remarks on zoo-geographical regions (pp. 157-160). Detailed literature, lists and synonymies are not included, but references to all important works, where earlier literature will be found, are given as foot-notes. Kobelt's work referred to above is throughout cited as " Kobelt's Monograph."

The literature on the fossil species is very scattered and it has entailed unremitting labour for some months to get together the works on the forms of different areas. In this connection I have to acknowledge the great help I received from Dr. W. Wenz of Frankfurt a. Main, Germany, and from the staff of the Geological Department of the British Museum (Natural History), South Kensington, London, during the time that I was working in that institution. Cossmann's work [2] contains a review of the various fossil genera and subgenera and a list of the main distinguishing forms of the different strata in different areas, but the work is far from satisfactory.

As an introductory chapter I have included some remarks about the methods of dispersal of the members of this family, while the question of the evolution of the family and its relationships are discussed at the end.

In view of the excellent figures of both recent and fossil Viviparidae that have been published in recent works by most of the authors cited in the text, I have not thought it

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[1] Kobelt, W., *Martini and Chemnitz Conch.-Cab.* (*n.f.*), *Paludina* Lam.—*Vivipara* Montf., pp. 96-430, pls. xv-lxxvii (1906-09). The exact dates of publication of this work are pp. 97-128, pls. xv-xix, xxi (1906), pp. 129-200, pls. xx, xxii-xliv (1907), pp. 201-312, pls. xlv-lvii, lx-lxiv (1908), pp. 313-430, pls. lviii, lxix and lxv-lxviii, (1909).

[2] Cossmann, M., *Essais Palèoconch. Comp.* XII, pp. 176-187 (Paris, 1921).

necessary to give many figures. A plate showing the more interesting types of the members of this family, and also the various types of sculpture is, however, published at the end of this paper.

The work was mainly carried out in the Zoological Department of the Edinburgh University, and I have to record here my great indebtedness to Professor J. H. Ashworth for his kind help and valuable criticisms. I am also indebted to Dr. F. A. Bather, Keeper of the Department of Geology of the British Museum, London, Mr. L. R. Cox in charge of fossil, and Mr. G. C. Robson in charge of the recent Mollusca in the same institution for the facilities given me for examining the collections under their charge. Dr. F. Haas, Frankfurt a. Main, and Professor Dr. F. Drevermann of the Senckenberg Museum, were also kind enough to give me all facilities for examining the very rich collections in their Museum. I am also indebted to Dr. Bryant Walker of Detroit, Michigan, Dr. P. Bartsch of the United States National Museum, Washington, Dr. P. Dautzenberg of Paris, Dr. L. Germain of the Natural History Museum, Paris, Dr. L. F. de Beaufort and Dr. T. van Benthem-Jutting of the Natural History Museum, Amsterdam, Dr. J. Thiele of the Berlin Museum, and Mr. W. A. Lindholm of the Zoological Museum, Leningrad, for material and information regarding the collections of Viviparidae. Last, but not least, I have to acknowledge the very great courtesy of the authorities of the Universitets Zoologiske Museum, Copenhagen, for sending me on loan some of the type-specimens out of the collection of O. F. Müller.

2. DISTRIBUTION.

Before discussing the distribution of the Viviparidae it is necessary to consider the methods of dispersal of these molluscs, as without a consideration of these facts it is impossible to understand the various factors which have determined the past and the present distribution of the family.

All the members of this family, with the exception of the estuarine genus *Larina* A. Adams,[1] are freshwater forms, and none are found in marine or brackish-water areas. They inhabit rivers, streams, lakes, ponds, pools, marshes, etc., and are particularly abundant in areas where the right type of succulent aquatic vegetation is common. In this connection it is of interest to note here that though *V. bengalensis* (Lam.) is quite common in the rice-fields on the islands in the reclaimed area of the Gangetic Delta, I have never found any living individuals of the species in the brackish-water streams which run in between these islands. This may partly be due to the absence of the right type of food in these streams, but the main factor inhibiting the occurrence of the species in these streams is, in my opinion, the salt in the water.

The food of these animals consists mainly of succulent aquatic plants, algae, etc., but occasionally they become carnivorous and feed on the dead carcasses of snails, etc.[2]

The respiration of the Viviparidae is entirely aquatic and is carried on by means of a ctenidium. The mantle[3] also in some cases has been assigned as an accessory respiratory organ, but the entire respiration must be aquatic, and save under very exceptional circumstances, and then only temporarily (see Sewell, *loc. cit.* p. 285), the animals are not able to breathe oxygen directly from the atmosphere. In this connection reference may be made

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[1] As is discussed further on (p. 165), the genus *Larina* A. Adams is doubtfully included in the Viviparidae.

[2] See Sewell, R. B. S., *Rec. Ind. Mus.* XXII, p. 287 (1921).

[3] See Annandale, N., *Rec. Ind. Mus.* XXII, p. 349 (1921) and *Proc. Roy. Soc. London* (B) XCVI. p. 73 (1924).

to the structure of the respiratory organ or ctenidium. The monopectinate ctenidium or gill consists of a large number of roughly triangular lamellae hanging into the branchial chamber from its roof somewhat to the right of the middle line. Respiration is carried on by a more or less continuous stream of water entering the branchial chamber over a channel formed by the right pseudoepipodial lobe. The water after washing the branchial lamellae passes out over the left pseudoepipodial lobe.

The Viviparidae are operculate Gastropods, and are able to withdraw themselves entirely within their shells, the aperture of the shell being closed by a tightly fitting horny or semi-calcareous operculum. In this condition they are able to live for short periods. The only definite observation on the subject, so far as I can find from the literature, is that of Christy,[1] who kept *V. viviparus* (Linn.) dry for a period of over three weeks exposed on dry ground without in any way injuring the animals. Under exceptional conditions of drought, temperature, etc., species are capable of aestivating for varying periods.[2] At such times they lie deeply embedded in the semi-dried mud at the bottom of pools, lakes, etc., with the animals withdrawn into the shells, but there can be no doubt that they cannot live in this condition for very long periods.

Low temperature probably plays an important part in the distribution of the Viviparidae but beyond the fact that they are not found in the polar regions, there are no definite observations available as to the exact influence of this factor.

The family, as the name suggests, is viviparous, but some authors have described it as ovo-viviparous. The uterus of the female contains embryos in various stages of development, and whereas the oldest embryos are fully developed, those in the upper part of the uterus are still in the very early stages of development. There are no records of any observations regarding these very young embryos being shed at the same time as the fully developed young, and their ability, or otherwise, to develop further in the open. In the case of *V. viviparus* (Linn.) that were kept in aquaria I found that normally none of the young embryos are shed at the time of the birth of the fully-developed ones, and those that were accidentally extruded were unable to develop further and perished. The family, therefore, appears to be entirely viviparous. The fully developed embryos differ from the adults in size and in having the shell ornamented with three spiral rows of minute curved chaetae on the shells. These curved chaetae are of the nature of protective organs, and can not possibly be of any use in the dispersal of these snails. The only observations on the numbers of the embryos in the uterus of the different members of the family are those of Swammerdam,[3] Sewell,[4] Annandale[5] and Rao.[6] From these observations and the large number of forms examined by me it is clear that, in species which live in streams and other areas where the struggle for the perpetuation of the species is very keen owing to the chances of large numbers of the embryos being destroyed by floods and other causes, the number of embryos is very large and the latter are consequently of small size. In the case of the essentially lacustrine species, on the other hand, as was noted by Annandale for *Taia intha,* and as I can confirm for

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[1] Christy, R. M., *Zoologist* (3) V, p. 181 (1881), and Kew, H. W., The *Dispersal of Shells*, p. 28 (London, 1893).

[2] See Benson, W. H., *Gleanings in Science*, I, pp. 363-365 (1829), and II, pp. 125, 126 (1830).

[3] Swammerdam, J., *The Book of Nature* (English translation by T. Flloyd), pp. 76-78 (London, 1758).

[4] Sewell, R. B. S., *Rec. Ind. Mus.* XXII, p 235 (1921).

[5] Annandale, N., *Proc. Roy. Soc London* (B) XCVI, p. 70 (1924).

[6] Rao, H. S., *Rec. Ind. Mus.* XXVII, pp. 129-135 (1925).

Neothauma tanganyicense (Smith) and a number of species of the sub-genus *Dactylochlamys* Rao from the Philippines, the number of embryos is decreased in correspondence with the increase in size of the full-grown embryos. With this great increase in size, which involves a correspondingly longer period of gestation, the chaetae on the embryonic shells are also reduced or even entirely lost before the young are born.

As is well known, the Viviparids are unisexual, and for these snails to be established in any new area after transplantation it is essential that at least two individuals of a species, a male and a female, or in exceptional cases a gravid female must be transported at the same time.

With reference to the question of transportation, whether active or passive, by birds and other animals, the difficulties in the case of these snails are too great to be surmounted. The adult shells are too big to be carried sticking to the mud on the feet of the animals and they do not possess any special organs of attachment.[1] The embryonic shells are too delicate to withstand long journeys, and would most probably be crushed by the drying up of the mud during transportation. Further, the difficulty in the way of transplantation of the species, unless males and females were carried at the same time, has already been referred to. The extinct reptiles, as suggested by Sollas,[2] could not have played any important part in the distribution of the family.

From the above it is clear that the only factor for the dispersal of this family, therefore, is the water-channels.

In flowing streams the snails could easily be carried by the current and spread throughout the watersheds of the rivers. Floods are probably responsible for their occurrence in areas at present cut off from the main streams. In this way many species of the family have become established in areas where no Viviparids were found before.

Man is also responsible for the introduction of the snails of this family in certain areas, where the conditions are suitable, but where no members of this family were found owing to the areas being not connected with any of the river-basins in which the family flourished. An example of this type is the introduction of some Japanese species in various places along the Pacific coast of North America within recent years by the Japanese labourers who use the snails as articles of diet.[3]

3. ZOO-GEOGRAPHICAL REGIONS.

Various views have been held by different authorities as to the limits to be assigned to zoo-geographical studies, and it is necessary, therefore, to outline the plan followed in this paper. Older authorities like Wallace, Huxley, Sclater, Sharp and others mainly considered the present-day distribution of the various groups of the Animal Kingdom with only a casual reference to the geological history, and from the data obtained attempted to divide the surface of the earth into zoo-geographical regions or realms. In fact, as Ortmann[4] has

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[1] See Kew, H. W., *The Dispersal of Shells*, p. 86 (London, 1893), who rightly concluded that the operculate snails can not for any length of time become attached by entrapping any part of the animals between the aperture and the operculum.

[2] Sollas, W. J., *The Age of the Earth*, pp. 183, 184 (London, 1905).

[3] See for example Hannibal, H., *Nautilus*, XXII, p. 33 (1908) and XXV, pp. 31, 32 (1911). Also Walker, B., *Univ. Michigan, Miscellan. Pub.* VI, p. 126. (1918).

[4] Ortmann, A. E., *Proc. Amer. Phil. Soc.* XLI, p 271 (1902).

rightly remarked, " any research in this direction is deemed incomplete that is not finished by the creation or discussion of ' regions ' " This method resulted in the division of the earth's surface into a varying number of realms or regions, 21 according to Schmarda,[1] 6 according to Sclater[2] and Wallace,[3] 2 according to Huxley,[4] 7 according to Blyth,[5] 9 according to Gill,[6] 3 according to Blanford,[7] 4 according to Dahl,[8] and various others. The regions were further sub-divided into subregions or provinces, and no two authors agreed as to their number or limits. In most of these schemes the divisions were mainly based on the distribution of mammals and birds, but even in these cases, as pointed out above, there was no agreement upon a uniform scheme. In spite of Wallace's[9] stout defence of his slightly modified scheme of Sclater as being applicable to all groups it is clear that no one scheme will serve equally for all groups. A detailed history of the subject is to be found in the works of Wallace (*loc. cit.*), Blanford (*loc. cit.*), Gadow,[10] Lydekker,[11] Ortmann,[12] the Sclaters,[13] the introductory pages of Bartholomew's Atlas[14] and Dahl (*loc. cit.*) and it is not necessary to go into details here.

The more recent trend of zoo-geographical studies, on the other hand, has been to work out the present distribution of the various groups in different areas, and, so far as possible, correlate it with the distribution of the allied forms in adjacent areas, collating it with the geological history of the group with a view to elucidating the relationships and probable lines of evolution and migration of the various members at different periods of the earth's history. This introduction of Palaeogeography into zoo-geographical studies has led to very interesting results, and the zoo-geographical regions in these cases have been used merely as a matter of convenience. Palaeogeography in its relation to zoo-geography has been dealt with in detail for all groups of the Animal Kingdom by Arldt in his voluminous work,[15], and reference may be made to it for the earlier literature.

As remarked in the introductory chapter, the distribution of the Viviparidae in the following pages is treated according to the geographical rather than the zoo-geographical regions. This course was found more satisfactory than proposing a new scheme for this family of molluscs only. As will be clear from the sketch-map the distribution does not correspond to any of the accepted schemes, nor do the relationships of the forms found in adjacent areas justify the division into regions of the types hitherto accepted.

Except for the maps in the Atlas of Bartholomew referred to already, no maps of the distribution of the various families of aquatic gastropods are available. The authors in this

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[1] Schmarda, K., *Die geographische Verbreitung der Thiere.* (Wien, 1853).

[2] Sclater, P. L., *Journ. Proc. Linn. Soc.* (*Zool.*) II, pp. 130-145 (1858).

[3] Wallace, A. R., *The Geographical Distribution of Animals, etc.*, Vols. I, II. (London, 1876).

[4] Huxley, T. H., *Proc. Zool. Soc. London*, pp. 294-319 (1868).

[5] Blyth, E., *Nature*, III, pp. 427-429 (1871).

[6] Gill, T., *Proc. Biol. Soc. Washington*, II, pp. 1-39 (1884).

[7] Blanford, W. T., *Proc. Geol. Soc. London*, pp. 76, 77 (1890).

[8] Dahl, F., *Ökologische Tiergeographie*, I, pp. 102-106 (1921).

[9] Wallace, A. R., *Nature*, XLIX, pp. 610-613 (1894).

[10] Gadow, H., *Vogel* in *Bronn's Kl. & Od. Thier-Reichs*, II, pp. 283-297 (1893).

[11] Lydekker, R., *A Geographical History of Mammals*, pp. 25-27. (Cambridge, 1896).

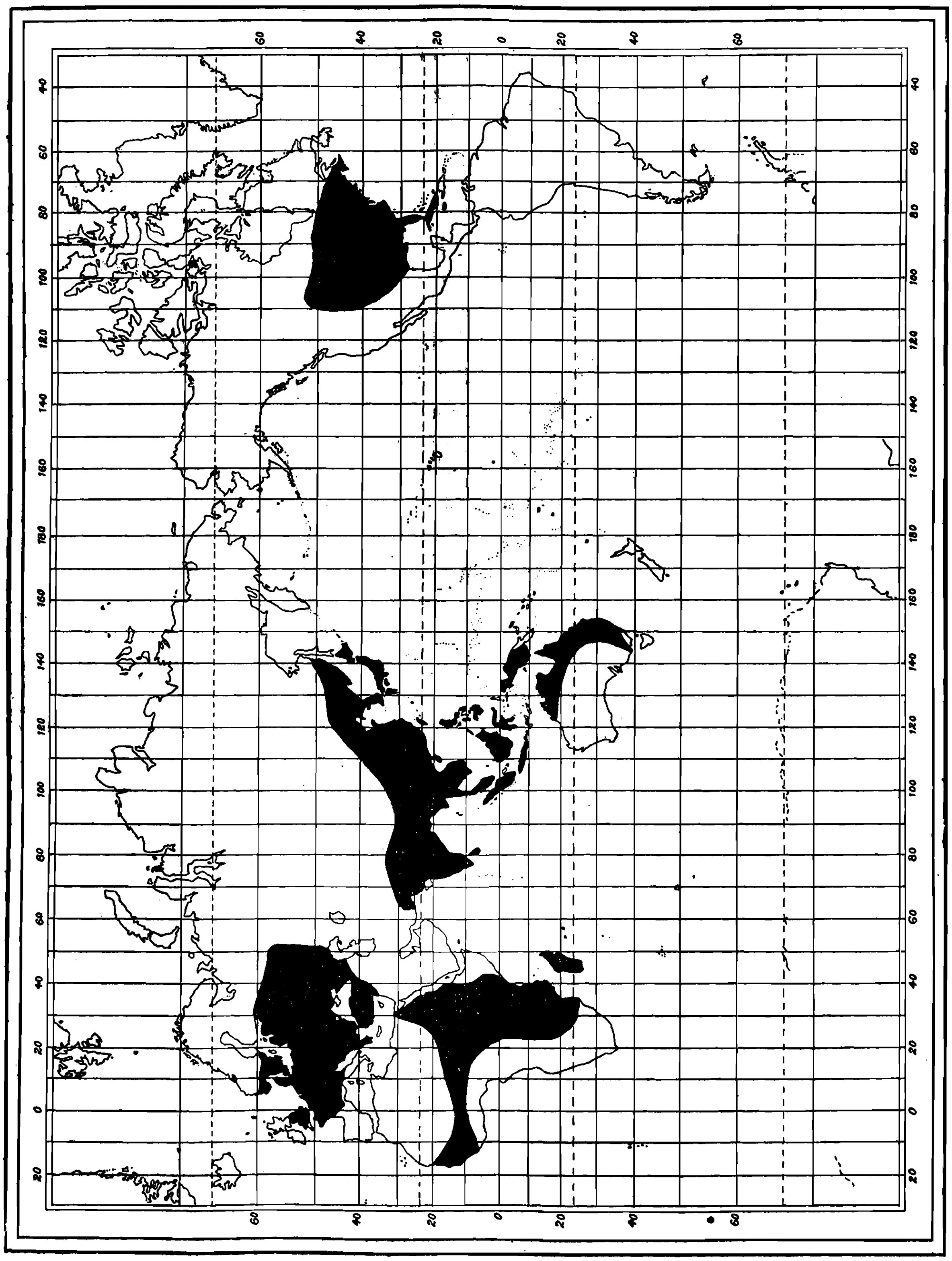
[12] Ortmann, A. E., *Grundzüge der marinen Thiergeographie*, pp. 1-14. (Jena, 1896).

[13] Sclater, W. L., & P. L., *The Geography of Mammals*, pp. 7-15. (London, 1899).

[14] *Atlas of Zoo-geography* in *Bartholomew's Physical Atlas*, V, pp. 4, 5 (Edinburgh, 1911). See also Germain, L. *Ann Geogr.* pp. 20-28 (1912).

[15] Arldt, T., *Handbuch der Palaeogeographie*, Vols. I, II. (Leipzig, 1917-22).

atlas published a map of the distribution of the Viviparidae (pl. XXVIII, map i), but the map is far from correct and does not even correspond to the authors' account of the distribution of the family (*op. cit.* p. 51). For the maps illustrating the distribution of the family in certain areas only, reference may be made to the map of North America by Call,[1] and the



Sketch Map illustrating the distribution of the Recent Viviparidae. The dark areas represent the regions from which members of the family have been recorded.

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[1] Call, R. E., *Amer. Journ. Sci.* XLVIII, map (1894).

one illustrating the distribution, of certain forms only, in Africa by Germain.[1] In the present paper only a single map illustrating the distribution of the family over the whole world is published, while detailed accounts of the distribution of the various members in different areas are included in the text. For want of sufficient information, separate maps for different areas have not been prepared.

4. RECENT VIVIPARIDAE.

The name Viviparidae was proposed by Gray[2] in 1847 for a number of genera with the genus *Viviparus* Montfort as the type of the family; of the other genera assigned to the family none is at the present day included in it. Some authors, namely von Martens and certain others, however, objected to the name *Viviparus*, with a masculine ending, as being inappropriate for a genus all the members of which bring forth living young ones, and adopted either the name *Vivipara* Lamarck (1809, suggested as the French word " Vivipare," and hence not available) or *Paludina* Lamarck suggested by this author in 1812, two years after Montfort's name. Kobelt in his Monograph tried to get over the difficulty by suggesting *Vivipara* Montfort *emend.* Kobelt, as the name for the genus, but that would lead to confusion with Lamarck's name which for a long time has been adopted by various authors. The masculine ending is not a serious difficulty as so many of the generic names are certainly incorrect either etymologically or because of their incorrect genders. If changes were to be made simply for the sake of emending the grammatical mistakes on the parts of the authors who proposed generic names, many well known names would require modification.[3] The generic name *Viviparus* and the family name Viviparidae have been adopted by most of the workers in the British Isles and in America, and I propose to employ these designations in this paper.

The question of the recent genera to be included in the family was discussed by Clessin [4] at length, and, basing his conclusions on the differences in the radula and in the form of the shell and of the operculum he distinguished the genera *Vivipara*, Lamarck, *Campeloma* Rafinesque *Tulotoma* Haldeman, *Lioplax* Troschel and *Cleopatra* Troschel. Fischer[5] among the recent forms only recognised the genera *Paludina* Lamarck and *Lioplax* Troschel, and for the fossils also included the genus *Tylopoma* Brusina. In the genus *Paludina* he included as subgenera *Paludina*, *Neothauma* Smith, *Cleopatra* Troschel, *Melantho* Bowdich (=*Campeloma* Rafinesque) and *Tulotoma* Haldeman, but he changed the latter from its incorrect tymology to *Tylotoma*. In the subgenus *Paludina* he further recognised the sections *Paludina* s.s., *Mekongia* Crosse and Fischer, ?*Margarya* Nevill, and *Eyrisia* Fischer.

Kobelt's proposed emendation of the generic name *Viviparus* has been referred to above. In his Monograph he considered Fischer's sections *Neothauma* and *Margarya* and the sub-

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[1] Germain, L., *Res. Sci. Voy. G. Babault dans l'Afrique Orient. Angl., Moll. Terr. et Fluv.* I, p. 231, fig. 111. (Paris, 1920). Since this paper went to the press, I have received a reprint of Pilsbry & Bequaert's valuable work on the Aquatic Molluscs of the Belgian Congo (*Bull. Amer. Mus. Nat. Hist.* LIII, pp. 69-602, 1927), in which the authors have published a map showing the distribution of the genus *Viviparus* in Africa (Map 1, p. 204).

[2] Gray, J. E., *Proc. Zool. Soc., London,* XV, p. 155 (1847).

[3] In this connection see also Dall, W. H., *Trans. Wagner Inst. Philadelphia,* III, pp. 332-335 (1892) and Smith, E. A., *Proc. Zool. Soc. London,* pp. 635, 636 (1893).

[4] Clessin, S., *Malakozool, Blätt.* (n. f.) II, pp. 161-196 (1880).

[5] Fischer. P., *Man. Conchyliol.*, pp. 732-734. (Paris, 1885).

genus *Cleopatra* as being of generic rank, but made no remarks about the others. He, however, added that Heude's genus *Rivularia* from China should be added to the list. Kobelt does not mention the section *Idiopoma* which was proposed by Pilsbry[1] in 1901 for an Indian species, but this, as is discussed further, is only a synonym of the Vivipari Dissimiles Group.

Since the publication of Kobelt's Monograph Hannibal [2] proposed the name *Cipangopaludina* as a section of *Idiopoma* Pilsbry, for the Japanese species *Paludina malleata* Reeve. This name, in spite of the incorrect relationships as understood by the author, will have precedence over *Lecythoconcha* Annandale. Three other generic names *Taia* Annandale *Heterogen* Annandale and *Dactylochlamys* Rao have since been proposed for the Asiatic forms.

Thiele [3] has recently removed *Cleopatra* Troschel to the sub-family Paludominae, but the present state of our knowledge of the anatomy of this genus does not warrant this course. In the family Viviparidae he includes only the genera *Viviparus* Montfort (=*Paludina* Lamarck), *Rivularia* Heude, *Margarya* Nevill, *Neothauma* Smith, *Campeloma* Rafinesque and *Lioplax* Troschel.

With the exception of the genera *Cleopatra* Troschel and *Larina* A. Adams, which I include provisionally in the family, I am of opinion that all the other divisions are of the rank of subgenera only. The anatomical differences, so far as they are known, would not justify their being considered as distinct genera. These subgenera with their distribution are as follows :—

Viviparus Montfort.—Europe, Africa, Asia, Australia and North America.
Cipangopaludina Hannibal.—Asia.
Dactylochlamys Rao.—Asia.
Taia Annandale.—Burma, Asia.
Margarya Nevill.—Yunnan, China, Asia.
Rivularia Heude.—China, Asia.
Heterogen Annandale.—Japan, Asia.
Mekongia Crosse & Fischer.—Siam, Cambodia, etc., Asia.
Neothauma Smith.—Africa.
Tulotoma Haldeman.—North America.
Campeloma Rafinesque.—North America.
Lioplax Troschel.—North America.

In the subgenus *Viviparus s.s.* it is possible to distinguish five groups of forms, (i) European, (ii) Asiatic, (iii) Australian, (iv) African, and (v) North American. These groups differ from one another in having different numbers of colour-bands on the shells. The European species have three colour bands, the Asiatic are uniformly coloured or with many bands, while there is a varying number of bands confined to above the periphery in the Australian, the African forms are uniformly coloured, and the North American species have four bands. Anatomically the five groups are very similar, and the shells also do not show any other

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[1] Pilsbry, H. A., *Proc. Acad. Nat. Sci. Philadelphia*, LIII, p. 189 (1901).

[2] Hannibal, H., *Proc. Malacol. Soc. London*, X, p. 194 (1912).

[3] Thiele, J., In Kükenthal & Krumbach *Handbuch der Zoologie*, V, p. 83, (Berlin, 1925).

distinguishing characteristics. I have some doubts about the Australian forms being genetically connected with the Asiatic forms, but, as is discussed further on, the other three groups must have originated from separate ancestral forms, and the similarity in the form of the shells and the animals is only an example of parallel evolution, or in other words the genus, as hitherto understood, has arisen polyphyletically. For this reason it may later on be desirable to separate these groups into distinct genera or subgenera, but for the present I propose considering them as all members of the heterogenous name *Viviparus s.s.*

The relationships and the evolution of the various subgenera are discussed later.

The distribution of the recent Viviparidae of different regions is considered in detail in the accounts of the various areas, but it may be noted here that no recent forms are known from the whole of South America, New Zealand, Tasmania, Polynesia and various parts of the different continents mentioned in the detailed account further on.

I. ASIA.

The Viviparidae, both recent and fossil, have a very peculiar distribution in Asia. As is shown in the sketch map, no Viviparids are found in the greater part of Asia Minor, Arabia, Iraq, Persia, Afghanistan, Tibet, the whole of Central Asia, Mongolia, the greater part of China and, with the exception of the Amur Basin, the whole of Asiatic Russia. Members of this family, however, form a very important element in the freshwater fauna of Eastern Asia and India, and this region may be defined as forming a broad band starting from the Amur Basin in the north, and broadening down south to include the greater part of south-eastern China including Yunnan, French Indo-China, Siam, the Malay Peninsula and Burma, India and Baluchistan to the eastern frontiers of Persia. In the Indo-Pacific Islands the family is well represented in the Japanese Islands with the exception of Sakhalin, Formosa (Taiwan), Hainan, the Philippine Islands, Celebes, the greater part of New Guinea, and most of the islands of the groups of Great and Small Sunda Islands.

India and Burma.

I propose treating the Viviparids of India and Burma[1] first, not because it is the central region of the distribution of this family but because I am better acquainted with the forms of this region. Further, the species of this area are better known both in regard to their anatomy and their distribution than those of any other country. Leaving aside the estuarine genus *Larina* A. Adams, there are in addition to *Viviparus s.s.* three other sub-genera, *Cipangopaludina* Hannibal, *Dactylochlamys* Rao and *Taia* Annandale, known from this region. In the genus *Viviparus s. s.*, I recognise two groups for which I have adopted the names Vivipari Bengalenses and Vivipari Dissimiles as proposed by Annandale.[2]

Vivipari Bengalenses Group :—The central species of this group I consider to be the widely distributed Indo-Burmese species *V bengalensis* (Lamarck) (pl. xix, fig. 1). It seems to be a direct representative of the European species *V viviparus* (Linn.)—the type species of the genus, but there can be no question that the two species are not even remotely

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[1] For literature on the Viviparids of this area see in addition to Kobelt's Monograph, Hanley, S. & Theobold, W., *Conch. Indica*, (London, 1870-76) ; Nevill, G., *Hand-List Moll. Ind. Mus.* II, pp. 18-31 (Calcutta, 1886); Preston, H. B., *Faun. Brit. Ind. Freshw. Moll.* pp. 83-94 (London, 1915).

[2] Annandale, N., *Rec. Ind. Mus.* XIX, p. 112 (1920) and XXII, p. 543 (1921).

connected and certainly have not descended from the same ancestors. As is discussed further (p. 245) these banded species found in such widely separated areas as North America, Europe and Eastern Asia afford a very nice example of Parallel Evolution of smooth-shelled species with varying numbers of colour-bands on the shells. With Annandale [1] I include in this group all the Indo-Burmese species with a thin, more or less smooth shell, and having a varying number of more than three colour-bands on the shells. The embryonic shell is delicate and thin, and has three primary rows of chaetae on low ridges on the various whorls. Of the three ridges the lowest or the peripheral forms a regular keel and is the best developed. In some cases secondary ridges are also developed between the primary ones and these also bear chaetae. In addition to the forms included by Annandale in this group I assign to it *V. nagaensis* Preston.

Vivipari Dissimiles Group :—With Annandale I consider *V. dissimilis* (Müller) (pl. xix, fig. 2) to be the central species of this group, but differ from him as to the forms which are to be included in the group. His Vivipari Sindicae Group is also a synonym of the Vivipari Dissimiles. From my examination of the Viviparids of all parts of Eastern Asia I believe that the members of this group have migrated all over this area, and though the type-species is confined to India and Burma only, nearly related species or forms derived from it are found in China and Japan on the one hand and in the Malay Peninsula, Siam, Cambodia, Cochin-China, Annam and the East Indies on the other. The main distinguishing feature of the group is the entire absence of colour-bands on the shell. The typical forms have a smooth shell, but feebly ridged and even keeled forms are also found. The three primary ridges bearing cheatae are developed on the embryonic shells, and in addition a number of secondary ridges are also developed.[2] Pilsbry's[3] section *Idiopoma*, based on differences in the operculum, is only a synonym of this group.

In addition to *V. dissimilis* (Müller) and its varieties *assamensis* Nevill and *kutchensis* Nevill, I include in this group *V. variatus* (Frauenfeld) and its vars. *pseudohelicina* Kobelt and *peguensis* Kobelt, *V. ceylanica* (Dohrn), *V. crassus* (Benson), *V. remossi* (Philippi), *V. henzadensis* Pilsbry, *V. micron* Annandale, *V. heliciformis* (Frauenfeld) and its var. *viridis* (Reeve), and *V. sindica* Nevill.

It may also be noted that Swainson's *Paludina carinata* [4] is only a synonym of *V. dissimilis.*

Cipangopaludina Group :—The generic name *Lecythoconcha* was proposed by Annandale [5] for the species *Paludina lecythis* Benson (pl. xix, figs. 8-10) from Manipur, Assam. The species belongs to the same subgenus as the Japanese *Paludina malleata* Reeve, and this species had earlier been separated under the subgeneric name *Cipangopaludina* by Hannibal,[6] who, however, treated it as a section of *Idiopoma* Pilsbry. This latter conclusion is quite wrong, but Annandale's name must be replaced by the earlier *Cipangopaludina* Hannibal. The adult shell is large, globose, with broad swollen whorls. The shell is smooth and without any trace of ridges or any other kind of sculpture. The colour of the

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[1] Annandale, N., *Rec. Ind. Mus.* XXII, pp. 267-278, pls. i, ii (1921).

[2] Annandale, N., *Rec. Ind. Mus.* XXII, p. 245, fig. 10 (1921).

[3] Pilsbry, H. A., *Proc. Acad. Nat. Sci. Philadelphia*, LIII, p. 189 (1901).

[4] Swainson, W., *Zool. Illustra.* Ser. I, pl. xciii (London, 1820-23).

[5] Annandale, N., *Rec. Ind. Mus.* XIX, p. 114 (1920).

[6] Hannibal, H., *Proc. Malacol. Soc. London*, X, p 194 (1912).

shells is uniform and no colour-bands are to be seen either externally or inside the shell. The embryonic shell, as Rao[1] has recently described and I can confirm from my own observations, is also unbanded. The very young shell has a well developed peripheral keel and two faint ridges above it; all the three ridges bear curved chaetae. In slightly older shells the upper ridges become obsolete and the peripheral keel is also much less prominent. I believe that the genus is closely allied to the Vivipari Dissimiles and is to be derived from species of that group. It is represented by a single species, with a number of phases, in India in the Manipur Valley, and in Upper Burma from near Tenasserim, whence it was recorded by Nevill as *Paludina siamensis* var. *burmanica* Nevill.[2] The Indian species and its phases have been fully discussed by Annandale[3] and I have nothing to add to his account. The further range of the genus is interesting. It extends through Burma, Siam, Cochin-China into China, Korea and Asiatic Russia in the Amur region, and thence to Japan on the one hand, and through the Philippines into Java on the other.

Dactylochlamys Group:—Rao [4] has recently proposed to separate the peculiar thin-shelled and hollow-ridged species *Paludina oxytropis* Benson (pl. xix, fig. 11) from the Loktak Lake, Manipur, Assam, into a new genus for which he has proposed the name *Dactylochlamys*. The shell is of fair size, rather thin and delicate and ornamented with a number of hollow, spiral ridges. The colour of the shell is uniform but the ridges appear rather darker. As will be seen under the account of this subgenus (*infra* pp. 175, 176) I assign a number of solid-ridged species also to this group, as I believe that they have been developed by greater deposits of shell substance on the inner surface. The embryonic shell is rather elongate and has a very well developed peripheral keel and, in very young embryonic shells, only two more ridges above it ornamented with long curved chaetae. In older shells a number of other ridges with chaetae are also formed. The subgenus is represented by the type-species *D. oxytropis* (Benson) and *D. microchaetophora* (Annandale) [5] in the Manipur Valley, Assam, and probably also extends into Burma. I believe that *Dactylochlamys* is also allied to the Vivipari Dissimiles and is evolved from some thin-shelled species of this group. The genus, if my interpretation of its development is correct, has a very wide range in the Malay Peninsula, Sumatra, Java, Celebes, the Philippines on the one hand and in China and Japan on the other.

Taia Group:—The name *Taia* was proposed by Annandale[5] for a very interesting group with a peculiarly developed callus of recent and subfossil species of the family Viviparidae from the Inlé Lake Basin, Southern Shan States, Burma. The species have been fully discussed by Annandale [6] and later by Annandale and Rao[7] and I will here include only a few notes regarding the evolution of the sculptured species from smooth-shelled forms and discuss the relationship of the subgenus.

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[1] Rao, H. S., *Rec. Ind. Mus.* XXVII, pp. 133, 134 (1925).

[2] Nevill, G., *Hand-List Moll. Ind Mus.* II, p. 26 (1885).

[3] Annandale, N, *Rec. Ind. Mus.* XXII, pp. 552-557, pls. v, vi (1921).

[4] Rao, H S., *Rec. Ind. Mus.* XXVII, p. 132 (1925).

[5] Annandale, N., *Rec. Ind. Mus.* XX, pp. 546-548, fig. 4 (1921).

[6] Annandale, N., *Rec. Ind. Mus.* XIV, pp. 123-137, pls. xv-xviii (1918), also see *Proc. Roy. Soc. London* (B) XCVI, pp. 68-72 (1924).

[7] Annandale, N. & Rao, H. S., *Rec. Ind. Mus.* XXVII, pp. 118-126 (1925).

The adult shell varies from conical-ovate to conoid or even conical in form, and is never very thick. The sculpture consists of spiral striae or ridges which may be broken up into nodular or squamous tubercles. The embryonic shell is variable according to the species to which it belongs, but in all cases there are three primary ridges ornamented with chaetae ; of the three ridges the peripheral keel representing the lowermost ridge is best developed. Later in older embryos the ridges become obsolete or prominent and broken up into tubercles. There are in all cases three colour-bands to be distinguished, these are present even on the embryonic shells. *Taia* is closely allied to the Vivipari Bengalenses and appears to have been evolved from some species of this group.

In considering the evolution the sculpture (pl. xix, figs. 19-74) we may begin with a species like *T. naticoides* (Theobald). The shell of this species is not very elongate and has three very distinct colour-bands, the sculpture consists of three low, spiral ridges. In *T. theobaldi* (Kobelt), which resembles *T. naticoides*, the spiral ridges on the shell are a little more prominent. In *T. naticoides* var. *noetlingi* (Kobelt) [1] the shell is more elongate than in the typical form, and the spiral ridges, which are more prominent, are often broken up into tubercles, particularly on the bodywhorl. The tubercles in some specimens take the form of subspiniform scales. In *T. crassicallosa* Annandale and Rao the shell is rather squat and globose and the ridges are better developed ; sometimes they are broken up into irregular, squamous tubercles. In *T. shanensis* (Kobelt) the shell is globose-conoidal and not very high. The ridges on the shells are better developed, and the peripheral ridge consists of more or less regular and prominent subspiniform scales. Above this ridge there are two spiral rows of tubercles and there are two rather low ridges below it. In *T. elitoralis* Annandale the shell is much more elongate and slender than in the forms hitherto considered, and the scaly tubercles are developed even on the penultimate whorl. Other ridges are also more tuberculate. The final stage in the evolution of the sculpture in the species of this subgenus is found in *Taia intha* Annandale. The shell is more elongate than that of *T. shanensis*, and the sculpture is also better developed on the penultimate whorl. All the ridges are very tuberculate and the one corresponding to the peripheral consists of squamous tubercles. On the bodywhorl the upper two ridges are broken up into tubercles and sometimes the tubercles of the two rows become confluent. The peripheral ridge is very prominent, and its projections are in " the form of short spiniform processes, blunt at tip and concave outwards and forwards (Annandale)." Below the peripheral there are two other ridges.

The evolution of the sculpture has taken place in the same way as in the Yunnanese subgenus *Margarya* Nevill, but I do not think that the two subgenera are in any way related. Further, I do not believe that *Taia* is in any way related to the North American *Tulotoma* Haldeman or the Chinese *Rivularia* Heude with which Annandale also compared it.

Larina Group :—The genus *Larina* A. Adams, as is discussed further (p. 179), was proposed by the author for an Australian species of doubtful relationships, and was later referred to the family Viviparidae. Blanford[2] referred doubtfully to this genus the species *L. burmana*

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[1] Annandale's *Taia naticoides* var. *intermedia* is, as I am able to confirm by examination of the types, identical with *V.* (*naticoides* var. ?) *noetlingi* Kobelt (*op. cit.* pp. 204, 205, pl. xlii, figs. 1, 2) and should be called *T. naticoides* var. *noetlingi* (Kobelt).

[2] For references to literature on the Indo-Burmese species of the genus *Larina* see Nevill, G., *Hand-List Moll. Ind. Mus.* II, p. 18 (Calcutta, 1886).

Blanford from the Irrawadi Delta, Burma, while H. Nevill described a species from Ceylon —*ceylanica*—under the new name *Robinsonia ;* this was later rightly referred by the Nevills to the genus *Larina.* Shells of *L. burmana* were later recorded by Nevill from Port Canning in the Gangetic Delta, and a new species *L. cincta* was described from near Puri, Orissa. The three species are all closely allied and are also undoubtedly related to the species found in New Guinea and Australia. No forms of the genus are so far known from the intervening area of the East Indies, but as is discussed further no great weight can be attached to the distribution of the members of this estuarine genus for zoo-geographical conclusions.

Baluchistan and Seistan.

In this area there is an extension of a form of the Vivipari Dissimiles Group. The species was described by Kobelt [1] as *V.* (*dissimilis* var. ?) *hilmendensis* from the basin of the Helmand River, Seistan, on the Western boundary of Baluchistan, but as Annandale [2] pointed out the specimens figured are out of the series of *V. sindica* Nevill, a form of *Viviparus dissimilis.* The Seistan form is distinct and should be known as *V. helmandica* Annandale. The species probably occurs in Baluchistan and may also have wandered into Afghanistan through the Helmand River. This extension of an Indian Viviparid into Seistan is quite similar to that of the Indian Unionid *Lamellidens marginalis* var. *rhadineus* Annandale and Prashad (*loc. cit.* p. 59) into the same area.

So far as I can find from the available literature, no Viviparids have been described from the Eastern half of Asia Minor, Arabia, Mesopotamia, Persia or Afghanistan. Issel's record of *Paludina mamillata* Küster [3] from Palaeston, Imertia, coast of Asia Minor in his Memoir on the Mollusca of Persia has wrongly been included by Westerlund[4] as the record of a Viviparid from Persia.

China.

In China[5] a relatively small-shelled, banded form of the type of *V. viviparus* or *V. bengalensis* [6] does not seem to exist, and its place has been taken by a large number of forms of the Vivipari dissimiles and the Lechythoconcha groups. I do not agree with Annandale [7] that the majority of the Chinese species of the subgenus *Viviparus* belong to a peculiar group which we may call Vivipari Angulares. It is possible to distinguish five types among the Chinese Viviparids which I call as follows :—1. Vivipari Dissimiles Group ; 2. Cipangopaludina Group ; 3. Dactylochlamys Group ; 4. Rivularia Group ; and 5. Margarya Group. Of these the Rivularia and Margarya Groups are found only in China.

Vivipari Dissimiles Group. :—Authorities will probably differ as to whether the Chinese Viviparids which I assign to this group are so closely allied to the Indian species *V. dissimilis*

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[1] Kobelt, W., *Op. cit.* p. 285, pl. lix, figs. 9-12. See also Annandale, N. and Prashad, B., *Rec. Ind. Mus.* XVIII, pp. 27,28 (1919).

[2] Annandale, N., *Rec. Ind. Mus.* XIX, p. 114 (1920).

[3] Issel, A., *Mem. Acad. Sci. Torino* (ii) XXIII, p. 18 (1865).

[4] Westerlund, C. A., *Fauna Palaearct. Reg. leb. Binnenconch.* VI, p. 8 (1886). The species is recorded under *P. subfasciata* Bgt.

[5] See Heude, R. P., *Mem. Empire Chinois*, I, pp. 172-179, pls. xxxix-xli (1890), and Kobelt's Monograph. Reference to different genera are given further.

[6] This idea will have to be modified if the species described as *Paludina subcostata* by Gray (Griffith's *Animal Kingdom* pl. xxvi, fig. 3) came from China. This species is undoubtedly of the Vivipari Bengalenses Group, but is based on a single worn specimen, and no further material of the species has since come to hand.

[7] Annandale, N., *Journ. As. Soc. Bengal* (n. s.) XIX p. 407 (1924).

(Müller) as to be included in this group. From my examination of a large number of specimens of all ages from different parts of China, however, I am quite certain that they had an ancestor closely resembling the Indian species and that they are all evolved from it. In this group I include *V. quadratus* (Benson) (pl. xix, fig. 3) and a number of forms closely allied to it.

The earlier authorities and even Kobelt in his Monograph have confused *V. quadratus* with Müller's *Nerita angularis*, but Heude (*loc. cit.*) understood the species correctly and figured it on plate xl (fig. 10) of his work cited already. Annandale recently (*loc. cit.* pl. xvii, fig. 2) gave a good figure of the cotypes of Benson's species in the Indian Museum, Calcutta, and pointed out the differences from Müller's species. The shell of the typical form of the species is elongate, subcylindrical, not greatly swollen, with the whorls flattened vertically. The sculpture consists of three spiral ridges corresponding to the three primary ridges of the embryonic shell, with the peripheral keel rather more marked than the other ridges, and a number of feebly-developed secondary ridges. The var. *reevei* (Dautzenberg and Fischer) has a more elongate shell, but the ridges, though better developed, are not very prominent. In var. *aeruginosus* (Reeve) the shell is a little more elongate, and the ridges, which are very pronounced, appear to be quite solid. In var. *heudei* (Dautzenberg and Fischer) the shell is not so elongate, but the spiral sculpture is a little better developed than in the typical form.

There is some uncertainty about *V. boettgeri* Kobelt [1] (pl. xix, fig. 6) from the Island of Hainan. The shell of this species is elongated, very thick and has 4-5 ridges above the peripheral keel and 2 below it; the primary ridges are distinguished by being more prominent than the secondary ones. All the ridges are raised and quite solid. In spite of the very regular, solid ridges on the shell I believe that Kobelt was right in considering this species to be an insular form of *V. quadrautus*, which has become very highly evolved and must be considered as a distinct species. It may also be noted that it has no relationship with the solid-ridged species of the subgenus *Dactylochlamys* Rao (see p. 176).

The species *V. delavayana* (Heude), *V. lapideus* (Heude) and *V. stelmaphora* (Bourguignat) form a peculiarly modified group. The shell of all these species is very large and it appears as if they were tending to converge to the large-shelled subgenus *Cipangopaludina* Hannibal. As regards their sculpture the three species mentioned above show a gradual degeneration of the ridges in a descending series. It would probably be more correct to consider them in a reversed order and take *V. stelmaphora*, in which, except for the peripheral keel, the other ridges are more or less obsolete and the shell appears nearly smooth, as the least highly modified form of the group, and from an ancestor like which all the three species have been evolved. In *V. lapideus* the ridges are better developed, but are not very prominent, while *V. delavayana* is very distinctly ridged and has 2-3 secondary ridges in addition to the three primary ones.

The group of species referred to above appears to be closely allied to the species which may be next considered. These are *V. lithophagus* (Heude), *V. demolitus* (Heude), *V. fontozianus* (Heude), *V. purificatus* (Heude), *V. lappilorum* (Heude), and *V. magnacianus* (Heude).

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[1] Kobelt refers this and a number of other species described and figured for the first time to Möllendorf, but as the latter author never described the species his names are nothing more than *nomena nuda*, and Kobelt must be considered as the author of all these new species.

The shells of these species are small to medium sized, never very elongate like those of the typical *V quadratus*, and with the whorls distinctly swollen. As to the sculpture the species mentioned above show an ascending series in the development of ridged forms from a nearly smooth-shelled species like *V lithophagus*, in which there is only the trace of a peripheral keel and which in both form and sculpture is very near *V dissimilis*, to *V magnacianus*, in which there are three well-developed ridges corresponding to the three primary ridges of the embryonic shell ; traces of some of the secondary ridges are also to be seen in some cases.

Kobelt's species *V rivularis* from Hunan is also to be referred to this group. It has a thick, nearly smooth, uniformly brownish green shell. It appears to be one of the least modified species of this group, and probably represents the ancestral form of the subgenus *Rivularia* Heude. I do not agree with Kobelt (*loc. cit.* p. 216) that the species is in any way related to *Cipangopaludina limnophila* (Mabille), which I consider to be the ancestral form of the subgenus *Margarya* Nevill.

It may also be noted here that the adults of all the Chinese species of this group have uniformly coloured, unbanded shells which, as noted above, may be nearly smooth or provided with spiral ridges. In the case of all the species of which I have been able to examine the animals the young embryonic shells were found to have the three primary ridges ornamented with minute curved chaetae.

Cipangopaludina Group :—I have already discussed the reasons for adopting the name *Cipangopaludina* Hannibal in preference to *Lecythoconcha* Annandale (p. 163), and it need only be noted that the subgenus has reached its highest development in China where it appears to replace the family Ampullariidae. The shells of the Chinese species are further specialized in having an elongated spire and in this they differ from the species of the subgenus found in most other areas. Unfortunately, I have not had sufficient material at my disposal to decide the status of most of the species described from China, and in the following list I follow Kobelt (*op. cit.* pp. 111-120) in considering most of them as varieties of the species *C. chinensis* (Gray). The varieties are *cathayensis* (Heude), *compacta* (Nevill), *ventricosa* (Heude), *fluminalis* (Heude), *hainanensis* (Kobelt), *diminuta* (Heude), *leucostoma* (Heude), *aubrayana* (Heude), *patris* (Kobelt), *lecythoides* (Benson) and its form *latissima* (Dautzenberg and Fischer), *wingatei* (Smith) and *haasi* Prashad (*nom. nov.* for *longispira* Heude which is pre-occupied for a Japanese species).[1] *C. limnophila* (Mabille) which I consider to be the ancestral form of the subgenus *Margarya* Nevill (*infra*, p. 171) is also a member of this group.

Dactylochlamys Group :—The characters of the subgenus have already been noted (p. 164). In China it is represented by *D. oxytropoides* (Heude), which is found in Yunnan, and which, as the name indicates, is closely allied to the type-species of the subgenus. I also believe that Müller's *Nerita angularis* [2] is to be referred to this group. The difficulty, however, in this connection has been the uncertainty which has existed regarding Müller's species and its exact provenance. Müller gave the locality distinctly as China, but Küster[3] and other authorities, and more recently Bartsch[4] believed the species to have a wide dis-

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[1] See Smith, E. A., *Journ. Conch.* V, p. 37 (1886), where a Japanese species is described under the same name. I dedicate this form to Dr. F. Haas of Frankfurt in recognition of the help he gave me in examining the collections under his charge.

[2] Müller, O. F., *Hist. Verm.* pt. II, p. 187 (1774).

[3] Küster, H. C., *Martini und Chemn. Conch. Cab. Paludina*, pp. 26, 27 (1852).

[4] Bartsch, P, *Proc. U. S. Nat. Mus.* XXXII, pp. 135, 136 (1907).

tribution and confused it with the East Indian *D. costatus* and the Philippine *D. burroughiana.* Koblet, on the other hand, while recognising it as distinct from these species, confused it with the other Chinese species *V. quadratus* (Benson), and used the two names indiscriminately both in his Monograph and on the labels of his collection. Walker [1] and Annandale [2] have discussed the whole question at length, and while the former author has discussed the literature and synonomy of the species, the latter has given the distinguishing characters of the two species. For figures of the two species reference may be made to Annandale (pl. xvii, figs. 1, 2). Walker has also published good figures (pl. viii, figs. 1, 2) and the species was correctly understood by Heude (pl. xl, fig. 7), while of Kobelt's figures numbers 1, 2, on pl. xxv represent the species most nearly. It is a thin-shelled species with three somewhat hollow, spiral ridges on the bodywhorl, and with three ridges on each of the preceding whorls as is mentioned by Müller in the original description of the species. In my opinion *D. angularis* is closely allied to the type-species of the subgenus *D. oxytropis* (Benson).

Of *Paludina thersites* (Hanley *mss.*) Reeve I have examined the type-specimens in the British Museum (Natural History), London, and the specimens figured by Kobelt (pl. xxiv, figs. 1-8) now in the Senckenberg Museum, Frankfurt a. Main, and I agree with Kobelt that they are nothing more than abnormal specimens in which the spire has been depressed inwards and the whole shell has become deformed in response to some peculiar environment.

I do not agree with Kobelt that the form he described as *quangdugensis* is a variety of *V. quadratus* allied to var. *heudei.* It is a solid-ridged species of the subgenus *Dactylochlamys* similar to the species found in the Philippines and in Celebes, and is, in my opinion, quite distinct.

Rivularia Group :—Heude [3] separated the small, thick-shelled Viviparids, which are found in the more or less clear waters of the hill-streams of Hunan and adjacent areas in China, into a distinct genus under the name *Rivularia.* The species were at one time referred to the American subgenus *Melantho* Bowdich (=*Campeloma* Rafinesque), and one of them was described as a *Paludomus.*

The shells are elongate-ovoid to subglobose in outline and are comparatively very thick. Some of the species are smooth, but in others, like *R. auriculata* (Martens) var. *bicarinata* Kobelt (pl. xix, figs. 30-31), two spiral, low and solid ridges are present on the whorls ; these are best marked on the bodywhorl. In young shells the traces of a third ridge are also to be made out below the peripheral. Externally the shell is uniformly greenish, but on the inner surface of the shell three brownish colour-bands are present on a white background. There is a well-developed columellar callus, and the aperture next to the callus is drawn out into a spout-shaped structure. This elongation of the aperture seems to be an adaptation for life in hill-streams.

I have not been able to obtain any spirit material of this subgenus but I have examined a large number of shells. The species are fully treated by Kobelt (*op. cit.* pp. 178-187, pls. xxxv, xxxvi).

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[1] Walker, B., *Nautilus* XXXII, pp. 114-117, pls. viii, ix (1919).

[2] Annandale, N., *Journ. Proc. As. Soc. Bengal* (n. s.) XIX, p. 408 (1924).

[3] Heude, R. P., *Mém. Empire Chinois,* I, no. 3, p. 179 (1890).

The subgenus appears to have been evolved from a species like *V. rivularis* Kobelt (*op. cit.* pp. 215, 216, pl. xliv, figs. 1-4) from Hunan, which has a *Rivularia*-like shell but is a true *Viviparus* of the group of Vivipari Dissimiles.

Margarya Group :—Nevill[1] called the very large, elongate and highly sculptured Viviparids from the Lake Tali (Er-Hai), Yunnan, *Margarya.* Neumayr (*loc. cit.*) considered it to be identical with the North America *Tulotoma* Haldeman, and included it as a subgenus of *Viviparus.* Other authors, however, have rightly considered the forms to be quite distinct. The subgenus is apparently confined to Lake Tali, and the area round about it. The various recent forms of the genus described by the authors referred to are only growth stages of the type-species, *M. melanoides* Nevill. Neumayr's var. *carinata* and Mabille's *francheti* may, however, be treated as distinct varieties.

Among the quaternary sub-fossil forms it is possible to distinguish a group of varieties of which var. *monodi* Dautzenberg and Fischer may be taken as the central form. In this variety the shell is similar to that of the type-species in shape, but instead of the tuberculate ridges there are 4-5 solid, uniform, spiral ridges on the bodywhorl. On the upper whorls also the ridges are similarly arranged. In var. *mansuyi* Dautzenberg and Fischer the shell is narrower and more elongate and the ridges are fewer and less prominent. In var. *obsoleta* Dautezenberg and Fischer the shell is still narrower and more or less smooth.

The sculpture of the type-species *M. melanoides* (pl. xix, figs. 25-29) may be considered here in some detail and for this it will be best to begin with an account of the very young shells. The youngest shell, which I have examined, is more or less globose, and appears to be a worn embryonic shell. It consists of $2\frac{1}{2}$ whorls. The first $1\frac{1}{2}$ whorls are rather weathered, but the sculpture on the main whorl is well preserved. It consists of an upper discontinuous ridge lying close to the suture and consisting of rounded tubercles. The second or middle ridge similarly consists of rounded tubercles and is the most prominent of the three ridges. The marginal ridge is the lowest and is like a distinct keel not broken up into tubercles. Traces of two other feeble ridges are also to be seen below the marginal.

In an older shell consisting of $4\frac{1}{2}$ whorls the embryonic region of the shell has the same type of sculpture as in the younger shell described above. On the penultimate whorl all the ridges are tuberculate, and so are the ridges of the bodywhorl but on these the tubercles are relatively larger. The uppermost ridge has further shifted close to the suture. Below the marginal ridge the secondary ridges are very prominent and consist of more or less vertical thickenings formed by the union of 4-5 rows of tubercles running into one another.

In a shell consisting of $5\frac{1}{2}$-6 whorls the sculpture on the first $3\frac{1}{2}$-4 whorls is similar to that of the shell of that age. The suture is, however, more impressed and the sculpture on the last $1\frac{1}{2}$-2 whorls is quite different. On the penultimate whorl there are only two more or less continuous spiral ridges and the peripheral is covered up by the bodywhorl. On the bodywhorl the three ridges are seen distinctly, but the third is rather feeble and the secondary ridges are also greatly reduced. The peripheral ridge on this whorl, corresponding to the second of the three primary ridges, is broken up into elongate areas of varying lengths.

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[1] Nevill, G., *Journ. As. Soc. Bengal*, XLVI, p. 30 (1877), and *op. cit.* L, p. 155, pl. v, fig. 1 (1881). Also see Mabille, J., *Bull. Soc. Malacol. France*, III, pp. 65-76, p. ii (1886); Neumayr, M., *Wiss. Ergebn. Reise Bela Szechenyi in Ost-Asien*, II, pp. 649-651' pl. iii (1898); Dautzenberg, P. & Fischer, P., *Journ. Conchyliol.* LIII, pp. 420-425, 1 pl. (1905); Kobelt, W., *loc. cit.* pp. 187-193 pls. xxxvii-xxxix (1907); Mansuy, H., *Bull. Serv. Geol. Indo-Chine*, V, fasc. iii, pp. 1-15, pls. i, ii (1918); and Annandale, N., *Proc. Roy. Soc. London* (B) XCVI, pp. 60-76 (1924).

In full-grown shells the only part needing description is the bodywhorl, as the other whorls either resemble the young shells or the sculpture becomes worn and indistinct. The uppermost or first ridge lies just next to the suture and is not very prominent; it consists of a low, more or less continuous ridge which in some places shows traces of small tubercular thickenings. The peripheral ridge, which here also represents the second of the primary ridges, consists of elongated ridged areas of varying lengths ending in scaly tubercles of an inverted V-shaped appearance directed towards the aperture of the shell. These remind one of the subspiniform scales of some species of the subgenus *Taia* (p. 165). In some specimens such scaly tubercles are also found on the penultimate whorl.

Annandale (*op. cit.* pp. 65, 66) considered *Margarya* to have been evolved from a smooth-shelled elongate Viviparid which he called *V. margaryoides.* From a careful comparison of the descriptions and figures of Mabille's species *Paludina limnophila* and *P. secernendus* (*op. cit.* pp. 72, 74, pl. ii, figs. 5, 4) from Lake Tali, the area from whence Annandale's species was described, I have no doubt that they all represent growth stages of the same species. The species belongs to the subgenus *Cipangopaludina* Hannibal, and the name of the species must be *limnophila.* Mansuy's *Viviparus margaraeformis* found fossil at Chi-li-pou-tang in the lacustrine basin of Mong-Tseu, Yunnan, is undoubtedly very closely allied to *C. limnophila,* and is probably only a variety of it.

It may also be noted here that the shells of the species of *Margarya* are all uniformly coloured, and that there are no colour bands to be seen either inside or on the outer surface of the shells.

Korea.

The only Viviparid so far known from the Korean Peninsula is a form of *Cipangopaludina chinensis* (Gray).[1] It undoubtedly has wandered from China, and probably represents the route along which the species of the subgenus wandered from China into Japan.

Asiatic Russia.

In the whole area of Asiatic Russia there are no Viviparids except in the extreme south-east in the basin of the Amur River and its tributaries, and these are apparently an extension of the Chinese forms which have become established in this area.[2] There are only two species and they belong respectively to the Cipangopaludina Group and the Dactylochlamys Group. Through the kind offices of Mr. W. A. Lindholm of the Zoological Museum, Leningrad, Russia, I have been able to examine both the species preserved in alcohol, and am therefore able to assign the two forms with confidence to their respective groups.[3]

Cipangopaludina Group :—Gerstfeldt's species *praerosa* is closely allied to *C. abbreviata* (Reeve), and like that species is undoubtedly a member of the subgenus *Cipangopaludina.*

Dactylochlamys Group :—This group is represented by the species *D. ussuriensis* (Gerstfeldt), which differs very slightly from the Japanese species *D. iwakawae* (Pilsbry), and is

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[1] See von Martens, E., *Zool. Jahrb.* Suppl. VIII, p. 25 (1905).

[2] See Dall, W. H., *Land and Freshw. Moll. Alaska,* p. 11 (1905), who considers the Amur Valley Viviparids as "probably variants of the Chinese forms."

[3] Gerstfeldt, G., *Mem. Acad. Imp. St. Petersbourg* IX, pp. 3-6, pl. i (1859) ; Schrenck, L. V., *Reise und Forsch in Amur-Lands, Zool.* II, pp. 605-619, pl. xxvi (1859-67) ; and Kobelt, W., *op. cit.* pp. 108-111, pl. xviii, figs. 1-4 (1906).

closely related to the Chinese *D. angularis* (Müller). The shell is larger than the Chinese species and the ridges are less hollow, but there can be no doubt as to their affinity.

Japan.

In the Japanese Archipelago the family is represented in all the islands with the exception of Sakhalin.[1] The Viviparids of this area[2] show a very distinct affinity to those of China, and are divisible into four groups. The peculiar lacustrine subgenus *Margarya* Nevill and the paludine *Rivularia* Heude are absent, but another lacustrine subgenus *Heterogen* Annandale has been evolved in Lake Biwa. The groups found in Japan are :— 1. Vivipari Dissimiles Group ; 2. Heterogen Group ; 3. Cipangopaludina Group ; and 4. Dactylochlamys Group.

Vivipari Dissimiles Group :—The two species *V sclateri* (Frauenfeld) (pl. xix, fig. 5) and *V histricus* (Gould), which I assign to this group, are closely allied to the Chinese *V quadratus* (Benson). On the embryonic shell there are three spiral rows of chaetae, while the adult shell has two faint spiral ridges and a well-developed peripheral keel.

Heterogen Group :—Annandale (*loc. cit.* p. 399) described a new species of his monotypic genus from Lake Biwa under the name *H. turris.* The species had, however, been described many years before by Smith[3] under the name *Paludina longispira* in a paper which seems to have escaped the notice of all later workers on the Japanese forms. The name of the species will, therefore, be *H. longispira* (Smith) (pl. xix, fig. 7). The form was previously confused with *V ingalsiana* (Lea) and *V sclateri* (Frauenfeld). In this peculiar Viviparid the embryonic shell is different from that of any other known species in having a very obtuse blunt apex, while the whorls, which are smooth, have two smooth spiral ridges separated by a broad deeply concave area. The apex of the adult shell is similarly blunt, as is very well shown in Annandale's figures. Annandale compared the young shell with that of *Rivularia* Heude, and added that it has a superficial resemblance to that of the young shell of *Margarya* Nevill. The relationship of the subgenus is uncertain, but it appears to have been evolved from the Vivipari Dissimiles Group, as the adult shells resemble in form and the sculpture is only slightly different.

Cipangopaludina Group :—Annandale (*loc. cit.* p. 401) provisionally assigned the species *malleata* of Reeve, *sclateri* of Frauenfeld and *japonica* of von Martens to his genus *Lecythoconcha* in ignorance of the work of Hannibal, who as noted already (p. 163) had established the subgenus *Cipangopaludina* for Reeve's *malleata.* I have examined extensive material of the Japanese species and have compared it with Viviparids from adjacent areas, and find that Annandale's conclusions except for *V sclateri* are correct. It may also be noted that *Paludina malleata* of Reeve, as was believed by Pilsbry, is not the same as *Paludina laeta* of von Martens. On the other hand Reeve's *Paludina abbreviata* is synonymous with von Martens's species *P. laeta,* which latter owing to its having been described three years earlier,[4]

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[1] For details as to the distribution of the species see Iwakawa T., *Cat. Japan. Moll. Nat. Hist. Dept. Tokyo Imp. Mus.* pp. 68-72 (Tokyo, 1919).

[2] Kobelt., W., *Abhandl. Senckenberg. Nat. Ges.* XI, pp. 120-127, pl. xi (1879) ; Iwakawa, T., *Annot. Zool. Japon.* I, pp. 83-92, pl. i (1897) ; Pilsbry, H. A., *Proc. Acad. Nat. Sci. Philadelphia*, pp. 115-119, pl. ix (1902) ; and Annandale N., *Mem. As. Soc. Bengal*, VI, p. 46 (1916) and pp. 399-401 (1921).

[3] Smith, E. A., *Journ. Conch.* V, p. 57 (1886).

[4] von Martens, E., *Malakozool. Blätt.* VII, p. 45 (1860).

has priority over Reeve's name. The sculpture of the Japanese species, like that of the other species of the genus, is feeble, and only in exceptional cases obsolete spiral ridges are to be distinguished. In half-grown individuals there is a prominent peripheral keel, but this disappears in older shells. In *C. laeta* (von Martens), according to Pilsbry, short bristles are to be distinguished on punctured spiral ridges in well preserved adult shells.

Dactylochlamys Group :—I have examined full-grown specimens of *Vivipara japonica* var. *iwakawae* Pilsbry (pl. xix, fig. 12) from Nippon and find that the shells have no relationship with *L. japonica.* They belong to a distinct species of the genus *Dactylochlamys* Rao, and are undoubtedly allied to the species *D. oxytropis* (Benson) from Manipur, India, and *D. oxytropoides* (Heude) from China. The species should be known as *D. iwakawae* (Pilsbry). There are three somewhat hollow ridges on all the whorls, but the peripheral lies next to the suture and in the upper whorls is covered over by the adjacent whorls. The shell for the size of the species is very thin and fragile.

Malay Peninsula, Siam, Cambodia, Cochin-China and Annam.

For the sake of convenience I propose treating the Viviparids of these countries[1] together. In this area there are five groups of Viviparids. Of these the sub-genus *Mekongia* Crosse and Fischer is truly endemic in the area and is not found elsewhere; the other four types are common to adjacent countries. Following the nomenclature adopted for the Indo-Burmese Viviparids with which the forms of the area under consideration show distinct affinities, the species may be grouped as follows :—1. Vivipari Bengalenses Group; 2. Vivipari Dissimiles Group; 3. Cipangopaludina Group; 4. Dactylochlamys Group; and 5. Mekongia Group.

Vivipari Bengalenses Group :—The forms from this region which I assign to this group have a more or less smooth shell with colour-bands like that of the typical *V. bengalensis* (Lam.), and the form of the shell is also very similar. The species are *V. filosus* (Reeve), *V. polygrammus* (Martens) and its various varieties, *V. penangensis* Martens and *V. martensi* (Frauenfeld) from Siam, *V. thomsoni* (Morlet), *V. chalangensis* (Deshayes), *V. obscuratus* (Deshayes) and *V. speciosus* (Deshayes) from Cambodia.

Vivipari Dissimiles Group :—The characteristics of this group have already been considered (p. 163). In some of the more highly differentiated species, as in *V. ingalsiana* (Lea), the remains of the embryonic primary and secondary ridges persist on the bodywhorl of the adult shell, while the peripheral ridge is quite prominent as a keel. I assign the following species to this group :—*V. ingalsiana* (Lea), *V. sabinae* (Morlet) and *V. subciliatus* Kobelt from Siam, *V. kelantensis* Kobelt and *V. perakensis* Kobelt from Perak, *V. speciosus* (Deshayes), *V. vignesi* (Jullien), *V. tiranti* (Morlet), *V. cambodjensis* (Mab. & Mes.), *V. danieli* (Morlet), *V. paviei* (Morlet), *V. simonis* (Bavay), *V. fulvus* (Reeve) and *V. luridus* (Morlet) from Cambodia, *V. basicarinatus* Kobelt from Annam and *V. cochinchinensis* (Morlet) from Cochin-China.

V. ciliatus (Reeve) from Siam, with a number of low, feebly ciliated ridges, is also to be referred to this group. The large number of ridges represent the primary, secondary and

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[1] See Fischer, P., *Cat. Distrib. Geog. Moll. Terr.-Fluv. & Mar. Indo-Chine* (Autin, 1891); and Fischer, P. & Dautzenberg, P., *Mission Pavie Indo-Chine*, III, pp. 390-450 (Paris, 1904).

tertiary ridges all of which are more or less equally developed and on which the cilia have persisted.

I refer *V polyzonatus* (Frauenfeld) from French Indo-China also to this group. Its shell with low solid and rather darker ridges appears to have been evolved in a manner similar to that of *V boettgeri* Kobelt from Hainan, but the ridges are less regular and not so strongly developed.

Cipangopaludina Group :—The only species which can definitely be assigned to this group is *C. laosiensis* (Morlet) from the Mekong Valley, Laos and Tonking. The shell in form and sculpture closely resembles that of *C. chinensis* (Gray), and probably represents a southward extension of the species of that group from China.

Dactylochlamys Group :—With some hesitation I assign the species *Paludina fischeriana* Mabille and Le Mesle and *P. largrandieri* Bavay to the subgenus *Dactylochlamys* Rao. Both the species are of small size, greatly compressed from above downwards, and have rather thick, solid shells. The ridges on the whorls are similar in arrangement to those of the hollow-ridged species of the subgenus, and it is probable that they have been derived from the more primitive species by the shells becoming thick and the ridges becoming solid. Probably *D. umbilicatus* (Reeve), *D. trochoides* (von Martens) and *D. occultus* (Fulton)[1] are also species of this subgenus, but in these species only the sutural and the peripheral ridges have persisted and the median is quite obsolete. The shells are solid and uniformly coloured.

Mekongia Group :—Crosse and Fischer[2] proposed the generic name *Mekongia* for the species *Paludina turbinata* Deshayes from Cambodia. Kobelt included a number of other species in this subgenus, but did not believe that the subgenus was in any way different from the other Viviparids from the same area. From my examination of a large number of species of this group I am of opinion that the species enumerated below form a separate group. They are paludine forms, and probably a number of the so-called species are based only on shells which were found in rapid or sluggish streams. The shell is usually thick and has a Neritoid facies (pl. xix, fig. 32). In specimens from rapid streams the margin of the aperture is thickened all round and it appears as if there was a thick callus extending all round. In young shells the remains of the three primary ridges are to be distinguished but the adult shells are quite smooth. The shells are uniformly coloured and no colour-bands can be distinguished. The subgenus *Mekongia* is to be derived from a species like *V lurida* (Morelet) of the Vivipari Dissimiles Group; the rather small, thick-shelled species are an adaptation to the peculiar type of environment in which these forms live.

Fischer's section *Eyriesia* [3] with *Paludina eyriesi* Morelet as type is only a synonym of *Mekongia*.

I assign the following species to this group :—*M. turbinata* (Deshayes), *M. jullieni* (Deshayes), *M. sphaericula* (Deshayes), *M. moreleti* (Deshayes), *M. eyriesi* (Morelet), *M. rattei* (Crosse and Fischer) and its var. *elongata* (Dautzenberg and Fischer) from Cambodia, *V lamarckii* (Deshayes) from Ca-Lyniou Island, and *M. siamensis* (Frauenfeld), *M. moreleti* var. *fruhstorferi* (Kobelt), *M. hainesiana* (Lea), *M. swainsoniana* (Lea), *M. braueri*

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[1] Fulton, H. C., *Proc. Malacol. Soc. London*, XII, p. 241, fig. (1917).

[2] Crosse, H. & Fischer, P., *Journ. Conchyliol.* XXIV, p. 316 (1876).

[3] Fischer, P., *Man. Conchyliol.* p. 733 (Paris, 1885).

(Kobelt) from Siam. Probably *Paludina kmerianus* Morelet is also allied to the subgenus *Mekongia* and should be referred here.

East Indies.

In the East Indies [1] the Viviparids are found in all the islands of the Greater Sunda Islands group, and in the Smaller Sunda Islands they are known from as far east as Lombok and Sumbawa, but none have so far been recorded from Timor. The species found in these islands show a marked affinity with the Viviparids of the Malay Peninsula and India, and are apparently to be derived from them. I am able to distinguish the following four groups :—1. Vivipari Bengalenses Group ; 2. Vivipari Dissimiles Group ; 3. Cipangopaludina Group ; and 4. Dactylochlamys Group.

Vivipari Bengalenses Group :—This group is represented in the islands by *V. sumatrensis* (Dunker), *V. hamiltoni* (Metcalfe) and *V. hendrici* Prashad. All the species are banded and only rarely, as in *V. sumatrensis*, is there a trace of fine spiral ridges on the shell.

Vivipari Dissimiles Group :—*V. javanica* (v. d. Busch) and its various forms, *V. deliensis* Kobelt, and *V. hortulanus* Kobelt are to be included in this group. The ridges on the surface are feeble, but the shell is unbanded and apparently is very near the ancestral type from which the more highly evolved species have been derived. *V. rouyeri* Bullen is also a member of this group, but is more highly evolved and has a well-developed peripheral keel, and resembles *V. ceylanica* (Dohrn) from Ceylon and the unicarinate forms of *V. unicolor* (Olivier) of Africa.

Cipangopaludina Group :—*Paludina semmenlinki* Schepmann from Borneo is undoubtedly a member of this subgenus. The shell is large, without bands, and except for being rather thick is similar to that of the Indo-Chinese species of the subgenus. The young shells have a peripheral keel, but this disappears in the adults. I have not been able to examine any preserved material of the species.

Dactylochlamys Group :—Quoy and Gaimard's species *Paludina costata* is closely allied to *D. angularis* (Müller), and should be referred to the subgenus *Dactylochlamys* Rao. The shell of *D. costatus* is medium sized, thin and rather fragile. There are a varying number, 3-5, of hollow or channelled ridges above the peripheral keel, and two fairly prominent ridges of the same type below it. The species occurs in Java, Borneo and the Celebes.

Vivipara grossicostata von Martens is, in my opinion, also to be referred to the subgenus *Dactylochlamys*. It has evolved from a species like *D. costatus* by the shell becoming thicker and the ridges solid and more prominent.

Celebes.

The Viviparids of Celebes [2] are similar to those of the adjacent islands of Sumatra, Java and Borneo, but the group of Vivipari Bengalenses is apparently not represented. They are divided into three main groups :—1. Vivipari Dissimiles Group ; 2. Cipangopaludina Group ; and 3. Dactylochlamys Group.

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[1] See Mousson, J. R. A., *Land u. Süssw. Moll. Java*, pp. 61-63, pl. viii (Zurich, 1849) ; von Martens, E., In *Weber's Zool. Ergebn. Niederland Ost. Indien*, IV, pp. 19-25, pl. ii (Leyden, 1897) ; and Prashad, B., *Rec. Ind. Mus.* XXII, pp. 479-483 (1921).

[2] In addition to Kobelt's Monograph see P. & F. Sarasin, *Süsswasser-Mollusken von Celebes*, pp 59-67, pl. x (Wiesbaden, 1898).

Vivipari Dissimiles Group :—*V javanica* (v. d. Busch), as vars. *virescens* (Reeve), *celebensis* Martens, *macassarica* Martens, and *laevior* Martens, is found in Celebes, and this species as already shown (p. 175) is a member of this group. *V gratiosus* (von Martens) *V rudipellis* P. and F. Sarasin, and *V. lutulentis* P. and F. Sarasin are also to be referred to this group.

Cipangopaludina Group :—The species described by P. and F. Sarasin as *Vivipara crassibucca* is undoubtedly a *Cipangopaludina.* The very open umbilicus and the recurved aperture are distinctive, but the shell otherwise is like other species of the subgenus.

Dactylochlamys Group :—The question of including Quoy and Gaimard's species in the subgenus *Dactylochlamys* Rao has already been discussed (p. 175). The typical form of the species occurs in Celebes; it is only slightly modified and has three channelled ridges on the bodywhorl.

I also consider that the species *Vivipara persculpta* P. and F. Sarasin (pl. xix, fig. 16) from Lake Posso, is, like *D. grossicostatus* from Sumatra, to be referred to this genus. In young shells of this species the shell is not very thick and the ridges are hollow. In adults, however, the shells are very thick and the ridges are filled up and in some shells are quite solid. The number of ridges varies, being 2-3 above and an equal number below the peripheral keel.

I have examined some shells of *D. costatus* from Tondanao in the Amsterdam Museum, and these are undoubtedly like the ancestral type from which *D. persculptus* (P. and F. Sarasin) has been evolved.

Aru Islands and New Guinea.

The Viviparids of the Aru Islands and New Guinea are undoubtedly an extension of the forms found in the Celebes. The only exception is that of the peculiar species of the genus *Larina* A. Adams, which has certainly come over from Australia during the time when Australia and New Guinea were connected with each other.

The various forms from these islands are divisible into the following three groups :—
1. Vivipari Dissimiles Group ; 2. Dactylochlamys Group ; and 3. Larina Group.

Vivipari Dissimiles Group[1]:—The species of this group in the islands under consideration are undoubtedly related to *Viviparus javanica* (v. d. Busch), and represent the eastermost extension of the species of this group. The species are *V decipiens* (Tapp.-Can.), *V constantina* Kobelt, *V kowiaensis* (Brazier), *V laevigatus* (Bavay) and *V novoguineensis* Leschke from New Guinea, and *V. decipiens* var. *aruana* Boettger from the Aru islands.

Dactylochlamys Group :—Bavay from an examination of the unique type of Lesson's species *tricostatus* described in 1830 (*Voy. de la Coquille, Zool.* II, p. 349, Paris) was able to decide that the species is quite distinct from *D. costatus* (Quoy and Gaimard), but there is no doubt that it is allied to it and belongs to the same group. The species is unfortunately based on a young shell, which shows three faint ridges on the whorls. The two varieties of *D. tricostatus* described by Bavay, *multifuniculatus* and *elegans*, show a great variation as

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[1] In addition to Kobelt's Monograph see Tapparone-Canefri, C., *Ann. Mus. Civ. Stor. Nat. Genova,* XIX, pp. 20, 21, pl. i (1883) ; Brazier, J., *Proc. Linn. Soc. N. S. Wales,* X, p. 483 (1886) ; Bavay, A., *Nova Guinea* (Zool.), V, pp. 269-292, pl. xiv (Leiden, 1908) ; Leschke, M., *Jahrb. wiss. Anstal. Hamburg,* XXIX, Beiheft ii, p. 130 (1911) ; Preston, H. B., *Proc. Malacol. Soc. London,* IX, p. 113, fig. (1910) and Boettger, C., *Abhandl. Senckenberg. Nat. Ges.* XXXV, p. 135, pl. viii, fig. 7 (1915).

regards the development of the ridges on the shell. I have examined the types of these varieties in the Zoological Museum, Amsterdam, and have no doubt as to their relationship. *D. fragilis* (Preston) from Lake Manswon Bien, Central Arfak Mountains, Dutch New Guinea, also appears to be allied to *D. costatus*.

Larina Group :—Tapparone-Canefri's species *Pa ludina paulciana*, from the Fly River New Guinea, was from the characters of the operculum assigned to the Viviparidae. Kobelt was doubtful as to whether the species had rightly been assigned to the family.

I have examined only dry shells, but have no doubt that the species is closely allied to the Australian *Larina strangei* A. Adams (*vide infra* p. 179). It is a small sized Viviparid with a Neritoid facies, and has apparently been evolved in response to its paludine habitat.

Philippine Islands.

Our knowledge of the Viviparidae of the Philippine Islands, in spite of the two detailed papers of Bartsch,[1] is in a very confused state. Kobelt cleared up the confusion to some extent, and Walker[2] has elucidated the synonymy of some of the species, but the species as a whole still need a careful revision. I do not propose attempting this here, and will only, as in the case of the Viviparidae of adjacent areas, group the species into sub-genera or groups.

The Viviparidae of the Philippines are similar to those of the Great Sunda Islands and Celebes, and are divisible into the following three groups :—1. Vivipari Dissimiles Group ; 2. Cipangopaludina Group ; and 3. Dactylochlamys Group. The subgenus *Cipangopaludina* appears to be dominant in the area, and is represented by a large number of forms.

Vivipari Dissimiles Group :—I am not absolutely certain about the species which I assign to this group as the material at my disposal was not enough to enable me to decide satisfactorily the status of the several species. All of them are more or less smooth-shelled and unbanded forms, and appear to be allied to *V. javanica* (v. d. Bucsh). The species are :—*V. javanica* var. *luzonica* Kobelt, *V. cebuensis* Bartsch, *V. mindanensis* Bartsch and its varieties *bangangensis* Bartsch and *mamanua* Bartsch, and *V. zamboangensis* Bartsch with the varieties *tubayensis* Bartsch, *danaoensis* Bartsch and *surigensis* Bartsch.

Cipangopaludina Group :—This group is very poorly represented in the Philippines. I refer to it *C. pseudocarinatus* Walker (= *Paludina carinata* Reeve), *C. bartschi* Walker (= *V. carinata* Bartsch *nec* Reeve), *C. buluanensis* (Bartsch) and its variety *boholensis* (Kobelt) and *C. cumingianus* Walker(= *P. cumingii* Hanley *mss.* Reeve).

Dactylochlamys Group :—The question of the identity of Müller's species *Nerita angularia* has already been discussed (p. 168). It is a Chinese species and is not found in the Philippines. The species described as such by Bartsch from the Philippines is, as Kobelt (*loc. cit.* p.231) pointed out, a form very different from the Chinese species, but is closely allied to *D. costatus* (Q. & G.). The species is characteristic of the Philippines, and, with Walker, I call it *D. burroughiana* (Lea). Other forms to be referred to this group are the varieties *philippinensis* (Nevill), *ecarinatus* (Kobelt), *samarensis* (Kobelt), *lagunensis* (Kobelt) and *trinominis* Walker

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[1] Bartsch, P., *Proc. U. S. Nat. Mus.* XXXII, pp. 135-150, pls. x, xi (1907), and Vol. XXXVII, pp. 365-367, pl. xxxiv (1909).

[2] Walker, B., *Nautilus*, XXXII, pp. 109-124, pls. viii, ix (1919).

(=*Paludina carinata* Val.) of *D. burroughiana*, *D. mearnsi* var. *misamiensis* (Bartsch)[1], *D. gilliana* (Bartsch), *D. clemensi* (Bartsch), *D. lanaonis* (Bartsch) and its varieties *alpha* to *lambda*, *D. pagodula* (Bartsch) (pl. xix, figs. 14, 15) and *D. tricarinatus* (Anton).

The Philippine species of the subgenus *Dactylochlamys* are very interesting from the point of view of the great development of the hollow, channelled ridges of the shell on the one hand, and continuous solid ridges or solid ridges broken up into scaly tubercles on the other.

The exact relationship of *D. partelloi* (Bartsch) (pl. xix, fig. 18) is not clear, but I believe that it has been evolved from the more primitive species of the sub-genus *Dactylochlamys* by the reduction of all the ridges except the third or the peripheral keel. This sidge, further, instead of remaining uniform and continuous is, owing to uneven development, broken up into scaly tubercles similar to those found in some species of the Burmese subgenus *Taia* Annandale and in the Yunnanese *Margarya* Nevill.

D. mainitensis Bartsch(=*Vivipara multisulcata* Moellendorf *mss.*) (pl. xix, fig. 17) and *D. mearnsi* (Bartsch) are also more highly evolved forms of this group. In *D. mearnsi* the shell is not so thick and the ridges not very prominent, but in *D. mainitensis* the shell is very thick and the ridges very solid, prominent and regularly running spirally on the whorls This latter species lives with *D. burroughiana* var. *ecarinatus* (Kobelt) in Lake Mainit Mindanao, and probably represents the ancestral form of *D. mainitensis* (Bartsch).

II. AUSTRALIA.

I have not been able to obtain any material preserved in alcohol of the Viviparidae from Australia, and my notes are mainly based on the collections in the British Museum (Nat. Hist.), London. The Viviparids of this region have, so far as can be judged from the literature,[2] a very peculiar distribution. They are; as is shown in the sketch-map, found to about longitude 120° E. in the West and their area of distribution is a band-shaped region above latitude 20°S. in the northern parts of Australia, while they are also known to occur in Queensland and East Australia. The distribution of the family in Australia, however, needs further investigation.

So far as is known the Australian species can be distinguished into three groups :—1. Vivipari Sublineati Group ; 2. Vivipari Ampullaroides Group ; and 3. Larina Group.

Vivipari Sublineati Group :—This group appears to be closely allied to the Vivipari Dissimiles, and may actually be synonymous with it. The species which I include in it are *V sublineata* (Conrad) from various parts of Queensland, *V intermedia* (Reeve) and *V alisoni* (Brazier) from Dalmatia River, Queensland. These species resemble *V dissimilis* (Müll.) in being uniformly coloured, and in a large series show evenly rounded to uni-or even bicarinate forms.

Vivipari Ampullaroides Group :—The group to which I refer *V ampullaroides* (Reeve), *V waterhousei* Adams and Angas, *V kingi* Adams and Angas, *V tricinctus* Smith and *V dimidatus* Smith has medium sized to large shells with colour-bands. The bands, however,

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[1] I agree with Kobelt (Monograph p. 224) that it is impossible to understand Bartsch's reasons for describing *misamiensis* as a variety of his species *mearnsi*. It does not appear to have any relationship with *mearnsi*, and for the present I propose leaving it as a distinct species allied to *D. burroughiana*.

[2] For literature see Smith, E. A. *Journ. Linn. Soc. London* (*Zool.*), XVI, pp. 262-266, pl. vii (1882).

as Smith (*loc. cit.* pp. 262, 263) pointed out are not found below the periphery. The group appears to be confined to North Australia, and probably is to be derived from the banded shells of the Indo-Malayan Archipelago through the former connection along the Smaller Sunda Islands.

Larina Group :—The genus *Larina* was proposed by A. Adams [1] for *L. strangei* A. Adams from Moreton Bay, Queensland. In his original description A. Adams believed the genus to be a marine form of uncertain position, but later the brothers Adams [2] referred it to the Viviparidae, and were of opinion that the species must have come from the freshwater streams or water-courses from the vicinity of Moreton Bay. The species is very similar to the New Guinea form *L. paulciana* (Tapp.-Can.), which I also refer to this genus, and from the latter species being found in freshwater streams, it is possible that the Adams were right in their conclusion. The genus, as has already been remarked, is a very peculiar paludine type, and so far is only known from Australia, India and New Guinea.

III. AFRICA.

The distribution of the family Viviparidae in Africa is very peculiar, but the question, except for the publication of a chart showing the distribution of some species of the genus *Viviparus* by Germain,[3] has not been dealt with by any author. The family is distributed along the course of the river Nile not extending beyond the longitude 25° E. to the west, and not above latitude 15° N. in the Sudan. The family is not represented in the whole of north-west Africa except for the basin of the river Senegal, where a species of the genus *Viviparus* and probably some species of the genus *Cleopatra* are found in a rather triangular area including Senegal, Guinea, Sierra Leone and Liberia. In Central Africa its range of distribution is along a rather broad band-like region along the basin of the river Niger, but there are no records of any species having been found below latitude 8°N. Further to the east the family is well represented in a part of French Africa, Belgian Congo, Anglo-Egyptian Sudan and in Uganda. In Abyssinia Viviparidae are only found in the south-western part of the country, while none are known from Italian Somaliland, except for species of the genus *Cleopatra* recently described by Connolly.[4] The Kenya Colony and Tanganyika Territory have a very rich fauna so far as the Viviparidae are concerned, and a large number of species are known from the lakes in this area. There are no records of any members of the family ever having been found in British South Africa or South-west Africa, and apparently the family is not found to the west of longitude 20°E.

The family is represented in Africa by the subgenera *Viviparus s.s.*, *Neothauma* Smith, and *Cleopatra* Troschel. Of these *Cleopatra* and *Viviparus* are found all through the area detailed above, and some species of the genus *Cleopatra* are also found in Madagascar. The subgenus *Viviparus* is not represented in Madagascar, and Kobelt's [5] record of *V.*

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[1] Adams, A., *Proc. Zool. Soc. London*, p. 41, pl. xxvii, fig. 3 (1854).

[2] Adams, H. and A., *The Genera of Recent Mollusca*, II, p. 624 (London, 1858).

[3] Germain, L., *Res. Sci. Voy. G. Babault d. L'Afrique Orient. Angl. Moll. Terr. et Fluv.* I, p. 231, fig. 111 (Paris, 1920). As has been noted already (p. 160 footnote 1) Pilsbry and Bequaert have recently published a sketch-map showing the distribution of the genus *Viviparus* in Africa. This map slightly differs from the map reproduced in this paper (p. 159).

[4] Connolly, M., *Ann. Mag. Nat. Hist.* (9th ser.), XVI, pp. 244, 245 (1925).

[5] Kobelt, W., *Abhandl. Senckenberg. Nat. Ges.* XXXII, p. 91 (1909).

madagascarensis Smith is undoubtedly wrong, as no such species was ever described by the late Mr. E. A. Smith of the British Museum (Nat. Hist.), London. The peculiar lacustrine subgenus *Neothauma* Smith is confined to the lakes Tanganyika and Mweru in Central Africa.

The African forms of the family may be distinguished as :—I. Vivipari Unicolores Group ; 2. Neothauma Group ; and 3. Cleopatra Group[1]

Vivipari Unicolores Group :—I agree with Germain (*loc. cit.* pp. 51, 52, 229) that *V unicolor* (Olivier) is the central species of all the African species of the sub-genus *Viviparus*. It probably represents the ancestral species from which all the recent African species have been derived. Küster,[2] and following him most of the earlier palaeontologists, considered *V unicolor* to be identical with the French Tertiary species *V semicarinatus* (Brard), but there is no true relationship between the two species, and all recent authors have rightly separated the two. On the other hand, as was hinted by Jickeli,[3] *V unicolor* appears to be very closely allied to the Indian *V dissimilis* and the two species appear to be genetically connected and have probably migrated from the same centre. All the African species including *V unicolor* have uniformly coloured shells like those of the Indian species, and no colour-bands are to be found either in the young or the adult shells. Further, the various forms and varieties of *V unicolor*, and the other species derived from it, show an evolution of keeled and ridged species from evenly rounded forms similar to that of the Indian species. This condition has been considered by Germain to be a polymorphism of the sculpture, and in view of its great interest a few notes on some of the species and their forms are included here.

Considering first the species *V unicolor*, we find that the typical form of it, which Germain calls " normalis," has the shells perfectly smooth and neither on any of the upper whorls nor on the bodywhorls is there the slightest trace of any carination. This form corresponds to the typical *V. dissimilis* (Müller) of India. In the " unicarinate " form there is a well developed keel about the middle of the bodywhorl and traces of it are also to be seen on the penultimate and upper whorls. The keel corresponds to the lowermost of the three primary rows of ornamented ridges of the embryonic shell, and following Annandale's terminology[4] it may be called the third primary ridge or the peripheral keel. The keel is equally marked in the young and the adult shells. In some specimens both the young and the adult shells show traces of a second keel which from its position most probably corresponds to the first primary ridge. Similar forms are found in the case of the Indian *V. dissimils* and the Chinese *V. quadratus* (Benson). The form " bicarinata," or the *V biangulata* (Küster) of most authors, has two well developed keels. Of these the inferior corresponding to the peripheral keel of the unicarinate form is the more prominent of the two, and the upper or the first is also more highly developed than in that form. The form " bicarinata " is fairly common and is found living with the unicarinate form. In certain localities, as for example certain regions of Lake Chad according to Germain, the bicarinate form is more abundant. The

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[1] For literature on the African species of the family see Küster's Monograph in *Martini & Chemnitz Conch.-Cab.* (1852), Kobelt's Monograph (*op. cit.*) pp. 162-177, Martens, E. von., *Beschalte Weichthiere Deutsch-Ost-Afrikas*, pp. 173-188 (1897), Connolly, M., *Ann. S. African Mus.* XI, pp. 260-262 (1912), Dautzenberg, Ph. and Germain, L., *Rev. Zool. Afric.* IV, pp. 52-60, pl. iv (1914) and Germain, *loc. cit.* (1920).

[2] Küster, C. H., *op. cit.* pp. 21, 22 (1852).

[3] Jickeli, C., *Nov. Act. K. Leopl. Carol. Deutsch. Akad. Naturf.* XXXVII, p. 237 (1874).

[4] Annandale, N., *Rec. Ind. Mus.* XXII, pp. 244-246, fig. 10 (1921), and *Proc. Roy. Soc. London* (B), XCVI, p. 61 (1924).

last form of this series, which is the rarest of all and which Germain calls " tricarinata," has a much less prominent third keel corresponding to the second primary ridge, intercalated between the first and the third ridge.

We will next consider some well marked varieties and also some species closely allied to and evolved from *V unicolor*. In the var. *conoidea* von Martens, a subfossil from near Lake Albert Edward, the shell is more elongate than in the typical form, but without any keel and resembles the *forma normalis*. The var. *elatior* von Martens from Lake Victoria Nyanza also has a more elongate shell and shows traces of a peripheral keel; it thus leads on to the *forma unicarinata*. Germain's var. *lefanti* from Lake Chad resembles *forma bicarinata* in having two ridges. Frauenfeld's species *jefferysi* and *robertsoni* from the basin of Lake Nyassa are, as von Martens (*loc. cit.* pp. 177, 178) and Germain (*loc. cit.* pp. 218-222) have shown, only forms or varieties of *V unicolor*. The shell of these forms is not so elongate, but is more ovoidal and has a relatively broader bodywhorl. As regards their sculpture they represent a form nearly allied to the unicarinate form. *V spekei* (Smith), from between Latitude 6° and 7° South of the equator along the eastern coast of Africa, is peculiar in that it has a large number of low, spiral rows, as many as 30 on the bodywhorl, with slightly marked tubercles. These ridges represent a large number of secondary and tertiary ridges of Annandale's nomenclature, all of which are more or less equally developed. The condition is somewhat similar to that of *V polyzonatus* (Frauenfeld) from French Indo-China, and that of *V quadratus* var. *heudei* (Dautzenberg & Fischer) from China. *V. cepoides* Smith is, except for its very large size and certain differences in the proportions of the whorls and aperture, similar to the *forma unicarinata* ; in some fully grown individuals, however, the peripheral keel is obsolete. *V abyssinica* (von Martens) from Lake Dembea and other localities in Abyssinia is, as Germain (*loc. cit.* p. 223) has pointed out, nothing more than a form of *V unicolor*. Its shell has a well developed peripheral keel on the bodywhorl and resembles the unicarinate form. *V rubicundus* (von Martens) and its var. *subturritus* von Martens from Lake Victoria Nyanza and other localities are only slightly modified forms of *V unicolor*. The embryonic shell of these forms has traces of the peripheral keel but the adults resemble the *forma normalis*. *V meta* von Martens from the same area as *V rubicundus* is nearly allied to it and resembles it in the type of sculpture. *V constrictus* (von Martens) from Lake Victoria Nyanza has a prominent peripheral keel and a low one corresponding to the first primary ridge next to the suture ; sometimes traces of a third intercalated between the two are also to be seen. It apparently is in an evolutionary stage intermediate between the bi- and the tricarinate forms of *V unicolor* referred to above. In var. *phthinotropis* von Martens, from the same locality as the typical species, the ridges except for the peripheral keel are much less prominent. As to the var. *trochlearis* von Martens, the author (*op. cit.* p. 181, pl. vi, figs. 19-21) did not differentiate between the various forms. He figured and described one form with two ridges apparently representing the first and the third primary ridges, and a second one which has only the peripheral keel or the third ridge ; they respectively represent the bi- and the unicarinate forms. In var. *pagodella* von Martens (pl. xix, fig. 33) the peripheral keel only has persisted, but it is very highly developed and owing to the greatly impressed suture and the flattened sloping nature of the whorls it appears as if the keel is a different structure from the peripheral keel of the other forms. There can be no doubt, however, that the ridge is certainly the third primary ridge and that the form *pagodella* has evolved from an ancestor like *trochlearis* (pl. xix, fig. 34).

E. von Martens remarked (*op. cit.* p. 182) that full-grown embryos of var. *trochlearis* taken out of the uterus are devoid of any hairs or chaetae on the shells similar to those found on the shells of the common European species. The case is very similar to that of *Neothauma tanganyicense* (Smith), (*vide infra*, p. 184), in which the fully developed embryos are without chaetae, but the younger ones, which lie higher up in the uterus, were found to have chaetae on their shells. The long period of gestation, as is clearly indicated from the enormous size to which the embryos grow in these forms, is probably responsible for the loss of the chaetae during the uterine period of their existence.

V duponti de Rochebrune, which Bourguignat considered to be a *Cleopatra*, and for which Jousseaume had created a new genus *Bellamya*, has been considered by Dautzenberg and following him by Germain (*loc. cit.* pp. 209-217) to be a variety of *V unicolor.* It would, however, appear to be a well characterised species found in the basin of the River Niger in Senegal, Guinea, etc., and is considered as a distinct species in the following account. The species is very common and is found in streams, rivers, ponds, etc. Like *V unicolor* the species has forms with uni-, bi- and tricarinate shells, and appears to have followed the same line of evolution. *V leopoldvillensis* (Putzeys) from the Belgian Congo is closely allied to *V duponti* and is probably only a variety of it.

The group of forms of the type of *V capillatus* (Frauenfeld) is the last to be considered here. They have a wide distribution in the basin of the River Zambesi, Zanzibar, Rhodesia and Lorenzo-Marques in East Africa. The typical form of this group, *V capillatus*, was considered to be only a synonym of *V unicolor* by Newton [1]. Germain (*loc. cit.* pp. 224-229) considered it as a representative species of *V unicolor* from which it is evolved, but believed that in the basin of the Zambesi it forms a distinct local race or what he terms " especé gèographique." Germain did not clearly differentiate between the various forms of this group, and only considered them to represent different stages in the development of the sculpture of the shell corresponding to the different degrees of the development of the animal. The form *sambesiensis* Sturany of the group of *V capillatus* has shells with perfectly rounded whorls, and with a moderately developed but very reticulate type of sculpture; there are, however, no ridges on the shell. It corresponds to the *forma normalis* of *V unicolor.* In the species *V capillatus* the whorls have in addition to the three primary ridges a number of secondary and tertiary ridges with low, curved chaetae on them. In this case all the ridges are more or less equally developed and the presence of the chaetae is only a retention of the larval character of the shell. The shell whorls are also somewhat angulate and resemble those of the biangulate form of *V unicolor.* In the var. *densistriata* Preston the sculpture resembles that of *V capillatus* but the ridges are less well developed and there are no chaetae on them. This group of forms represents a parallel evolution of the shell sculpture to that of some forms of *V unicolor* and also some of the Asiatic species of the Vivipari Dissimiles Group, but the main point of difference is the more or less equal development of all the ridges and the retention of the chaetae on them; this last is nothing

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[1] Newton, R. B., *Quart. Journ. Geol. Soc. London*, LXVI, p. 240 (1910).

more than the persistence of one of the larval characters and is not to be confused with the formation of the tubercles or nodules on the shells of some forms.

In summing up this review of the various forms of the African species of the genus *Viviparus*, it may be noted that they are not very highly specialized forms, and are apparently all to be derived from the central species *V. unicolor.* The more highly sculptured forms are all found in lakes or other big areas of water in which the conditions of life are uniform, and where almost always species of different families and genera become specialised. In the case of the group of *V. capillatus* the shells retain embryonic characters in the adult stage, and as was confirmed by examination of the soft-parts of the var. *sambesiensis* this is correlated with the specialised structure of the mantle edge of these species.

Neothauma Group.—Smith[1] from the peculiarities of the shell alone originally considered *Neothauma* to be a highly specialised Viviparid quite distinct from the genus *Viviparus,* but in a later paper,[2] agreeing with Pelseneer,[3] united it with the latter genus. Moore[4] on anatomical grounds again separated it from *Viviparus,* and I believe that the differences in the shell and the soft-parts are quite enough to justify the separation of the form as a distinct sub-genus. The sub-genus was originally believed to be confined to Lake Tanganyika, but the discovery of a species, *N. mweruensis*[5] (Smith), in Lake Mweru, has considerably extended the range. *N. mweruensis* further throws a great deal of light on the origin of the sub-genus *Neothauma.* The Lake Mweru species is derived from a form like *V. crawshayi* Smith, also found in the same lake, in which the shell is rimate-carinate, but is tending to have the umbilicus reflected and the posterior angle drawn out into a canal-shaped structure. The shell itself does not differ in shape from that of the unicarinate forms of *V. unicolor,* but the peripheral keel is more pronounced. The evolution is further advanced in the form described as var. *pagodiformis* of *V. mweruensis* by Smith (*loc. cit.* p. 638, pl. lix, fig. 7), which I consider to be a separate species of the sub-genus *Viviparus.* In this species the suture is much more impressed and lies next to the peripheral keel. The peripheral keel is well developed and is quite sharp ; there are also traces of two other spiral ridges above the peripheral. The canal-shaped prolongation of the mouth is also more marked. In *N. mweruensis* the shell is not so thick as in *N. tanganyicense* (Smith) and only the peripheral keel is well developed, while the sutural ridge, which is quite marked in *N. tanganyicense,* is very feeble. The aperture is similar to that of *N. tanganyicense* (pl. xix, fig. 38) but the canal is less marked. It may also be noted that a similar though less highly developed condition of the aperture has also been observed by Germain[6] in the case of *Viviparus duponti* de Rocheburne, from Senegal.

In view of the differences in the form of the shells of the two species and their occurrence in different lakes I believe that they evolved independently in the two areas.

The embryonic shell (pl. xix, fig. 39) is similar to that of the various species of the sub-genus *Viviparus,* and bears on the young shells the three rows of chaetae on low ridges.

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[1] Smith, E. A., *Proc. Zool. Soc. London,* p. 349 (1880).

[2] Smith, E. A., *Proc. Zool. Soc. London,* p. 635 (1893).

[3] Pelseneer, P., *Bull. Mus. Roy. d'Hist. Nat. Belgique,* IV, p. 105 (1886).

[4] Moore, J. E. S., *Proc. Zool. Soc. London,* p. 466, pls. xxv, xxvi (1901) and *Tanganyika Problem,* pp. 264, 265, figs. 44-46 (London, 1903).

[5] Smith, E. A., *Proc. Zool. Soc. London,* p. 638, pl. lix (1893).

[6] Germain, L., *Res. Sci. Voy. G. Babault d. L'Afrique Orient. Angl. Moll. Terr. et Fluv.* I, p. 214 (Paris, 1920).

The full-grown embryonic shell loses the chaetae while still within the uterus, and is of exceptionally large size, one specimen taken out of a gravid female measured 16·5 mm. × 16·1 mm. The shell shows traces of the three colour bands, but these disappear with age. The adult shell has a very marked peripheral keel, and there is a second ridge corresponding to the sutural ridge lying next to the suture.

Bourguignat[1] described a number of the species from the Tanganyika Lake, but they are all based on individual variations of the type-species *N. tanganyicense.* The second species from Lake Mweru has been mentioned above.

Cleopatra Group.—Like the sub-genus *Neothauma, Cleopatra* Troschel is endemic in Africa, and with the exception of Madagascar has not been found anywhere else.

The genus at the present day is most abundant in the coastal region of Eastern Africa extending in the north to Egypt and in the south to the mouth of the Zambezi river, while species have also been recorded from West Africa and from Madagascar. Kobelt (*loc. cit.* p. 164) considers the genus *Cleopatra* to have been evolved in Europe in the Mediterannean basin and to have wandered into Africa. Among the Createaceous Viviparids the species *Paludina deshayesiana* (Matheron) from Provenance, South France, has been believed by Oppenheim[2] to be a species of the genus *Cleopatra,* and apparently it was this record which led Kobelt to consider Europe as the region in which *Cleopatra* had originated. The shell of the fossil *V deshayesiana* superficially resembles the shells of *C. bulimoides* (Olivier), but there is no justification for assigning the fossil species to the genus *Cleopatra.* It is only a small shelled species of the genus *Viviparus.* I do not believe that *Cleopatra* wandered to Africa from Europe, but am of opinion that it must, as is discussed below, have been evolved in Africa itself.

The genus has often been referred to the Melaniidae and Paludominae,. and Thiele [3] has recently again placed it with the latter subfamily. Until, however, its anatomy has been fully compared with that of *Paludomus* and its inclusion in that subfamily justified, I propose leaving it with the Viviparidae.

A large number of species[4] of this genus have been described by various authors, but many of them appear to be only varieties or even to be based on individual variations, and the genus needs revision. Like other Viviparids *Cleopatra* shows a parallel evolution of keeled and ridged species from more or less smooth shelled forms (pl. xix, figs. 35-37). *C. guillemeti* Bourguignat shows faint traces of ridges on the bodywhorl; of these spiral ridges the peripheral is the most prominent. The same condition is to be observed in *C. broecki* Putzeys and *C. hargeri* Smith. In *C. johnstoni* Smith and *C. emini* Smith there are two ridges on the bodywhorl and traces of these are also to be seen on the other whorls. In *C. soleilleti* Bourguignat and *C. percarinata* Bourguignat the shell is more elongate and the ridges are wide apart. In *C. mweruensis* Smith the upper whorls have three ridges, while the body-

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[1] Bourguignat, J. R., *Ann. Sci. Nat. Zool.* (2) X, pp. 24-39, pls. ii, iii (1890).

Dr. L. Germain, who has examined the types of Bourguignat's species of *Neothauma* in the Paris Museum, was kind enough to inform me that my surmise about all these species from Lake Tanganyika being synonyms of *N. tanganyicense* (Smith) is correct. In the western area of the lake, however, between Pambété and Kibanga, the form *bicarinata* with two carinae has become fixed as a distinct local form.

[2] Oppenheim, P., *Palaentographica* XLII, pp. 328-331, pl. xvi, figs. 22, 24 (1895).

[3] Thiele, J., Kükenthal and Krumbach *Handbuch der Zoologie,* V, p. 83, (Berlin, 1925).

[4] See Kobelt, W., *loc. cit.* pp. 382-409, pls. lxxv-lxxvii (1909).

whorl has as many as seven; of these the three primary ones are more prominent. *C. grandidieri* (Crosse & Fischer) and *C. exarata* (Martens) and a number of other species were referred by the authors to the genus *Paludomus*, but they are true Cleopatras, and Kobelt has rightly referred them to this genus. The shell in these species has a large number of ridges closely placed in the same way as in *D. mainitensis* (Bartsch) from the Philippines (see *antea* p. 178). Reference may also be made here to the extraordinary forms with well developed sculpture described by Dautzenberg and Germain (*loc. cit.*) from the branches Lualaha and Luapala of the River Congo in Belgian Congo. The ridges are solid and the shells appear somewhat cancellated. The species similarly vary with reference to colour bands. Some of them, like *C. brincatianus* (Bourguignat) and *C. bulimoides* (Olivier), are banded while others like *C. aurocincta* Martens and most of the ridged species are uniformly coloured.

IV. EUROPE.

In treating the Viviparids of Europe I include with them the Western border of the Palaearctic Region. In this area the family at the present day is represented by a single genus—*Viviparus* Montfort, and all the forms are smooth-shelled species belonging to what I term *Viviparus s. s.*

As is shown in the sketch-map, the distribution of the species in this area is very interesting. In the British Isles there are no Viviparids in Scotland, Ireland and the greater part of Wales. In England proper the area of distribution may be roughly taken as the drainage system of the Thames, from whence the Viviparids have spread by connecting canals northwards to York and westwards to Montgomery, Glamorgan and Devonshire.[1]

In France the Pyrenees basin to the south-west and the greater part of the Mediterranean coastal area is without any representatives of the family, and so is the whole of the Iberian Peninsula. With the exception of *V. viviparus* var. *isseli* (Bourguignat),[2] which has been found at Pisa, no species are found south of the Apennine Mountains in Italy.

In Belgium and Holland the two common species of the European fauna are found in rivers, streams, and other freshwater areas beyond the tidal range, and the same appears to be the case with Denmark. In Scandinavia[3] the range does not appear to extend beyond latitude 58° N., and this seems to be the northern limit even for Russia. In the east the Ural Mountain chain and River Volga form the boundary line of their eastern limit of extension, while in the south-east they are found in the Trans-Caucasian region and Asia Minor to about 30° East. In Central and Eastern Europe they are well represented.

In spite of the great amount of work that has been done on the European Viviparidae our knowledge of these forms is in a very confused state. Bourguignat[4] divided the species

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[1] See *Roebuck Mem. Number* in *Journn. Conch.* XVI, p. 178, pl. vii (1921).

[2] See Kobelt, *loc. cit.* p. 306 (1908).

[3] See Westerlund, C. A., *Faun. Moll. Terr. Fluv. Sveciae Norv. Dan.* pp. 445-455 (Stockholm, 1871-73) and *Land-och Sotvatt. Moll. Exkurs.* pp. 56, 57 (Stockholm, 1884).

Bourguignat, J. R., *Recen. Vivipara système Europ.* pp. 1-52 (Paris, 1880).

of the area into seven sub-groups and recognised no less than 50 species. Westerlund[1] distinguished 20 good species and an equal number of varieties. Kobelt[2] originally distinguished 5 " Formenkreise " or geographical groups, but later,[3] apparently following Clessin,[4] he distinguished two main types of forms, 1. *Vivipara contecta* Millet, and 2. *Vivipara fasciata* Müller. He is not quite definite about the range of the former, but stated that it is found over the whole of the European area, though the forms included under it, and for which he employed a trinomial nomenclature, do not extend east of the Volga and certainly not into Greece and Turkey. The group of *V. fasciata* he divided into 4 sub-groups which according to him correspond to the " Hauptflussgebieten " or the main river-basins. These according to the regions of their distribution are :—1. Nördliche, occupying the whole of the area north of the Alps, except for the regions mentioned already, and running from the Pyrenees basin to the Trans-Caucasian area with *V fasciata* as the central type; but becoming gradually replaced to the east by the species *V okaensis* Clessin and *V duboisiana* Mousson ; 2. Südliche in the region of the southern Alpine lakes and in the basin of the river Po, with *V pyramidalis* (Jan.) Rossmässler as the central form ; 3. Isterkreis or the Donauformen in the Lower Danube and probably extending through the Balkans to the Dardenelles and reminding one of the probable course of the Danube in the late Tertiary or the Old-Diluvian times. The central form of the group is *V danubialis* Bourguignat ; and 4. Dinarische Kreis in the lakes and streams of the eastern part of the Balkan Peninsula with *V mammilata* Küster as the central species.

The above system of Kobelt is not very satisfactory, and the species of the European area need a thorough revision. It may also be noted that the names given to the two main groups by Kobelt can not be upheld owing to the fact that his *V contecta* (*non* Millet[5]) is what should be called *V viviparus* (Linn.) and his *V. fasciatus* (Müll) is the same as *V contectus* (Millet), but though the name of Müller has to be adopted owing to its being earlier, its definition as given by Kobelt is not correct. This was first established by Kennard and Woodward[6] by an examination of the Müllerian and Linnean types, and I am able to confirm their work from a re-examination of the same material.

V. AMERICA.

As has been noted already (p. 162) no members of the family are found in South America. In North America the area of distribution as shown in the map does not extend north of latitude 52° N. and they are not found in Mexico or Central America. To the west the Rocky Mountains seem to form the furthest boundary line of their distribution. In the West Indies the family is only represented by a single species in Cuba. Call [7] has published a map show-

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[1] Westerlund, C. A., *Faun. Palaearct. Binnenconch.* Hft. VI, pp. 3-11, (Berlin, 1886).

[2] Kobelt, W., *Monograph.* (*loc. cit.*) pp. 298-374, pls. lx-lxxiv (1908-09).

[3] Kobelt, W., *Rossmässler's Icon.* (n.f.) XIII, pp. 21-32, pls. cccxlii-cccxlvii (Wiesbaden, 1907).

[4] Clessin, S., *Malakozool. Blätt.* (n f.) I, pp. 3, 4 (1879).

[5] Dr. L. Germain informs me that from the examination of specimens from the type-locality of *V. contectus* (Millet), he has come to the conclusion, that this form, as was suggested by other authorities, is not synonymous with *V. fasciatus* (Müller), but is a distinct form allied to *V. viviparus* (Linn.).

[6] Kennard, A. S. and Woodward, B. B., *Proc. Malacol. Soc. London,* XIV, pp. 88-90 (1920) ; see also the same authors' *Synonomy of British Non-Marine Mollusca* pp. 9-14 (London, 1926) and Caziot, E., *Bull. Soc. Zool France, Paris,* XLVIII, pp. 8-11 (1923).

[7] Call, R. E., *Amer. Journ. Sci.,* XLVIII, pp. 132-140 (1894).

ing the geographical and hypsometrical distribution of the Viviparidae in the United States and this may be consulted for details of the exact distribution of the genera and species.

In addition to the older literature on the subject the critical Catalogue of the Freshwater Molluscs of North America north of Mexico,[1] published by Mr. Bryant Walker of Michigan, has served for the following notes on the Viviparids of this region. I am also greatly indebted to the same authority for sending me further notes which have proved of immense use. I have also examined the collections of the Viviparidae of this area in the British Museum (Natural History), London, for doubtful points.

In North America there are four sub-genera of the family, *viz.*, *Viviparus* Montfort, *Tulotoma* Haldeman, *Campeloma* Rafinesque, and *Lioplax* Troschel. Of these *Viviparus* alone is found in other parts of the world, and the other three sub-genera are characteristically American. The reference of some fossil species from various European strata to these genera by different authorities is, in my opinion, without any justification. In the following notes the members of the four genera are dealt with on similar lines as those of the various groups found in other parts of the world.

Viviparus Group.—In considering the species of this group I have not taken into account the European species *V. fasciatus* (Müll.) = *V. contectus* (Millet) of the earlier authors, or the Japanese species *Cipangopaludina malleata* (Reeve) and *C. japonica* (von Martens), as these have undoubtedly been introduced by human agency during recent years. The European species *V. fasciatus* is found in various parts along with the true American species in the eastern parts of the States, while the Japanese species have become established in a number of localities on the Pacific coast in both Canada and the United States.[2] As to the true American species there is no doubt that they are all direct descendants of the very rich Cretaceous and probably earlier Viviparid faunas of the Laramie Beds and other areas (*vide* p. 249), and are most richly represented in the basins of the Missouri and the Mississippi; in other parts the extension is of a much later date and has apparently been brought about either by artificial means or by the spreading of the species along the basins of the various rivers and streams. The ancestral species appears to me to be the more or less smooth-shelled form *V. leai* (Meek & Hayden). All the recent species are smooth with more or less evenly rounded whorls and with only the trace of a peripheral carina, and have four colour bands instead of three as in the European species. Hannibal [3] has recently proposed a new sub-genus *Callina* with *V. intertextus* (Say) as the type, but as Walker (*op. cit.* p. 126) has shown, there does not seem to be any justification for this division of the American species into two groups. I follow Walker in considering the following as good species :—*V. contectoides* Binney, *V. georgiana* (Lea), *V. halliana* (Lea), *V. intertextus* (Say), *V. subpurpureus* (Say), *V. troostiana* (Lea), *V. waltoni* Tryon, *V. warneana* (Shuttleworth) and *V. walkeri* Pilsbry & Johnston.

Campeloma Group.—Walker, in following Meek, has given good reasons for adopting the name *Campeloma* Rafinesque [4] in preference to *Melantho* Bowdich or *Ambloxis* Rafinesque.

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[1] See Binney, W. G., *Smithsonian Misc. Coll.* CXLIV, (Washington, 1865) ; Tryon, G. W. Jun.—*A Monograph of the Freshw Moll. U.S.* (Philadelphia 1870) ; and Bryant Walker, *Univ. Michigan Mus. Zool. Miscellaneous Publ.* No. 6 (1918) for earlier literature and the figures and descriptions of the American Viviparidae.

[2] See Bryant Walker, *Op. cit.* p. 126 for references.

[3] Hannibal, H., *Proc. Malacol. Soc. London*, X, p. 193 (1912).

[4] Rafinesque, C. S., *Journ. Phys.* LXXXVIII, p. 422 (1819).

The sub-genus is distinguished from *Viviparus* by its more solid thick shell, thickened inner lip and in most species the wavy outline of the outer lip of the aperture. The shell is smooth or with faint vertical ridges and is uniformly coloured. The operculum is concentric with a simple inner margin. The radular teeth are simple and very minutely crenulated. Lewis[1] originally proposed dividing the species of the sub-genus into four groups, but later [2] found that this division was not possible. A monograph of the species was published by Call,[3] and I follow Walker in considering the following as good species:—*C. decisum* (Say) (pl. xix, fig. 40), *C. integra* (Say), *C. ponderosa* (Say), *C. rufa* (Haldeman), *C. subsolida* (Anthony), *C. exilis* (Anthony), *C. genicula* (Anthony), *C. limum* (Anthony), *C. milesii* (Lea), *C. floridense* Call and *C. lewisii* Walker.

The embryos of most species are stated to be evenly rounded and I can confirm this from my examination of the young of *C. decisa*, but from the poor material at my disposal I am unable to add anything regarding the presence or absence of the rows of chaetae on the shell. The embryos of *C. spillmani* Lea (= *?C. limum* (Anthony), however, are according to Walker "strongly and acutely bicarinated."

Lioplax Group.—The sub-genus *Lioplax* Troschel [4] is mostly found in streams and so far as I can find from the literature the more highly sculptured species are confined to the lower reaches of the streams in Alabama and Florida. The shell is uniformly coloured and has no colour-bands. The whorls of the adult shells of most species are smooth, but in some cases they are shouldered and there may be vertical ridges near the suture. In young shells and in some cases on the adult shells also it is possible to distinguish the remains of spiral ridges. The operculum is concentric with a subspiral nucleus. The radular teeth are smooth and not serrated at the apices. Walker recognizes the following as good species:—*L. subcarinata* (Say) (pl. xix, fig. 41) with a wide distribution, *L. cyclostomatiformis* (Lea), restricted to Alabama and the adjacent territories, *L. eliotti* (Lea) found in Georgia and Florida, *L. contorta* (Shuttleworth) in Alabama and *L. pilsbryi* Walker in Florida.

I have examined spirit material of *L. subcarinata*, but unfortunately none of the specimens were gravid, and I am, therefore, unable to add anything about the form or the structure of the embryonic shells.

Tulotoma Group. The sub-genus *Tulotoma* Haldeman [5] is confined to rivers in Alabama. Through Dr. Bryant Walker's kind help I have had an opportunity of examining preserved material of the type-species—*T. magnifica* (Conrad). The general anatomy is very similar to that of *Viviparus,* but the radula and the subspiral operculum, with the inner margin reflected to form an elevated marginal fold, are characteristic of the genus. The embryonic shell is of moderate size with the whorls somewhat swollen, and the surface with three spiral ridges covered with curved chaetae as in the case of *Viviparus.* The adult shell (pl. xix, figs. 42—44) is of fair size with the whorls moderately swollen, and the surface smooth or with well developed tubercles. The three species of the sub-genus enumerated below form a regular series in the evolution of the thick-shelled highly sculptured form,

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[1] Lewis, J., *Amer. Journ. Conch.* IV, pp. 133-136 (1868).

[2] Lewis, J., *Amer. Journ. Conch.* V, pp. 33-36 (1869).

[3] Call, R. E., *Washburne Coll. Bull.* I, pp. 149-168 (1886).

[4] Troschel, F. H., *Gebiss der Schnecken,* I, p. 100 (Berlin, 1857).

[5] Haldeman, S. S., *Monograph Freshw. Unival. Moll.* Suppl. ii, p. 36 (1840).

like *T. magnifica*, from *T. coosaensis* with a thin shell and practically without any sculpture ; *T. angulata* has a moderately thick shell and the sculpture is intermediate between that of the two species mentioned already. All the three species are paludine forms, and are only found in Alabama in the Coosa River, *T. coosaensis* and *T. angulata* in the upper reaches of the river where the waters are rapid and *T. magnifica* in the lower slow running parts of the stream. From its geological history there can be no doubt that *Tulotoma* has evolved from the genus *Viviparus* in Cretaceous times in the same way as *Taia* Annandale and *Margarya* Nevill have done in Asia from other forms of the same genus. There is, however, no justification for considering the European Levantine fossil species as being congeneric with *Tulotoma*. *Tulotoma* was discussed in detail by Wetherby,[1] and the following three species are referred by recent authors to it:—*T. magnifica* (Conrad), *T. angulata* (Lea) and *T. coosaensis* (Lea).

Cuba.

The only Viviparid known from Cuba is D'Orbigny's species *Paludina bermondiana*.[2] It is a smooth-shelled species apparently allied to the other North American species of the sub-genus *Viviparus*.

5. FOSSIL VIVIPARIDAE.

The records of the fossil Viviparidae range from the Jurassic strata of the Inferior Oolite age (Bajocien) upwards to recent times. The record of a supposed form of the genus from the Carboniferous strata of Yorkshire, England, by Garwood [3] under the name *Viviparus carbonarius* is undoubtedly based on incorrect identification. As is discussed further on it is even doubtful whether the two species of *Viviparus* from the Jurassic strata, which were described as *V. scotica* Tate [4] and *V. langtonensis* Hudleston,[5] are correctly referred to this family. From the Cretaceous onwards, however, there is no doubt that the members of this family became definitely separated from the ancestral marine and estuarine forms, and took to a freshwater life. The earliest Jurassic and Cretaceous species, which are found in the Purbeckian Beds and the Wealden Strata of England and Germany, were referred by Sandberger [6] to the recent North American sub-genus *Lioplax* Troschel. As Kobelt rightly pointed out in his Monograph, the shells of these forms do not at all resemble those of the fossil or the recent species of *Lioplax*, while there is no possibility of determining the form of the operculum or the radula on which the distinction of the sub-genus from other Viviparids depends. It appears moderately certain, however, that we should not be far wrong in considering these species as being the earliest known forms of the genus *Viviparus.s.l.*, from the Old World regions. In North America there are two fossil forms which have doubtfully been considered to have come from strata of the Jurassic Period, but all certain records from this part of the world are also from the Cretaceous onwards.

Of palaeontological literature on the Viviparidae, the pioneer work of Sandberger (*loc. cit.*) has first to be considered. In this work the author based his conclusions on insufficient

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[1] Wetherby, A. G., *Quart. Journ. Conch.* I, pp. 207-215 (1876) ; also see Call, R. E.—*loc. cit.* pp. 132-141 (1894).

[2] See Reeve, L., *Conch. Icon.* XIV, *Paludina* Sp. 28, pl. v (1863), and Y. Molina, *Contr., Faun. Malacol. Cubana*, p. 139 (Habana, 1878).

[3] Garwood, E. J., *Geol. Mag. London*, LIV, pp. 289-293, pl. xiii (1922).

[4] Tate, R., *Quart. Journ. Geol. Soc. London*, XXIX, p. 349, pl. xii, fig. 3 (1873).

[5] Hudleston, W. H., *Mon. Pal. Soc. London*, p. 488, pl. xliv, figs. 1*a*, *b* (1896).

[6] Sandberger, C. F. L., *Die Land–u. Süssw. Conchyl. Vorwelt*, pp. 59-62, pl. ii, figs. 15-17 (Wiesbaden, 1870).

data, and referred the European fossil species indiscriminately to the recent genera and sub-genera of the Viviparidae; his comparisons of the fossils with the recent species are also far from justifiable. Zittel [1] gave a short general account of the fossil species, but his remarks, which are mainly based on Speyer [2] and Sandberger, lack sufficient support. According to him the species of this family are found from the Middle Jurassic strata upwards, and he is obviously wrong when he says that the Viviparidae " sind über die ganze Erdoberfläche verbreitet." Fischer's treatment of the fossil genera has already been referred to (p. 160).

I do not propose to deal in the following account with the casual remarks of various authors regarding the family as a whole, but will limit the review to a consideration of the more important general treatises.

Meek [3] in his work on the American fossils included useful notes on the genera and sub-genera, as I call them, found in North America; they are the same as the recent forms and no further remarks about these are, therefore, necessary. Hannibal,[4] however, has again reverted to the old arrangement of separating *Campeloma* Rafinesque and *Lioplax* Troschel from the rest and placing them into a distinct family Lioplacidae Gill. As I have stated already, I consider both these as only sub-genera of *Viviparus*, and it is not justifiable even to separate them into a separate sub-family.

Reference may also be made to the remarks of Stefanescu,[5] who, after discussing the question of the nomenclature of the type-genus of the family at length, adopted the name *Vivipara* Lamarck for it. He, like Sandberger (*op. cit.* pp. 694, 695), referred the sculptured species of fossil Viviparids of Eastern Europe indiscriminately to the North American sub-genus *Tulotoma* Haldeman, which, owing to its incorrect etymology, he, like Fischer, changed to *Tylotoma.*

Brusina [6] proposed the new genus *Tylopoma* for some small-sized species of Eastern Europe which have smooth or sculptured shells. Cobalcescu[7] described a number of species allied to the type-form of *Tylopoma—T avellana* (Neumayr)—under the generic name *Bythinia*, but these were later referred to the genus *Tylopoma* by Stefanescu. Cossmann[8] has also included the genus in the Viviparidae, but I do not think that it is a member of this family, and all the species ought to be referred to the Hydrobiidae.

As to the species referred to *Tulotoma* Haldeman, I do not consider that the fossil species of Eastern Europe are at all genetically connected with the North American species. In the European fossil species only the sutural and the peripheral ridges are well developed and become tuberculate, while in the North American species, both recent and fossil, the median ridge is also equally developed and broken up into tubercles. The species of Annandale's new sub-genus *Protulotoma*[9] are not to be distinguished from other sculptured

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[1] Zittel, C., *Handbuch Palaeozool.* II, pp. 225, 226 (München and Leipzig, 1881-85).

[2] Speyer, O., *Palaeontographica*, XIX, pp. 83, 84 (1871).

[3] Meek, F. B., *U. S. Geol. Surv. Terr.* IX, pp. 576-588 (1876)

[4] Hannibal, H., *Proc. Malacol. Soc. London*, X, p 195 (1912).

[5] Stefanescu, S., *Mém. Soc. Géol. France, Paléontol.* VI, pp. 82-87 (1896).

[6] Brusina, S., *Beitr. zur Paläont. Osterreich-Ungar.* II, pp. 37, 38 (1882).

[7] Cobalcescu, G., *Studii Geol. Palaeont. Ter. Tert. Roman.* p. 139 (Bucaresci, 1883). See also Stefanescu, S.—*loc. cit.* pp. 100 103 (1896).

[8] Cossmann, M., *Essais Paléoconch. comp.* XII, p. 181 (Paris, 1921).

[9] Annandale, N., *Proc. Roy. Soc. London* (B) XCVI, p. 64 (1924).

fossil species which he considered to belong to the genus *Tulotoma*, and I believe it would be better to drop it altogether and call the European species, whether smooth or sculptured, *Viviparus*. Lörenthey's name *Carinia*,[1] which he proposed as a sub-genus for *V rothi* Lörenthey from the Balaton Lake, cannot also be considered to have any value and must be dropped.

Annandale's new genus *Palaeotaia* (*loc. cit.* p. 73) with *Melania hellespontica* Calvert and Neumayr as type has nothing to do with the Viviparidae, but is, as I am able to co-firm from an examination of the type-species and other allied forms like *M. hollandrei* and *M. ornatus*, to be referred to the family Melaniidae.

Finally reference may be made to Cossmann (*loc. cit.* pp. 176-189) who has, in addition to the genera and sub-genera already considered, included in the Viviparidae *Aegionia nom. mut.* in place of *Aegea* Oppenheim,[2] which is undoubtedly a *Valvata*; *Adelina* Contr.[3] with *A. elegans* as the type-species, which Oppenheim (*op. cit.* pp. 463, 464) had rightly referred to the Melaniidae (Tiaridae), and *Saccoia* Brusina,[4] which is undoubtedly a Hydrobiid. Cossmann's creation of the new section *Paludotrochus* with *V trochiformis* (Meek & Hayden) as type, and also his treatment of the subgeneric names *Melantho* Bowdich and *Campeloma* Rafinesque as two distinct sections are also unjustified.

In the following account the fossil species are reviewed according to the areas from which they are known, and their relationship to recent species and forms from adjacent areas is so far as possible, discussed.

I. ASIA.

India.

The earliest account of the fossil Viviparidae of India is that of J. de C. Sowerby,[5] who described a species from the Intertrappean Beds of the Deccan series of Late Cretaceous period, under the name *Paludina deccanensis*. Newton,[6] apparently from the figures and the meagre description of the species only, considered this form to be a valid species of the genus *Viviparus s.s.* I have examined the types of the species in the British Museum (Natural History), London, and am of opinion that they are not Viviparids but Hydrobiids. The types consist of a large number of very small shells deeply embedded in a piece of rock, and unfortunately in not one of the specimens is it possible to see the aperture. A more extensive account of the fossils of the Intertrappean Beds was published by Hislop,[7] who described a heterogeneous group of species under the generic name *Paludina*. Annandale[8] when revising the Indian fossil Viviparidae did not have access to either Sowerby's or Hislop's types, and had to rely entirely on the figures and descriptions of the two authors. Of

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[1] Lörenthey, I., *Res. Wissen. Erfor. Balatonsees, Anhang Palaeontol.*, IV, and iii, p. 161, pl. iii, fig. 19 (Wien, 1911)

[2] Oppenheim, P., *Zeitschr. Deutsch. Geol. Ges.* XLIII, p. 463 (1891).

[3] The name *Adelina* is preoccupied in Coleoptera (see Chevrolat in Dejean, P.F.M.A., *Cat. Coléopt. ed.* 2, IV, p. 315 (Paris, 1835). The name *Velutinopsis* Sandberger (*loc. cit.* p. 700 (1873) is, however, available for this genus.

[4] Brusina, S., *Boll. Soc. Malacol. Italiano,* XVIII, p. 49 (1893).

[5] Sowerby, J. de. C., *Trans. Geol. Soc. London* (2) V, pl. xlvii, figs. 20, 22 (1840). The description of the species is given in the explanation of the plate.

[6] Newton, R. B., *Ann. Mag. Nat. Hist.* (9) V, p. 247 (1920)

[7] Hislop, S., *Quart. Journ. Geol. Soc. London,* XVI, pp. 166-176, pls. v-viii (1860).

[8] Annandale, N., *Rec. Geol. Surv. Ind.* LI, pp 362-367, pl. xi (1921)

Hislop's species he considered *Paludina normalis* to be a true *Viviparus*, but was rather doubtful about *P. rawesi*. As to the other species he left their generic position unsettled. From my examination of the types I find that with the exception of *P. conoidea* Hislop, which is undoubtedly based on young shells of *V normalis*, all the other species described by Hislop are to be referred to the Hydrobiidae and Melaniidae (Tiaridae).

Forbes [1] in his account of the Siwalik Molluscs of Falconer's collections identified one of the species as " allied to *Paludina Bengalensis* but apparently distinct " and further added " though extremely near *P. Bengalensis* must be regarded as its representative than its homologue." The other species he considered to be " *P. unicolor* which is found amongst the shells of the Paris Basin, and also in the mammiliferous Crag of England. At present the species ranges from Egypt to India." Theobald [2] later identified the two species as *Paludina bengalensis* and *P. melanostoma*; his fossils it may be noted came from the Nerbuddah Gravel. Lydekker,[3] on the authority of G. Nevill, included in his lists *P. bengalensis* from the Nerbuddah Siwaliks and *P. dissimilis* from the Nerbuddah and Jumna Siwaliks. Blanford [4] described *P. bugtica* from the Bugti Hills, Baluchistan. In addition to the above are the papers of Annandale [5] in which he described new species from various parts and revised the Viviparidae of the whole area. His account is of special importance in view of his comparison of the fossil with the recent species. It is also of interest to note here that no members of the family Viviparidae were found by Stoliczka [6] in the Cretaceous rocks of Southern India. An analysis of the fossil species will now be made on the same lines as that of the recent species.

The oldest Indian fossil Viviparid, so far known, is *V normalis* (Hislop) from the Intertrappean Beds. It was rightly considered by Annandale to be closely allied to *V dissimilis* (Müller), and it probably represents the ancestral form of the Vivipari Dissimiles Group. It will not be out of place here to include a few remarks on the beds in which the species was found. The beds contain fossils of the freshwater Gastropods *Paludestrina*, *Limnaea* (*s. l.*), and *Bullinus*, and Pelecypods, Unionids and *Pisidium*, and in addition a great variety of estuarine and marine genera. Annandale[7] from a careful analysis of the conditions came to the conclusion that *Bullinus prinsepii* (Sowerby) must have lived under conditions which may be described as " paludine rather than lacustrine or fluviatile," and the same appears to have been the case with the Viviparids, though some of them may have lived in the streams. Originally the beds were assigned to the Tertiaries, but Neumayr [8] pointed out their similarity to the Laramie Beds of North America, and they have since been accepted as being Late Cretaceous or at the latest intermediate between the Cretaceous and Eocene.

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[1] Forbes, E., in *Falconer's Palaeont. Mem.* I, pp. 389, 390 (London, 1868).

[2] Theobald, W., *Mem. Geol. Surv. Ind.* II, pp. 284, 285 (1860).

[3] Lydekker, R., *Rec. Geol. Surv. Ind.* XV, pp. 106, 107 (1882).

[4] Blanford, W. T., *Mem. Geol. Surv. Ind.* XX, p. 131, pl. i, figs. 6, 7 (1883).

[5] Annandale, N., *Rec. Ind. Mus* XIV, pp. 159-168 (1918), *Rec. Geol. Surv. Ind.* L, pp. 231-238, pls. xxxi-xxxiii (1919), LI, pp. 362-367, pl. xi (1921) and LV, pp. 100, 101, p. vii (1924).

[6] Stoliczka, F., *Mem. Geol. Surv. Ind., Pal. Indica* (5) II, p. 268 (1868).

[7] Annandale, N., *Rec. Geol. Surv. Ind.* LI, pp. 52, 53 (1921). See also Oldham, R.D., *A Manual of the Geology of India* (2nd dn.), p. 276 (Calcutta, 1893)

[8] Neumayr, M., *Neues Jahrb. Min. Geol.* I, pp. 74-76 (1884), also in *Rec. Geol. Surv. Ind.* XVII, pp 87, 88 (1884)

Newton (*loc. cit.* pp. 243-249) compared *P. deccanensis* with an unidentified species from Matabeleland, Central South Africa, and from the analogy of the similar assemblage of fossils found in the two areas, he assigned the South African formation to the same period. As has, however, been pointed out *P. deccanensis* is not a Viviparid, but Newton's comparison applies equally to *V. normalis* (Hislop). Corresponding forms in other areas are *V. leai* (Meek & Hayden) from the Laramies of North America, *V. sublentus* (d'Orbigny) from the Tertiaries of Paris, and *V. lentus* (Solander) from beds of about the same age in England.

The two fossil species *V bugtica* (Blanford) and *V. atavia* Annandale, from the Bugti Hills, Baluchistan, are both from the Gaj Stage of Oligocene or Miocene Beds. Both species, as Annandale rightly pointed out, are closely allied to the recent *V helmandica* Annandale from Seistan, and apparently lived under similar conditions in more or less paludine basins. As I have shown already (p. 166), *V. helmandica* belongs to the Vivipari Dissimiles Group, and represents the north-western limit of the distribution of the Oriental Viviparidae. The Baluchistan fossils enable us to follow the change from the Cretaceous to the Oligocene or the Miocene in the species of the Vivipari Dissimiles Group. This change from smooth shells with evenly rounded whorls is very slight indeed compared to the changes undergone by the forms in the Laramie Beds in North America, or the evolution that has taken place in the recent species of the group in various parts of Asia and in members of the allied group of Vivipari Unicolores in Africa. It may, therefore, be assumed that the paludine environment in which these fossil forms lived remained more or less uniform during these long geological periods, and that little evolution took place in either the form or sculpture of the shells.

The only fossils of the Vivipari Bengalenses Group so far discovered have been found in the Nerbuddah Gravel and in recent alluvium, and probably are not older than the Pliocene. They were designated by Annandale " phase *pachydolicha* " and are identical with some of the living forms. The fossils are of too recent a date to help in reconstructing the past history and the origin of the group, but it appears certain that the Vivipari Bengalenses Group was evolved from some species like *V normalis* (Hislop) of the Vivipari Dissimiles Group.

The fossil species of the sub-genus *Taia* Annandale are, like the recent species, confined to Burma. They are not older than Pleistocene, and that probably represents the time when the sub-genus was evolved from the Vivipari Bengalenses Group. The evolution of the sculpture on the shells of the various members of this sub-genus in the exceptionally favourable lacustrine conditions in the S. Shan States, Burma, has already been discussed (pp. 164-166), and it need only be added that the sub-genus offers a very interesting example of parallel evolution to the sculpture of fossil species found in certain parts of Eastern Europe.

The two species *V dubiosus* Annandale and *V gregoriana* Annandale from the Oil Measures of the Dawna Hills, Burma, appear to me to be allied to the sub-genus *Dactylochlamys* Rao. The two species which are about Middle Tertiary in age are not greatly modified, and closely resemble the more primitive members of the sub-genus *Dactylochlamys*. They point to the origin of the sub-genus in the early Tertiaries from the Vivipari Dissimiles Group.

Rivularioides spinifera Annandale was considered by the author to belong to a new sub-genus of his genus *Taia*. I, however, consider that both *Taia* and *Rivularioides* are of the same rank. This species was found in the Oil Field region of Upper Burma, and, so far as can be judged from the associated fossils, it must have inhabited the upper reaches of streams which opened into estuarine areas. It has an elongate-ovoid shell, with an elongate aperture and a well developed broadened columellar callus of the same type as is found in various species of the sub-genus *Taia* Annandale and some forms of the Chinese *Rivularia* Heude. The sculpture consists of two spiral rows of spiny projections on the bodywhorl. The outer surface of the bodywhorl is band-like, and is somewhat concave between the sutural and the peripheral ridges which bear the spines. The flattening of the bodywhorl and the development of the spines on only two ridges, corresponding to the sutural and the peripheral, affords a very interesting parallel to the condition in the sculptured fossil Viviparids of Slavonia (p. 205). In view of there being only two ridges on the shells of *Rivularioides* the comparison and relationship of this sub-genus to *Rivularia* Heude, as suggested by Annandale, is also untenable. The similar development of the columellar callus is only an instance of the development of similar adaptive structures in response to similar habitats, and does not indicate community of descent.

China.

In addition to the quaternary and subfossil forms of the sub-genus *Margarya* Nevill, and its ancestral forms of the genus *Viviparus* discussed already (p. 170), the record of a fossil species from the Upper Tertiaries of China from the banks of the Sie-ho Stream in Hupe by Schlosser [1] has to be considered. The author recorded the species as *Paludina angularis* Müller, but from his comparison of the form with *V. ingallsiana* (Lea) and the fact that for a long time *D. angularis* (Müll.) was confused with *V. quadratus* (Benson), there can be little doubt that the fossils in question belonged to the latter species and were of the Vivipari Dissimiles Group.

Asiatic Russia.

The only fossils from this area are those described by von Martens from the banks of the Irtish stream near Omsk in the extreme west, and as their relationships are undoubtedly with the European species, they are discussed below (p. 215) with the species of that area.

East Indies.

Martin [2] described a species under the name *Vivipara eastoni* from Silat River Beds in Borneo, but the species was later considered by Icke and Martin [3] to be a *Faunus* and was referred to a new sub-genus for which the name *Eastonia* was proposed by the authors.

The only fossils of the family from Java are the ones which were recorded by Martin [4] as *Paludina* (*s.s.*) *javanica* var. probably from Pleistocene Beds. These have rightly been referred to *V. javanica* (v.d. Busch) and its variety *moussoni* von Martens by Oostingh.[5]

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[1] Schlosser, M., *Ann. Mus. Nat. Hung. Budapest*, IV, p. 39 (1906).

[2] Martin, K., *Verslag. Natur. Afd. Konik. Akad. Wetensch. Amsterdam*, VII, p. 305, fig. (1899). In English edition of the same work the description of the species is reproduced on p. 248.

[3] Icke, R. and Martin, K., *Leiden Samml. Geol. Reichsmus.* VIII, pp. 106-144 (1906).

[4] Martin, K., *Samml. Geol. Reichsmus, Leiden* (*n.f.*) I, Hft. ix, pp. 249, 250, pl. xxxvii, figs. 601-604 (1905).

[5] Oostingh, C. H., *Meddl. Landbouwhoogeschool.* XXVI, paper 3, pp. 55, 56 (Wageningen, 1923).

II. AFRICA.

The very interesting fossil Viviparid from Matabeleland in South Africa, and the peculiar assemblage of freshwater forms found associated with it, rightly led Newton [1] to the conclusion that the formation was comparable to the Intertrappean Beds of Peninsular India, and was like these Beds to be referred to the Cretaceous period. The " Botletle Schichten " in the south of the Kalahari area in Bechuanaland described by Passarge,[2] and the " Chalcedonic Quartzite " in the Bakota Gorge of the Zambesi River described by Lamplugh,[3] were also believed by Newton to be contemporaneous with the Matabeleland formation, and he, therefore, concluded that this Upper Cretaceous formation extends from the Zambesi River to Cape Colony. The fossil species of the genus *Viviparus*, which, owing to the badly preserved material, was neither named nor described by Newton, however, closely resembles the recent African *V unicolor* (Olivier), and, as has been discussed already, is also allied to the Indian Intertrappean form *V normalis* (Hislop). From the great similarity of the Matabeleland fossils Newton reaffirmed the land-connection between Peninsular India and East Africa, and considered it to be the remains of the Gondwana Land of the Upper Palaeozoic times. The land connection, he added, was probably submerged by the Tertiary Sea at the close of the Cretaceous.

If the above noted conclusions of Newton are correct, as they appear to be, then the species described as *V passargei* by von Martens [4] from the Kalahari area, Bechuanaland, is also probably of a much earlier age than was assumed by the author, and may be an Upper Cretaceous species. It was described as being closely allied to but distinct from *V. unicolor*, and from the description and figure of the species, I believe it to be an intermediate form between the Matabeleland fossils and the typical form of the recent *V. unicolor*. It may, however, be noted that no recent species of Viviparidae are found so far west as Bechuanaland in South Africa, and the occurrence of a fossil species in the area shows that the family had a more extensive distribution in earlier times.

Chronologically the next fossils to be considered are two species of *Cleopatra* Troschel. *C. bulimoides* (Olivier) and *C. exarata* (von Martens) were recorded by Newton [5] from the Burdigalien or the Lower Miocene strata of Nira. Both the species are recent forms, and are only of interest as showing that the genus *Cleopatra* is probably not very old, and that some of its species have remained unchanged from the Lower Miocene to the present day.

Newton [6] recorded fossils from the quaternary deposits of Nyassaland as *V. unicolor*, and added that amongst the large series of fossils it was possible to distinguish connecting forms between *V. unicolor*, *V robertsoni* (Frauenfeld) and *V. capillatus* (Frauenfeld). From a comparison of recent and fossil specimens he concluded that all these supposed species were to be referred to *V unicolor*.

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[1] Newton, R. B., *Ann. Mag. Nat. Hist.* (9) V, pp. 241-249, pl. viii (1920).

[2] Passarge, S.. *Die Kalahari*, pp. 196, 285, 648 (Berlin, 1904).

[3] Lamplugh, G. W., *Quart. Journ. Geol. Soc. London*, LXIII, p. 198 (1907).

[4] Martens, E. von. *Die Kalahari*, p. 753, fig. 3 (Berlin, 1904).

[5] Newton. R. B., *Quart. Journ. Geol. Soc. London*, LXX, p. 193 (1914).

[6] Newton, R B., *Op cit.* LXVI, pp 240, 241 (1910).

Other records of *V unicolor* are from the Quaternary deposits of the Nile Valley near Wadi Halfa by Blanckenhorn,[1] subfossil ones from the Libyan Desert by Jickeli,[2] and of the var. *conoidea* von Martens[3] from the southern banks of Lake Albert Edward. The more recent records of the same species are all summed up in Germain's[4] work to which reference may be made for details[5].

III. EUROPE.

Before dealing with the Viviparids of various European countries in detail I propose giving a short general account of the forms found in different parts.

In England, leaving aside the doubtful species *V. langtonensis* (Hudleston) and *V. scotica* Tate, the Purbeckian (Jurassic) and the Inferior Oolite (Cretaceous) species are the first to be considered. Of these *V. fluviorum* (Mant.) may be taken as the typical form and this has been considered by Kobelt (Monograph, p. 298) to be the ancestral form of all the Palaearctic species of the family. This is followed in Tertiary times by forms like *V lentus* (Solander) and through species like *V diluvianus* (Kunth) which leads on to the recent species *V viviparus* (Linn.) and *V fasciatus* (Müll.).

The oldest known fossil species from France is *V aurelianus* Cossmann from the Bathonian strata of the Cretaceous times; its relationship is not quite clear, but it or related forms gave rise to *V. beaumontiana* (Matheron), *V aspersus* (Michaud) and *V sublentus* (d'Orbigny). From these forms species like *V burgundiana* (Tourn.) were evolved, and these were followed by the recent species, which are the same as those found in England.

The Inferior Oolite species in Germany are identical with those found in England. The Eocene species *V hammeri* (DeFrance) is followed by *V splendidus* (Ludwig), which corresponds to and is probably closely allied to the English species *V lentus* (Solander). In the Miocene are species like *V varicosus* (Krauss), which is allied to French species of the same age, and is succeeded by *V diluvianus* (Kunth) and the common recent species.

The earliest record for Italy is that of the Tertiary species *V pollonerae* (Sacco)[6] from the deposits near Piemonte. It is closely allied to the French Tertiary species *V burgundiana* (Tourn.) and *V dresseli* (Tourn.) and was probably derived from the same ancestral form.

The ancestral species of the Pliocene forms of Slavonia and the adjacent areas is *V neumayri* Brusina. Its ancestral form is undoubtedly *V achatinoides* (Deshayes) from the Miocene Beds of Eastern Europe, which in turn is allied to species like *V ventricosus* (Sandberger) and *V splendidus* (Ludwig) of Western Europe. From *V neumayri*, the ancestral species of the Slavonian species, *V suessi* Neumayr, *V fuchsi* Neumayr and *V robustus* Brusina were evolved, and these were followed by the highly specialised and sculptured forms of the Lake-Beds of Eastern Europe. The Servian species *V. vinmatica* Brusina is

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[1] Blanckenhorn, M., *Zeitschr. Deutsch. Geol. Ges.* LIII, p. 432 (1901).

[2] Jickeli, C. F., *Nov. Act. k. Leopold Deutsch. Akad. Naturf.* XXXVIII, p. 237 (1874).

[3] Martens, E. von, *Beschalte Weichthiere Deutsch-Ost-Afrikas,* p. 176 (Berlin, 1897).

[4] Germain, L., *Moll. Terr. et Fluv. Voy. G. Babault d. l'Afrique Orient. Angl.* I, pp. 233, 234 (Paris, 1920).

[5] Since this paper went to press, I have received from Mr. L. R. Cox his paper on the Fossil Mollusca of Kaiso Bone Beds, Uganda Protectorate. A number of new records and new species of *Viviparus, Neothauma ?* and *Cleopatra* are described in this paper—*Uganda Protectorate Geological Survey Department, Occ. Pap.* II, pp. 53—71, pls. viii, ix (1926).

[6] Sacco, F., *I Moll. Terr. Terz. Piemonte Liguaria,* XXVIII, p. 45, pl. i, fig. 128 (Torino, 1895).

closely allied to *V neumayri*, and there can be little doubt that species like *V metohiensis* Pavlovic are also to be referred to the same ancestral form.

Pavlov in his recent memoir has published numerous figures of Viviparids from the basin of the River Volga and the southern part of European Russia, and these show that the central form of the later species of this region was also *V achatinoides* (Deshayes).

V. megarensis Fuchs from the Neogen of Greece and *V. bukowski* Oppenheim of Asia Minor correspond to *V. fuchsi* Neumayr, and apparently both of them are evolved from *V. achatinoides*. From the Island of Rhodes we have the large shelled species like *V. rhodensis* Bukowski, which is allied to *V. bukowski* of Asia Minor. The sculptured species of this island are also related to the species found in Cos.

The ancestral form of the highly sculptured species of the Island of Cos is *V. calverti* Neumayr, which in this island represents *V. neumayri* Brusina of Slavonia, and like it has probably evolved from *V achatinoides* (Deshayes).

The above short review gives an idea of the probable lines of evolution and migration of the Viviparidae of Europe and Asia Minor. Though the forms found in different areas in strata of different ages are not specifically the same, there can be no doubt as to their affinities, and hence a community of descent may be admitted. The centre of origin of the family was certainly somewhere in the extreme west, and in view of the oldest fossils occurring in England, this area may be accepted as the home of the first members of the family. The migrations must have taken a west to east and south-east direction,[1] but with our present knowledge it is not possible to lay down the exact lines of evolution and migration. As, however, the means of distribution of the members of this family are, as already discussed, necessarily very limited, it may be assumed that the forms which spread from the west to the east must have travelled along water-channels of rivers or streams which connected adjacent areas, or there must have been extensive water-basins connected with one another and forming a regular chain from one end to the other at different periods of the geological history of this continent.

In connection with the highly sculptured and otherwise specialised species of the Pliocene Lakes of Eastern Europe it is only necessary to note that the very rich series of forms, which had been produced under the very favourable lacustrine conditions, were not able to adapt themselves to the changing conditions and all perished without leaving any descendants whatsoever. The less specialised smooth-shelled species persisted and spread over the entire area, where they are found to-day as *V viviparus* (Linn.), *V fasciatus* (Müll.) and forms derived from them.

British Isles.

The fossil Viviparids of the British Isles are not of very great interest except from the point of view of their antiquity, and the fact that they represent the earliest known forms, from any area. They are all smooth-shelled forms, not at all specialised, and seem to have undergone very little change from the earliest known species to the recent forms found in the country. The distribution of the recent forms has already been discussed, and it is

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[1] See Oppenheim, P., *Zeitschr. Deutsch. Geol. Ges.* XLII, p. 486 (1891), who also believed in a west to east migration of the freshwater Mollusca of the Pliocene times of Europe, but his assertion that " die heutige Fauna Nordamerikas ihre directen Nachkommen darstellt " is quite unwarranted.

only necessary to remark that the fossil species, if they are rightly assigned to the family, seem to indicate a much wider distribution.

The earliest record of a Viviparid from this area is that of *Viviparus carbonarius* Garwood [1] from a supposed freshwater bed at the base of the Lower Carboniferous strata at Horton in Ribblesdale, Yorkshire. The specimens do not seem to have been very well preserved, but were described as not exceeding 14 mm. in length, and consisting of 4-5 smooth, tumid whorls. The suture was deep, not running very obliquely, and beyond feeble growth lines no sculpture was to be distinguished. In view of the associated fossils being *Pleurotomaria* and other marine forms, I am inclined to consider the fossils as being wrongly assigned to the family. In any case the name *carbonarius* is preoccupied by *Paludina carbonaria* Roemer,[2] for a species which Sandberger [3] has rightly considered to be synonymous with *Viviparus* or what he calls *Lioplax fluviorum* (Mant.). In view of the very doubtful nature of this fossil I do not propose considering it in the following account.

The next record and apparently the earliest for any species of the family is that of *V. langtonensis* (Hudleston)[4] from the Jurassic strata of the Inferior Oolite age (Bajocien), from Langton Bridge. The author rightly compared it to *V viviparus*, and noted that it differs from the latter in being smaller, having more convex whorls and more sloping sutural angle. He also referred to its resemblance to the Hebridean species *V scotica* Tate,[5] which was found in approximately the same horizon (Callovien according to Cossmann,[6] who also doubts whether the species is a Viviparid at all) on the coast of Skye. These two are doubtful species of the family and were certainly not freshwater forms.

The first extensive occurrence of the Viviparidae, and one which can without any doubt be assigned to the family, is that of the Purbeckian forms of Mid-Jurassic age and those found in the Wealden strata of the Lower Cretaceous age. The three species, which form the main constituents of the Purbeck Marbles, are *V. fluviorum* (Mant.), *V elongatus* (Sowerby) and *V inflatus* (Sandberger)[7]. The species were referred to the recent North American sub-genus *Lioplax* Troschel by Sandberger, but there is no justification for this course. There is no similarity in the form of the shells, while the operculum and the radula, the chief distinguishing features of the American sub-genus, are not known for the fossil species; I, therefore, propose considering them as belonging to *Viviparus*. The general form of the shell is not very different from that of the recent species of the genus and there is no special sculpture on the shells.

Newton's [8] list of the Eocene and Oligocene species is very complete and it is only necessary to make a few remarks about the species here. The species described by Sowerby [9] as *Phasianella angulosa* and *P. orbicularis* from Bembridge Beds of Oligocene age are the

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[1] Garwood, E. J., *Geol. Mag. London*, LIX, pp. 289-293, pl. xiii (1922).

[2] Roemer, F. A., *Verstein. Norddeutsch. Oolit. Gebirg.* p. 160, pl. ix, fig. 28 (Hannover, 1836).

[3] Sandberger, C. F. L., *Die Land-. u. Süssw. Conchyl. Vorwelt,* p. 59, pl. ii, figs. 15, *a-c* (Wiesbaden, 1870). Roemer's second species *P. nitida* (*op. cit.*) from near Rehburg and Lockum is also synonymous with *V. fluviorum* (Mant.).

[4] Hudleston, W. H., *Mon. Pal. Soc. London,* p. 488, pl. xliv, figs. 1, *a-o* (1896).

[5] Tate, R., *Quart. Journ. Geol. Soc. London,* XXIX, p. 349, pl. xii, fig. 3 (1873).

[6] Cossmann, M., *Essais Paléoconch. comp.* XII, p. 179 (Paris, 1921).

[7] Sandberger, C. L. F., *Die Land-und Süssw. Conch. Vorwelt.* pp. 59-62, pl ii, figs. 15-17 (Wiesbaden, 1870). All earlier references will be found in this work.

[8] Newton, R. B., *Syst. List Edwards Coll. Brit. Olig. Eoc. Moll. etc.* pp. 225, 226 (London, 1891).

[9] Sowerby, J., *Min Conch.* pl. clxxv, figs. 1, 2 (London, 1817).

same and are undoubtedly a form of the genus *Viviparus.* Newton doubtfully assigned some shells from the same Bembridge Beds to Deshayes's[1] species *Paludina distinguendus* from the Paris Beds. I have examined the specimens and have no doubt that they represent either the same species or are very closely allied to it. *V. lentus* (Solander)[2] from the Oligocene Beds in Hampstead, Bembridge, etc., and the Woolwich Beds of Lower Eocene age is another interesting species found in the strata under consideration. Specimens were described under this name by Deshayes [3] from the Parisian Beds, but these were later considered by d'Orbigny[4] to belong to a distinct species to which he gave the name *P. sublenta.* The specimens referred to under the name *V. vestitus* Edwards (Mss.) by Newton are also to be referred to the species *V lentus.* The Eocene and the Oligocene forms are all smooth-shelled species very much resembling the recent forms, and are of interest only from the fact that they show a very close relationship between the forms found in England and those found in the Parisian Beds ; the significance of this resemblance is discussed below (p. 240).

For a list and synonymy of the species from the Post-Tertiary to recent times, reference may be made to the recent work of Kennard and Woodward,[5] while descriptions and figures of the species will be found in the earlier work of Wood.[6] In this connection it may be noted that the species recorded as *P. clactonensis* by Wood is, as was shown by Kennard and Woodward,[7] the same as *V. diluvianus* (Kunth),[8] while Wood's *P. contectus* was re-described as *P. gibbus* by Sandberger.[9] In Kennard & Woodward's list the Tertiary species *V medius* (Woodward), which replaced the older heterogeneous names *unicolour, lenta, semicarinata,* etc., is not included ; it appears to be a good species allied to *V gibbus* (Sandberger). The various species with their distribution in time are as follows :—*V. viviparus* (Linn.), Holocene to Recent ; *V fasciatus* (Müller), Pleistocene to recent ; *V gibbus* (Sandberger), Cromerian ; *V glacialis* (Wood), Pliocene and Cromerian ; and *V medius* (Woodward), Pliocene. The species including the recent ones resemble the forms found on the Continental area of Europe, and are of no special interest either from the point of view of the strata in which they occur or from their relationships.

France.

The earliest known fossils of the family from France is *V. aurelianus* Cossmann [10] from Bathonian Strata at Saint Gaultier, Indre. The species is conical-ovoid, with a greatly swollen bodywhorl and an acuminate apex. The author compared the species to the recent *V. viviparus,* and it appears as if this is one of the ancestral forms from which the later species were evolved.

The fossils from the Cretaceous strata of Provence and its vicinity are the next oldest known. A good account of these was published by Oppenheim [11] to whose work reference

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[1] Deshayes, G. P., *Descr. Anim. sans Vertéb.* II, p. 486, pl. xxxii, figs. 27, 28 (Paris, 1862).

[2] In G. Brander's *Fossil. Hanton Mus. Brit.* p. 29, pl. iv, fig. 60 (London, 1866).

[3] Deshayes, G. P., *Descr. Coq. Paris,* II, p. 128, pl. xv, figs. 5, 6 (Paris, 1825).

[4] d'Orbigny, M. A., *Prodrome Paleont.* etc. II, p. 299 (Paris, 1850).

[5] Kennard, A. S. and Woodward, B. B., *Syn. Brit. Non-Mar. Moll. Rec. Post-Tert.* pp. 9-14 (London, 1926).

[6] Wood, S. V., *Mem. Pal. Soc. London,* XXV, pp. 68-70 (1872).

[7] Kennard, A. S. and Woodward, B. B., *Proc. Malacol. Soc. London,* VI, pp. 66, 67 (1904). See also Brusina, S., *Nachrbl Deutsch. Malacozool. Blätt.* XXXIX, pp. 40-45 (1907).

[8] Kunth, A., *Zeitschr. Geol. Ges. Berlin,* XVII, p. 331, pl vii, figs. fia, *b* (1865).

[9] Sandberger, C. L. F., *Palaentographica,* XXVII, pp. 97, 98, pl. xii, figs. 2-2a (1880).

[10] Cossmann, M., *Bull. Soc. Geol. France,* (3) XXVII, pp. 141, 142, fig. 4 (1899).

[11] Oppenheim, P., *Palaenotographica,* XLII, pp. 328-331, pl. xvi (1893).

may be made for earlier literature and descriptions of the species. I will content myself here with adding only a few notes on the generic or sub-generic position of the fossils concerned. The species *Paludina deshayesiana* Matheron, which Oppenheim compared with the African *Cleopatra bulimoides* (Olivier) and referred to the genus *Cleopatra* Troschel, is not a Viviparid but a Hydrobiid. Of the other species *V beaumontiana* (Matheron), *V bosquiana* (Matheron), *V dieulafaiti* (Roule) and the doubtful species *V globulosus* (Roule), which was described by Roule [1] as a species of the North American genus *Melantho* Bowdich (=*Campeloma* Rafinesque), appear to belong to the same group. The shells of the species are not very elongate, but are globose-ovate with the bodywhorl greatly swollen, and a rather short spire; the shells are smooth and there is no sculpture. They all appear to be closely allied to *V aurelianus* Cossmann. *V novemcostatus* (Matheron) from the same strata is the most interesting of all the species. The shell is not very large, but appears to have been elongate-ovoid, and had 7-9 quite sharp spiral keels, 3 above and 4-6 below the periphery, running spirally round the whorls. The ancestral form of this species appears to be *V cingulatus* (Matheron)[2] with *V subcingulatus* (Sandberger) and *V mazeli* (Roule) closely allied to or even synonymous with it.

The species of the Paleocene and Eocene times are *V aspersus* (Michaud), *V proavius* (Deshayes), *V desnoyersi* (Desh.), *V matheroni* (Desh.), *V orbignyi* (Desh.), *V obliquatus* (Desh.), *V novigentiensis* (Desh.), *V intermedius* (Desh.), *V inaspectus* (Desh.), *V disintenguendus* (Desh.), *V suessoniensis* (Desh.), *V rimatus* (Michaud), *V sublentus* (d'Orbigny) and *V soriciensis* (Noulet) from the environs of Paris and other areas.[3] The species are all smooth-shelled forms and neither in form nor in the structure of the shells differ very much from those found in strata of later ages or from the recent species; they are closely allied to the fossil species found in England and those found in Central and Eastern Europe.

With the above mentioned species we may also consider the species described as *Paludina burgundiana* and *Paludina dresseli* from the Tertiaries of the upper valley of the Saone and from near Vancia, Lyon, by Tournouër.[6] Both the species are closely allied to the recent species and were rightly compared by the author with *V lentus* (Solander) and the recent species.

The Viviparids of La Bresse on the banks of the River Saone are of special importance in connection with the fossils of Central and Eastern Europe. Pavlov[5] has very well defined this area as " déposée dans la grande depression entre le massif du Jura à l'Est et Beaujolais et Bourgogne à l'Ouest." The Viviparids of the area are fully discussed in the work of Delafond and Depéret,[6] but Pavlov in the paper cited has recently introduced many changes in the nomenclature and greatly multiplied the number of species. I quote from Pavlov the following passage to show his idea in thus encumbering the already unwieldy literature on

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[1] Roule, L., *Ann. Malacol. Paris*, II, p. 210, pl. i, fig. 9 (1886).

[2] Matheron, P., *Cat. Méthod. descr. foss. Bouches-du-Rhône*, p. 223, pl. xxxvii, figs. 17, 18 (Marseilles, 1843).

[3] For a detailed account and figures of the species see Deshayes, G. P., *Descr. Coq. Foss. Paris*, II, pp. 125-127, pl. xv (Paris, 1824), Deshayes, G. P., *Descr. Anim. sans Vertéb.* II, pp. 478-485, pls. xxxii, xxxiii (Paris, 1864), Cossmann M. and Pissarro, G., *Icon, compl. Coq. foss. Eocène Paris* II, pl. xiii (Paris, 1910), Noulet, J. B., *Mem. Coq. Foss. Terr. Sud-Ouest France* p. 95 (Toulouse, 1868).

[4] Tournouër, R., *Bull. Soc. Géol. France*, (2) XXIII, pp. 791, 792, fig. (1866), and Ser. 3, III, pp. 743, 744, pl. xxviii, fig. 2 (1875).

[5] Pavlov, A. P., *Mem. Soc. Géol. Sec. Ami. Sci. Nat. etc. Moscou*, Liv. V, pp. 158-161, 202-213 (1925).

[6] Delafond, F. and Depéret, C., *Les terr. tert. de La Bresse etc. Etudes d. Gites miner. France*, (Paris, 1893).

the subject—" Dans cet ouvrage j'ai tâché d'utiliser largement les différences morphologiques des formes que j'étudie et de séparer sous les noms particuliers toutes les Paludines qu'on peut discerner suivant (misprinted suivaut) leurs caractères, si elles ne présentent pas des déviations uniques peut-être accidentelles. Avec cela il est bien possible que les mâles et les femelles de la même espèce reçoivent des noms différents, mais ce ne sera au détriment de la stratigraphie comparée des dépots qui fait le but principal de cet ouvrage (misprinted ouvaage in the original)." In addition to the author having altogether ignored the question of variation and the individual differences, he has often given names for species which it would be impossible for any other worker to recognise, and I may here quote Brusina's [1] remark about the multiplication of species in Slavonia and the adjacent areas—" Man ist in der Aufstellung der Arten oder Formen der glatten *Vivipara* aus Slavonian und Rumänien zu weit gegangen."

In the following notes I consider the species according to the names given to them by Delafond and Depéret, and have also indicated the names given to them by Pavlov.

In the lowest strata of Pliocene age designated Mollon Inférieur by the French authors, the commonest species discovered was *V. ventricosus* (Sandberger). This smooth-shelled species, which was originally described from near Montpellier from beds of Middle Pliocene age, is undoubtedly closely allied to if not actually a form of the widely distributed *V. achatinoides* (Deshayes) of Central and Eastern Europe. Pavlov considers the species figured by the French authors to be *V. casaretto* (Rouss.) which, however, is nothing more than *V. achatinoides*. I would prefer to keep the French species distinct as *V. ventricosus*.

I agree with Pavlov that the species recorded as *V. neumayri* by Delafond & Depéret from the Mollon Supérieur is not correctly named, and should be called *V. tardyana* (Locard). *V. leiostracus* Delafond & Depéret *nec* Brusina has been divided by Pavlov into two species, but, in my opinion, is identical with *V. burgundiana* (Tourn.), and corresponds to the Slavonian *V. leiostracus.*

From the beds of Sermenaz Delafond & Depéret recorded a species under the name *V. fuchsi* Neumayr, this Pavlov has divided into four species. I consider the specimens described and figured to be nothing more than individual variations of *V. dresseli* (Tourn.), which in La Bresse strata corresponds to *V. fuchsi,* and from which species like *V. burgundiana* have evolved.

Of the species from Saint-Amour I consider the species recorded as *V. burgundiana* to be *V. dresseli,* while *V. sadleri* Delafond & Depéret *nec* Neumayr I consider to be *V. bressana* (Ogérien).

The Auvillars species recorded as *V. burgundiana* is certainly distinct, and may be known by the name *V. depereti* (Pavlov), though I do not agree that the same species, as asserted by Pavlov, is found in Southern Russia. It corresponds to *V. rumana* (Tourn.) from Rumania, *V. megarensis* Fuchs from Greece and *V. rhodensis* Bukowski from Rhodes.

Pavlov is certainly wrong in considering the species recorded as *V. falsani* (Fischer) from the Trevoux horizon as being in any way allied to *Tylopoma melanthopsis* (Brusina) ;

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[1] Brusina, S., *Zeitschr. Deutsch. Geol. Ges.* XLIV, p. 489 (1892).

it is a more highly evolved species of the *V. burgundiana* series in which the sutural and the peripheral ridges have become better developed and the area between the ridges is somewhat channeled.

Germany.

In considering the fossil Viviparidae of Germany we may start with the species from the Wealden strata which was described by Ebert [1] as *Tulotoma degenhardti.* This is, as Oppenheim [2] rightly suggested, not a Viviparid but a *Pyrgulifera.*

From the Lower Cretaceous Beds of North Germany Roemer [3] described two species as *Paludina carbonaria* and *P. nitida* both of which are synonyms of the earlier described English species *V. fluviorum* (Mant.) found in beds of the same age. At the same time it may be noted that the other two English species *V. elongatus* (Sowerby) and *V. inflatus* (Sandb.), found in strata of the same age, are also found in Germany.[4]

The Upper Eocene species *V. nobilis* (Klein), which was stated by the author to have been found near Nordlingen, Bavaria, is considered by Sandberger (*loc. cit.* p. 224) to have come from Buxweiler and to be synonymous with the earlier described species *V. hammeri* (DeFrance). I have seen specimens of this species in the collections of the Geological Department, British Museum (Natural History), London, from Ulm, Wurttemburg.

The Oligocene species *V. splendidus* (Ludwig) [5] from Kirchhain in Kurhessen is not very different from *V. lentus* (Solander) of England and *V. sublentus* (d'Orbigny) of France, and appears to represent an extension of this group in Germany.

The Miocene species *Paludina varicosa* of Krauss, which was referred to the North American genus *Melantho* Bowdich (=*Campeloma* Rafinesque) by Sandberger (*loc. cit.* p. 559), is a true *Viviparus*, and appears to be allied to the group of *V. beaumontiana* (Matheron) from Provence. To the same group also belongs the species *V. gerhardti* (Boettger)[6] from near Budenheim, Hessen.

The other species to be included here are *V. diluviana* (Kunth), *V. viviparus* (Linn.) and *V. fasciatus* (Müll.); they occur as fossils from the Pliocene to recent times, and the last two are the recent species found in this area.

Yugo-Slavia.

In considering the Viviparids of this area I will deal with the species of different parts of the country separately as those of different parts are not equally known and in many cases it is not possible fully to correlate the species of the different areas.

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[1] Ebert, T., *Jahrb. König. Preuss. Geol. Landeanstal.* pp. 558, 559 (1884).

[2] Oppenheim, P., *Zeitschr. Deutsch. Geol. Ges.* XLIII, p. 478 (1891).

[3] Roemer, F. A., *Verstein. Norddeutsch. Oolit. Gebirg.* p. 110, pl. ix, figs. 28, 29 (Hannover, 1836).

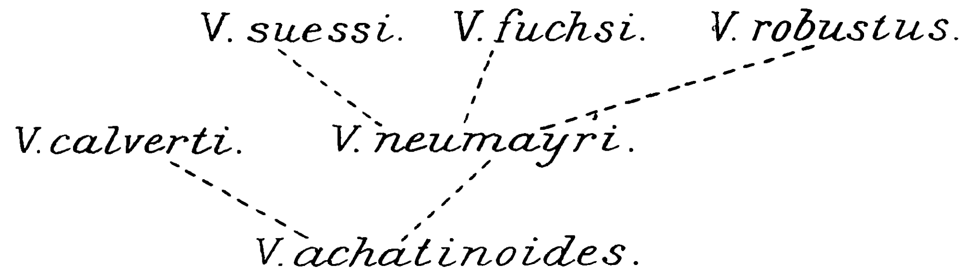
[4] See Sandberger, C. F. L., *Die Land-u. Süssw. Conchyl. Vorwelt,* pp. 59-62, pl. ii, figs. 15-17 (Wiesbaden, 1870).

[5] Ludwig, R. *Palaeontographica,* XIV, p. 89, pl. xxi, figs. 15-17 (1865).

[6] Boettger, O., *Notizbl. Ver. Erdkunde Darmstadt,* IV, hft. vii, p. 7 (1886); also see *Nachrbl. Deutsch. Malakozool. Ges.* p. 156 (1908).

Slavonia.

The fossil Viviparids of Slavonia do not date further back than the Pliocene. They have attracted attention from early times and the literature [1] on the subject is very extensive. *V. achatinoides* (Deshayes),[2] which was considered by Neumayr as the ancestral form of the Viviparids of this area, has not, so far as I can find from the literature, been found in Slavonia, but from its wide distribution there can be no doubt that it was one of the forms which occurred in Slavonia during Miocene times. For the Slavonian and some of the allied species Neumayr (*op. cit.*, 1875, pl. x) constructed a diagram illustrating the probable relationships and lines of evolution of the different forms, but later,[3] in view of his studies of the Cos Viviparidae, he found it necessary to modify his scheme in a few minor details. Penecke (*op. cit.* p. 27) introduced further modifications, and a different diagram of the evolution of some of the species is included in Bogatchev's paper.[4] Unfortunately Bogatchev's paper is in Russian, and I have not been able to understand the exact modifications suggested by him, but his diagram shows a distinct advance on the works of the authors mentioned above. My idea of the main lines of evolution of the fossil species are shown in the following table, and the various series of species, as I call them, are treated separately in the following pages.



The question of the evolution of the sculptured species as a whole may also be considered here. Leaving aside the discussion of the factors which influenced and brought about these changes the only points for consideration are the lines of evolution and the correlation of these in the fossil and the recent species. The question of evolution has been considered by various authors. Neumayr (*loc. cit.*, 1875, p. 97) considered the various forms to be mutations [5] of the less highly evolved species, and from his genealogical tree and descriptions it is clear that he considered the various series as having developed along parallel lines. This was further elaborated in a later paper [6] in which he definitely assigned a triphyletic origin to the sculptured Viviparids of Slavonia, and drew attention to similar evolu-

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[1] Hörnes, M., *Abhandl. k. k. Geol. Reichanstal. Wien,* III, pp. 581, 582, pl. xlvii fig. 17 (1856); Brusina, S., *Fossile Binnen-Moll. Dalmat. etc.* pp. 71-88, pls. i, ii, vii (Agram, 1874); Neumayr, M., *Jahrb k. k. Reichanstal,* XIX pp. 373-378, pls. xiii, xiv. (1869); Neumayr, M., *Abhandl. k. k. Geol. Reichanstal. Wien,* VII (Hft. iii), pp. 50-73, pls. iv, vi, viii (1875); Penecke, K. A., *Beiträge Pal Österreich-Ungar.* IV, pp. 26-33, pl. ix, (Wien, 1884); Brusina, S., *Matér. Faun. Malacol. Dalmat. etc.* p. 24, pl. xii (Agram, 1897); and Brusina, S., *Icon. Moll. Foss. Tell. Tert. Hungar. etc.* pl. xxii (Agram, 1902). Also see Annandale, N., *Proc. Roy. Soc. London* (B) XCVI, pp. 61-76 (1924).

[2] Deshayes, G. P., *Mem. Soc. Géol. France,* (i) III, p. 44, pl. v, figs. 4-7 (1838).

[3] Neumayr, M., *Denkschr. k. Akad. wiss. Wien.* (*Math.-Naturwiss. cl.*) XL, p. 305, foot-note (1880).

[4] Bogatchev, V., *Mém. Com. Géol. Petrograd* (*n.s.*), Liv. CXXXV, pp. 184-208 (1924).

[5] See also Neumayr, M., *Erdgeschichte,* II, pp. 15, 16 (Leipzig & Wien, 1895).

[6] Neumayr, M., *Zeitschr. Deutsch. Geol. Ges.* XXVII, p. 871 (1875).

tion of the Ammonites. This view was fully subscribed to by Oppenheim[1] who, without being definite, stated that "Alle diese Erscheinungen mahnen somit zur Vorsicht und lassen uns die Hypothese einer polyphyletischen Entstehung vieler Mollusken-Gattungen und vielleicht auch-Arten nicht als so unmöglich und ungereimt erscheinen." Koken,[2] who adopted the identifications of the fossils by Neumayr and other workers, believed that the genus *Tulotoma* is found in various parts of the World, and that there can be no doubt about "seine unabhängige Entstehung zu verschiedenen Zeiten und an verschiedenen Orten." This he called the phenomenon of Recurrence, and explained it as being due to Convergence. Blanckenhorn [3] casually referred to the origin of the sculptured species, and traced the lines followed by the sculptured or rather the ridged species in their evolution from the smooth forms. The last and undoubtedly the most important contribution on the subject is the paper by Annandale[4] who, on the analogy of the structure of the mantle in the recent sculptured species of the family, believed that the sculpture of the fossil forms was also produced in the same way. He explained the various stages of evolution of the sculptured species very carefully, and I cannot do better than quote his remarks in extenso—"The main line of shell-evolution in the Viviparidae was manifested, at the period and in that particular part of the world, by the appearance in the first instance of a vertical flattening of the profile of the bodywhorl. At a slightly later stage this flattening became a definite spiral constriction with raised margins, which formed ridges on the shell. Then the ridges became irregular and assumed a tuberculate form. Finally a third ridge made its appearance below the other two." So far the author was quite right, but in his further comparisons of the recent species of the North American *Tulotoma* Haldeman with the European fossil species he confused the ridges of the primary and the secondary series. The two main ridges on the less highly specialised species correspond to 1 and 3 of Annandale's terminology,[5] as proposed for the ridges on the embryonic shells of recent Viviparids, while the third ridge mentioned above is not the ridge 2 of the same series, but is one of the secondary series and probably corresponds to 3. In accordance with their situations on the shell I propose calling the three primary ridges of the adult shells the sutural, the median and the peripheral. It will be seen that the two ridges on the European fossils under consideration are the sutural and the peripheral, while the third ridge is not the median, and hence the forms in which a third secondary ridge, not corresponding to the median, is developed are not identical with the North American *Tulotoma* or the Yunnanese *Margarya* Nevill, in both of which it is the primary series of ridges which are equally developed and are tuberculate. The reference of the European fossils to any of the recent genera, therefore, is not justified, while the sub-generic name *Protulotoma* proposed by Annandale (1924, p. 64), with *V. dezmaniana* Brusina as type, is in view of the polyphyletic species which will have to be referred to it, superfluous. There can be no doubt that Annandale was quite right about the various cases of these sculptured forms being instances of parallel evolution, and the sculptured forms, whether among the recent or the fossil forms, being often produced polyphyletically.

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[1] Oppenheim, P., *Zitschr. Deutsch. Geol. Ges.* XLIII, p. 478 (1891).

[2] Koken, E., *Die Vorwelt und ihre Entwicklungsgeschichte*, pp. 440, 622 (Leipzig, 1893).

[3] Blanckenhorn, M., *Palaeontographica*, XLV, pp. 103-105 (1897).

[4] Annandale, N., *Proc. Roy. Soc. London* (B), XCVI, pp. 60-76 (1924).

[5] Annandale, N., *Rec. Ind. Mus.* XXII, pp. 244, 245, fig. 10 (1921).

I will now give a short account of the various kinds of changes which can be distinguished among the fossil species of Eastern Europe.

The simplest kind of evolution, to use the word in a very general sense, was an increase in size. The shells of the species grew to a very large size, the increase being both in length and in regard to the swelling of the whorls. The species produced resemble the forms of the recent sub-genus *Cipangopaludina* Hannibal, which is common in south-eastern Asia and like the species of this sub-genus the shells of the fossils were also more or less smooth. Examples of this type are *V rumana* (Tourn.) from Rumania, *V megarensis* Fuchs from Greece, *V hectoris* Hoernes from near Constantinople, *V bukowski* Oppenheim from Asia Minor, and *V rhodensis* Bukowski and allied species from Rhodes.

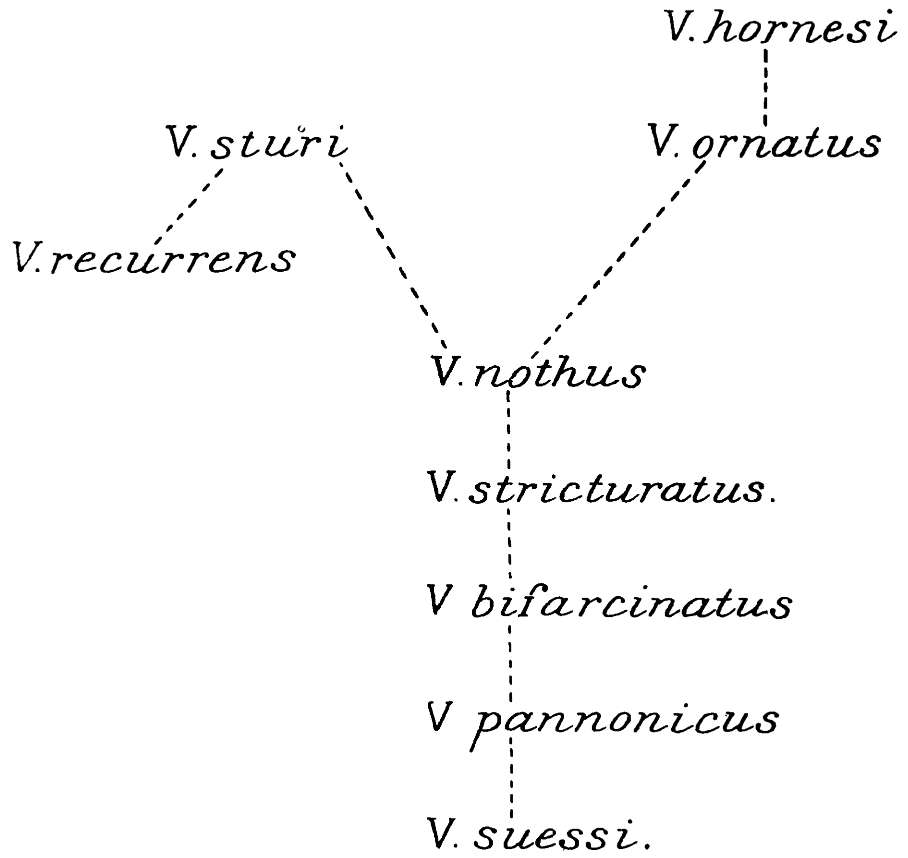
The second type of evolution consisted in the shells becoming rather elongate, and correspondingly narrower, and a number of the primary and secondary ridges became prominent thus forming a ridged shell. Examples of this type are *V böckhi* Halaváts, *V artesica* Hal., etc., from Hungary, and probably *V aulacophorus* Brusina of Yugo-Slavia. From this type were evolved the more highly ridged species with either a single highly developed ridge, as in the case of *V mazuranici* Brusina and *V. vucotinovici* Frauenfeld, or with two of the primary ridges well developed as in *V bicingulatus* (Zujovic) Pavlović and allied species from Servia, and lastly with all the three primary ridges well developed and forming distinct keels as in *V viquesneli* (Deshayes), *V spratti* Fuchs and *V lacedaemoniorum* Oppenheim from Greece and adjacent areas. From this last group species with a large number of ridges on the shells, as in the case of *V novemcostatus* (Matheron) from France, *V dautzenbergi* Brusina in Croatia, *V pauli* Brusina in Yugo-Slavia and *V apamae* (Blanckenhorn) in Asia Minor, were evolved.

The last type to be considered is that of the forms in which only two of the three primary ridges, *viz.*, the sutural and the peripheral, became specially developed, and later owing to unequal development broke up into tubercles. In this type the immediate ancestral forms were different, but the general lines of the evolution of the species were the same ; these have been discussed by Annandale from whose work I have quoted above (p. 204). It is only necessary to point out that the evolution in the form of the shell in these species is also very varied. They either became elongate, as in *V fuchsi-mojsisovicsi* series, greatly swollen and very globose as in *V robustus* series, or remained more or less like the ancestral forms as in the various series of *V suessi* and *V. fuchsi.* The production of ridges culminating in tuberculated types was evolved in at least six different series and is undoubtedly of multiple origin.

Of the Slavonian species Neumayr rightly considered *V neumayri* Brusina as the least modified, and derived all the other forms from it. This species has a conical-ovoid shell consisting of 5 moderately swollen, smooth whorls, without any spiral ridges or other specially pronounced sculpture. The aperture is subcircular and only slightly pointed posteriorly. Details as to the localities and the horizons in which this species occurs will be found in the memoirs cited already and it is only necessary to point out here that the species has a wide distribution and occurs in the lowest strata of the Pliocene age.

The authors, cited already, considered that from *V neumayri* there were two lines of evolution of the species, but in view of the material I have examined and the descriptions which I have seen, I am of opinion that there were three distinct lines with distinct ancestral species. The three species are *V suessi* Neumayr, *V fuchsi* Neumayr and *V robustus* Brusina. These three main series evolved on more or less parallel lines, and in the following pages are considered separately.

V suessi series :—The ancestral form of this series is a little more highly evolved than *V. fuchsi* and *V robustus*. It has a more or less conical shell with the whorls not very closely appressed. The whorls are not evenly rounded, but are flattened from the suture downwards ; in many of the specimens in the upper third of the whorls there is the beginning of a spiral constriction bounded by rather raised margins corresponding to the sutural and the peripheral ridges. The suture is moderately impressed, and the aperture, which is circular, has the angle at its posterior extremity a little more marked than in *V neumayri*. From *V. suessi* the next species of the series, *V pannonicus* Neumayr, differs only in the form of the shell and in the constriction on the whorls being more marked. In *V bifarcinatus* (Bielz) the constriction becomes more concave, and the two ridges bounding it, particularly the sutural, become more marked. *V stricturatus* Neumayr has the shell more elongate, and the ridges as also the constriction are more pronounced. In *V nothus* Brusina the shell is still more elongate, and the two ridges are more elevated, while the constriction becomes a flat, band-shaped structure.



From *V. nothus* the series branched along two lines, which may be called *ornatus-hörnesi* and *sturi-recurrens* respectively. These species are highly ornamented, and the two series differ only in the form of the shell, *ornatus-hörnesi* species being elongated, while *sturi-recurrens* are not so elongate but are more swollen.

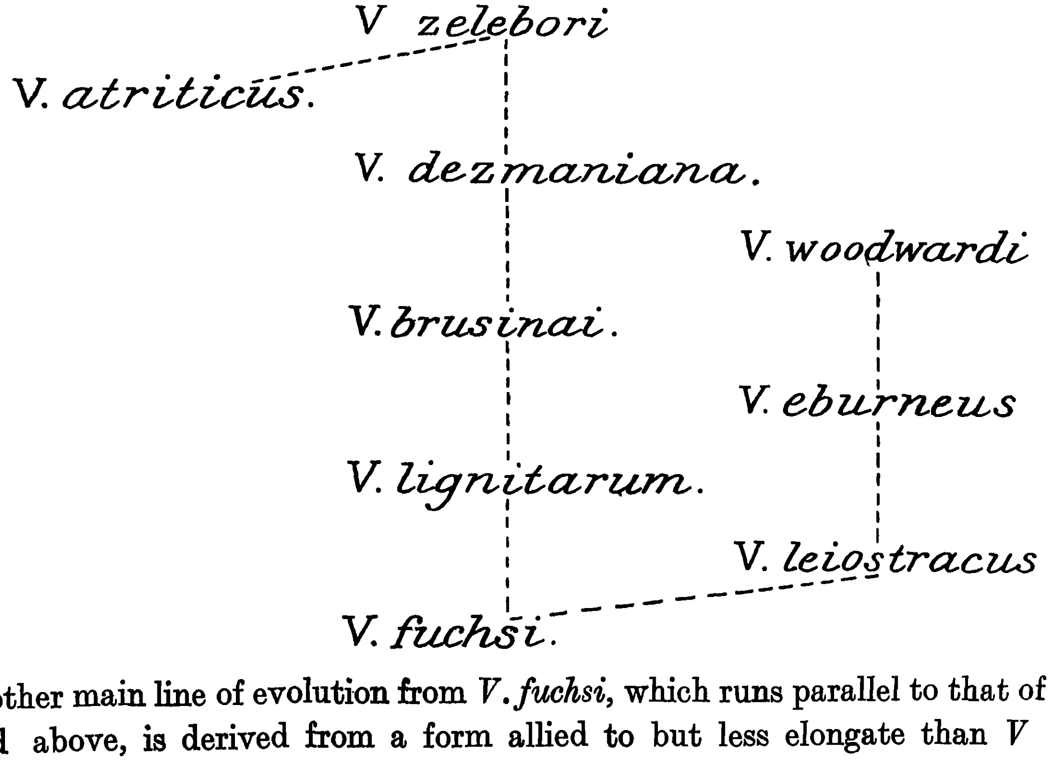
In *V ornatus* Neumayr the sutural and the peripheral ridges, which only rarely are tuberculate, are still better developed, and a number of secondary ridges are also developed below the peripheral. *V hörnesi* Neumayri, the most highly evolved species of this series, has a tuberculated peripheral ridge, and in some specimens even the secondary ridges below it are also broken up into tubercles.

V sturi Neumayr, which corresponds to *V hörnesi,* has a very tuberculate peripheral ridge, and even the sutural becomes wavy owing to uneven development. In *V recurrens* Penecke, which I regard as only a mutation of *V sturi,* the peripheral ridge on the bodywhorls has again become smooth and is not broken up into tubercles ; on the earlier whorls, however, it is tuberculated in the same way as in *V sturi.*

V fuchsi series :—In *V fuchsi* Neumayr, the ancestral form of this series, the shel is conical-ovoid, but proportionately broader than that of *V suessi* Neumayr. There are 5 whorls, which are not evenly rounded, but show the beginning of a flattening of the upper half or thereabout. The aperture is ovate.

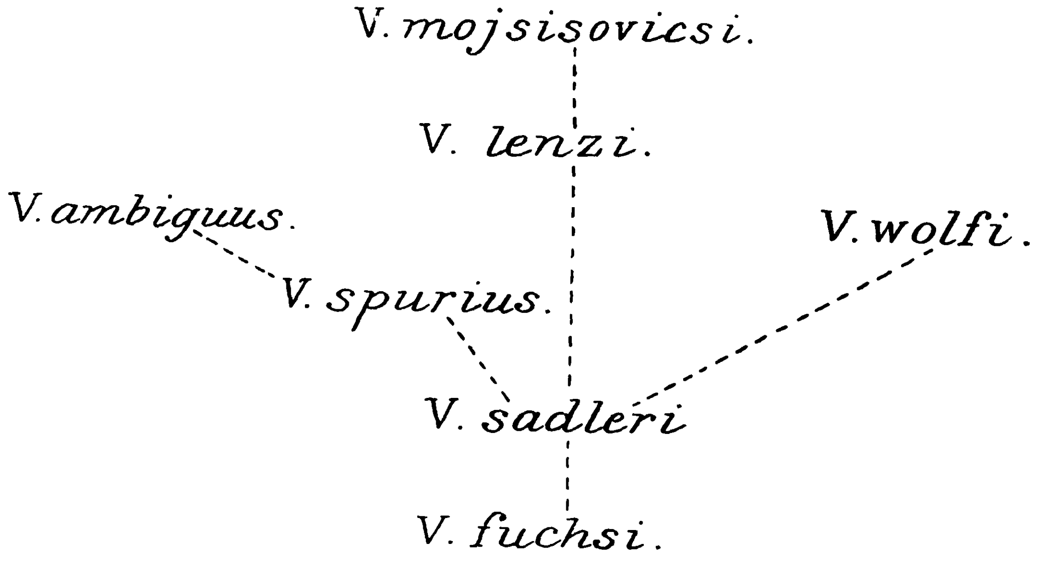
From *V. fuchsi* it is possible to distinguish 3 distinct parallel lines of evolution, and these I propose calling *fuchsi-zelebori, fuchsi-mojsisovicsi* and *fuchsi-vucotinovici.*

The majority of species in the Slavonian Beds belong to the series which I propose calling *fuchsi-zelebori* series. From *V fuchsi* the first species to be evolved in this series is *V leiostracus* Brusina. It has an elongate-conical, smooth shell, of a medium size, with the whorls evenly rounded, except for the last two which show a marked flattening next to the suture. From *V. leiostracus* is derived the more elongate form *V eburneus* Neumayr ; in this species the whorls are more flattened. In *V woodwardi* Brusina (= *V ambiguus* Cobalcescu *non* Neumayr), the next of the series, the whorls are more flattened and slightly constricted in the upper third of the whorls ; the sutural and peripheral ridges are also better marked.



The other main line of evolution from *V. fuchsi,* which runs parallel to that of the species considered above, is derived from a form allied to but less elongate than *V leiostracus,* and this I consider to be Neumayr's *V lignitarum.* The shell of this species owing to the shorter spire is less elongate, but the whorls are more flattened. In *V. brusinai* Neumayr the whorls are more flattened and there is the beginning of a constriction in the upper third of the whorl. On the shells of *V. dezmaniana* Brusina the constriction is very well developed and is bounded by evenly raised sutural and peripheral ridges. *V. altecarinatus* Brusina is closely allied to and probably identical with *V. dezmaniana*. *V. zelebori* Hörnes, the most highly evolved species of the series, is to be derived from *V. dezmaniana* ; in it both the ridges on the shells are tuberculate. *V. atriticus* [1] Neumayr appears to resemble *V. recurrens* of the *V. suessi* series, and as in the case of that species the peripheral keel has, apparently, secondarily become even.

The series from Syrmien which I propose calling *fuchsi-mojsisovicsi* series is quite distinct from the forms in adjacent areas. The series starting with *V. fuchsi* leads on to *V. sadleri* (Partsch) Neumayr, from which apparently three side-branches separated as *V. spurius* Neumayr, *V. lenzi*, Neumayr and *V. wolfi* Neumayr. In all the three species the shell whorls are flattened and somewhat concave, the sutural and the peripheral ridges distinctly marked, the sutural a little more so than the peripheral, and the aperture is smaller and narrower. The three species, however, as shown in the figure below, are not in a direct line of descent, and show different degrees of specialization. *V. spurius* Neumayr appears to have a parallel in *V. cyrtomorphus* Brusina of Hungary. *V. ambiguus* Neumayr, with its slightly more elongate shell, the broadly concave depression on the bodywhorl and more elevated sutural and peripheral ridges, has certainly no relationship with the Cos species. On the other hand it appears to be a derivative of *V. spurius* Neumayr. The final form of the series is *V. mojsisovicsi* Neumayr, with an elongate, conical-ovate shell, but otherwise resembling *V. lenzi* from which it appears to have been evolved.



The species *fuchsi-vucotinovici* and related species form another separate group. Neumayr in his Monograph (p. 63) derived the species from *V. sadleri*, with *V. altus* and *V. herbichi* as intermediate forms. As was, however, shown by Penecke (*op. cit.* p. 27) this is not correct, and he derived the species *V. vucotinovici* direct from *V. fuchsi* with his new species *V. rudolphi* as the intermediate form. Brusina [2] later rightly considered *V. rudolphi* Penecke to be only a synonym of *V. aulacophorus* Brusina,[3] and also figured a new species

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[1] This species was described under the above name in *Jahrb. k. Geol. Reichanstal.* XIX, p. 375 (1869), but in a later work is referred to as *V. arthritica.*

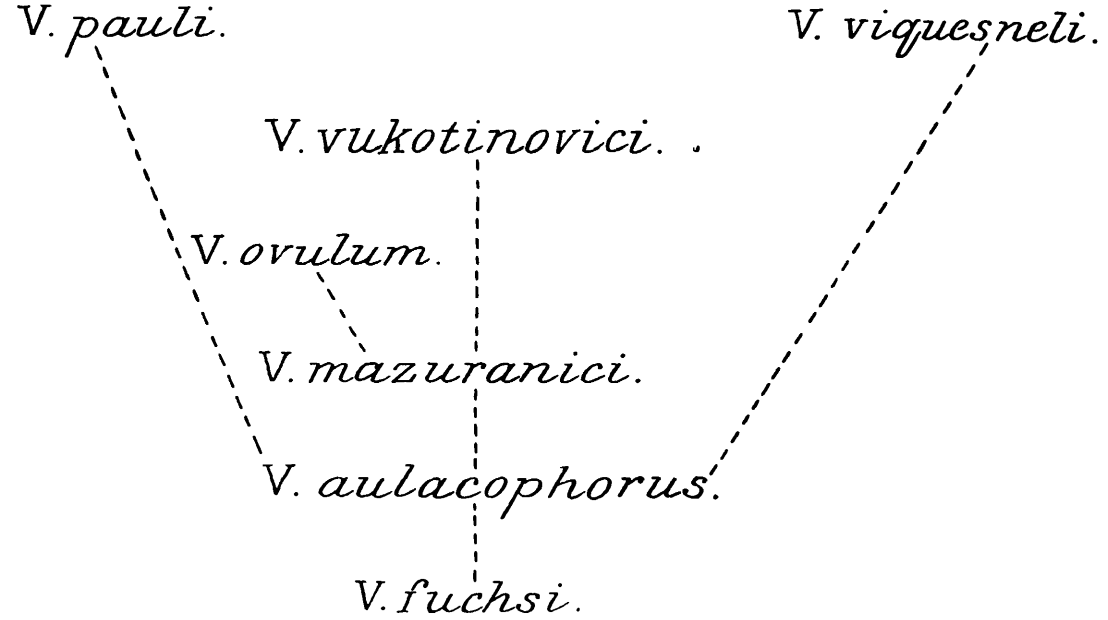
[2] Brusina, S., *Matér. Faun. Malacol. Dalmat. Croat. Slavon., etc.*, p. 24 (Agram, 1897).

[3] Brusina, S., *Fossile Binnen-Moll. Dalmat. Kroat. Slavon., etc.*, p. 88, pl. ii, figs. 14, 15 (Agram, 1874).

V. mazuranici [1] which clears up the evolution of the series. In *V. aulacophorus* all the three primary ridges on the whorls are distinct but only feebly developed. In *V. mazuranici* the peripheral becomes specially marked and the surface of the whorls instead of being rounded slopes sharply towards this ridge. This becomes still more pronounced in *V. vucotinovici*, and the ridge appears as a sharp keel in the same way as in the recent African species *V. constrictus* (Martens) and its varieties. *V. ovulum* Neumayr appears to be allied to *V. vucotinovici*, but is not in the direct line of evolution.

V. viquesneli (Deshayes) [2] from Ipek with three equally well developed sharp spiral keels and a number of secondary ridges has also, I believe, been derived from an ancestor like *V. aulacophorus.*

V. pauli Brusina, with 7-9 spiral ridges, 3-4 above the periphery and 4-5 below it, and appearing beautifully ridged like the recent species *D. persculptus* (P. & F. Sarasin) from the Celebes, and *D. mainitensis* (Bartsch) from the Philippines, is also to be referred to this series, and has probably originated from a form like *V. aulacophorus.* Other fossil species showing a similar type of evolution of the shell-sculpture are *V. dautzenbergi* Brusina from Croatia, *V. novemcostatus* (Matheron) from Provence, and probably *V. apamae* Blanckenhorn from Syria.



The very primitive Servian species *V. viminatica* Brusina [3] and the highly specialised forms described by Pavlović [4] require consideration. Nothing is known about *V. viminatica* beyond the figures of Brusina, but there can be little doubt that it is closely allied to *V. neumayri* Brusina.

The species described by Pavlović from the Tertiaries of Kosovo and Metohia in Southern Servia enable us better to understand the relationships of the species from the Ipek or Pec beds. The species were indiscriminately referred by the author to the genus *Viviparus*

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[1] Brusina, S., *Icon. Moll. Foss. Tell. Tert. Hungar. Croat. Slavon., etc.*, pl. xii, figs. 8-12 (Agram, 1902).

[2] Deshayes, G. P., *Mém. Soc. Géol. France* (1) V, p. 88, pl. xx, fig. 7 (1842) ; Also see Bukowski, G. V., *Denkschrift. k. Akad. Wiss. Wien*, LX, p. 270 (1893), and Pavlović, P. S., *Ann. Géol. Pénin. Balkan Belgrade*, VI, pp. 594, 595 (1908).

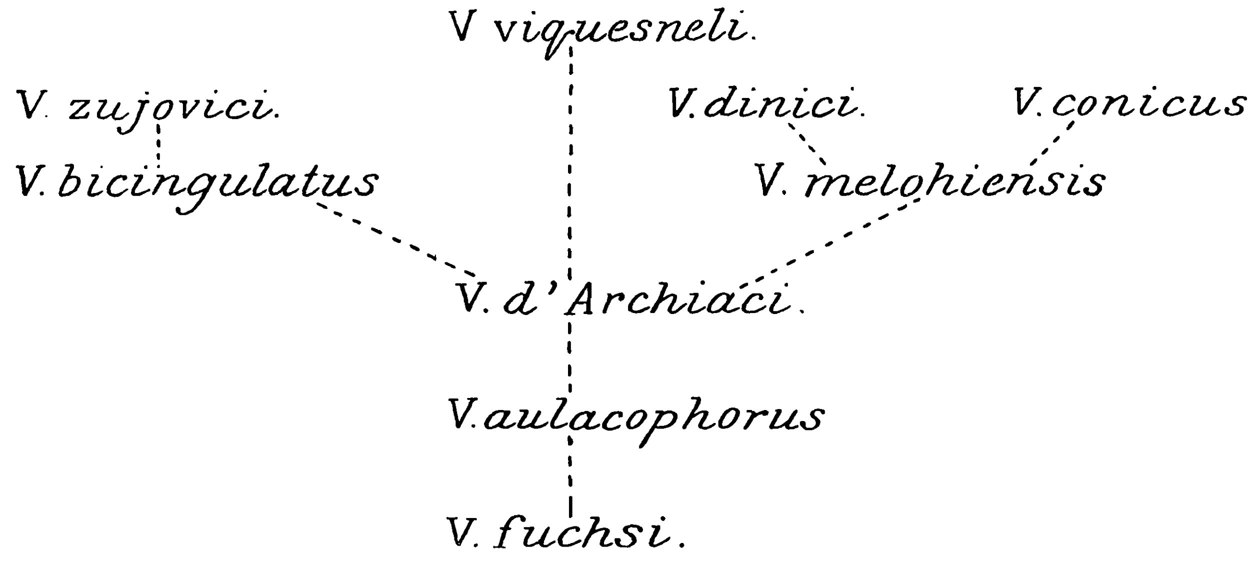
[3] Brusina, S., *Icon. Moll. Foss. Tell. Tert. Hungar-Croat. Slavon, etc.* p. 24, pl. xii, figs. 39-41 (Agram, 1902).

[4] Pavlović, P. S., *Ann. Géol. Pénin. Balkan Belgrade*, VI, pp. 580-608, pls. I-vi (Separate in 1908 1911).

and the sub-genus *Tulotoma*, but there is no doubt that they are all derived from *V. fuchsi*, and are allied to the *fuchsi-vucotinovici* series.

From *V. fuchsi* a form like *V aulacophorus* leads to *V d'Archiaci* Pavlović, which has a conical-elongate shell with the whorls flattened and band-shaped, and well developed sutural and peripheral ridges appearing like keels. In a direct line of evolution *V d'Archiaci* appears to lead on to *V viquesneli* (Deshayes), which was originally described from the Ipek beds, but also occurs in this area and has a wide distribution. In *V viquesneli* three distinct ridges, corresponding to the sutural, median and the peripheral, are well developed, and in some specimens the ridges appear tuberculate. In the series figured by Pavlović (*op. cit.* pl. ii, figs. 14-21) it is possible to distinguish a regular series of forms leading from *V d'Archiaci* to *V viquesneli.*[1]

The second group of species consisting of *V bicingulatus* (Zujovic) Pavl. and *V. zujovici* Pavl. have, in addition to the sutural and the peripheral ridges, two closely placed ridges running about the middle of the space between the primary ridges, and as a result the species appear tetracarinate. This group with the same type of shells as those considered above is also derived from *V d'Archiaci.*



In the three species from the Methohia Basin, which were described as *Vivipara* by Pavlović, the shell is similar in shape to that of *V d'Archiaci*, but the ridges appear to be differently developed. *V metohiensis* Pavl., the least evolved species of the series, has the whorls flattened and band-shaped. The sutural and the peripheral ridges are well developed and in addition there are traces of one or two secondary ridges in between. *V. conicus* Pavl. and *V dinici* Pavl. appear to be parallel branches developed from *V. metohiensis.*

Croatia.

The forms from this area are not well known, and the records are rather scanty, but there can be no doubt that the species recorded are the same as those from other parts of Yugo-Slavia and apparently represent westward extensions of the range of these species.

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[1] In this connection also see Prashad, B., *Ann. Mag. Nat. Hist.* (9) XIX, pp. 136-138, pl. ix (1927), where I have described a new species, *V. coxi*, which is intermediate between the species mentioned above.

Among the forms known are *V stricturatus* Neumayr of the *V suessi* series, *V mazuranici* Brusina of *V. fuchsi* series and other forms of this type. The greatly ridged species *V. dautzenbergi* Brusina, of the type of *V. pauli,* which is found in Croatia, has already been mentioned.

Austria.

The only species known from the Vienna Beds is *V fuchsi* Neumayr. [1] Apparently the area was not suitable for the Viviparidae, and the primitive species, which migrated there from the adjacent areas, did not flourish and produce the highly specialised types which were evolved in more congenial surroundings.

Hungary.

The Viviparids of this region may be considered under two separate heads, according to the separate areas in which they occur, as they appear to belong to two different groups. These are, 1. The Alföld Beds, and 2. The Balaton Lake or Platten See deposits.

The Alföld Beds [2] are imperfectly known and it is not possible to understand their exact relationship with our present knowledge of the forms. They are, according to Pavlov,[3] related to the Rumanian and South Russian forms, but the conclusions of the author appear to me to be based on insufficient evidence. The three species from the area are *V böckhi* Halaváts, *V artesica* Hal. and *V zsigmondyi* Hal. They are all elongate-conical species, smooth or with one or two low ridges on the surface and the whorls only moderately swollen but not flattened. They appear to be allied to *V sadleri* (Partsch) Neumayr.

The Viviparids of Balaton Lake are considered by Halaváts [4] to have been brackish water forms during the earlier epochs, and he suggests *V semesyi* Halaváts as the ancestral form of the species in this area. This is certainly correct for one group of species, the *semesyi-kurdensis* series, but the other series, *fuchsi-cyrtomorphus,* must have migrated from Slavonia into this region.

Semesyi-kurdensis series:—*V semesyi* Hal., with its smooth ovoid shell, appears to be closely allied to *V suessi* Neumayr, and they probably had a common ancestor. The next species from it is *V loczi* Hal., which is more elongate and may be described as conical, but the shell is still smooth. This leads on to *V balatonica* Neumayr (syn. *V gracilis* Lörenthey) in which the sutural and peripheral ridges are well marked, but the flattening of the whorls has not proceeded very far. In *V kurdensis* Lörenthey the shell is still more elongate, the whorls flattened and somewhat concave, and the sutural and peripheral ridges very prominent. This species in its general appearance resembles *V stricturatus* Neumayr, but is in no way related to it.

Fuchsi-cyrtomorphus series :—*V fuchsi* Neumayr has not so far been recorded from Balaton Lake, but the occurrence of *V. sadleri* (Partsch) Neumayr points to this or some

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[1] Hörnes, M., *Abhandl. k. k. Geol. Reichanstal; Wien,* III, pp. 581, 582, pl. xlvii, fig. 17 (1856) ; the species was recorded under the name *Paludina concinna* Sowerby, but Neumayr rightly considered it as distinct from the English species of that name and renamed it *V. fuchsi.*

[2] Halaváts, J., *Mittl. Jahrb. K. Ungar. Geol. Antstal.* VIII, pp. 183, 184, pl. xxxii, figs. 1-3 (1888), and pp. 226, 227, pl. xxxiv (1889).

[3] Pavlov, A. P., *Mem. Sec. Géol. Soc. Ami. Sci. Nat. etc. Moscou,* Liv. V, pp. 165, 166 (1925).

[4] Halaváts, J., *Res. Wiss. Erfor. Balatonsee. Anh. Palaeontol.* IV (ii), pp. 40-44, pl. i (Wien, 1911).

related form having migrated into Hungary. *V sadleri* has already been discussed and only *V cyrtomorphus* Brusina need be considered here. The shell of this species is not very elongate, but is comparatively more swollen and the whorls are flattened and slightly concave with the sutural and the peripheral ridges distinctly marked.

Lörenthey, in recording the species mentioned by Halavâts, added another interesting species of doubtful relationship, for which he proposed a new sub-genus *Carinia.*[1] This species, *V rothi* Lörenthey, has all the three ridges well developed, and the median ridge appears to form a very prominent keel on the middle of the whorls.

The accounts of Weiss [2] and Kormos [3] are not of sufficient interest to be considered here ; both the authors deal with only subfossil species.

Rumania.

The literature [4] on the Viviparids of Rumania is very extensive, and the variety of forms found in the country is also very great. The region, lying as it does in a central position, has received species from Hungary and Yugo-Slavia in the west and Russia on the east.

Pavlov [5] has introduced many unnecessary new names and complicated the question of the species found in Rumania. In the following notes I consider the Siebenbürgen series of *fuchsi-herbichi,* the forms allied to *V bifarcinatus* (Bielz) and the Wallachian group of *robustus-novskaensis* separately. The smooth-shelled species of Rumania and the peculiar giant forms found in this region are also discussed separately.

The characteristic smooth-shelled form of Eastern Europe, with the whorls evenly rounded, was rightly recorded by Stefanescu from Rumania under the name *V achatinoides* (Deshayes), but Pavlov has, without any justification, proposed to separate it as *V pseudo achatinoides.* He has similarly separated the Rumanian *V neumayri* Brusina (from Rumania) as *V pseudo-neumayri.* The two species are similar in every respect to the typical forms and I consider Pavlov's names as synonyms of the older names. *V craiovensis* (Tourn.) and *V popescui* Cobalcescu and its var. *tumidus* Stefanescu are nothing more than varieties of *V neumayri.* The species recorded as *V leiostracus* Brusina by Porumbaru was rightly considered by Stefanescu to be distinct, and renamed *V mammata.* Pavlov considers it to be a multiple species and has divided it into *V mammata, V böckhi* Halavâts and *V. cretzensis* nov. I consider this quite unjustified, and believe that *V mammata* is a variable species allied to *V böckhi* and through it to *V sadleri* (Partsch) Neumayr, which also is found in Rumania. From *V mammata* probably the species *V. rumana* (Tourn.), with its very large, greatly swollen shell, has been evolved. It may also be noted that Cobalcescu described a number of species under the name *V euphrosinae, V alexanderieni, V murgescui,*

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[1] Lörenthey, I., *Res. Wiss. Enfor. Balatonsee. Anh. Palaeontol.* IV (iii), pp. 157-163, pls. ii, iii (1911).

[2] Weiss, A., *Op. cit.* IV, (v), p. 25 (1911).

[3] Kormos, T., *Op. cit.* IV (vi), p. 33, pl. (1911).

[4] Neumayr, M., *Verhandl. k. k. Geol. Reichanstal. Wien,* p. 367 (1876) ; Tournouër, R., *Journ. Conchyliol.* (3) XIX, pp. 261, 262 (1879) ; id., (3) XX, p. 96 (1880); Cobalcescu, G., *Mem. Geol. Scol. Milit. Din. Iasi,* Mem. I, *Stud. Geol. Palaeontol. Ter. Tert. Rom.* pp. 125-137, pls. xi-xiii (Bucuresci, 1883) ; and a criticism of it by Brusina, S., *Verhandl. k. k. Geol. Reichanstal. Wien,* pp. 161, 162 (1885) ; Fontanes, F., *Arch. Mus. Hist. Nat., Lyon,* IV, pp. 338-343, pl. xxvi (1886) ; Stefanescu, S., *Mém. Sec. Géol. France Paléontol.* VI, pp. 82-103, pls. viii-x (1896), and *Bull. Soc. Géol. France,* (3) XXV, pt. i, p. 312, pl. viii (1897).

[5] Pavlov, A. P., *Mém. Sec. Géol. Soc. Ami. Sci. Nat., etc., Moscou,* Liv. V, pp. 162-164, 202-213 (1925).

etc., all of which are only based on specimens of different ages of *V rumana*. *V rumana* is allied to *V megarensis* Fuchs, *V hectoris* Hoernes and *V rhodensis* Bukowski. Probably *V stefanescui* Stefanescu and *V transitorius* Stefanescu represent intermediate forms of the same series.

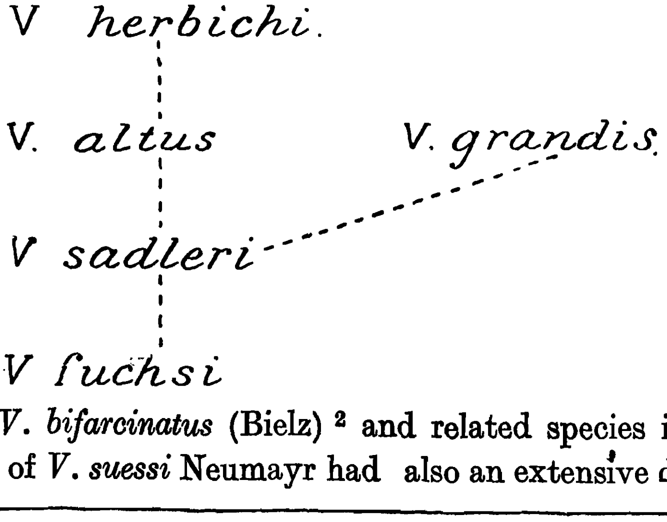
V dezmaniana Brusina and *V altecarinatus* Brusina of the *fuchsi-zelebori* series also occur in Rumania, as also *V woodwardi* Brusina of the same series.

The Wallachian series of *robustus-novskaensis* has representatives like *V turgidus* (Bielz), a form more evolved than *V robustus* Brusina, *V turgidus* var. *jiani* Stefanescu, *V. pilari* Brusina and probably also *V woodwardi* var. *argensis* Stefanescu.

The Pliocene Viviparids of Siebenbürgen, Rumania, are not very highly evolved, but offer very interesting parallels with some of the recent species of the family. Neumayr[1] dealt with the species in a special paper and later included them in his memorable Monograph on the Slavonian forms. It is, however, now possible to compare the forms better with the Hungarian species, and to ascertain the probable line of evolution of the species of the area.

V. fuchsi Neumayr, which as has been shown already, is to be derived from *V neumayri* Brusina, and has a very simple type of shell, occurs in this area also, and is apparently the ancestral form from which the species of the area were derived. From this species we get the rather widely distributed species *V sadleri* (Partsch) Neumayr. This smooth-shelled species with only slightly flattened whorls leads to *V grandis* Neumayr, which has a larger and more elongate shell, with the whorls more flattened and the peripheral ridge still more prominent. In *V. altus* Neumayr the form of the shell is similar to that of the preceding species, but the sutural keel has become more distinct. In the specimen which Neumayr figured as the " Ubergang " to *V herbichi* Neumayr (pl. xvi, fig. 5) the shell has all three primary ridges well developed. In *V herbichi*, as in the intermediate forms, the three keels are all well marked, but the median is situated rather higher up. Neumayr's comparison of this form with the recent Chinese species *V quadratus* var. *aeruginosus* (Reeve) is correct, and the species in Siebenbürgen show a similar evolution of the ridges on the shell to that shown by the various forms of *V quadratus* (Benson) in China.

The line of evolution of the species is represented in the following figure :—



The occurrence of *V. bifarcinatus* (Bielz)[2] and related species in Siebenbürgen shows that species of the group of *V. suessi* Neumayr had also an extensive distribution in this area

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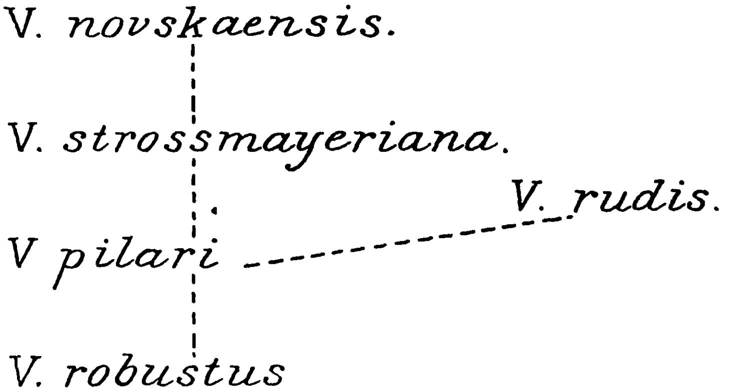
[1] Neumayr, M., *Jahrb. k. k. Geol. Reichanstl.* XXV, pp. 413-415, pl. xvi (1875).

[2] Bielz, E. A., *Verhandl. siebenbürg. Ver. Naturwiss.* p. 77 (1864).

V robustus series :—The species of this series were considered by both Neumayr and Penecke to be derivatives of *V dezmaniana* Brusina, but there is no doubt that they could not have evolved from this species. The ancestral form of this series was described by Brusina as *V robustus*,[1] but the author did not recognize its relationships. *V robustus* Brusina is a large sized species with a swollen, globose shell. The species resembles *V. fuchsi* Neumayr, but differs in its larger size, more swollen and less flattened whorls, the suture more impressed and a shorter spire. It probably originated from *V neumayri*. In *V pilari* Brusina, the next species of the series, the upper third of the whorls is flattened and the sutural and peripheral ridges begin to be marked out as low keels. In *V strossmayeriana* (Pilar) Brusina the ridges are better developed, and the peripheral ridge is tuberculate. In *V novskaensis* Penecke, the most highly evolved species of the series, both the sutural and the peripheral ridges are tuberculate. As shown in the diagram below I consider *V. rudis* Neumayr to be a side branch of *V pilari*, and not in the direct line of evolution of the series; it has a more elongate shell than any of the other species and both the ridges are feebly tuberculate. All the species are more globose than any of the other forms in Slavonia and grew to a much larger size.



Southern Russia.

Pavlov, in his monograph,[2] referred to so often in connection with the Viviparids of the adjacent areas, has dealt with the Neogen deposits of Southern Russia extending from Rumania along Bessarabia, Kherson, the area surrounding the Black Sea and the Sea of Azov to the north, the basin of the River Volga and the Caspian depression to the Caspian and the Trans-Volgaic region. He has figured a large number of species of Viviparidae, but as remarked already (p. 201) his identifications are open to question, and he has undoubtedly described far too many species. I have unfortunately seen no material from this extensive area, and as the greater part of Pavlov's work is in Russian, I have had chiefly to depend on the French Summary at the end of his paper. The Viviparids of those areas, however, clearly show that the range of distribution of the family in Eastern Europe was much more extensive than it is today, and that the forms found there were related to those of the regions to the west and south-west whence apparently they had migrated. Another point brought out by Pavlov's work is the fact that the forms found in the easternmost regions are similar to forms like *V diluvianus* (Kunth) and the recent species, and not to the more highly evolved

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[1] Brusina, S., *Journ. Conchyliol.* XXVI, p. 352 (1878) and *op. cit.* p. 25, pl. xii, figs. 19, 20 (1897).

[2] Pavlov, A. P., *Mém. Sec. Géol. Soc. Ami. Nat. etc. Moscou*, Liv. V, pp. 1-217, pls. i-viii (1925).

species of the earlier Pliocene times, which would seem to indicate that the migration of these forms in the far east of Europe took place at a much later date.

Western Siberia.

I propose including with the European Viviparids the very scanty records of fossil and subfossil Viviparidae from the extreme limit of the Western Siberian region, as I have no doubt that they represent only the easternmost extension of the European Viviparids. They certainly have no relationship with the forms found in Asia, and the conclusion of von Martens [1] that " dieses deutet also, wie die Paludinen und die eine Cyclas, auf eine Aehnlichkeit der vergangenen europäisch-westsibirischen Fauna mit der gegenwärtigen von Ostsibirien und Nordamerika " has, from the distribution of the Viviparidae, no support whatsoever.

The only record of a recent Viviparid east of the Volgaic Basin is that by Middendorf,[2] who recorded *V. achatinoides* (Desh.) from Lake Aral. Boettger [3] was not able to obtain any specimens from this area, and believed that the record was probably based on subfossil shells of *V. diluvianus* (Kunth). Kobelt [4] considered that the species, probably *V. achatinoides,* had become extinct within recent times.

Among the fossil forms from this area the species *V. columna* von Martens, a form of *V. diluvianus, V. achatinoides* and *V. tenuisculptus* von Martens,[5] also a form of *V. achatinoides,* from the banks of the Irtish stream near Omsk, are the only ones to be noted. Bogatchev [6] has recently proposed to consider *V. tenuisculptus* as a variety of the Amur Basin species *Dactylochlamys ussuriensis* (Gerstfeldt), apparently basing his conclusion on the unfortunate comparison made by von Martens of his species *V. tenuisculptus* with *D. ussuriensis.* It may further be noted that the specimens reproduced on pl. vii, figs. 32-35 of Bogatchev's work have nothing in common with *V. tenuisculptus,* but probably represent a distinct species with the same type of sculpture as *V. novemcostatus, V. pauli,* etc.

Greece and Turkey in Europe.

The species from various parts of Greece described by Fuchs [7] are few, but are interesting in that they provide the connecting forms between those found on the mainland and those found on the islands of the Grecian Archipelago.

V. megarensis Fuchs with an elongate-ovoid shell, which is nearly smooth and has evenly rounded to rather flattened whorls, is the most primitive form known from this area. Fuchs compared the species to forms of the *fuchsi-herbichi* series from Siebenbürgen (*antea* p. 213) while Neumayr [8] considered it to be allied to *V. aulacophorus* Brusina, another derivative of *V. fuchsi.* Pavlov [9] rightly considers *V. megarensis* to be closely allied to the Cos

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[1] Martens, E. von, *Zeitschr. Deutsch. Geol. Ges.* XVI, p. 351 (1864).

[2] Middendorf, A. T. von, *Reise Nord. Osten. Siberiens etc.* II, p. 312, (St. Petersburg, 1851).

[3] Boettger, O., *Zool. Jahrb. Systematik,* IV, p. 971 (1889).

[4] Kobelt, W., *Studien zur Zoogeograpie,* I, p. 217 (Wiesbaden, 1897).

[5] Martens, E. von, *Zeitschr. Deutsch. Geol. Ges.* XVI, pp. 345-347, figs. 1, 2 (1864) and XXVI, pp. 741, 742, pl. xx, fig. 1 (1874).

[6] Bogatchev, V., *Mém. Com. Géol. Petrograd (n. s.)* Liv. CXXXV, p. 206 (1924).

[7] Fuchs, T., *Denkschr. k. Akad. wiss. Wien (Math.-Naturwiss. cl.)* XXXVIII (2) pp. 1-42, pls. i-v (1877).

[8] Neumayr, M., *Denkschr. k. Akad. wiss. Wien (Math.-Naturwiss, cl.)* XL, p. 261 (1880).

[9] Pavlov, A. P., *Mém. Sec. Géol. Soc. Ami. Sci. Nat. etc. Moscou,* Liv. V, pp. 165, 170 (1925).

species *V pyleensis* (Pav.), and has according to the form of the shell distinguished a number of varieties. His comparisons of these with the recent species are unjustifiable, though there is no doubt that *V. megarensis* is very near the ancestral form of the recent species of the area.

V incertus Fuchs from Livonates appears to me to be closely allied to the Servian *V. aulacophorus.* The elongate shell with not very prominent sutural, median and peripheral ridges point to a close relationship between the two species. In *V graeca* Fuchs the sutural and peripheral ridges are better developed, and even broken up into tubercles. *V spratti* Fuchs and *V lacedaemoniorum* Oppenheim [1] are of uncertain relationship. In both cases there are the three ridges on the shells, but while *V spratti* appears to be related to the Servian *V d'Archiaci* Pavlovic, *V lacedaemoniorum* with its Clinoconchous type of shell appears to be allied to the Cos forms.

V hectoris Hoernes [2] from Renkioi near Constantinople is, as Hoernes rightly remarked closely allied to the Grecian *V megarensis* Fuchs, and needs no further consideration.

Asia Minor.

Only two species of Viviparidae are known from this vast area, and as both of them belong to very widely separated groups they do not help us in reconstructing the past history or the relationship of the forms found here.

V. bukowskii Oppenheim,[3] which was described from near Efflatum-Bunar in Pisidia, is, as the author rightly believed, closely allied to *V megarensis* Fuchs, and also shows some relationship to the group of *V fuchsi.* It is a smooth-shelled form, of moderate size and has the whorls greatly swollen.

V. apamae (Blanckenhorn),[4] which was referred by the author to the sub-genus *Tulotoma* Haldeman, has a rather narrow elongate shell, with a narrow aperture and with prominent spiral ridges running over it. The species resembles *V pauli* Brusina and *V dautzenbergi* Brusina, but its relationship is uncertain.

Cos.

The Viviparids of the Island of Cos in the Greek Archipelago are of special interest from the fact that it was their discovery, by Spratt and Forbes [5] about the middle of the Nineteenth century, which led to the study of the changes in the form and sculpture of the shells of allied species probably descended from the same ancestral form, and found in the different strata of a single area. The question of the strata and the species in Cos has been discussed by various authors,[6] and I will only include here an analysis of the different forms found in this island.

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[1] Oppenheim, P., *Zeitschr. Deutsch. Geol. Ges.* XLIII, pp. 461, 462, pl. xxvi, figs. 3, 3a (1891).

[2] Hoernes, R., *Sitzungsber, k. Akad. wiss. Wien* (*Math.-Naturwiss. cl.*) LXXIV, (I abt.), p. 25, pl. i, figs. 16a, b (1877).

[3] Oppenheim, P., *Zeitschr. Deutsch. Geol. Ges.* LXX, pp. 207, 208, pl. ix, fig. 6 (1918).

[4] Blanckenhorn, M., *Palaeontographica,* XLV, pp. 103-105, pl. viii, figs. 9-14, pl. x, fig. 22 (1897).

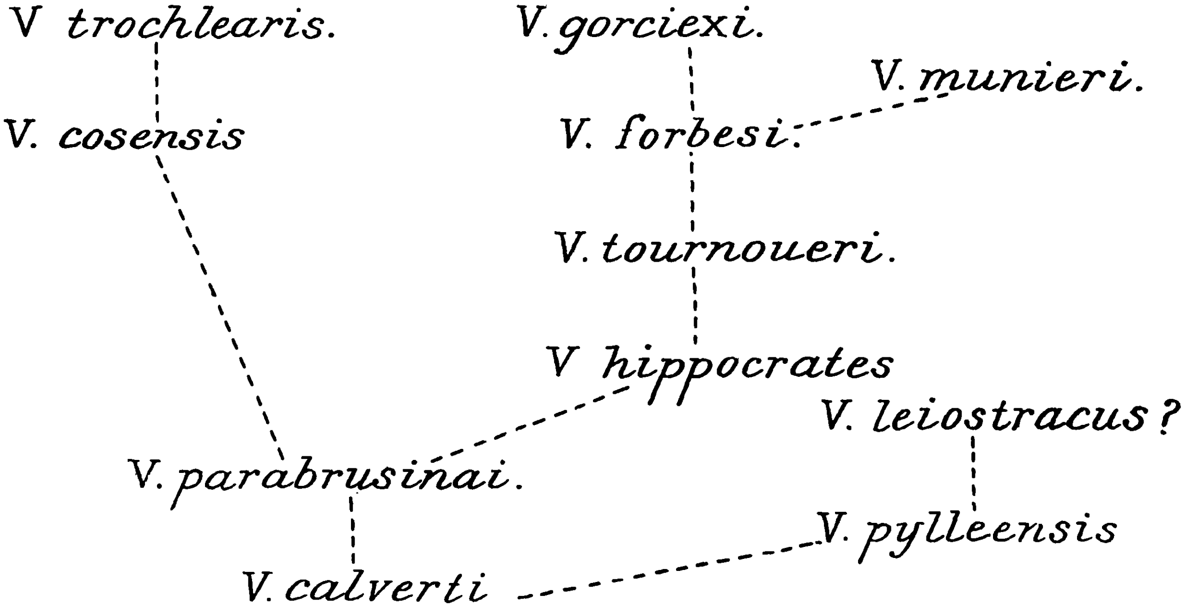
[5] Forbes, E., In Spratt, T. A. B. & Forbes, E., *Travels in Lycia, Milyas, Cibyratis, etc.* II, pp. 199-206 (London, 1847).

[6] Forbes, E., *Edinburgh New Phil. Journ.* XLII, pp. 271-295 (1847); Tournouër, R., *Journ. Conchyliol.* XXIII, pp. 77, 78 (1875); Tournouër, R., *Ann. Sci. l'Ecole Norm. Sup.* (2) V, pp. 457-462, pl. iii (Paris, 1876); Neumayr, M., *Denkschr. k. Akad. wiss. Wien.* (*Math.-Naturwiss. cl.*) XL, pp. 298-304, pl. ii (1880); Newton, R. B., *Proc. Malacol. Soc. London,* IX, pp. 363-368 (1911); Annandale, N., *Proc. Roy. Soc. London* (B) XCVI, pp. 60-76 (1924).

The Cos species show a great resemblance to the Slavonian forms, and Neumayr actually considered some of them as being identical in the two regions. The difference in the form and sculpture, however, were not properly understood by Neumayr, and were explained by him as being only a type of mutation. He called the Cos species Clinoconchous forms of the Orthoconchous type of species found in Slavonia etc. Pavlov[1] has, in my opinion, rightly separated one of the Cos species as distinct from the Slavonian forms, and one of the other species must similarly be separated and designated by a new name.

The most primitive species of the series in this island was originally designated *V coa* by Neumayr, but later, owing to the same name having been used by Tournouër for another Cos species, he changed the name of the species to *V. calverti* Neumayr. The species corresponds to and is certainly closely allied to the Slavonian *V. neumayri* Brusina. The shell is similar in shape, but the whorls are somewhat flatter, not so evenly rounded, and the aperture is rather narrower. From this species evolution proceeded along two lines, one along the series for which Neumayr considered *V. fuchsi* as the central species, and the other which he designated *V brusinai.*

Neumayr's *V. fuchsi* from Cos has been renamed *V pylleensis* by Pavlov (*loc. cit.* p. 211, pl. ii, figs. 52, 53), and he has rightly compared it with *V. megarensis* Fuchs from the Neogen of Greece. The shell of the species is much larger than that of the Slavonian form, the whorls more flattened, but still rounded and without any concavity or ridges. I am not certain as to the form recorded as *V leiostracus* from Cos, and in the following figure have provisionally placed it next to *V pylleensis.* Probably it is quite distinct from the Slavonian species, but I have seen no specimens.



Neumayr's *V brusinai* (*loc. cit.* p. 300, pl. ii, figs. 5-9) is not the same as the species recorded under that name from Slavonia. Its greatly slanting and oblique whorls, and the peripheral ridge lying very near the base of the whorls are the main distinguishing characters, and I propose to call it *V parabrusinai* nov. It is the ancestral form of most of the Cos species and these forms can be separated into two different series.

In *V. coa* (Tournouër), which in his later paper was named *V cosensis* to avoid confusing it with *V. coa* Neumayr, and in *V trochlearis* (Tourn.) all the three primary ridges, the sutural,

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[1] Pavlov, A. P., *Mem. Sec. Géol Soc. Ami. Sci. Nat. etc. Moscou,* Liv. V, pp. 155-213, pls. i-iv (1925).

the median and the peripheral, are well developed and not the sutural and the peripheral only as in the other species.

The relations of the second branch, which consists of *V hippocrates* Neumayr, *V tournoueri* Neum., *V forbesi* (Tourn.), *V gorciexi* (Tourn.) and *V munieri* (Tourn.), are shown in the figure, and it is only necessary to note that the series has evôlved along parallel lines to the species of the *V suessi* series in Slavonia.

Cibyrates.

Forbes described from this area a species under the name *Paludina cibyratica.*[1] Unfortunately the description is very incomplete and the figure unsatisfactory, and it is not possible to be certain as to what the species was. There is no example of the species in Forbes's collections in the British Museum. It appears to be a species of the type of *V. hippocrates* Neumayr, and is not the young of *V vukotinovici* as Neumayr [2] surmised.

Rhodes.

The Viviparids from the Plaisancian Beds of Rhodes are very interesting in spite of the fact that it is not possible fully to trace their genealogy and relationships.

Bukowski [3] recorded from these beds *V forbesi* (Tournouër), a species found in Cos, but owing to the small half-grown specimens which he figures, it is not possible to be sure as to whether they are correctly referred to this species. The specimens having only two of the three primary ridges appear to belong to the same group as *V. forbesi.* On the other hand they might represent the ancestral form of the highly sculptured species of the area *V clathratus* (Deshayes).[4] This species, with its various varieties described and figured by Bukowski in his memoir, is very interesting in that in addition to the sutural and the peripheral ridges there are two secondary ridges running spirally between them. The ridges are unequally developed and as a result the shell appears to have four rows of tubercles. It shows a superficial resemblance to species of the sub-genus *Taia* Annandale of Inlé Lake, Burma. The relationship of this species is uncertain, but it may be noted that it has nothing to do with *Melania hellespontica* Calvert and Neumayr,[5] with which Annandale proposed to associate it in a new genus to which he gave the name *Palaeotaia.*[6]

The two smooth-shelled species *V rhodensis* Bukowski and *V acramitus* Buk. are of a large size with the whorls rather swollen, but flattened in the middle between the very feeble sutural and peripheral ridges. The flattened region also shows traces of fine spiral ridges. Bukowski compared the species to the Rumanian species *V murgescui* Cobalcescu and *V. maracineni* Cob., both of which, as is discussed in the account of the Rumanian species

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[1] Forbes, E., in Spratt, T. A. B. & Forbes, E., *Travels in Lycia, Milyas, Cibyratis etc.* II, p. 177, fig. b (London, 1847).

[2] Neumayr, M., *Denkschr. k. Akad. wiss. Wien* (*Math.-Naturwiss. cl.*) XL, p. 266 (1880).

[3] Bukowski, G V., *Denkschr. k. Akad. wiss. Wien* (*Math.-Naturwiss. cl.*) LX, pp. 265-306, pls. i, ii (1893).

[4] Deshayes, G. P., *Expéd. Sci. De Morée*, III, pt. i, Zool. pp. 148, 149, pl. xxv, figs. 3, 4 (Paris, 1833); Tournouër, R., *Mém. Soc. Géol. France* (3) I, pp. 40-44 (1877).

[5] Calvert, F. & Neumayr, M., *Denkschr. k. Akad. Wiss. Wien* (*Math.-Naturwiss. cl.*) XL, p. 374, pl. ii, fig. 14 (1880).

[6] Annandale, N., *Proc. Roy. Soc. London* (B) XCVI, p. 73 (1924).

(p. 212), are only forms of *V. rumana* (Tournouër). Pavlov's[1] comparisons of these species with the Hungarian forms are certainly very strained. They appear to me to be only giant forms evolved from the ancestral smooth-shelled species of the sculptured forms of Rhodes along parallel lines to the Rumanian species.

The exact relationships of the Rhodes species are not clear, but there can be little doubt that they are related to the Cos species on the one hand, and the Rumanian and Asia Minor species on the other.

IV. NORTH AMERICA.

The earliest known species of the fossil Viviparidae of North America were found in strata which were doubtfully referred to the Jurassic period. A very complete series of forms is found in the Laramie Beds, about the exact age of which also the various authorities differ, while the records for the Tertiaries as a whole are very few.

The supposed Jurassic fossils were described by Meek and Hayden[2] from Black Hills in the Upper Missouri Valley under the names *Lioplacodes nucalis* and *Viviparus gillianus*. The authors were doubtful as to the age of the strata, but provisionally assigned them to the Jurassic period and in all recent accounts[3] the fossils are referred to as Jurassic. For the species *nucalis* the authors proposed the new genus *Lioplacodes*, but there is little justification for considering it as distinct from the species later referred to the sub-genus *Lioplax* Troschel. I consider it as a species of the sub-genus *Lioplax*, and as the ancestral form of the fossil and the recent species of both *Lioplax* and *Campeloma* Rafinesque. *Viviparus gillianus* is a small sized, smooth-shelled species and, in my opinion, represents the ancestral form of the fossil and the recent species of the genus *Viviparus* in North America.

The Laramie fossils are the next to be considered, and, in view of their importance, it will not be out of place to preface my remarks about these species with a few notes on the area and the conditions under which these beds were laid down. White[4] after a detailed discussion of the area came to the conclusion that the Laramies are intermediate between the Caenozoic and Mesozoic eras, and form the border line between the Cretaceous and the Tertiaries. These beds to quote from White extended "from Northern New Mexico on the south to the British Possessions on the north, and from the vicinity of the Great Salt Lake on the west to a present known distance out upon the Great Plains of more than 200 miles of the eastern base of the Rocky Mountains. It has been traced within the western boundary of both Kansas and Nebraska." This area was, according to the same author, a broad stretch of the open sea in the Cretaceous period and separated the western part of the North American continent from the eastern. At the close of the Cretaceous period the sea became land-locked, and the enclosed area of the ocean formed the inland Laramie Sea. The huge area of this sea was gradually divided into a number of lakes, which were connected with a large number of streams and rivers, thus according to White forming an "unfinished river-system." The conditions in the area were generally lacustrine, but

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[1] Pavlov, A. P., *Mém. Sec. Géol. Soc. Ami. Sci. Nat. etc. Moscou.* Liv. V, p. 169 (1925).

[2] Meek, F. B. & Hayden, F., *Palaeontology of the Upper Missouri*, pp. 115, 116 (1876).

[3] See for example Grabau, A. W., & Shimer, H. W., *North American Index Fossils Invertebrates*, Vol. I, p. 725 (New York, 1909).

White, C. A., *Third Annual Rept. U. S. Geol. Surv.* pp. 411-486 (1883), and *Bull. U. S. Geol. Surv.* V, no. 34, pp. 1-32 (1886) the water in the greater part of it was brackish. This conclusion is confirmed by the occurrence of brackish-water forms co-mingled with those of freshwater species. From the distribution of the fossils of freshwater species also there is no doubt that they were deposited in the main and shifting part of the sea, but a large number of them are also found in the beds of the streams of the times. In a later communication White [1] considered the Laramie Beds to be the uppermost of the Cretaceous series though he added that "its molluscan fauna might with propriety be referred to the Tertiary." He was further of opinion that the "genetic successions of each fauna have descended in a continuous freshwater habitat," thereby adhering to his previous idea that the main river-systems of the present day, the Missouri for example, represent the ancient river-systems of the Cretaceous.

Stanton,[2] who considered the Laramie as the last conformable Cretaceous series of the Colorado Sea, believed that "soon after the Benton, however, large areas west of the Front range in Colorado and Wyoming and west of the 108th Meridian in Montana previously covered by the sea began to emerge, either by uplift or by filling up of the basins with sediment, and as they came up to sea level or a few feet above it, land and marsh flats became established and all the conditions became favourable for the formation of coral beds. Land animals also came in and the streams and freshwater lagoons received their appropriate population from adjacent areas, while the bays and estuaries were inhabited by brackish-water forms." Osborn[3] considers the Laramie as being the same as the Upper Cretaceous. Schuchert's [4] account and his palaeogeographical maps, as also those of Arldt [5] based on the works of de Lapparent, Haug, Willis and other workers, confirm the ideas of White and Stanton. To sum up, therefore, the area in the Late Laramies or Upper Cretaceous and even the early Tertiaries consisted of a large number of lakes surrounded by estuarine and freshwater zones, and had a large network of streams opening into it.

In the following account no distinction is made between the true Cretaceous and the Laramie fossils, and the two are treated together.

Of the Laramie Viviparids I consider *V leai* (Meek and Hayden) [6] as the least modified form. It occurs in great numbers in Fort Union Beds, Yellow Stone Beds and in other areas. The species has also been recorded by Dowling [7] from the Coal Field Region of Souris River, Canada. The shell of the species, which is very variable, is conical-subovate and nearly smooth. As has been noted already it resembles *V normalis* (Hislop) from the Intertrappean Beds of Peninsular India, and also has a superficial resemblance to *V sublentus* (d'Orbigny) from the Paris Beds and *V lentus* (Solander) of England. Among the recent American species Meek rightly considered it to be near *V subpurpureus* (Say).

The next group of species consists of *V peculiaris* (M. & H.), *V. conradi* (M. & H.) and *V panguitchensis* White.[8] The shell of the forms of this series has increased in length,

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[1] White, C. A., *Smithson. Misc. Pub.* XLVIII, pp. 75-88 (1905).

[2] Stanton, T. W., *Journ. Geol.* XVII, p. 403 (1909), and *Proc. Washington Acad. Sci.* XI, p. 280 (1909).

[3] Osborn, H. F., *The Age of Mammals*, p. 99 (New York, 1910).

[4] Arldt, T., *Handbuch Palaeogeogr.* I, pp. 399-401, figs. 56, 57 (Leipzig, 1919).

[5] Schuchert, C., *Bull. Amer. Geol. Soc.* XX, pp. 594-596, pls. xciv-xcvi (1909).

[6] Meek, F. B., *U S. Geol. Surv. Terr.* IX, pp. 576-588, pls. xlii-xliv (1876) also see White, C. A., *Third Ann. Rept. U. S. Geol. Surv.* pp. 466-470, pls. iii, viii, xxiv, xxv, xxviii (1883).

[7] Dowling, D. B., *Ann. Rept. Geol. Surv. Canada*, XV, p. 16F (1904).

[8] For details as to the descriptions and the figures of these species reference may be made to the works of Meek and White cited already.

the suture is more deeply impressed, and a well marked peripheral keel, corresponding to the third or the peripheral embryonic ridge, has been developed. In some species like *V panguitchensis* traces of other secondary ridges are also to be seen on the various whorls. This group of forms appears to have evolved in the same way as some of the species of the Vivipari Dissimiles Group in Asia and of the Vivipari Unicolores Group in Africa.

The two species *V. marylandicus* Clark and *V arlingtonensis* Clark[1] apparently represent the extension in eastern areas of the above noted group in the early Cretaceous, while *V turneri* Hannibal and *V washingtonianus* Hannibal[2] are their direct descendants preserved in Eocene rocks.

In the species *V prudentius* White, *V. retusus* (M. & H.), *V trochiformis* (M. & H.) and *V. formosus* (M. & H.) [3] the shells did not become very elongate, but the whorls were tumid and the general form of the shells may be described as elongated-ovoid. The ridges on the whorls including the peripheral, which is well developed in the form of a regular keel, are also better developed. Cossmann[4] has separated *V trochiformis* into a separate section for which he has proposed the name *Paludotrochus.* The species, however, is a typical form of the genus *Viviparus* and there is no justification whatsoever for placing it in a new section. The species considered above with well-developed primary and secondary ridges indicate a type of evolution similar to that of the more primitive members of the Asiatic sub-genus *Dactylochlamys* Rao.

V leidyi (M. & H.), *V reynoldsianus* (M. & H.) and *V couessi* White form a group resembling the species of the sub-genus *Cipangopaludina* Hannibal of Asia. The shell of these is very large, elongate and greatly swollen. The primary and the secondary ridges, though indicated on the earlier whorls, are greatly reduced and may even be obsolete on the penultimate and the bodywhorl. The group illustrates a successful attempt on the part of the Laramie Viviparids to evolve into large sized, more or less smooth shelled species, and offers a very good example of parallel evolution to what occurred at a later date in the case of the species of the sub-genus *Cipangopaludina* in Asia.

From the Cretaceous of Montana Stanton[5] has described a species *V montanaensis* which according to the author is very similar to *V gillianus* (M. & H.), but differs in its smaller size, shape of the aperture and in having the whorls distinctly shouldered.

The Tertiary Eocene species *V paludiformis* Hall, *V wyomingensis* (Meek), *V lyelli* (Conrad) and probably *V subglobosus* (Emmons) all have more or less smooth shells and resemble the recent North American species of the genus. They are not of any great interest except for illustrating the fact that at the end of the Laramie all the large shelled highly specialised and sculptured forms, with the exception of the species of the sub-genus *Tulotoma* Haldeman which is separately considered below, perished, and that only the very primitive smooth-shelled forms persisted and have given rise to the recent species. In this connection reference may be made to the remarks of Call,[6] who believed that from the

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[1] Clark, W. B., *Md. Geol. Surv. Lower Cretaceous, Baltimore,* pp. 211-213, pl. xxi (1911).

[2] Hannibal, H., *Proc. Malacol. Soc. London,* X, pp. 193, 194 (1912).

[3] I consider *V. formosus* (M. & H.) to be a distinct species and not a variety of *V. leidyi* (M. & H.) as it was described by the authors. The form of the shell and the sculpture are quite different in the two species.

[4] Cossmann, M., *Essais Paléoconch. comp.* XII, pp. 185, 186 (Paris, 1921).

[5] Stanton, T. W., *Proc. Amer. Phil. Soc.* XLII, pp. 195, 196, pl. iv, fig. 5 (1903).

[6] Call, R. E., *Amer. Journ. Sci.* XLVIII, p. 132 (1894).

Laramie region "as a center all recent forms have been derived."[1] Walker[1] similarly put forward the view that the Viviparidae originated in North America, though he is not definite as to the time and the region in which the forms first took to a freshwater life. From North America the family migrated to Asia over the Behring Bridge and spread into the Old World; this aspect of the question is discussed below (pp. 242, 243).

The sub-genus *Tulotoma* Haldeman is represented by a single fossil species, *T thompsoni* White. The fossils of this species are found in the Laramie Group in Southern Wyoming, west of the Rocky Mountains and in Colorado, east of the same mountain chain. In the evolutionary series of this species, which is very completely represented in the two areas, the most primitive form with three well-developed spiral ridges on the various whorls is hardly distinguishable from *V trochiformis* (M. & H.), which also is found with it and very probably represents its ancestral species. In the more highly evolved shells the ridges are more prominent, and, owing to uneven development, appear tuberculate. The tubercles, however, it may be noted are along all the three primary ridges. The species is closely allied to the recent species, and is the ancestral form of the more highly evolved species like *T. magnifica* (Conrad) and *T angulata* (Lea). The rather unfortunate comparison of the evolutionary series of *T. thompsoni* with the various forms of *Neothauma tanganyicense* (Smith) by Sollas [2] may be referred to here. The series of *N. tanganyicense* does not offer an example of a parallel evolution to that of *T thompsoni*, but a similar evolution is to be seen in the case of the sculptured species of Viviparids of Eastern Europe. Even the last example is, however, nothing more than an instance of parallel evolution, for as is discussed already (p. 190), in the European species only two rows of tubercles along the sutural and peripheral ridges are developed while in the case of the American forms the median ridge is similarly tuberculated and there are thus three rows of tubercles on the shells.

As to the sub-genus *Campeloma* Rafinesque, in spite of its general resemblance to *Viviparus*, there can be no doubt that it became differentiated from the general stock at a very early date. As has been mentioned already, I believe that *Campeloma* evolved about the same time as *Lioplax*, and probably from the same ancestral forms. The differences between the fossil species of *Viviparus* and *Campeloma* are, according to Meek and White, as well marked as they are in the recent species. I consider *C. multistriata* (M. & H.) with its small-sized shell, with only slightly swollen whorls, and with a very feeble sculpture, as the least highly modified of the fossil species. It has a wide distribution in the Laramies of the United States. In *C. multilineata* (M. & H.), or rather *C. nebrascensis* (M. & H.)[3] as the species should be called, which is found in the Laramie Beds of the United States and in Canada, the shell is more elongate and striated, the whorls next to the suture are distinctly angulate, and the bodywhorl shows a flattening or even a transverse band-shaped depression below the angulation. The species resembles the recent *C. decisum* (Say). In *C. vetula* M. & H. the shell has a more marked Viviparus-facies, being of a medium size, not greatly swollen and with a feeble vertical striation on the whorls. *C. macrospira* Meek, the final species of the series, was probably evolved from *C. vetula*. The shell of this species is large, more elongate, conical-ovoid, while the whorls are distinctly swollen. It

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[1] Walker, B., *First Rept. Michigan Acad. Sci.* p. 58 (1900).

[2] Sollas, W. J., *The Age of the Earth*, p. 214, fig. 79 (London, 1905).

[3] See Henderson, J., *Nautilus*, XXXII, p. 63 (1918).

resembles the recent species *C. ponderosum* (Say) and *C. subsolidum* (Anthony), and probably represents the ancestral form of these species. *C. harlowtensis* Stanton [1] from the Cretaceous of Montana is nearly allied to *C. macrospira.* The records of the sub-genus from the Tertiaries are very scanty and do not offer any points for comment.

The supposed Jurassic species of the sub-genus *Lioplax,* which was put in a new genus *Lioplacodes*, has already been referred to. From the Laramie strata the only species known was described by White as *Campeloma* (*Lioplax ?*) *producta.* It appears to be intermediate between the sub-genera *Campeloma* and *Lioplax,* but from its small size, general facies and sculpture, I am of opinion that it should be referred to *Lioplax. Lioplax andersoniana* Hannibal [2] from the Eocene Beds of Tejon formation, California, is closely allied to the recent *L. subcarinata* (Say).

V. SOUTH AMERICA.

As has been remarked already (pp. 162, 186) there are no recent members of this family in South America, and the records of fossils are also very limited.

Philippi [3] described a species from the Tertiaries (exact age not specified) of Chile under the name *Paludina araucana.* The species has not been found since, and has been generally considered to be a doubtful member of the family as now restricted. Recently another species was described by Duello-Juardo [4] from the Upper Cretaceous of the Rio-Negro area. This species, *V wichmanni*, is a true *Viviparus*, and from its description and figures appears to belong to the same group as Philippi's species. The two records, insufficient as they are, prove that the family was represented in South America from at least the Upper Cretaceous to the Early Tertiaries. It is not possible to be certain about the causes which led to the extinction of the family there, as other freshwater molluscs, like the Ampullarids and the Hydrobiids, are quite common in that area. Probably after the severance of the connection of South America with Africa in the Early Tertiaries, the flooding over of the areas in which the family flourished by the sea was responsible for the disappearance of the family from the freshwater fauna.

The relationships of the South American species, so far as they can be deduced from the descriptions and figures, are undoubtedly with the African *V unicolor* (Olivier), and the above mentioned connection of South America with Africa points to their migration from Africa. The South American forms can not be derived from the North American Viviparids ; the absence of members of this family, both recent and fossil, in the whole of Central America is sufficient to disprove this. The possibility of an independent origin of the family in South America is, in view of the absence of any recent members in this area, too remote to be seriously considered.

6. PALAEOGEOGRAPHICAL NOTES.

Before going on with the palaeogeographical notes on the various areas it is necessary to include a few remarks about the much debated question of whether the various continents

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[1] Stanton, T. W., *Proc. Amer. Phil. Soc.* XLII, pp. 196, 197, pl. iv, figs. 11, 12 (1903).

[2] Hannibal, H., *Proc. Malacol. Soc. London,* X, p. 196, pl. viii, fig. 3 (1912).

[3] Philippi, R. A., *Die Tert. Quart. Verstein. Chile,* p. 79, pl. ix, fig. 10 (Leipzig, 1887).

[4] Duello-Juardo, M., *Physis,* V, pp. 329, 339, figs. 1-3 (1922).

and oceans have remained unchanged in the earth's history, or have undergone great changes in reference to the respective areas occupied by land and water at various times. This question of the permanence of land and ocean basins, as it is termed, has been discussed by various authors in detail, and reference may be made to Dacqué [1] and to Arldt [2] for its history and the opinion of different authors. It need only be noted that though the very extensive changes as propounded by some of the authors may not be justified, the general principle of the different parts of the continental shelves having been under the sea at one time or another is accepted by all. The transgressions of the sea over the continents can not, owing to the fossil marine deposits of various ages, be denied, while similarly geological and biological grounds necessitate the acceptance of extensive land areas or land-bridges over long stretches of the sea and connecting either the various continents with one another, or the adjacent insular and peninsular areas with the mainlands. The great difficulty in this connection, as Suess [3] pointed out, has arisen from the fact that authors have not distinguished between " the outlines of the seas and of the sea basins. The outlines change, and not without reason are transgressive or supracontinental seas distinguished from the deep basins. The former are produced by changes in the shape of the hydrosphere, the latter by deformations of the lithosphere. The outlines of the transgressions change ; the deep basins also change."

In the following account I do not propose going into details about the changes that have taken place in the respective positions of various continents and oceans, but will only include short summaries of the conclusions of different authors so far as they are of interest in connection with the past history and distribution of the family Viviparidae. The account is based on the works of the authors cited in the text, and I have, as far as possible, tried to correlate the same with my results on the distribution of the family. Some of the areas are treated in greater detail than others, but this has been inevitable owing to the varying degree of information that is available. The various areas are, so far as possible, treated separately, but in some cases the connections of some of the continental areas have been considered together.

1. ASIA (EXCLUDING INDIA) AND AUSTRALIA.

a. *Asia.*

In the following account I propose considering various parts of Asia separately from India, as in my opinion this gives a better understanding of the connections of this continent with the others, while it also allows of a better plan of dealing with the connections of India with other areas.

As an introductory remark it may be noted that the connections between north-eastern Asia and North America over the Behring Straits,[4] or the land-bridge which is supposed to have connected Japan with America, are not considered here. Though molluscs of different

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[1] Dacqué, E., *Grundlagen und Methoden der Paläogeographie*, pp. 157-185 (Jena, 1915).

[2] Arldt, T., *Handbuch Palaeogeogr.* I, pp. 3-35 (Leipzig, 1919).

[3] Suess, E., *The Face of the Earth*, IV, p. 600 (Oxford, 1909). See also Wegener, A., *Die Entstehung der Kontinente und Ozeane*, pp. 18, 19 (Braunschweig, 1922).

[4] For detailed accounts of the connections see Scharff, R. F., *Distr. and Origin of Life in America*, pp. 83-100 (London, 1911), and Arldt, T., *Handbuch Palaeogeogr.* I, pp. 103-118 (Leipzig, 1919).

families and other animals[1] and plants migrated over these connections from one continent to the other, it may be safely concluded that no interchange of the Viviparidae took place along these channels (see also p. 243).

Geologically, leaving aside Burma and the Malay Peninsula, the eastern regions of the continent of Asia consisting of north-eastern Siberia, south-eastern China, Cochin-China and a part of Siam, form a more or less complete tectonic unit. As Suess [2] has shown the region consists of the old archaic and palaeozoic rocks forming in the north-east the eastern parts of Siberia and China, and in the south the areas with the folded mountain ranges of Tonkin and Annam.

From his detailed studies of the geology of China Frech [3] concludes that the north of China was covered by sea from the Cambrian to the Silurian times, while the southern area was similarly under the sea up to the Devonian times. During the succeeding epochs there were great changes in the relative positions of the land and water areas, and the mountain chains became elevated, but it was not till the end of the Triassic times that China finally became land by the retreat of the sea. In Jurassic times China formed a part of the Palaearktis, and for the greater part was separated from the united Lemuris and Palaeonotis.[4] For the Lower Cretaceous Ortmann,[5] following Neumayr and Suess, extends the Sino-Australian continent over the Indo-Malayasian Archipelago, Australia and Antarctica to South America, but as Uhlig[6] and Arldt have shown this extension of the Sino-Australian continental mass is not supported by the geological formations of the intervening areas. Koken[7] and Arldt show Angaris (the eastern continental area of the Palaearktis) as extending in the south to Szechuan and Formosa, which at the time was united with the continental shelf. Lapparent[8] includes the islands of Hainan and part of the Philippine Islands also in this south-eastern extension, while Haug[9] extends it still further south-east to Mindanao and Borneo.

In Upper Cretaceous, according to Ortmann, the Sino-Australian continent was cut up into the Sinic (the Asiatic) and the Australian (Australia and Antarctica with the latter of which South America was connected); he shows the Sinic as broadly connected with Lemuris or the Peninsular Indian region. Koken and Arldt extend the Sinic, Angaris or the Palaearktis to South China and Formosa, while according to Lapparent and Kossmat[10] it extended as far south as the Malayan Archipelago.

For the Caenozoic era the authorities differ as to the connections of Palaearktis with Lemuris and the exact southern extension of the continental shelf, but they are all agreed

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[1] See Dall, W. H., *Popular Sci. Month.* LXVII, pp. 362-366 (1905) and *Harriman Alaska Exped. Mollusca,* XIII, p. 1-171 (1905).

[2] Suess, E., *The Face of the Earth,* II, pp. 210-242 (Oxford, 1906).

[3] Frech, F., *Mittl. Ferdinand von Richthofentages,* pp. 38-61 (Leipzig, Berlin, 1912).

[4] For descriptions of these names and their history see Arldt, *loc. cit.* pp. 283-301. In the following account I have adopted the names proposed by Arldt for the various continents and oceans.

[5] Ortmann, A. E., *Proc. Amer. Phil. Soc.* XLI, pp. 320-324 (1902).

[6] Uhlig, V., *Mittl. Geol. Ges. Wien,* IV, pp. 329-448 (1911).

[7] Koken, E., *Die Vorwelt u. ihre Entwicklungsgeschichte,* pls. i, ii, (Leipzig, 1893).

[8] Lapparent, A. de., *Traite Géol.* (5th Edn.) p. 1297 (Paris, 1906).

[9] Haug, E., *Traité Géol.* II, p. 1358 (Paris, 1908-11).

[10] Kossmat, F., *Palaeogeographie,* map 5 (Leipzig, 1908).

that China and the adjacent areas were above sea-level, and formed a part of the northern continent.

We may also refer here to the Hanhai or the Dry Sea of the Chinese. This great inland sea was first referred to by von Richthofen,[1] who believed that the site of the existing Gobi Desert was at one time covered by an inland sea. This sea has been discussed by many authors, and reference may be made to Kobelt,[2] Suess[3] and Arldt[4] for details. Leaving aside the consideration of the earlier epochs it may be noted that in Tertiary times according to Suess " large parts of Asia were covered by freshwater lakes of vast dimensions, together with numerous smaller ones," and these probably represented the remnants of the Hanhai. This Hanhai, it must be remarked, is different from the one referred to by Arldt (*loc. cit.* p. 539, and Vol. II, pp. 842, 843) for explaining the peculiarities of the fauna of Lake Baikal. Arldt believed that the Hanhai during the later epochs was not in communication with the Pacifik, but was connected with the Obik or the southward extension of the Arctik, which separated the western part of the Palaearktis from the eastern. The importance attached to the remains or the extensions of the Hanhai for explaining the similarity and relationship of the Tertiary freshwater Molluscs with those of China and Central Asia is quite unjustified. Fuchs,[5] from the resemblance of the Viviparidae of Lake Tali Fu (Er-hai), Yunnan, to those of the Levantine Paludina-Beds of Eastern Europe, considered the latter to be of Japano-Chinese character. He also remarked on the similarity of the other molluscs, and the entire absence of the Melanopsids, which form a very important element in the fossils of Eastern Europe, mentioned already. Neumayr[6] went into greater detail, confirmed Fuchs's ideas about the resemblance of the Levantine faunas of Eastern Europe with the recent ones in Asia and North America, and concluded that " der See von Talifu ist das letzte der Becken der levantinischen Stufe, das bis in die heutige zeit erhalten hat."[7] Kobelt (*loc. cit.* p. 124), while considering Neumayr's explanation as plausible, remarked that the acceptance of the connection between the European Levantine areas and Hanhai through the Danube is impossible as there are no remains of these faunas in the whole of Central Asia, and more particularly in areas like the Aral and the Caspian. Suess (*loc. cit.* I, p. 598 (1904)), on the other hand, agreed with Neumayr, and considered the explanation as the only way of accounting for the remarkable similarity of the faunas in two such distant areas. Koken [8] believed in the independent origin of similar forms at different times and in widely separated areas. Annandale[9] came to the same conclusion, and showed that the similarity which is purely superficial is an instance of convergence or parallel evolution. My studies of the fossil and recent Viviparidae fully uphold this view (see p. 204). It may, therefore, be concluded that even as early as the Jurassic there could have been no connection between the Hanhai and the basin in Eastern Europe, and that the only possible connection of this inland sea with the marine

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[1] Richthofen, F. von, *China*, I, pp. 24, 25 (Berlin, 1877).

[2] Kobelt, W., *Studien zur Zoogeographie*, I, pp. 113, 119 (Wiesbaden, 1897).

[3] Suess, E., *The Face of the Earth*, III, pp. 56-59 (Oxford, 1908).

[4] Arldt, T., *loc. cit.* pp. 539, 540.

[5] Fuchs, T., *Verhandl. k. k. Geol. Reichsanstal. Wien*, pp. 297-300 (1879).

[6] Neumayr, M., *Neues Jahrb. Mineral. Geol.* I, pp. 21-26 (1883) and in Béla Széchenyi's *Reise in Ostasien*, II, (Süsswasser-Mollusken) pp. 649-651 (1898).

[7] Neumayr, M., *Erdgeschichte*, II, p. 405 (Leipzig, Wien, 1895).

[8] Koken, E., *Die Vorwelt u. ihre Entwicklungsgeschichte*, p. 440 (Leipzig, 1893).

[9] Annandale, N., *Rec. Geol. Surv. Ind.* L, pp. 209-213 (1919).

areas was with the Arctik through the Obik. In Tertiary times the inland sea broke up into a number of lakes, and some of these have persisted up to the present day.

Reference may here be made to the probable changes that have occurred in the river-systems of Asia. The question of the Indian rivers is considered separately (p. 234), but it may be noted that these also must have had much closer connections with the rivers of eastern Asia. In connection with the rivers of Asia there is very little information available, but there can be no doubt that Arldt (*loc. cit.* Vol. II, pp. 785, 786, fig. 81) is right in considering the plateau of Hochasien, as he calls it, as the area of great changes in the rivers of Asia. His reconstruction of the probable courses of the rivers of south-east Asia in the pre-quaternary times is by no means the last word on the subject, but shows that the rivers of this region all arose in the above-mentioned plateau, and that in the past they were much more closely connected with one another.

Japan.

According to Frech [1] Japan became separated from the mainland of Asia in Quaternary times. Lapparent, Koken, Handlirsch and others agree that as late as the Miocene Japan was broadly connected with the mainland both in the north and the south, and attempts have been made by Matthew and Arldt to explain the various stages of the separation of the different islands. Matthew[2] considers the Korean Straits to have been formed in the Miocene, and believes that even after this separation in the south Japan retained a broad connection with Siberia through Sakhalin. Arldt [3] on the other hand believes the first separation to have been in the north along the Gulf of Tartarv, which cut off Sakhalin from Siberia about the end of the Miocene. In the early Pliocene Sakhalin was cut off as an island by the formation of the La Perouse Straits, and Hokaido or Yeso was separated by the Tsugaru Straits appearing about the same time. This was followed by the formation of the Korean Straits, which resulted in the separation of the Liu Kiu islands from Nippon, but the latter remained connected with China by a land-bridge till the late Quaternary. With the separation of Nippon as an island, its breaking up into the islands of Honshu, Kyushu and Shikoku was brought about by the formation of the narrow straits which separate these islands. The absence of Viviparidae in Sakhalin and their general distribution in the various islands supports Arldt's hypothesis, but owing to the absence of any fossil forms too much stress can not be laid on these facts.

East Indies, etc.

In view of the importance of this region and the rather arbitrary limits which I assign to it, it is necessary to define the region which I propose considering. This area consisting of a large number of islands in the Indo-Pacific lies between the Latitudes 5°N. and 10°S. of the equator, and the Longitudes 95°E. and 145°E. of Greenwich. It includes the three Great Sunda Islands, Sumatra, Java and Borneo ; the chain of the Smaller Sunda Islands up to Timor ; the Celebes ; Moluccas and New Guinea west of Longitude 145°E. In view of the great similarity and close relationship of the Viviparids of the Philippines, and the con-

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[1] Frech, F., *Mittl. Ferdinand von Richthofentages*, p. 49 (Leipzig, Berlin, 1912).

[2] Matthew, W. D., *Bull. Amer. Mus. Nat. Hist.* XXII, p. 366 (1906).

[3] Arldt, T., *Entwicklung der Kontinente etc.* pp. 295, 296 (Leipzig, 1907) and *Handbuch Palaeogeogr.* I, p. 541 (1919).

nections of these islands in comparatively recent geological times with Celebes and the Sunda Islands, I will consider this area also here. The region defined above does not correspond to any recognised scheme of zoogeographical divisions, but is a very uniform one for the Viviparidae.

A few notes about the zoogeography of this area may preface the account of its geological history. These islands have attracted eminent naturalists from early times, and excellent accounts of the zoogeography of the area are available in the works of Wallace,[1] Kükenthal,[2] Weber,[3] the Sarasins,[4] van Kampen,[5] Barbour[6] and others. I will here only refer to the question of the regional limits in the form of artificial boundary lines like the "Wallace's Line" of Huxley and the "Weber's Line" of Pelseneer. As von Martens,[7] Weber and others have shown there is no justification for accepting a sharp boundary line between the islands of Bali and Lombok, and running northwards between Borneo and Celebes and to the east of the Philippines. "Weber's Line" was based on the distribution of molluscs by Pelseneer,[8] and was described as running through the Malacca Straits and Banda Sea to the east of Celebes and Timor. As van Kampen and Barbour have shown, it is not possible to draw any sharp dividing line between the faunas inhabiting the areas, though in some places a transitional zone between the Indian and Australian types of faunas inhabiting the area is to be distinguished. No such line is indicated by the Viviparidae.

The various views regarding the geological history of the area for the earlier epochs have been dealt with already (pp. 224, 225), and it is only necessary to consider the history during Tertiary times.

According to Koken [9] during the early Tertiary times there were a number of separate islands in the hilly areas of Sumatra, Borneo, Celebes, Luzon, Mindanao, Ceram, Flores and Timor, and Ortmann [10] and Arldt (*loc. cit.*) generally agree with his conclusions. Matthew [11] does not consider Ceram, Timor and Flores to have been above the sea at this time, while he shows Java also as an island. Jhering [12] in his map of the Eocene times does not show any of these islands, and, apparently, according to him, all of them were covered over by the sea. Handlirsch [13] believes Borneo, Celebes, the Moluccas and the Philippines to have been united to form a single island, while a second big island included Sumatra, the Andamans, the Nicobars, Banka and Belitong and this was probably also connected with Burma. Java and Flores at this time formed separate islands.

Ortmann extends the mainland during the Miocene to Java, Borneo and the Philippines, while Lapparent,[14] who unites Celebes with the mainland, shows the Philippines as forming

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[1] Wallace, A. R., *The Geographical Distribution of Animals,* Vols. I, II, (London, 1876), and *Island Life* (London, 1902).

[2] Kükenthal, W., *Abhandl. Senckenberg. Naturforsch. Ges.* XXII, pp. 1-321 (1896).

[3] Max Weber., *Der Indo-Australische Archipelago etc.* (Jena, 1902).

[4] Sarasin, P. & F., *Materialen z. Naturges. Insel Celebes,* Vols. I-IV (Wiesbaden, 1898-1901).

[5] van Kampen, P. N., *Amer. Natural.* XLV, pp. 537-560 (1911).

[6] Barbour, T., *Mem. Mus. Comp. Zool. Harward,* XLIV, pp. 1-203 (1912).

[7] Martens, E. von., *Weber's Zool. Ergebn.* IV, p. 298 (Leiden, 1897).

[8] Pelseneer, P., *C. R. Sixieme Cong. Internat. Zool. Berne,* pp. 550-552 (Geneve, 1905).

[9] Koken, E., *Die Vorwelt etc.* pl. ii (Leipzig, 1893).

[10] Ortmann, A. E., *Proc. Amer. Phil. Soc.* XLI, p. 383, fig. 7 (1902).

[11] Matthew, W. D., *Bull. Amer. Mus. Nat. Hist.* XXII, pp. 359-370 (1906).

[12] Jhering, H. von, *Archhelenis und Archinotis,* Map (Leipzig, 1907).

[13] Handlirsch, A., *Sitzungsber. Akad. Wiss. Wien (Math.-Naturwiss. Cl.)* CXXII, Abt. I, pp. 361-481 (1913).

[14] Lapparent, A. de, *Traité Géol.* (5th Edn.) p. 1607 (Paris, 1906).

a separate island. Matthew on the other hand includes Borneo, Sumatra and Java with the mainland; Celebes with Ceram and Buru formed an island while Palawan and the Philippines are shown as two other separate islands. Arldt's extension of the mainland is to Cochin-China only; Borneo, Celebes and the Philippines were united as a separate island, and Sumatra also formed a distinct island.

In Pliocene and Quaternary times Matthew shows Sumatra, Java and the chain of the Smaller Sunda Islands as forming a peninsula united to the mainland, while Borneo, Palawan, Celebes and the Philippines, according to him, formed separate islands. In Late Quaternary times the Sunda Chain was cut off first and then Java and Sumatra were separated. According to Arldt the Asiatic Continent at the beginning of the Pliocene extended as far as Celebes and Timor, but in early Pliocene Celebes was cut off by the formation of the Macassar Straits, and some of the Smaller Sunda Islands by the Lombok Straits. The Philippines separated about the same time by the formation of the Mindanao Straits and the Sulu Sea, and soon after the large insular region of the Philippines broke up into its constituent islands. In Quaternary times Mentawi Islands were cut off from Sumatra, and Java separated by the formation of the Sunda Straits and the Java Sea. Borneo was the next to separate from Sumatra, and about the same time Malacca Straits cut off Sumatra from the mainland. The Malay Peninsula now extended to Belitong; this island and Banka were the last to separate from the mainland. The Moluccas were never included in the south-east extension of the continental shelf of Asia.

Celebes.

From their detailed geological and zoological studies the Sarasins (*loc. cit.*) concluded that Celebes did not rise above sea-level before Late Eocene. For the Miocene the relations of these islands have been considered already (p. 228).

During Pliocene times the Sarasins consider Celebes, as a single island, to have been connected with Java, the Philippines, the Moluccas and Flores by separate land-bridges, and derive their faunas from these sources. The situation of these land-bridges, according to the authors, is still traceable along submarine shallows or chains of islands. Weber (*loc. cit.*), basing his views on the comparative poverty of the fauna of Celebes and its relationships, is of opinion that Celebes arose by the union of small islands which earlier on were connected with adjacent areas. Similar views in slightly modified forms are suggested by van Kampen and Barbour, and though there can be no doubt as to the connections by means of land-bridges, it is not possible to be certain as to their exact situations.

Arldt (*loc. cit.* pp. 633-637), as a result of the geological considerations and the distribution of the various groups of the Animal Kingdom, does not agree with the Sarasins in most details. According to him Celebes in the beginning of the Pliocene was broadly connected with Borneo, and this area extended to Lombok, while still earlier the Philippines were also connected with Celebes. He thus does away with the land-bridges, and postulates an extensive land area for the Early Pliocene extending from Talaut in the north to Lombok in the south. The detailed sequence of the separation of the various islands, as postulated by Arldt, does not seem to be warranted by the data available.

Philippines.

During the Cretaceous Ortmann[1] considers the Philippines to have formed a part of the south-east extension of the Asiatic mainland, and though the connection was cut off during the early Tertiaries it is stated to have been re-established in the later Tertiaries. Weber (*loc. cit.* p. 32) from the presence of fossil Stegodonts of Pliocene times in the Philippines suggests a connection with Eastern Asia perhaps *viâ* Formosa. Matthew (*loc. cit.* p. 368) is not quite definite, but suggests that they may have had a connection before Pliocene. Arldt (*loc. cit.* p. 631), from the composition of the mammalian fauna of the islands, believes that the separation came about sometime in Pliocene and before the separation of the Smaller Sunda Islands from Java. According to him the more important land connections of the Philippines were with Borneo over Palawan and probably also over the Sulu Islands, along which routes the Asiatic element of the mammalian fauna must have migrated to these islands. The complicated scheme for the connection of the Philippines with Borneo and Celebes, as suggested by the Sarasins, [2] does not seem to be based on sufficient evidence.

New Guinea.

According to the accounts of the various palaeogeographers New Guinea was not connected after the Early Cretaceous with any of the islands of the East Indies or the areas which I have considered with them. The presence of a very distinct stock of Viviparidae of Asiatic origin in both New Guinea and the Aru Islands, however, suggests that probably as late as the Pliocene New Guinea had a direct or indirect connection or connections with either Celebes or the Sunda Island chain through Aru Islands.

The only other connection of New Guinea to be considered here is that with Australia. Though Lapparent and Handlirsch believe that in Miocene New Guinea and Australia were separated from one another by the Torres Straits, other authorities are agreed that from Eocene to Late Pliocene the two areas were broadly connected along York Peninsula. Weber,[3] from a consideration of the distribution and relationships of the freshwater fishes, definitely asserts that the connection subsisted to the Pliocene times. Arldt (*loc. cit.* p. 638) from the relationships of the mammals concluded that " Die Isolierung muss also unbedingt in Pliozän erfolgt sein, fruher dagegen kaum, da beide Gebiete immerhin unter den Säugetieren eine ganze Anzahl gemeinsame Gattungen aufzuweisen haben."

b. *Australia.*

With reference to Australia it is not necessary to consider the connections of this continent with South America through the Antarktis, or by the land-bridge which united New Guinea, with which Australia was then connected along Cape York Peninsula, through the Bismarck Archipelago, the Solomon Islands, New Hebrides, Fiji, New Caledonia and New Zealand and thence to Patagonia in South America.[4] Both these connections, which

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[1] Ortmann, A. E., *Proc. Amer. Phil. Soc.* XLI, pp. 378-385 (1902).

[2] Sarasin, P. & F., *Materialen z. Naturges. Insel Celebes*, IV, pp. 132-137 (Wiesbaden, 1901).

[3] Weber, Max., *Nova Guinea*, V, (Zool.), II, pp. 217-225 (Leiden, 1908). See also Hedley, C., *Rept. V Meeting Australian Ass. Adv. Sci. Sydney*, p. 445 (1893).

[4] See Hedley, C , *Proc. Roy. Soc. New South Wales*, XXIX, pp. 278-286 (1895), and Osborn, H. F., *Science* (*n. s.*), XI, pp. 561-574 (1900).

have been advocated by different authorities, are of no interest in connection with the distribution of the Viviparidae. Similarly the connections of Australia with India to the south of the Great Sunda Islands as hinted by Verbeek,[1] or through Timor and Sandalwood Islands and Borneo to the mainland of Asia as expressed by Barbour,[2] would be very ancient, and hence of no use for explaining the introduction of the family into Australia.

The only connection to be considered and which has been referred to already is that of Australia and New Guinea. This connection is suggested by Suess and by Ortmann. Matthew, Arldt and Basedow[3] all agree about the two areas having been broadly connected along Cape York Peninsula to at least the Pliocene times. Wegener[4] believes the Post-Pliocene to be the time when the third or the most recent migrants of the Asiatic fauna passed into north-eastern Australia from the Sunda Islands through New Guinea, thereby assuming a connection as late as the Post-Pliocene.

The only other points to be considered are the relative positions of land and sea areas in Australia from the Cretaceous onwards, and the probable river-basins of the area during Tertiary times. During the Cretaceous period the greater part of central and west Australia and the area south of the Murray River in east Australia was covered by the Cretaceous Sea. According to Basedow from this time onwards the sea was gradually cut off by a land-bridge from the Indian Ocean in the west. By the rising of land in the south and the east the sea receeded from these parts and was transformed into an inland sea. From the Cretaceous to Eocene times a large network of freshwater streams opened into this inland sea, gradually reduced the salinity of its waters and transformed it into a freshwater lake. In the south-eastern part of Australia the presence of undoubted deposits of Miocene age shows that this part must still have been covered by the sea.

The reconstruction of the probable river-channels of Australia by Arldt (*loc. cit.* Vol. II, p. 805) for the Tertiary times shows that the rivers in this region were more numerous than they are to-day, and that they were more intimately connected with one another. The distribution of the Viviparidae suggests a still closer connection between the river-systems of Australia.

II. INDIA.

The past history of the Mediterranean is intimately connected with the changes in Peninsular India during the Palaeozoic and Mesozoic eras, and because of its importance in connection with the origin and distribution of the Asiatic Viviparidae, I include here an account of the eastern extension of the Mediterranean and its connections with India.

The Mediterranean, the " Ozean " of earlier authors, the " Zentrales Mittelmeer " of Neumayr, the " Tethys " of Suess, the " Thetis " of von Jhering or the " Mediterranik " of Arldt[5] formed a closed oceanic belt running round the globe from at least the Carboniferous to the Eocene, and though its exact extent varied at different times, it separated a northern part of the world from a southern. About the Upper Carboniferous of European chronology

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[1] Verbeek, R. D. M., Cited after van Kampen, P. N., *Amer. Natural.* XLV, p. 546 (1911).

[2] Barbour, T., *Mem. Mus. Comp. Zool. Harvard,* XLIV, p. 154 (1912).

[3] Basedow, H., *Zeitschr. Deutsch. Geol. Ges.* LXI, pp. 342-344 (1909).

[4] Wegener, A., *Die Entstehung der Kontinente und Ozeane* (3 Auf.) pp. 59-62 (*Braunschweig,* 1922).

[5] Arldt, T., *HandbuchPalaeogeogr.* I, pp. 283-300 (Leipzig, 1919).

the Indian Peninsula, including Ceylon, formed a part of the great Gondwana Land of Suess.[1] This continental shelf comprised " South America from the Andes to the east coast between Orinoco and Cape Corrientes, the Falkland Islands, Africa from the southern offshoots of the Great Atlas to the Cape mountains, also Syria, Arabia, the Indian peninsula, and Ceylon," while it extended further eastwards below the Sunda Islands to include Australia ; it lay entirely to the south of the Mediterranean belt. To the north of this belt was the great continental mass called Angara Land (Suess) or Angaris (Arldt) in the east, and Nordatlantis further to the west. The exact relation and extent of these continents need not be discussed here, but it may be noted that about the end of the Triassic, while the vast continent of Gondwana was still intact, Peninsular India, according to Oldham,[2] was " a land area over which many large lakes were probably scattered, while on the land there were glaciers flowing down into these lakes and into the sea which covered part of the great Indian desert, the north-west Punjab, and a very large portion, if not the whole of the area occupied by the Himalayas west of the Ganges valley." The stretch of land which connected the Peninsula with Assam and the region now occupied by the eastern Himalayas in Silurian times most probably existed as a narrow bridge during the Gondwana era, and became much broader during the Cretaceous when, according to Oldham (*loc. cit.* p. 493), " the eastern coast line of the continent ran not very far from the east coast of India, across the Ganges delta, and along the south side of the Assam Hills " ; this is considered further below.

It is not necessary to consider the history of Peninsular India in the Mesozoic era before the Jurassic, when, as the presence of marine deposits in Asia Minor, Persia and the western Himalayas shows, the Mediterranik must have extended over the whole of this part, and cut off Peninsular India from the northern Eurasiatic continent. As Arldt (*loc. cit.* p. 375) has pointed out this does not, however, rule out the existence of connecting land-bridges for the intervening periods. During Dogger the Gondwanis was broken up by the sea flooding over the connecting areas, and Peninsular India became an island for which Arldt has proposed the name " Lemuris." During Upper Jurassic times the conditions remained more or less the same and there was no connection of Lemuris with either Asia or Africa.

For Early and Middle Cretaceous, geologists are generally agreed about the separation of Lemuris from Asia, but Oldham and Kossmat[3] believe that a land-bridge existed across Assam, and the same view is put forward by Ortmann[4] on zoogeographic grounds. According to this author " in the Middle and Upper Cretaceous, this peninsula became united with the Sinic continent, forming a bridge between the latter and Africa " ; the connections of Peninsular India with Africa are discussed below (p. 234).

In Eocene times according to Oldham (*loc. cit.* p. 494) " the eocene sea flowed over Western Rájputána and the Indus Valley to the west, over a large part of Balúchistán and Afghánistán, and over the whole of the north-west Punjab and the outer Himálayas as far east as the Ganges River." Oldham is not definite as to whether Peninsular India at this time was connected over the eastern part of the Gangetic Plain with Assam and eastern Asia, but from his account it may be assumed that he believed in such a connection. Pilgrim[5]

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[1] Suess, E., *The Face of the Earth*, IV, p. 500 (Oxford, 1909).

[2] Oldham, R. D., *A Manual of the Geology of India* (2nd Edn.) p. 403, (Calcutta, 1893).

[3] Kossmat, F., *Jahrb. k. k. Geol. Reichanstal.* XLIV, p. 463 (1894). See also *Rec. Geol. Surv. Ind.* XXVIII, pp. 44, 46 (1895).

[4] Ortmann, A. E., *Proc. Amer. Phil. Soc.* XLI, p. 330 (1902).

[5] Pilgrim, G. E., *Journ. Proc. As. Soc. Bengal* (*n. s.*) XV, p. 99, pl. i (1919).

considers that " the complicated drainage system and breadth of the Mahanadi so disproportionate with its length, as well as the entire absence of any fluviatile deposits older than Sub-Recent, such as we find on the Irawaddi, point to a Pliocene submergence of much of its former valley, and to a much wider extension of the Indian Peninsula over what is now the Bay of Bengal from the Eocene onward." In his map of Eocene times Pilgrim extends the Eocene Sea to Assam, while parts of Persia and Afghanistan are shown as forming a narrow strait cutting off the main Eocene Sea from its eastward extension. He also shows a narrow bridge connecting Peninsular India over Assam with China. Matthew [1] and Handlirsch [2] also suggest that Peninsular India was connected with the northern part of Asia, but Arldt (*loc. cit.* p. 409), while admitting the absence of any deposits of Lower Eocene age, denies such a connection. According to Matthew the south-eastern extension of Angaris or the Asiatic continent at this time included Borneo and Java. Ortmann and Handlirsch restrict it to Malacca, while Arldt includes Sumatra with it. For the Upper Eocene Arldt again suggests that India must have been separated from Angaris.

During the Oligocene Peninsular India was separated from Angaris according to Kossmat, Arldt and others, while Matthew and some authors believe the connections to have been the same as in the Eocene. The limits of extension of Angaris in the south-east are also different according to different authors.

In the Miocene Palaearktis, as Arldt calls the united northern regions of Angaris and Skandis, is believed to have been connected with Peninsular India. The connection, according to Arldt, was rather narrow, while Lapparent,[3] Ortmann (*op. cit.* p. 585) and Matthew (*op. cit.* p. 366), following Blanford, Oldham and other workers on Indian Geology, agree that the greater part of the Indo-Gangetic Plain had at this time risen above sea-level, and that the Peninsula was broadly connected with the mainland. Pilgrim shows the whole region of the Indo-Gangetic plain as land, and extends Peninsular India over a great part of the Bay of Bengal. He further shows a southward extension of land in the Arakan region along the Cape of Negrais, and this in Pliocene times is shown as including the Andaman and Nicobar Islands. Authorities differ as to the south-eastern extension of Asia, but they are all agreed that most of the islands of the Sunda Group were included in it.

During the Pliocene the conditions were similar to those in the Miocene except that the sea receeded further and the land assumed its present configuration.

The close of the Secondary Period is believed by Oldham to be the probable date of the elevation of the Himalayan chain, and following him Sarasin [4] considers the Oligocene or the Miocene to the Pliestocene to be the period when India was broadly connected with North Africa and South-eastern Europe over Baluchistan, Persia, Arabia and Turkey on the one hand, and with China and Eastern Asia on the other. At this time Sarasin considers the main migration of the " Siwalik Fauna " to have taken place. Wadia,[5] from a consideration of the recent work of Oldham, Hayden and others, places the elevation of the Himalayas during the Mid-Eocene to the end of the Tertiary time, during which period the elevation

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[1] Matthew, W. D., *Bull. Amer. Mus Nat. Hist.* XXII, p. 360, map 2 (1906).

[2] Handlirsch, A., *Sitzungsber. Akad wiss. Wien* (*Math.-Naturwiss. cl.*) CXXII, p. 472 (1913).

[3] Lapparent, A. de, *Traité Géol.* (5th Edn.) p. 1607 (Paris, 1906).

[4] Sarasin, F., *Zool. Jahrb. Suppl.* XII, p. 82 (1910).

[5] Wadia, D. N., *Geology of India*, pp 203, 204 (London, 1926).

took place in several intermittent phases. Reference may also be made to the Arabian region of dispersal of Jacobi[1] which extended from north-eastern Africa across Arabia to India, and along which the interchange of the Siwalik Fauna took place. As Ortmann (*loc. cit.* p. 332) rightly pointed out this region of dispersal only played a part in very recent times, probably Late Tertiary, while in the Early Tertiary and the Mesozoic this connection could not have existed.

Reference may also be made here to the " Siwalik River " of Pilgrim (*loc. cit.* pp. 81-99, pls. i, ii) or the " Indobrahm River " as this Tertiary river is called by Pascoe.[2] It is supposed to have run to the south of and parallel to the Himalayan chain from Assam in the east to the north-west corner of the Punjab, and then flowing south-west opened into the Miocene Sea. The formation of the Siwalik deposits along the Himalayas and in Baluchistan is ascribed by the authors mentioned above to this great river during the Middle Miocene to the Pliocene. The elevation of the Himalayas resulted in the breaking up of the great river into three systems, (i) the Indus, and (ii) the five rivers of the Punjab, both flowing as they do to-day into the Arabian Sea, and (iii) the rivers of the Ganges System, which took a south-easterly course and now open into the Bay of Bengal.

III. INDO-AFRICAN CONNECTIONS.

With reference to the connection of Peninsular India and Ceylon with Africa and Madagascar, it is not necessary to consider the connections in the Palaeozic era, as these connections are not of any importance for the distribution of the Viviparids.

In early Jurassic times " Äthiopische Mittelmeer " of Neumayr or Aethiopik of Arldt [3] formed a deep southward bay, and submerged the connecting land area between Peninsular India and Africa except in the extreme south where the Lemuris Peninsula still remained connected with Africa and Madagascar. In Meso-Jurassic times, according to some authors, this bay extended further south and separated Lemuris from Südatlantis while Neumayr, Arldt, Uhlig, Blanford and others believe that the connection was maintained during the whole of the Mesozoic era and even in the early Tertiaries. Authors similarly differ as to the Cretaceous, and Arldt (*op. cit.* p. 391) after a full discussion of the various views concludes that there was no connection after the Lower Cretaceous. Reference may also be made to Suess,[4] who stated that after the partial breaking up of the Gondwana Land " at the time of the middle Cretaceous there still existed a barrier running from south-west to north-east," and Depéret[5] who supposed the connection to have been broken up towards the end of the Cretaceous, but re-established during Tertiary times.

I give below a summary of the views regarding the supposed land connection between India and Africa based on the relationship of the recent faunas of the two regions.

Leaving aside the casual references of the earlier authors, the original idea of such a land connection was suggested by Sclater[6] who, from the relationship of the mammals of Mada-

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[1] Jacobi A., *Zeitschr. Gessellsch. Erdkunde Berlin,* XXXV, pp. 321-426 (1900).

[2] Pascoe, E. H., *Quart. Journ. Geol. Soc. London,* LXXV, pp. 138-157, pl. x (1919).

[3] Arldt, T., *Handbuch Palaeogeogr.* I, pp. 372-391 (Leipzig, 1919). References to earlier authors will be found in this work.

[4] Suess, E., *The Face of the Earth,* I, pp. 417-420 (Oxford, 1904).

[5] Depéret, C., *Les transformations du monde animal* (Paris, 1907).

[6] Sclater, P. L., *Quart. Journ. Sci. London,* I, pp. 213-219 (1864).

gascar, concluded that " anterior to the existence of Africa in its present shape, a large continent occupied parts of the Atlantic and Indian Ocean stretching out towards (what is now) America on the west, and to India and its islands on the east; this land connection was broken up into islands, of which some became amalgamated with the present continent of Africa and some possibly with what is now Asia, and that in Madagascar and the Mascarene Islands we have existing relics of this great continent, for which as the original focus of the " Stirps Lemurum " I should propose the name " Lemuria !" The name Lemuria or the Lemurian Continent has become intimately connected with the land connection between India and Africa, and though no definite date was assigned by Sclater to this connection, it has for various times and in different senses been utilised for explaining the relationship of the Indian and the Aethiopian faunas.

A. von Pelzeln,[1] though he did not use the name Lemuria for this connection, considered that in India there are two different types of faunas intimately mingled; (1) an old Malayan derived from the old continental area which in the Lower and Middle Miocene extended from the Sunda Islands to Madagascar, and probably also included a part of Africa, and from which certainly the faunas of the Mascarene Islands and Madagascar were derived, and (2) an Aethiopian-Indian fauna probably dating from the Indo-African connection of Upper Miocene times, along which the interchange of the Indian and Aethiopian faunas took place from India to Africa and *vice versâ*.

Blanford,[2] as a result of his studies on the relations of mammals and birds of India with the African forms, suggested a connection between the two areas. He did not definitely assign any date to the continental connections, but added that in the Late Tertiaries the two faunas were probably more alike than they are at the present day.

Wallace [3] agreed that in order to explain the similarities of the Ceylonic subregion, which included the greater part of Peninsular India with Madagascar, there must have been a land-connection, probably like Sclater's Lemuria, in the Early Tertiaries. In his later work,[4] however, he modified his views, and concluded that the connection, if it existed, must have disappeared at the latest in Early Miocene.

Hartlaub,[5] from a study of the birds of Madagascar and the neighbouring islands, suggested a continental connection from Africa over Madagascar, the volcanic islands like Bourbon and Mauritius to Southern India and Ceylon. He did not assign any age to this hypothetical continent but considered it to be the same as Sclater's Lemuria.

Blanford [6] considered in detail the geological and biological evidence and concluded that " every circumstance as to the distribution of life is consistent with the view that the connexion between India and South Africa included the Archaean masses of the Seychelles and Madagascar, and that it continued throughout Upper Cretaceous times, and was broken up into islands at an early Tertiary date." In two later papers [7] he considered the Dravidian

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[1] Pelzeln, A. von, *Verhandl. zool.-bot. Ges. Wien*, XXV, pp. 58-62 (1875).

[2] Blanford, W. T., *Ann. Mag. Nat. Hist.* (4), XVIII, pp. 280-293 (1876).

[3] Wallace, A. R., *The Geographical Distribution of Animals*, I, pp. 328-361 (London, 1876).

[4] Wallace, A. R., *Island Life* (3rd Edn.) pp. 422-426 (London, 1902).

[5] Hartlaub, G., *Die Vögel Madagascars, etc.* pp. viii, ix (Halle, 1877).

[6] Blanford, W. T., *Proc. Geol. Soc. London*, pp. 87-99 (1890).

[7] Blanford, W. T., *Proc. Roy. Soc. London*, LXVII, pp. 486-489 (1900), and *Phil. Trans. Roy. Soc. London*, (B) CXCIV, p. 419 (1901).

element in the Cisgangetic subregion as the remnant of the fauna which was found in the region which connected India and South Africa across the Indian Ocean in the Secondary and Early Tertiary times.

Lydekker [1] in connection with the distribution of the mammals referred to an earlier continental, probably the Gondwana Land, connection, and a later which persisted during Jurassic and Cretaceous to Pliocene in the Tertiaries. Similar views were again affirmed by Sclater [2] for the Lemurian continent.

Kobelt[3] from his studies on the distribution of the Land Molluscs referred to the close relationship of the South Indian and African forms, but did not consider the question of the land connections. Later,[4] however, he stated that the land connection between the two areas could not have existed in Tertiary times.

Jacobi[5] agreed with Wallace that a continuous land bridge did not exist, but to explain the distribution of animals postulated a chain of islands, which in Pliocene times formed the means for the interchange of the faunas of the two areas. The main lines of migration from India to Africa and *vice versâ,* however, he believed to have been over Syria and Arabia and through Baluchistan and Persia.

Ortmann[6] after a detailed discussion of the geological evidence and the distribution of some families of freshwater Decapod Crustacea concluded that a Lemurian bridge must have persisted between Peninsular India and Africa up to the Eocene.

Willey[7] after considering the constitution of the fauna of Ceylon believed that a great continental shelf extended from Ceylon and Southern India to Madagascar and probably Africa. He did not, however, assign any date to this connection.

The distribution of the members of the genus *Herpele* in Assam , West Africa and Panama and of the Pagurid Crabs led Alcock[8] to affirm the presence of a continuous continent from India through Africa to South America, and a continuous sea-belt from Japan, Southern Asia to north-west Africa and Europe. He did not assign any age to these connections, but from his comparison of these with Lemuria and Tethys it may be assumed they were intended for the Palaeozoic and Mesozoic eras.

As a result of his geological and zoogeographical studies Arldt[9] concluded that the Mesozoic Lemurian connection between India and Africa must have persisted to the end of Cretaceous times (p. 141) or even to a little later in the Tertiaries. He also postulated a second connection between India and Tropical Africa in the Pliocene south of Arabia and perhaps over Socotra, and which according to the author was the route for the migration of the Siwalik Fauna (p. 231). He also referred to migrations over Arabia to East Africa as postulated by Jacobi and others (p. 166).

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[1] Lydekker, R., *Geographical History of Mammals,* p. 23 (Cambridge, 1896).

[2] Sclater, P. L., *The Geography of Mammals,* pp. 236, 237 (London, 1899).

[3] Kobelt, W., *Studien z. Zoogeographie,* I, pp. 45, 46 (Wiesbaden, 1897).

[4] Kobelt, W., *Ber. Senckenberg. Naturfors. Ges.* pp. 89-104, map (1899).

[5] Jacobi, A., *Zeitschr. Gessellsch. Erdkunde Berlin,* XXXV, pp. 321-426 (1900).

[6] Ortmann, A. E., *Proc. Phil. Soc. Philadelphia,* XLI, pp. 326-333 (1902).

[7] Willey, A., *Spolia Zeylanica,* I, pp. 1-12 (1903).

[8] Alcock, A., *Ann. Mag. Nat. Hist.* (7) XIV, pp. 267-273 (1904).

[9] Arldt, A., *Die Entwicklung d. Kontinente, etc.* (Leipzig, 1907).

Sarasin [1] in connection with the fauna of Ceylon considered in detail the geological and zoogeographic evidence, and concluded that though there is the probability of a Palaeozoic and Early Mesozoic connection, there is no justification whatsoever for believing this connection to have persisted in the Late Cretaceous and the Early Tertiaries.

Gadow[2] supposes a permanent connection between India and Madagascar and also Africa from the Primary to the Oligocene; the connection was broken in the Late Oligocene.

Annandale,[3] without committing himself, stated that "geologists are apparently willing to admit that in late Cretaceous or early Tertiary times a land bridge, in the form either of a solid territory or of an archipelago, extended from what is now East Africa to what is now the Malabar Zone." This connection, he believed, was probably the explanation for the element of African Fauna in Southern India.

Stephenson [4] referred to the possibility of a land connection between Peninsular India and Madagascar in the Early Tertiaries, and used it for explaining the origin and evolution of certain genera of Indian Oligochaetes like *Hoplochaetella* and *Erythraeodrilus* from the genus *Howascolex* of Madagascar. In a later work,[5] however, following Matthew,[6] he is inclined to doubt not only Lemuria, but probably even the Gondwana Land of the Palaeozoic era.

Arldt[7] in his latest work has discussed in great detail the relationships of the animals and plants of Peninsular India and Madagascar, and concludes that there must have been a direct land connection between the two areas. In this connection he does not consider the relations of Peninsular India with Africa.

Reference may also be made to the two recent papers of Connolly,[8] who has referred East African species of Unionidae to the Indian genus *Indonaia* Prashad. This genus is not found in either North Africa or the intervening countries like Arabia, Asia Minor or Persia, and the presence of undoubted species of the genus in Africa may be attributed to a Lemurian connection in earlier times.

A note about the Mascarene Islands and the Seychelles may also be included here. As Germain [9] has pointed out, these islands are a remnant of the Old Gondwana Land, but he has not paid much attention to their connections in the later epochs. The only recent Viviparid found in the region is *Viviparus zonatus* (Reeve).[10] This species as Liénard, Nevill and Germain have pointed out is only a slightly modified form of the Indian *V bengalensis* Lam.), and has within very recent times been introduced into Mauritius with Indian plants. Its presence in the region is of no value for zoogeographic purposes.

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[1] Sarasin, F., *Zool. Jahrb. Suppl.* XII, p. 57 (1910).

[2] Gadow, H., *The Wanderings of Animals* (Cambridge, 1913).

[3] Annandale, N., *Ninth Internat. Cong. Zool. Monaco*, pp. 579-588 (Rennes, 1914).

[4] Stephenson, J., *Rec. Ind. Mus.* XIII, pp. 362, 363 (1917).

[5] Stephenson, J., *Proc. Zool. Soc. London*, pp. 138, 139 (1921).

[6] Matthew, W. D., *Ann. New York Acad. Sci.* XXIV, pp. 171-318 (1915).

[7] Arldt, T., *Handbuch Palaeogeogr.* I, pp. 162-172 (Leipzig, 1919).

[8] Connolly, M., *Rec. Alb. Mus. III*, pp. 265-267, pl. xii, figs. 1, 4 (1925) and *Trans. Roy. Soc. South Africa*, XII, p. 213 (1925).

[9] Germain, L., *Faun. Malacol. Terr. Fluv. Iles Mascareignes*, pp. 419-454 (Angers, 1921), and *Compt. rend. Congr. Soc. sav. Sci.* pp. 264-268 (1925).

[10] For references to this species see Germain's work (1921) cited above, pp. 355-357.

IV. AFRICA.

The continent of Africa is very old, and except for the northern area, which was covered by the Mediterranean up to Late Tertiary times, the greater part of the continent has remained above sea-level since the Cretaceous. The connection of Africa with Asia have already been considered (pp. 233, 234), and it is only necessary to refer to its connection with America. The connection of western Africa and a part of the Iberian Peninsula with Central America, which the French authors call the Atlantide,[1] is of no interest for the distribution of the Viviparidae, as all the areas connected by this bridge are without fossil or recent Viviparidae. The possible connection with South America has been referred to already (p. 223).

In connection with the distribution of the family in Africa reference may be made to the changes in the river-basins and the lake areas from Tertiary times to the present day. Haas and Schwarz [2] from the relationship of the freshwater fishes and molluscs believed that the extensive inland sea of the earlier times, which covered the inner area of the continent, broke up later into four main river basins, and that the series of lakes in East Africa was connected with one another and some of these basins by a network of rivers. The four basins, which they distinguished are (1) the Timbuktu basin in the region below the Sahara, and forming the source of the Niger and the Senegal, (2) the United Chad, (3) the Congo basins, which were situated in Central Africa and from which some of the tributaries of the Niger, the Congo and the old Chari took their origin, and (4) the Nagami basin in the Nagami Lake area. Arldt,[3] after discussing all the literature on the subject, concludes that after the retreat of the Cretaceous Sea a large basin corresponding to the first three basins of Haas and Schwarz occupied the area, and in it all the streams of the region opened or had their source. The separation of the Chad and the Congo basins he believes to have taken place about the end of the Pliocene, while the Timbuktu basin must have been cut off earlier. He also shows a large basin above Lake Rudolph, and considers this to have formed the source of the Nile-system ; it was also in connection with the main basin to the south-west. The chain of East African lakes is also shown in connection with one another and with the Congo area of the main basin by a network of streams ; it is also supposed to have been connected with the Zambesi and the Nagami basin in the south.[4] The connections and the course of the Nile are supposed to have been different. After a discussion of the views of the different authors, Arldt concludes that from the Oligocene to the Pliocene the course of the Nile lay much further to the west than it does to-day, and that the deposits of the Fayum resulted from that time. Another river, the Blue Nile, is supposed to have originated in the same basin as the Nile, and to have flowed to the east over the dry area of the Red Sea to the north, and to have been in connection with the Syrian river-systems in the Jordan Valley. This latter is believed to be the explanation of the African element in the fauna of Syria, and *vice versâ*.

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[1] See Germain, L., Joubin, L, and Davis, E. L., *Lé Géographie*, XL, Reprint pp. 1-13 (1923), and Germain, L., *Bull. Soc. Philomat. Paris*, Reprint pp. 1-24 (1924).

[2] Haas, F., & Schwarz, E., *Geol. Rundschau*, IV, 603-607, fig. 1 (1913).

[3] Arldt, T., *Handbuch Palaeogeogr.* II, pp. 798-804, fig. 83 (1922).

[4] A new map showing the probable extent and distribution of lake and river basins on the African continent towards the close of the Pleistocene, and a full discussion of the subject is included by Pilsbry and Bequaert in their recent Memoir, (*Bull. Amer. Mus. Nat. Hist.* LIII, pp. 545-549, Map 14, 1927) which, however, was published too late for review in this paper.

V. EUROPE.

In view of the earliest records of the family Viviparidae in Europe being of the Meso-Jurassic times, I will begin my account of the palaeogeographical conditions of this area about this time. Further, as the greater part of Europe was at this time covered by the Mediterranean or the Mediterranik as Arldt calls it, my remarks on this period will be limited to the British Isles and the adjacent areas.

Probably somewhat previous to the Bathonian age the Scoto-Scandinavian Land, as Jukes-Browne [1] has pointed out, " was increased by the addition of a broad tract of lowland along its southern side; a lowland never raised far above the sea-level of the period, and indented by the estuaries of several large rivers which drained a considerable area of the northern land." His account and map of the Bathonian Sea show that in areas like Langton Bridge and what is now Skye and probably also in other places the conditions were essentially estuarine, with the deltaic regions next to the sea and freshwater streams opening into them. The first ancestors of the European Viviparidae probably migrated into these estuarine areas, and we have their remnants in the Langton Bridge and Skye fossils. The occurrence of *V. aurelianus* Cossmann at Saint-Gaultiere, in strata which were doubtfully considered to be Bathonian, would confirm Jukes-Browne's idea that the Bathonian Sea of the British Isles was broadly connected with that covering parts of northern France. In this case *V aurelianus* would be an instance of an independent origin of the members of this family in France and the British Isles at about the same time and under similar conditions from identical ancestors.

In Upper Jurassic it is only necessary to consider the conditions for the British Isles and Germany. According to Lapparent,[2] England formed a peninsula connected with North America, but separated from the Scandinavian area. Jukes-Browne, however, believes it to have also been connected with Scandinavia, while a part of the eastern area was united with Belgium to form the Anglo-Belgian Island. The Portlandian Sea, which ran in between the two areas, was, according to Jukes-Browne (*loc. cit.* pp. 287, 288), " contracted into two parts, which were practically separate seas; the sea of the Portlandian limestones lying wholly to the south of Bedfordshire and opening south through France, while a northern sea extended from Germany into Yorkshire and Lincolnshire." It was in the estuarine areas along this sea that the ancestors of the Paludina-Beds, which form the famous Purbeck Marbles, must have lived. Jukes-Browne starting with the Lower Purbeck lagoons, which were apparently formed by the land-locking of portions of the Portlandian Sea, follows on to the more extensive Purbeck-Wealden Lake in England, while similar areas must have become enclosed in north Germany. Probably in these areas the Purbeckean and the Wealdean Viviparids migrated into estuarine and eventually freshwater areas both in England and in Germany. This again involves the supposition of independent origin of similar or even identical forms in separated areas, but as the intervening sea was the same, there can be no objection against the origin of similar species from identical ancestral types under approximately identical conditions.

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[1] Jukes-Browne, A. J., *The Building of the British Isles*, p. 274, fig. 44 (London, 1911).

[2] Lapparent, A. de, *Traité Géol.* II, p. 1258 (Paris, 1906).

Even during Cretaceous times Europe did not exist as a broad continental area. The greater part of what now forms the continent was at this time covered by the extensive Mediterranik, and Ortmann,[1] following Neumayr, shows a broad sea connecting the Arctic with the Mediterranean over Russia near the Ural mountain range, thus separating it entirely from the northern parts of Asia. According to other authors this broad sea did not appear till later in the Tertiaries. More or less isolated insular areas existed in parts of the Scandinavian region, the British Isles, France, Spain, Germany and in the region above the Black Sea. Ortmann, Lapparent, Haug and Arldt [2] consider the British Isles, France and Spain to have formed a broad islandic or peninsular area connected with Scandinavia over what is now the North Sea, and according to some of them also over Iceland and Greenland with North America. Others, however, do not believe that there was any connection with North America or even with Scandinavia. Neumayr and Koken show the various countries mentioned above as separate islands.

During the early Tertiaries the conditions in Europe as a whole were not very different from what they were in Cretaceous times. The Mediterranean covered the greater part of central and eastern Europe, and, according to most authors, was still broadly connected with the Arctik through the Obik. The British Isles were separated from the rest of Europe, while the land area in the west consisted of the Iberian Peninsula, which was sometimes united to France and at other times separated by a bay running along the Pyrenees, parts of France and Germany and connected with a part of Central Europe near the Black Sea. The Eocene and Oligocene species of Viviparidae of England, France and Germany, which represent nearly related species, are apparently descendants of the Cretaceous forms which had become established in suitable areas.

During the Miocene and Pliocene great changes occurred in the area now occupied by Europe. The extensive Mediterranean had started to shrink, and the various stages of its shrinkage and ultimate regression to the present outlines have been distinguished by Suess (*loc. cit.* Vol. I, pp. 279, 280) as the five Mediterranean Stages. The Pyrenees were not elevated till the beginning of the Oligocene, and the system of the Alps did not begin to rise till the close of the Oligocene. During this long period the British Isles were broadly connected with the mainland of Europe, and the Baltic did not exist as such. The greater part of the continent of Europe had arisen above sea-level, though there were inland seas or sea-basins occupying various extensive areas of central and eastern Europe. Two areas of special interest in this connection are the region of the Aegean and the area from the River Saone in France in the west to the Aral Sea in the east.

Until the Early Pliocene, as Suess (*loc. cit.* pp. 344, 345) concluded from the work of Spratt, Forbes, Neumayr and others, the Aegean region formed a broad land area, and served as the chief channel for the interchange of faunas between Asia and the existing areas of south-eastern Europe. In the third Mediterranean stage according to Suess "a deep freshwater lake stood over the site of the Aegean, a part of that Levantine chain of lakes which stretched from Slavonia to Asia Minor. The Mediterranean lay entirely to the south of this area." First the southern part of the land subsided, and later, according to Suess

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[1] Ortmann, A. E., *Proc. Amer. Phil. Soc. Philadelphia,* XLI, figs. 5, 6 (1902).

[2] For references to the other authors see Arldt, *loc. cit.* pp. 386-425.

‘in very recent times the Aegean continent completely subsided; Levantine freshwater deposits of great thickness and with broken edges indicate the new coast, the Mediterranean spread far and wide over the Pontic basin, and even overflowed the otherwise regular shores of this sea into the sea of Azov.” Arldt (*loc. cit.* pp. 525, 526) from the recent work of Cayeux, Blanckenhorn, Kessler and others divides the breaking up of this area into various stages, and the final subsidence and the connections of the Mediterranean with the Pontik are considered to have been more complicated than was hitherto supposed. The final subsidence is supposed to have been continued even in Quaternary times.

In his third Mediterranean stage, corresponding roughly to the Pliocene, Suess distinguished a Levantine Group in central and eastern Europe. This group was based on the occurrence of Levantine Beds of fossils of freshwater molluscs, chiefly Paludinas, and it was rightly assumed that the areas where these fossils are found were covered by extensive freshwater lakes. At the time of publication of Suess's famous work such beds were known from the valley of the Danube, Dalmatia, Bosinia, north Greece, Asia Minor and some of the Aegean Islands. Since then the work of the Russian geologists, a summary of which will be found in Pavlov's Memoir, cited already, and the work of Depéret in France have shown that such lakes extended from the valley of the Saone River in France in the west to the Sea of Aral and even eastwards. Arldt (*loc. cit.* Vol. II, pp. 821-827) has given a good summary of our knowledge of these Tertiary basins, and it is not necessary to go into detail here.

Reference may also be made to the changes undergone by the river-systems of Europe during Tertiary times. Haas [1] concluded from the distribution of the Unionidae that the Thames was a tributary of the Rhine in the Pliocene, when the North Sea did not exist, and England was broadly connected with the mainland. Arldt (*loc. cit.* Vol. II, pp. 757-784) includes a very useful summary of the views of various authors, and has constructed maps to represent the different views regarding the changes that have taken place in the Caenozoic era in the river systems of Europe. From these it is clear that the Thames, Seine, Rhine, Rhone, and Danube were at the time more closely connected than they are to-day, and there can be little doubt that they played a very important part in the distribution of the Viviparidae in Europe from the west to the east.

In addition to the Ural Mountain chain which forms an impassable barrier for the Viviparids from European to Asiatic Russia the main factor for this area appears to have been the large brackish inland sea of post-Tertiary or Pleistocene times as has been advocated by Karpinski.[2] This sea included the whole of the Caspian and the Sea of Aral, and extended north to the mouth of the Kama river in north Russia. This is further believed to have been connected with the Arctic Ocean by a system of narrow channels or lakes. Scharff[3] from the study of the European fauna appears inclined to the same view. Apparently this extensive barrier is responsible for the absence of the Viviparidae in the eastern areas,

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[1] Haas, F., *Proc. Malacol. Soc. London,* IX, pp. 106-112 (1910) and *Abhandl. Senckenberg. Naturfor. Ges.* XXXII, pp. 143-177 (1910). I am indebted to Mr. B. B. Woodward for drawing my attention to a paper by J. Trimmer, *Quart. Journ. Geol. Soc. London* IX, pp. 293, 294, pl. xiii (1853), in which the author published very instructive maps showing the probable connections of the British Isles with the main continent of Europe. Trimmer was probably the first author to suggest the linking of the Thames with the Rhine in the past.

[2] Karpinski, A., *Beitr. Kennt. Russ. Reich.* (3) IV, pp. 143-188 (1888).

[3] Scharff, R. F., *Proc. Roy. Irish Acad.* (3) IV, pp. 427-514 (1897), and *European Animals*, pp. 147, 153 (London, 1907).

and the brackish conditions which were brought about by the ingression of the Mediterranean in the later Tertiaries led to the extinction of the Levantine forms in the Aralo-Caspian area.

The effect of the Glacial Period on the distribution of the Viviparidae in the northern latitudes cannot be ignored, and in this connection reference may be made to the maps of this period published by Scharff (*loc. cit.* p. 455) and Arldt (*loc. cit.* p. 424). From these it is clear that most of the freshwater forms in the areas covered by ice must have perished, and that the recent distribution is probably of a date later than the Glacial Period.

VI. NORTH AMERICA.

From the records of the fossils of the family Viviparidae it is clear that they did not appear in North America till late in the Jurassic, and for the purpose of the present enquiry it will be sufficient to begin with the Meso-Jurassic times. For this time the palaeogeographical maps of Neumayr,[1] Lapparent,[2] Arldt[3] and Haug [4] agree as to main conclusions, while the work of Schuchert [5] on the North American region itself does not differ from these authors in any material details. Nordatlantis (Arldt) consisted of the whole of North America, north of Mexico, and included Greenland, Iceland and probably a part of the British Isles with which it was connected by a broad land-bridge. It was separated from Sudatlantis, or the united areas of South America and Africa, by the Mediterranean. With the Asiatic part of Palaearktis the Nordatlantis was connected by a land bridge over the Behring Straits. Somewhat later, about Upper Dogger, the Pacific Ocean of the time flooded over the greater part of the western area of Nordatlantis, and extended in the east to the area later occupied by the Laramie Sea.

From the occurrence of the first fossils of the Viviparidae about this time it may be assumed that they originated in America in this period.

The general changes in the continental area in the succeeding times up to the Middle Cretaceous are of no interest, but the formation of the Laramie Sea may be referred to here. This inland sea has been discussed already (pp. 219-220), and it is only necessary to note that it ran in a north-western to a south-eastern direction, and divided Nearktis into the main eastern part of the continent from a belt-like western. The area of the sea was about 2,000 miles long by about 500 miles broad, and with waters which were "sometimes salt, sometimes brackish and sometimes fresh." According to Chamberlin and Salisbury [6] "the Laramie series may be said to record the transition from the marine conditions of the Montana epoch to the freshwater and land conditions of the Tertiary in the region." It may also be noted that the great development of the freshwater and land faunas in the Laramies was foreshadowed in the Early Cretaceous.

For the later periods the configuration of the continent or the broad continental connections between the Nearktis and the Palaearktis over the Behring Straits in Oli-

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[1] Neumayr, M., *Denkscr. k. Akad. wiss. Wien* (*Math.-Naturwiss. Cl.*) L, pp. 57-142 (1885), and *Erdgeschichte*, II, p. 263 (Leipzig & Wien, 1895). Also see Uhlig, V., *Mittl Geol. Ges. Wien*, IV, pp 329-448 (1911).

[2] Lapparent, A. de, *Traité Géol* (5th Edn.) pp. 1154-1258 (Paris, 1906).

[3] Arldt, T., *Entwicklung Kontinente*, map. 18 (Leipzig, 1907), and *Handb. Palaeogeogr.* I, pp. 370-383 (Leipzig, 1919).

[4] Haug, E., *Traité Géol.* II, p. 1113 (Paris, 1908-11).

[5] Schuchert, C., *Bull. Amer. Geol Soc* XX, pp. 427-606 (1910).

[6] Chamberlin, T. C. & Salisbury, R. D., *Geology. Earth History*, III, p. 152, (London, 1906).

gocene, Miocene, Pliocene and possibly also in Quaternary times are of no use for the explanation of the distribution of the Viviparidae, as they have been used for the Unionidae,[1] the Pleuroceridae [2] or the Decapod Crustacea. Similarly [3] the connection with Europe[4] during the various geological periods does not contribute to the solution of this problem. Walker [5] was of opinion that " if we would assume that instead of coming from the Orient, the *Viviparidae* originated in North America, where from the earliest times there has been the greatest generic differentiation, and that like the *Camelidae* among the mammals,they passed around the mountains to the north and spread westward over the Behring bridge into the Old World, all such apparent inconsistencies would be obviated and theoretical conclusions would be in entire harmony with the known distribution." Against this hypothesis there is the occurrence of fossils of an earlier date in Europe. There are no recent or fossil Viviparids known from Alaska or the eastern Siberian region, and, with the exception of the Japanese species introduced by man in recent times, no Viviparids are known from the western parts of North America. It is, therefore, impossible to believe that members of this family migrated from America to Europe either along the eastern route or over Siberia and Asia, and the only course left open is to believe in independent origins of the family in America and other areas.

I have already referred to the opinion of different authors that the Viviparid fauna of to-day in North America represents the descendants of the Laramie one, and in this connection reference may be made to the map of the Late Tertiary river-systems constructed by Arldt (*loc. cit.* Vol. II, p. 789), which shows close connections between the Missouri and the rivers of the eastern States in these times, and greatly helps in elucidating the distribution of the recent species. In connection with the effect of the Glacial Epoch reference may be made to the works of Schuchert, cited already, Willis [6] and Arldt, which give details as to the limits of the areas which were covered by ice during this period.

7. RELATIONSHIPS, ORIGIN AND DISTRIBUTION.

Fischer,[7] Pelseneer,[8] Lang-Heschler [9] and most other authorities do not express any opinion on the relationships of the family Viviparidae, or the probable forms from which it is to be derived. According to Cooke [10] the origin of the family is doubtful, and its affinities cannot definitely be affirmed. Bouvier,[11] however, considers the family to be undoubtedly related to the Turbonidae and the Trochidae. In his genealogical tables he derives the Monotocardia from the Diotocardian families mentioned above, and considers the Viviparidae and the Littorinidae to be the intermediate forms. R. Perrier [12] subscribes to Bouvier's

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[1] Simpson, C T., *Proc. U. S. Nat. Mus.* XVIII, pp. 342, 343 (1895), and XXII, p. 508 (1900). Also see Walker, B., *Proc. Malacol. Soc. London,* IX, pp. 126-145 (1910).

[2] Walker, B., *First Rept. Michigan Acad. Sci.* p. 58 (1900).

[3] Ortmann, A. E., *Proc. Amer. Phil. Soc. Philadelphia,* XLI, pp. 316-319 (1902).

[4] In addition to authorities cited see Scharff, R. F., *Proc. Roy. Irish Acad.* XXVIII (B), pp. 1-28 (1909) and *Distribution and Origin of Life in America,* pp. 11-14 (London, 1911) and Germain, L., *Ann. Geogr.* XXIII-XXIV, pp. 394-406 (1915).

[5] Walker, B., *First Rept. Michigan Acad. Sci.* p. 58 (1900).

[6] Willis, B., *Journ. Geol.* XVII, p. 601 (1909).

[7] Fischer, P., *Manual Conchyliol.* pp. 732-734 (Paris, 1885).

[8] Pelseneer, P., *Mollusca* in Ray Lankester's *Treatise of Zoology,* V, (London, 1906)

[9] Lang-Heschler, *Mollusca* in *Lehrbuch vergl. Anat. Thiere* (Jena, 1902).

[10] Cooke, A. H., *Molluscs* etc. in *Cambridge Natural History,* p. 17 (London, 1895).

[11] Bouvier, E. L., *Ann. Sci. Nat.* (*Zool.*), (7) III, pp. 58, 72 (1887).

[12] Perrier, R., *Ann. Sci. Nat.* (*Zool.*), (7) VIII, p. 136 (1889).

views, and Haller [1] in his genealogical tree derives the Architaenioglossa, to which the Viviparids belong, from the Trochidae. Sollas,[2] apparently following Bouvier, derives the family from the Trochids and the Turbonids. In spite of certain objections to the suggested origin and the relationships of the family there is much in favour of this view. The families Trochidae and Turbonidae are both very old geologically, members of both occur in Silurian and in some cases even in Cambrian beds, while their anatomical characters, the ctenidia, the nervous system and the relationship of the heart and the rectum, suggest a close relationship with the Viviparidae. It is probable, therefore, that the Viviparidae arose from the less highly modified common stem of the families Trochidae and Turbonidae in the Early Jurassic period. An important objection against this hypothesis is the fact that none of the Trochidae or of the Turbonidae are estuarine, and it is difficult, if not impossible, to imagine the origin of a family of freshwater molluscs except from some intermediate estuarine forms.[3] The objection, however, is not so serious as it appears for, as in the case of the Neritinidae, there may have been some ancestral forms which gave rise to the Viviparidae on the one hand and the Littorinidae and the Rissoidae on the other. I do not agree with Bouvier that the anatomical differences between the Viviparidae and the Rissoidae, the Hydrobiidae (= Bouvier's Bythinidae) and the Littorinidae are so fundamental as to preclude their being closely related. The palaeontological history and the anatomy of these families point to a near relationship, and I consider them to form a uniform group. Among the Viviparidae themselves probably the genus *Larina* A. Adams is the least modified member of the family. It is an estuarine genus, and the shell of the various species has a Trochid-facies. As has, however, been remarked already, the relationships of *Larina* are doubtful and with the absence of any information about its anatomy, the genus cannot even definitely be included in the family.

Sollas, Cossmann and Arldt appear to be the only authors who have expressed any opinions on the time of origin of the family. Sollas (*loc. cit.*) suggested that they may have originated in the Devonian lakes, but owing to the absence of any fossils of the Carboniferous and Permian periods, he added that probably a later date must be assigned. Cossmann [4] is not definite, but his account may, in view of its interesting suggestions, be quoted here in extenso—" Il est posible toutefois que les *Naticopsidae* carbonifériennes, en émigrant dans les marais oú se formait la houille, aient subi une adaptation paludicole qui-tout en leur conservant á peu près le galbe naticoide-ait modifié leurs organes pour ce nouveau genre de vie, et qu' ensuite â travers le Trias où l'on ne connait pas jusqu'à presént de vestiges de formations palustres, ces animaux transformés aient atteint les époque stratigraphiques où leur présence a été authentiquement reconnue. Ce ne sont là, bien entendu, que des hypothéses qui exigeraient une confirmation materiélle, avant de prendre corps."

Arldt [5] in discussing the origin of the freshwater molluscs stated that "Als erste Familie treten uns die Paludinen entgegen. Sie sind seit der unteren Kreide fossil bekannt und damals wahrscheinlich in Europa ins Süsswasser übergangen. Aus dem Senon wird auch

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[1] Haller, B., *Studien über Docoglosse und Rhipidoglosse Prossobranchier etc.* p. 151 (Leipzig, 1894).

[2] Sollas, W. J., *The Age of the Earth*, p. 199 (London, 1905).

[3] In this connection see White, C. A., *Third Ann. Rept. U. S. Geol. Surv.* pp. 479-488 (1883), Pelseneer, P., *Bull. Acad. Roy. Belgique* (*Sci. cl.*), no. XII, pp. 699-741 (1905), and Prashad, B., *Proc. Twelfth Ind. Sci. Congress*, pp. 126-143 (1925).

[4] Cossmann, M., *Essais Paléoconch. comp.* XII, p. 177 (Paris, 1921).

[5] Arldt, T., *Handbuch Palaeogeogr.* II, p. 1164 (Leipzig, 1922).

eine nordamerikanische Art beschrieben. Das Hauptgebiet von *Paludina* (*Vivipara*) blieb aber die Palaearktis, von der aus vielleicht schon in Palaeogen Afrika erreicht wurde (*Cleopatra*)." These remarks are a verbatim copy of this author's statement about the family in an earlier paper,[1] with the only modification that he apparently now gave up his idea of the migration of the family from the Palaearctic to the Oriental region in Cretaceous times, as he originally believed. The question of the origin of the family is discussed below, but it may be noted that in view of the earlier Jurassic fossils, the family must have been evolved much earlier than the Cretaceous. Arldt's view that the Palaearctic is the main region of the distribution of the genus *Viviparus* is incorrect, for the greater part of the Asiatic area of the Palaearctic region has no Viviparids, while south-eastern Asia including the East Indies is the richest in members of the family, both as regards species and individuals. North America and Africa are also as rich in species of *Viviparus* as the European area of the Palaearctic.

From the results of my work on the distribution of the Viviparidae, the palaeogeographical connections of the different continents and the restricted means of distribution of the family I am convinced that these molluscs did not originate in any one area only. The different forms of the various members of the family found in the different areas do not justify the conclusion of the previous workers that they have descended from the same ancestral form in one area, while the palaeogeographical relations of the continents would not admit of their distribution from any one region. I am, therefore, of opinion that the family had a polyphyletic origin, and that it is possible to distinguish at least four main zones in which the members of this family evolved by taking to a freshwater life.

There are numerous examples of the polyphyletic origin of similar species of the genus *Viviparus* in the fossil species in Eastern and Central Europe, where apparently under the influence of similar conditions species developed along the same lines. More remarkable, however, is the evolution of identical species in the Inferior Oolite in Germany and the British Isles, two widely separated areas, as also in Bathonian times in France and England, from apparently marine or brackish water ancestors. The suggestion of the polyphyletic origin of the family, in widely separated areas, as put forward above is only a wider application of this principle, and certainly with our present knowledge no other explanation seems feasible. In this connection reference may be made to Bourne,[2] who suggested that probably many of the fluviatile Neritidae of widely separated regions, which appear so similar, had been independently derived from marine Neritidae. Similarly Hesse [3] has put forward the view that different marine species of *Cerithium* Adanson have probably independently evolved into apparently allied species of the estuarine *Potamides* DeFrance, in widely separated localities, but under the influence of similar changed conditions of life in brackish waters.[4]

The four zones in which the family evolved are :—(1) Western Europe, where the first members of the family had their origin in the Bathonian Sea ; (2) North America in the Jurassic extension of the Mediterranean in this area ; (3) Peninsular India in the eastern

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[1] Arldt, T., *Archiv Naturges.* LXXXI, Hft. 4, pp. 16-84 (1915).

[2] Bourne, G. C., *Proc. Zool. Soc. London*, p. 878 (1908).

[3] Hesse, R., *Tiergeographie*, pp. 103, 120 (Jena, 1924).

[4] This is also hinted at for freshwater Gastropods generally by Pilsbry and Bequaert (*Bull. Amer Mus. Nat. Hist. LIII*, p. 97 (1927).

extension of the Mediterranean in the Late Jurassic or the Early Cretaceous; and probably (4) Australia in the Cretaceous Sea. All the four zones formed part of the extensive Mediterranean, and the freshwater areas in which the family later flourished were formed by the enclosing of parts of this sea by land, and the waters gradually becoming fresher. The time of origin may roughly be taken as the Jurassic for all the zones, though the family is not so far known from Peninsular India or anywhere else in Asia from beds of an earlier age than the Cretaceous. These four zones will now be discussed separately and the distribution of the recent forms will, as far as possible, be correlated with the palaeogeographical conclusions.

I. ASIA AND AFRICA.

I believe that Peninsular India forms the central zone whence the Viviparids of Asia and Africa are derived. Either the Lemurian connection in Cretaceous times formed the channel along which the ancestral forms of the Indo-African species migrated from Peninsular India to Africa, or it must be accepted that closely allied ancestral forms evolved independently into similar types of Viviparids in both India and Africa about the same time. I am inclined to accept the former as the more likely course, and hence have included the two areas together.

Taking Africa first, I consider that the first members of the family established themselves somewhere in the south-east, and in view of the age of the Matabeleland fossils this area may be accepted as the central one for this continent. The genus *Cleopatra* must have branched off very early from the main stem, and evolved along more or less parallel lines to the other members of the family. Other species, which are to be referred to the group of Vivipari Unicolores, retained their primitive characters, and except in some specially suitable localities have persisted more or less unchanged to the present day. The distribution must have taken place from the south to the north, and from the central area to the west, and there can be no question of any migrations to or from Europe or Asia in the north. This suggested line of distribution, it may be noted, is different from the one suggested by von Martens[1] who believed that " Ihre reiche Entwicklung in Ostafrika ist daher ein nach Indien weisender Zug," but the difference is one of interpreting the direction from, instead of, to India.

The sub-genus *Neothauma* evolved undoubtedly in response to the peculiar lacustrine conditions, and I am inclined to consider the two species *N. tanganyicense* and *N. mweruensis* as having been evolved independently in Lake Tanganyika and Lake Mweru, but from similar ancestral forms.

As to the agencies for dispersal in Africa I agree with Haas and Schwarz and Arldt (pp. 238, 239) that the river-systems and lakes of Africa must have been closely connected in Tertiary times, and that along these channels the Viviparidae, like the other groups of animals considered by the authors, must have spread over the area where they are found to-day. It is not possible to define the causes for the absence of the family in parts of western Africa, and I cannot add anything to explain this mysterious problem. The absence of the Viviparidae in north Africa, with the exception of the Nile basin, is due to the area having

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[1] Martens, E. von, *Beschalte Weichthiere Deutsch-Ost-Afrikas*, p. 174 (Berlin, 1897).

been under the sea up to the Late Tertiaries, and the presence of the forms in the Nile basin dates undoubtedly from comparatively recent geological times.

I believe that the Viviparids of Asia, with the exception of the few forms in the extreme west, are all to be derived from the ancestral types which originated in the Cretaceous extension of the Mediterranean in Peninsular India. The earliest known fossil is *Viviparus normalis* (Hislop) from the Intertrappean Beds of Peninsular India, and this type is represented in the recent fauna of India and Eastern Asia as a whole, by what has been referred to as the Vivipari Dissimiles Group in my account of the recent forms of the area. This group spread over the whole of India and Ceylon, and probably with the Siwalik River it spread as far west as the Hamun-i-Helmand in Seistan, and to Assam in the east. The time of this migration I would place earlier than Miocene when, according to the palaeogeographical conclusions of various authors, the Indo-Gangetic Plain had risen above sea-level. About this time the Vivipari Bengalenses Group must have also been evolved from the Vivipari Dissimiles, and spread with it over the same area.

The sub-genera *Cipangopaludina* and *Dactylochlamys* must have evolved in the Assamese area about Miocene times and from there migrated southwards to Burma, and eastwards to China, and through Siam into the Malay Peninsula together with the ancestral type of the Vivipari Dissimiles and in some cases with the Vivipari Bengalenses. It is not clear why Vivipari Bengalenses did not migrate into China, or if they did, why they were not able to establish themselves there.

The forms of the East Indies are all to be derived from the types which had migrated into the Malay Peninsula, and apparently the time of migration was from the Middle to the Late Tertiaries. Some of the forms in the Philippines and the Celebes may also have come from China, as indications of these are to be found in the islands of Hainan and Formosa, but it is impossible to be dogmatic about the exact line of distribution. The New Guinea forms are related to the Asiatic forms, and, as has been remarked already (p. 230), indicate that there must have been some connection between New Guinea and the adjacent regions in the Late Tertiaries over which the forms were carried to these islands.

The Chinese and eastern Asiatic species of the regions like Korea and the Amur Basin must have travelled north-east from the Indian centre of distribution along the Yangtse Kiang and Hwang-Ho rivers, and in view of the absence of any Viviparids in Sakhalin, the migration into Japan could not have taken place till Late Pliocene.

The peculiar sub-genera *Taia*, *Margarya*, *Rivularia*, *Mekongia*, and *Heterogen* were all evolved in special areas, probably in response to the biological conditions, and are of no special interest in connection with their areas of distribution. Their relationships and probable ancestries have already been discussed in the account of these forms.

II. AUSTRALIA.

The absence of any fossils of Viviparidae in Australia might be taken to indicate that the family was introduced into the area in comparatively recent times. On the other hand this may be due to the area not having been sufficiently explored so far. With the exception of the estuarine genus *Larina* the recent species of the family do not show anything but a superficial resemblance to those found in the neighbouring areas of New Guinea or the East Indies. Any connection with these forms must, therefore, be of a very early date. It is, however, impossible to be certain as to whether these forms are to be derived from the Asiatic stock or whether they originated independently in Australia. I am inclined to the latter view, and believe that they probably originated in Australia independently in the Cretaceous Sea, and from there spread in the north-eastern belt-shaped zone which they occupy to-day. The absence of any species of the type of *Dactylochlamys* in Australia is a very important argument in favour of this view, for if the Australian forms were derived from the neighbouring areas of New Guinea or the East Indies, it would be difficult to explain why no forms of this type, which is dominant in all these parts, did not wander with the other types. Further the commoner type of the Australian Viviparidae is the banded one, and this is least represented in the neighbouring areas. I do not agree with von Martens[1] that the differences between the Asiatic or Indian Viviparidae and the Australian are to be explained as " Gegensatz nicht Indien und Australien, West und Ost, sondern Festland oder grössere Inseln gegenüber der kleineren."

III. EUROPE.

The recent Viviparids of Europe form a uniform group, and, as has been discussed already (p. 186), they are divisible into two main types. We are very well informed about the palaeontological history of the family in this region, and a scheme of evolution of the recent from the fossil has been given already, while a few notes on the distribution have also been included in the palaeogeographical considerations about this area. It is only necessary, therefore, to include a general summary here.

Europe, including Asia Minor, has at the present day only smooth, shining, not very thick-shelled and banded species. They are found in the area defined already, and the main distribution seems to have taken a direction from west to east. The chief barriers against the dispersal of the family appear to have been the absence of rivers flowing in the right direction or not connected with the centres of origin of the family, and the high mountain ranges like the Alps, except in the Alpine lakes where members of the family had apparently become established before the elevation of this mountain chain, the Pyrenees,[2] the Caucasus and the Ural Mountains. Reference has also been made to the influence of marine basins, such as the one in the Pyrenees basin in the Early Tertiaries, the Obik and later the marine Aralo-Caspian Basin connected with the Arctic ocean in eastern Russia, and above all the influence of the over-flooding of the various parts of Central and Eastern Europe by the Mediterranean during its various stages of regression and transgression. This last factor is undoubtedly responsible for the disappearance of the highly evolved and variously sculptured forms of Levantine Viviparids in Europe. To the Glacial Period must be attributed the absence of the family in the northern latitudes.

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[1] Martens, E. von, *Weber's Zool. Ergebn.* IV, p. 294 (Leiden, 1897).

[2] Dr. F. Haas has drawn my attention to a paper by J. Royo Gomez, *Comm. d. Invest. Paleont. Prehist.* Memoir XXX, p. 98, pl. xii, figs. 12, a, b (Madrid, 1922), in which the author has recorded a species as *Viviparus* aff. *ventricosus* Sandberger, from various localities in Spain. In the same paper references to the records of an unidentified species of the genus from various localities in Portugal are also to be found. These papers came to my notice long after the present memoir was ready for the press, and I can only add that the discovery of undoubted species of fossil Viviparidae in the Iberian Peninsula during the Miocene, does not in any way help in unravelling the problem of the peculiar distribution of the recent species in Europe. The Iberian species were probably an extension of the French species, but in the absence of actual specimens it is impossible to be certain about their exact relationships.

It is impossible to lay down definitely the exact region where the recent species first originated, and whence they migrated over the whole of the region, but there can be little doubt that it must have been somewhere in western Europe. The connections of the Tertiary river-systems and their courses during that time must have played an important part in the distribution from the west to the east, and it appears as if the Danube is the most important in this connection for the whole of central and eastern Europe, while the Rhine and its connections with the rivers of the western region determined the distribution in those areas.

IV. NORTH AMERICA.

The history of this region undoubtedly shows that the Viviparids of this continent are a distinct stock, and though most of the highly evolved types disappeared after the Laramie times, we may consider the recent forms as the descendants of the less highly evolved forms of that period. For the distribution of the recent members of the family we have to recognise the influence of the Missouri River, and it may in fact be assumed that the distribution of the family at the present day is a good index of the course and the relationships of the streams of this system with the rivers of the eastern area of the United States and the south-eastern parts of Canada.

As to what exactly determined the absence of the family in other parts it is impossible to be certain, but the Glacial Period in the northern regions, and the absence of any river connections between the Viviparid zone of North America and central America may be taken as the two main factors.

8. SUMMARY.

1. This paper is an attempt to determine the relationships of the various members of the family Viviparidae, and to divide into genera, subgenera and groups the various types found all over the World.
2. The methods of dispersal of the family are examined in detail (pp. 155-157), and it is concluded that freshwater streams are the main channels along which the members of this family have spread from one area to another.
3. The Zoogeographical Regions proposed by various authors for different groups of the Animal Kingdom are of no value for the Viviparidae, and the distribution of the family is, therefore, considered according to the continents and countries in which they are found (pp. 157-160).
4. The various genera and subgenera of Recent Viviparidae proposed by different authors are discussed. With the exception of *Cleopatra* Troschel and *Larina* A. Adams, which are only provisionally included in the family, *Viviparus, Cipangopaludina, Dactylochlamys, Taia, Margarya, Rivularia, Heterogen, Mekongia, Neothauma, Tulotoma, Campeloma* and *Lioplax* are accepted as valid, and all of these are considered as being of subgeneric rank.

In the subgenus *Viviparus* s.s., five groups of forms are distinguished according to the areas in which they are found, and a number of other groups are differentiated according to the types of shells of the species inhabiting different areas (pp. 160-189).

A sketch-map illustrating the distribution of the recent members of the family is appended.

5. Annandale's *Taia naticoides* var. *intermedia* must be known as *Taia naticoides* var. *noetlingi* (Kobelt), as the two forms are the same, and the latter name has priority (p. 165). A new name *Cipangopaludina chinensis* (Gray) var. *haasi* Prashad is proposed for *Paludina longispira* Heude, which name is preoccupied for a Japanese species (p. 168). Smith's name *Paludina longispira* has priority over Annandale's *Heterogen turris,* and the species should be known as *V* (*H.*) *longispira* (Smith) (p. 172).
6. The recent members of the family from different areas are examined in detail, and their relationships with one another are, so far as possible, determined (pp. 160-189).
7. The Fossil Viviparidae are treated on lines similar to those adopted for the recent species. With the exception of the North American types, which can be definitely assigned to recent subgenera, all others are referred to the subgenus *Viviparus* s.s. The relationships of the recent with the fossil species are also discussed (pp. 189-223).
8. Genealogical trees illustrating the mutual relationships of the various sculptured species of Central and Eastern Europe are included and it is shown that the various series of sculptured forms are all to be traced back to *V achatinoides* (Deshayes). The various series of sculptured forms in the region are shown to have evolved independently on parallel lines, and it is concluded that the origin of similar types of sculpture is of a polyphyletic type. The European species are further shown to have no genetic relationship with the Asiatic or the American sculptured Viviparids (pp. 202-219).
9. The evolution of the Fossil Viviparidae of Yugo-Slavia and other areas in Eastern Europe is considered in detail (pp. 202-206). The first type of evolution consisted in the mere increase in size, both in the height or the length of the shell, and in the swelling of the whorls. The second type resulted in the shells becoming rather elongate and correspondingly narrower, while the whorls developed a number of primary and secondary ridges. The three primary ridges, corresponding to the three hairy ridges of the embryonic shell, are from their positions on the shell distinguished as the Sutural, Median and Peripheral. The more highly sculptured European Fossil species show various grades in the development and evolution of the shell sculpture ; these are treated in detail, and the lines of evolution, so far as possible, determined. It is believed that the evolution of the sculpture had a polyphyletic origin, and the various series of forms evolved on more or less parallel lines. In most of the European species the sutural and the peripheral ridges played the most important part, and in this respect they differ from the recent sculptured forms like *Margarya, Taia* and *Tulotoma* in which all the three ridges become developed.

10. The new name *Viviparus parabrusinai* is proposed for the species recorded as *V brusinai* by Neumayr from the Island of Cos (p. 217).

11. The question of the permanence of Land and Ocean Basins is referred to, and it is concluded that though the very extensive changes in the configuration of the land and oceans as propounded by some authors are not justified, there can be no doubt that different parts of the continental shelves were at one time or another covered by the sea. Similarly there can be no question about extensive land connections over long stretches of the sea, connecting either the various continents with one another or the adjacent insular and peninsular areas with the mainland (pp. 223, 224).

12. The Palaeogeography of the various areas so far as it has a bearing on the distribution of the Viviparidae is discussed (224-243). A detailed review of the literature dealing with the Indo-African Connections based on the relationships of the Recent Faunas of the regions is included (pp. 234-237).

13. An examination of the relationships suggests that the family Viviparidae arose from the less highly modified common stem of the families Trochidae and the Turbonidae in the Early Jurassic Period (pp. 243, 244).

14. The Viviparidae apparently did not descend from a single common ancestral form. The family had a polyphyletic origin and it is possible to distinguish at least four main zones in which the members of this family evolved independently by taking to a freshwater life. The four zones (1) Western Europe, (2) North America, (3) Peninsular India, and (4) Australia—are considered separately and the probable time of origin in each area, the evolution of the different subgenera, and the lines of migration of the various types to different areas are fully discussed (pp. 243-249).

EXPLANATION OF PLATE XIX.

Fig. 1. *Viviparus bengalensis* (Lamarck), from Calcutta, India.

Fig. 2. *Viviparus dissimilis* (Müller), from Madras, India.

Fig. 3. *Viviparus quadratus* (Benson), from Canton, China.

Fig. 4. *Viviparus quadratus* (Benson) var. *aeruginosus* (Reeve), from Canton, China. The specimen figured is a half-grown shell.

Fig. 5. *Viviparus sclateri* (Frauenfeld), from Lake Biwa, Japan.

Fig. 6. *Viviparus boettgeri* (Kobelt), from Hainan Island, China Sea.

Fig. 7. *Heterogen longispira* (Smith), from Lake Biwa, Japan. The specimen figured is only a young shell.

Figs. 8-10. *Cipangopaludina lecythis* (Benson), from Loktak Lake, Assam, India. The three figures illustrate the changes in the form and sculpture of the species during growth.

Fig. 11. *Dactylochlamys oxytropis* (Benson), from Loktak Lake, Assam, India.

Fig. 12. *Dactylochlamys iwakawae* (Pilsbry), from Nippon Island, Japan.

Fig. 13. *Dactylochlamys costatus* (Quoy & Gaimard), from Lake Tondanao, North Celebes.

Figs. 14, 15. *Dactylochlamys pagodula* (Bartsch), from Lake Lanao, Mindanao Island, Philippines. Only the last two whorls are figured to show the highly channelled ridges.

Fig. 16. *Dactylochlamys persculptus* (P. & F. Sarasin), from Lake Posso, Celebes.

Fig. 17. *Dactylochlamys mainitensis* (Bartsch), from Lake Mainit, Mindanao Island, Philippines.

Fig. 18. *Dactylochlamys partelloi* (Bartsch), from Lake Lanao, Mindanao Island, Philippines. Copied after Bartsch (1909).

Fig. 19. *Taia theobaldi* (Kobelt), from Southern Shan States, Burma.

Fig. 20. *Taia naticoides* (Theobald) var. *noetlingi* (Kobelt), from S. Shan States, Burma.

Figs. 21. 22. *Taia shanensis* (Kobelt), from Inlé Lake, Burma ; adult and embryonic shell.

Figs. 23, 24. *Taia intha* Annandale, from Inlé Lake, Burma ; adult and embryonic shell.

Figs. 25-29. *Margarya melanoides* (Nevill), from Lake Er-Hai (L. Tali), Yunnan, China. Adult and young shells of various stages illustrating the evolution of the form and sculpture in this species ; in fig. 26 the body-whorl of another shell showing the *Taia*-like scaly tubercles is represented.

Figs. 30, 31. *Rivularia auriculata* (Martens) var. *bicarinata* Kobelt, Siangtchin, Hunnan, China ; adult and young shell.

Fig. 32. *Mekongia moreleti* (Deshayes) var. *fruhstorferi* Kobelt, from Eastern Siam.

Fig. 33. *Viviparus constrictus* (Martens) var. *pagodella* Martens, from Lake Victoria Nyanza, East Africa. Copied after Martens (1897).

Fig. 34. *Viviparus constrictus* (Martens) var. *trochlearis* Martens, from Lake Victoria Nyanza, E. Africa. Copied after Martens (1897).

Fig. 35. *Viviparus costulatus* (Martens) var. *triliratus* Martens, from Lake Victoria Nyanza, E. Africa. Copied after Martens (1897).

Fig. 36. *Cleopatra exarata* (Martens), from the coast of old German East Africa. Copied after Kobelt (1909).

Fig. 37. *Cleopatra mweruensis* Smith, from Lake Mweru, Africa. Copied after Smith (1893).

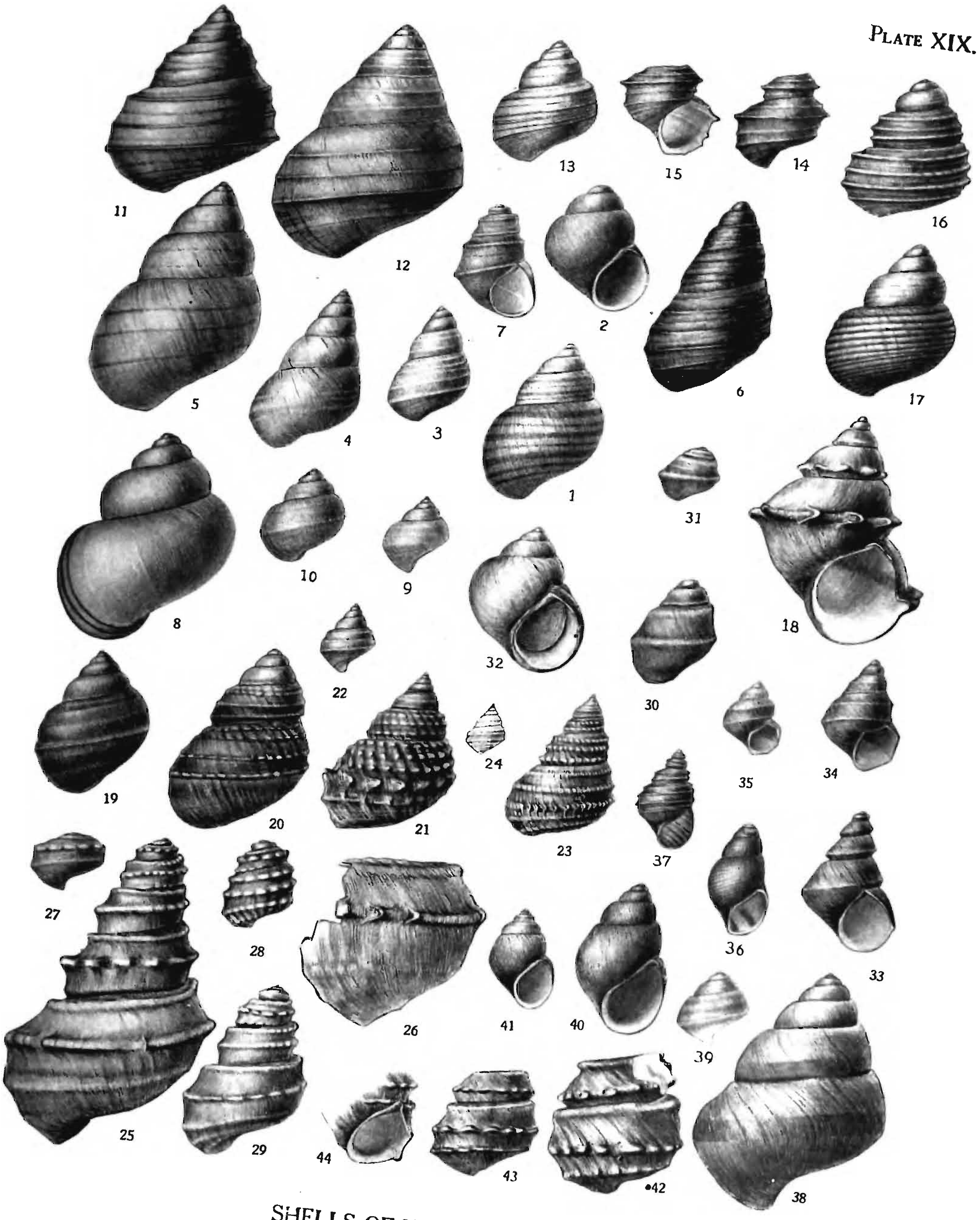
Figs. 38, 39. *Neothauma tanganyicense* (Smith), from Lake Tanganyika, E. Africa ; adult and embryonic shell.

Fig. 40. *Campeloma decisum* (Say), from Milwaukie River, U. S. A.

Fig. 41. *Lioplax subcarinata* (Say), Ohio River, Cincinnati, U. S. A.

Figs. 42-44. *Tulotoma magnifica* (Conrad), from Cossa River, Alabama, U. S. A. Figure 42 represents the last two whorls of an adult shell, and the other two figures the dorsal and ventral views of a younger shell.

PLATE XIX.



SHELLS OF VIVIPARIDAE.

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THE MANTLE AND THE SHELL OF THE VIVIPARIDAE.

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(Plates XX—XXIV.)

CONTENTS.

1. INTRODUCTION.

This paper is a continuation of the work of my late lamented chief, Dr. N. Annandale, on the problem of the shell sculpture in the family Viviparidae. He published two papers (1, 2)[1] on the subject, but his sudden death in April 1924 left the work unfinished. I was hoping to take up the elucidation of the problem from where he had left it earlier, but the pressure of other official duties did not allow of the work being started sooner. The collection of material from different parts of the world is also to some extent responsible for the delay. During the period of a combined leave spent in Europe, I devoted myself to the study of this interesting problem, and the results of my work are here presented.

In view of a number of closely connected questions being included in the paper, it would be useful to indicate the scope of the paper. Beginning with a review of the different opinions regarding the relation between the animal and the shell of the Gastropod Molluscs, the enquiry is limited to the mantle, which organ alone, at least in most forms, is responsible for the secretion of the shell. In this connection the macroscopic and the histological

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[1] The Arabic numerals in brackets refer to the literature cited at the end of the paper.

structure of the mantle margin of both adults and embryos of various members of the family is discussed in detail, and particular attention is devoted to special structures on the mantle margin which appear to be specifically responsible for the production of the sculpture. The question of the secretion of the various layers of the shell by specially modified regions of the mantle is discussed in detail, and a review of the literature for all families of molluscs is included. The later phases of the development of the shell-secreting area of the mantle of *Viviparus viviparus* (Linn.) have been investigated, and in view of the importance of the so-called shell-gland of the embryo and its relationship to the shell-secreting areas of the adult, a detailed survey of the literature on this structure in all classes of molluscs exclusive of the Cephalopoda, is given. An account of the minute structure of the shell of the different members of the family is included, and the question of the shell-sculpture is discussed. A separate summary of each part of the paper is given at the end of each part.

The work was mainly done in the Zoological Department of the University of Edinburgh, and I have great pleasure in acknowledging my obligation to Professor J. H. Ashworth under whose guidance the work was carried out. The constant interest, the valuable criticisms and the helpful suggestions of Professor Ashworth have been of the greatest value. I am indebted to Mr. G. C. Robson of the British Museum (Natural History), London, Dr. F. Haas of the Senckenberg Museum, Frankfurt a. Main, and Dr. L. F. de Beaufort and Dr. T. van Benthem-Jutting of the Zoological Museum, Amsterdam, for giving me facilities for examining the collections under their charge.

I have also to thank the Department of Education, Health and Lands of the Government of India for making a special grant in aid of the expenses in connection with this work.

2. MATERIAL AND METHODS.

The material of the Indian Viviparidae used in this work came mainly from the rich collections of the Zoological Survey of India, Indian Museum, Calcutta ; a few of the Chinese and Japanese species are also from the same source. The rest of the material from different parts of the world was received from the British Museum (Natural History), London ; Senckenberg Museum, Frankfurt a. Main ; Zoological Museum, Berlin ; Zoological Museum, Amsterdam ; Zoological Museum, Petrograd ; and the United States National Museum, Washington, U. S. A., and in this connection I am indebted to Mr. G. C. Robson, Dr. F. Haas, Dr. J. Thiele, Dr. T. van Benthem-Jutting, Mr. J. W. Lindholm and Dr. P. Bartsch for so kindly supplying me with the valuable material. Through the kind offices of Dr. Bryant Walker of Detroit, Michigan, U. S. A., I received from the University of Alabama Museum very valuable material of the peculiar American *Tulotoma magnifica* (Conrad) preserved in spirit. Dr. P. Dautzenberg of Paris was good enough to send me some interesting specimens of *Margarya.* Fresh material of the common European species, *Viviparus viviparus* (Linn.) and *V fasciatus* (Müll.), was obtained from near Manchester through Professor Ashworth's kind help.

I give below a list of the species which I have investigated from different parts of the world. In the case of the species marked with an asterisk, gravid females containing embryos were found in the collections, and this has enabled me to include notes on the condition of the embryonic mantle in the various species.

List of Species.

Europe—
*_Viviparus viviparus_ (Linn.), from near Manchester, England.
*_Viviparus fasciatus_ (Müll.), from near Manchester, England.
*_Viviparus pyramidalis_ (Jan.) Rossmässl., from Wörther Lake, Carinthia, Austria.
Viviparus duboisiana (Mousson), from Russia.

Africa—
*_Viviparus unicolor_ (Olivier), from Egypt.
*_Viviparus sambesiensis_ Sturany, from the Victoria Falls.
*_Neothauma tanganyicense_ (Smith), from Lake Tanganyika.
Cleopatra bulimoides (Olivier), from near Khartoum.
Cleopatra multilirata Ancey, from Akotra Lake, Madagascar.
Cleopatra trabonjiensis Smith, from Majunga, Madagascar.

Asia—
India—
*_Viviparus bengalensis_ (Lam.), from near Calcutta.
*_Viviparus dissimilis_ (Müll.), from near Madras.
*_Cipangopaludina lecythis_ (Benson), from Loktak Lake, Manipur.
*_Dactylochlamys oxytropis_ (Benson), from Loktak Lake, Manipur.

Burma—
*_Taia shanensis_ (Kobelt), from Inlé Lake, S. Shan States.
*_Taia naticoides_ (Theobald) var. _intermedia_ Annan., from the S. Shan States.
*_Taia intha_ Annan., from Inlé Lake, S. Shan States.
Taia elittoralis Annan., from Inlé Lake, S. Shan States.
*_Taia crassicallosa_ Annan. and Rao, from Yawnghwe.

Yunnan—
Margarya melanoides Nevill, from Lake Er-Hai (Lake Tali).

China—
*_Viviparus quadratus_ (Benson), from Foochow.
*_Viviparus delavayana_ (Heude), from Saifu, Szechuan.
*_Cipangopaludina chinensis_ (Gray), from Saifu, Szechuan, and its varieties _fluminalis_ (Heude) from Tsinanfu, and _diminuta_ (Heude), from Pingshiung.

Japan—
*_Viviparus sclateri_ (Frauenfeld), from Lake Biwa.
Cipangopaludina malleata (Reeve), from near Otsu.

Amur Basin, Asiatic Russia—
*_Cipangopaludina praerosa_ (Gerst.), Amur River.
Dactylochlamys ussuriensis (Gerst.), Lake Khanka.

Sumatra—
Viviparus sumatrensis (Dunker), from Kael, Boentsch.

Java—
*_Viviparus javanica_ (V. Busch), from Palimanan.

Celebes—
**Dactylochlamys costatus* (Quoy and Gaimard), from Minehassa.

New Guinea—
Viviparus laevigatus (Bavay), from Lake Yamoer.
Dactylochlamys tricostatus (Lesson), from Lake Sentani.

Philippine Islands—
**Dactylochlamys burroughiana* (Lea), from Luzon.
**Dactylochlamys lanaonis* (Bartsch) and vars. *iota* and *theta*, from Lake Lanao, Mindanao.
**Dactylochlamys pagodula* (Bartsch), from Lake Lanao, Mindanao.

North America—
Campeloma decisa (Say), from Potomac River, Maryland, U. S. A.
**Tulotoma magnifica* (Conrad), from Coosa River, Alabama, U. S. A.
Lioplax subcarinatus (Say), from Potomac River, Maryland, U. S. A.

The material received from various institutions consisted of specimens preserved in spirit, and was not specially preserved for histological work; in most cases, however, the preservation was found to be sufficiently good for general details. The Indian Museum material, except for the specimens of *V dissimilis* (Müll.), the species from the Loktak Lake and the extra-Indian species, was specially preserved for histological work. In the case of fresh material specimens were fixed in absolute alcohol, corrosive acetic solution with or without acetic, 5 per cent. formalin (neutralized), Zenker's fluid, Flemming's fluid weak and strong both with and without acetic, Hermann's fluid and Bouin's fixative.

Sections of the embryos were cut after double embedding in celloidin and paraffin according to the method described by me already.[1] For all other work the sections were prepared in the usual way after embedding in paraffin only. The sections of embryos were cut 3-4 μ thick, while the other sections ranged between 5-8 μ.

Only in exceptional cases was the material stained *in toto* before sectioning; the stains used being Grenacher's borax-carmine or Ehrlich's haematoxylin. In the case of sections stained on the slide Delafield's haematoxylin followed by eosin or Orange G. was usually employed. For all critical work and for tissues fixed in Osmic mixtures Heidenhain's iron haematoxylin and Dobell's iron haematin were used; the former of these gave the most satisfactory results. For embryological material Heidenhain's stain was found to be the most useful. For the differentiation of muscle fibres from connective tissue van Gieson's stain and its various modifications, and Mallory's stain were used. Specific stains like Methylene Blue, Mucicarmin, Thionin and Toluidin Blue were employed for differentiating the glandular areas. For the identification of calcareous particles, whether in the form of calcium carbonate or as calcium phosphate, I used Roehl's haematoxylin, purpurin, alizarin, Macallum's lead acetate and Cossa's silver nitrate method of micro-chemical reactions; full details of these methods will be found in Zill's paper (179). Of these Roehl's haematoxylin, purpurin and Cossa's silver nitrate stains were found to be useful, but really critical reactions were seldom obtained. The tissues used for these micro-chemical tests were fixed

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[1] Prashad, B.—*Ind. Journ. Med. Research,* V, p. 611 (1918).

in acid free solutions like neutralized formalin 5 per cent, corrosive sublimate solution without acetic, or absolute alcohol.

For the structure of the shells broken pieces of shell were examined, and in addition thin sections of shells were prepared by grinding on stones of various grades; the method employed being the one recommended by Flössner (51). Another method, which was found to be very helpful, was worked out in the Geological Institute of the University of Frankfurt a. Main, with the help of Herr A. Schwarz. Small pieces of shells varying in size from ¼-½ an inch in length and about a quarter of an inch in height were cut in the right plane by means of a steel saw, and embedded in Kollolith on a slide. The surface of the shell was carefully polished after all scratches and uneven areas had been smoothened by grinding, and the preparations were afterwards left in very dilute acetic acid (5 drops to 200cc.) for etching the surface. The etching was controlled under the microscope. Such preparations could, of course, only be examined by reflected light or very low powers of the microscope, but were found to be very useful for interpreting the structures.

For the drawings of my paper I am indebted to Frau Dr. Winter of Frankfurt, who prepared the same under my guidance with great skill and infinite patience. The microphotographs were mostly taken at Wetzlar, Germany, in the beautifully equipped microphotographic section of the well known optical works of Messrs. E. Leitz, and it is my very pleasant duty to record my great indebtedness to Dr. E. Leitz for unreservedly placing the resources of his works at my disposal during the time I was working there.

3. THE SHELL AND THE ANIMAL.

Stempell (162) has published a detailed critical summary of the literature dealing with the different views regarding the formation and the growth of the shells of molluscs, and it is not necessary, therefore, to repeat the same here. It may, however, be noted that recent work on the structure, formation and regeneration of shells has fully confirmed Réaumur's view (137, 138) of the growth of shells by *apposition*, and there is no justification for believing that growth of any shells whatsoever takes place by *intussusception*. The shells are the secretion products of the animals they enclose, and have no separate existence of their own. They can not increase in size except by the addition of fresh material secreted by the animal.

The animals and shells of molluscs were from quite early times supposed to be closely connected, but it was not till the announcement of Réaumur's experiments of 1709 (137) that the exact relation between the two was understood. Réaumur described the organic layer of the shell, corresponding to what is now known as the periostracum, as a secretion of the animal, and considered it as a mould on the inner surface of which the calcareous secretions were deposited in layers.

Bournon (13), as a result of his investigation of the shell structure of various Gastropods, stated that the shell layers were probably formed by crystallization of shelly secretions of the animal deposited in succession on the inner surface of the organic periostracum.

Gray (64), referring to the opinion of the earlier authors on the secretion of the shell by the mantle of the animals, remarked that the operculum and the shell of *Cymbia, Oliva. Ancellaria* and many other genera of Marine Gastropods is secreted by the upper surface of the foot. Philippi (130), Tullberg (169) and Cooke (30) also refer to the role of the foot of Gastropods in the formation of the shell, but this is apparently based on the remarks of Gray referred to above, and has not been confirmed by any recent work. It may, therefore, be safely concluded that the shell of the Gastropods is a secretion of the mantle, and that the increase in size and thickness can only take place by the deposition of fresh material on the already existing shell. I do not include in this general statement the secondary changes which are brought about in the shells of the Cypraeidae, the Auriculidae and other forms by the dissolving away of some of the earlier whorls.

Picard (131) appears to have been the first to differentiate definitely between the increase in size (en l'élongation) and the thickness (en épaisseur) of the shell. He distinguished the regions which secrete the shell in the two cases, and noted that the thickness of the shell resulted from the deposition of new layers by the epithelium of the mantle inside the already formed shell.

Bowerbank (18) considered the shell to be highly organised and vascular in structure, and added that it retained a vascular connection with the animal throughout life. With reference to the cellular nature of the shell he did not specify the area which secretes the membrane in which later the cytoblasts of the shell were supposed to develop.

Carpenter (25) could not find any vascular connection of the type described by Bowerbank, but agreed with the latter author regarding the cellular nature of the shell. He made no reference to the parts of the animal by which the shell is secreted.

In the mantle margin of the common garden-snail of Europe Meckel (114) described a very large number of small glands opening by minute pores. These glands, according to the author, are flask-shaped, and their slimy secretion contains large quantities of calcareous material for the formation and repair of the shell. He described the mantle epithelium as consisting of columnar cells in which also he found the calcareous granules.

Gegenbaur (61) described the process of shell formation in the mantle furrow of the embryos of some Pulmonates. He did not mention any glands in the furrow and it may be assumed that he believed the secretion of the shell to be confined to the epithelium lining the furrow.

Semper (152) considered the share of the mantle epithelium in the secretion of the organic part of the shell of Gastropods, and more particularly in the Pulmonates, as quite insignificant. In the thickened mantle margin he found large numbers of two kinds of mucous glands to which he assigned the secretion of the cuticular layer of the shell. He considered the epithelium on the surface of the thickened mantle margin to be too insignificant to have any share in the secretion of the organic part of the shell. The calcareous material of the shell was believed to be secreted through the epithelial cells of the mantle, apparently from the subepithelial connective tissue.

Leydig (103) referred to his earlier observations (102) on the shell in the embryos of *Viviparus*, where he suggested its secretion by the skin epithelium, (Hautepithel, apparently implying thereby the mantle epithelium). He was of the opinion that the calcareous part of the shell is deposited as polygonal particles on the inner surface of the cuticular shell. He considered the mantle margin as the area mainly responsible for the growth of the shell owing to the brownish pigment in the epithelial cells of this region being confined to zones which correspond exactly to the pigment bands of the shell. He agreed with Semper that the calcareous glands in the mantle do not play any important part in the formation of the shell, but that the calcareous fluid for the formation of the shells oozes (schwitze) out through the epithelial cells.[1]

Nalepa (124) described intercellular spaces between the epithelial cells of the mantle of Helicidae, through which he believed that the calcareous fluid from the blood-spaces in the connective tissue was directly conveyed to the exterior. These spaces were definitely denied by Moynier de Villepoix (121), while Burkhardt (22), who found some spaces particularly between the epithelial cells of the visceral mass, considered them as secondary modifications of no particular significance.

Tullberg (169) figured and described a mass of flask-shaped unicellular glands in the mantle margin of *Buccinum undatum*, but was doubtful as to their function. He suggested that they probably secreted the periostracum, but, in view of the secretion of the rest of the shell by the general mantle epithelium, he was doubtful that special glands should have been differentiated for the secretion of the periostracum. Dakin (32) confirmed the presence of the glandular mass in the mantle margin of the whelk, but made no mention of any pallial groove in his account. Owing to the absence of the glandular mass in the region of the mantle below the visceral mass, where no periostracum is formed, Dakin suggested that this area probably, as supposed by Tullberg, secreted the periostracum.

Longe and Mer (107), in land-snails and especially in *Helix*, found a peculiar modification of the anterior margin of the mantle in connection with shell secretion. They described an " appareil cutogène " consisting of a groove (sillon palléal) running parellel to the mantle margin, and a band of goblet-shaped epithelial cells (organe épithélial) behind the groove. At the bottom of the groove they found a large number of gland cells, which were supposed to secrete mucus in the form of conchiolin, while the goblet cells of the epithelial organ contained granules soluble in caustic potash but not in acids. The secretions of both these areas were supposed to form the periostracum of the shell. The deeper shell layers were believed to be secreted by the general surface of the mantle. The mantle margins show this modified structure till the snail is full-grown, when the goblet-shaped cells of the epithelial organ and the glands at the base of the groove atrophy; the groove itself, however, persists throughout life.

Nalepa (123) referred to the pallial groove having been observed by the earlier workers and described the structure of the mantle margin of *Helix arbustorum*. He found the band of goblet-shaped cells behind the groove, and, according to him, the cells are fully developed only during the period of growth. Like Longe and Mer he was of opinion that the cuticle of the shell is secreted by the cells of this band and the gland cells of the mantle furrow. The epithelium of the furrow, according to Nalepa, does not differ from that of the rest of the surface of the mantle. He added that the epithelium behind the band of goblet-shaped cells is generally absent or consists only of very young cells, and stated that this is probably connected with the secretion of calcareous substance by the connective tissue cells lying below it.

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[1] Various views have been held by different authors regarding the sub-epithelial mucous, calcareous and pigment glands of the Gastropods, and detailed accounts of these will be found in the recent papers of Herfs72) and Zill (179).

Moynier de Villepoix (120, 121) in his monumental works laid the foundation of our knowledge of the mantle margin and its relation to the secretion of the various shell layers. In the mantle margin of *Helix* he described a deep furrow (" gouttière palléale " corresponding to Longe and Mer's " sillon palléal ") to which and the glands at the bottom of the furrow he attributed the secretion of the periostracum. Behind the furrow he distinguished the pallial band (" bandelette *or* glande palléale " corresponding to the " organe épithélial " of Longe & Mer) consisting of flask-shaped gland cells which secrete the outer calcareous layers of the shell. To the general epithelium of the mantle lying behind the pallial band was, as by the earlier workers, assigned the secretion of the internal layers of the shell and the pigment for the shell. Biedermann (6), as a result of his studies on the structure of the shells of various Gastropods and the mantle of *Helix,* fully confirmed the work of Moynier de Villepoix. He concluded that the shells are formed by secretions of the epithelial cells of the mantle and probably also in part by the secretion of glands. The various layers of the shell differ in their structure and disposition from one another, and correspond to definite areas of the mantle by which they are secreted.

Meisenheimer (117) simply follows Moynier de Villepoix and Biedermann in his account of the shell secretion in *Helix.*

Burkhardt (22) investigated the structure of the mantle margin in *Helix pomatia* and came to the same conclusions as Moynier de Villepoix. Matthes (112) found the structure of the mantle margin of *Helix pisana* to be similar to that of *H. pomatia.*

Thiele (167, II) studied the shell of various molluscs in connection with the soft parts, and distinguished the three shell layers in it as periostracum, ostracum and hypostracum. In *Patella* and *Haliotis,* the mantle of which he specially studied, he did not distinguish any special zones in the mantle margin, but found a well developed groove running parallel to the margin. He remarked that only the epidermis of the mantle margin appears to be a derivative of the original (ursprünglichen) epidermis, while the epithelium of the visceral mass, which secretes the hypostracum, consists of modified connective tissue cells. Regarding the secretion of the Gastropod shells he agreed with Semper's view referred to above. Davis and Fleure (34) in the case of *Patella vulgata* found a large number of subepithelial glands near the edge of the mantle, which they stated secrete the outer shell layers.

Thiele's work on *Haliotis* was confirmed and extended by Fleure (50), according to whom the epithelium of the mantle furrow secretes the outer layers of the shell, while the inner shell layers are secreted by the " Haftepithel " and the cells adjacent to it on the upper surface of the mantle.

Haller (66) made contradictory statements about the mantle margin in Docoglossa, and it is not possible to understand his account of the secretion of the shell by the outer surface of the mantle margin and to correlate it with the histological structure of the area as described by him. In *Lottia* and *Scuttelina* he described two types of glands in the mantle margin, of these the upper series is described as consisting of unicellular, flask-shaped glands, while the lower series is shown as a large mass of greatly elongated and convoluted glandular sacs. As Haller had not been able to distinguish the nuclei in the sacs, Thiele (167, III) and Simroth (159) doubt as to whether his account can be accepted as correct, and Thiele definitely considers the glands as unicellular.

Jacobi (79) described the mantle furrow in *Amphidromus.* He regarded the furrow and the glands lining it as the apparatus for the secretion of the mucus which is found on the soft exposed parts of the animal. After a general review of the literature he assigned the secretion of the shell to the mantle as a whole.

Linden (105), without going into details, noted that there is a differentiation of the epithelium in the different regions of the mantle which secrete the various layers of the shell.

Simroth (159) gave a useful summary of the work of earlier authors, but omitted much of the recent work. He concluded that the upper or the outer surface of the mantle secretes the periostracum and the ostracum, while the rest of the mantle and the visceral mass epithelium secrete the hypostracum. In view of the contradictory accounts of Tullberg and Moynier de Villepoix, he was of opinion that our knowledge of the conditions in the higher Gastropods was not sufficiently advanced for exact demarcation of the different areas which secrete the various shell layers.

Stempell (162), in his valuable review of the literature on the formation and growth of the shell, paid little attention to the differentiation of the various areas in the mantle for the secretion of the different layers of the Gastropod shell.

Haeckel (65) could not distinguish any separate regions for the secretion of the various shell layers in *Chilina,* but found two kinds of glands evenly distributed in the mantle epithelium and was of opinion that these probably secreted the shell. In *Crucibellum* Scheidig (147) did not find any separate zones, but believed that the general epithelium of the mantle secretes the patelliform shell. Kleinstuber (85), as a result of his observations on *Trochita, Calyptraea* and *Janacus,* agreed with Scheidig and stated that in all these there is no differentiation of the mantle epithelium or of the glands for the secretion of the various shell layers.

Schumann (151) in *Gadinia,* Beck (5) in *Buliminus,* Küttler (91) in *Oliva,* Eckhardt (41) in *Vitrina,* Frank (57) in Trochidae, Wille (174) in *Stenogyra,* Weber (172) in *Cyclophorus* and Herfs (71) in *Cyclostoma* and *Amphipeplea* described the modification and demarcation of the different areas of the mantle margin for the secretion of the various layers of the shell corresponding to those in the Helicidae noted above. Bregenzer (19) did not describe the mantle margin of *Bythinella dunkeri* in detail, but from his figure of a transverse section of the mantle margin of this mollusc it is clear that the modifications of the mantle margin in this species also are similar.

Zill (179) stated that the subepithelial calcareous glands of the mantle have no share either in the formation or in the regeneration of the shell, but that both these functions are performed by the mantle furrow and the epithelium of the visceral mass. He does not mention the pallial band of unicellular glands situated just behind the mantle furrow.

A few observations on the much debated question of the origin of the unicellular flask-shaped gland cells may also be included here. Flemming (46) considered the cells to be derived from the connective tissue cells, but later (49) was of opinion that they are only modified epithelial cells. Simroth (156), Hoyer (78), Jacobi (79) and Plate (132) derive them from connective tissue cells. Leydig (103) considered the pigment and calcareous gland cells to be subepithelial in origin, while the other gland cells were believed to be modified epithelial cells. Boll (11), Techow (165, 166), Burkhardt (22) and Herfs (71, 72), on the other hand, consider them all to be modified epithelial cells.

From the above review of the literature it is clear that the mantle is the only structure that, with our present knowledge of the anatomy and histology of the Gastropods, can be definitely considered as responsible for the secretion of the shell.

My own observations are in agreement with this view; I have not been able to trace any connection between the shell and any other organ in the Viviparidae, and the present work is, therefore, limited to the structure of the mantle margin in various members of the family. The general epithelial covering of the mantle and the visceral mass which probably secretes the innermost layers of the shell is only casually considered here.

4. THE MANTLE OF THE VIVIPARIDAE.

I. *Previous accounts of the structure of the Mantle Margin.*

In the historical works of Swammerdam[1] (164) and Lister (106) there is no reference to the structure of the mantle or its relation to the secretion of the shell in *Viviparus.* Cuvier (31) generally described the mantle of *Viviparus,* but did not mention any processes on its margin, and made no remarks about the shell-gland area in it. Leydig (102), in his monograph on the anatomy and embryology of *V viviparus* (Linn.), did not devote much attention to the mantle except to its condition in the embryo. In the adult the margin of the mantle, according to his account, is uniform (ganzrandig), and does not show any traces of the embryonic processes. He does not refer to any ridge or groove running parallel to the mantle margin, and did not distinguish the shell secreting glands. In the embryo, however, without understanding their true nature, he described the calciferous glands as " dann erkannte ich bei Embryonen hinter den drei fingerförmigen Forsätzen des Mantelrandes gelbliche, cylinderförmige Drüsenschläuche von 0, 05‴ Länge und 0,008-0,0120‴ Breite, welche mit zelligen Inhalt angefült waren, am verdickten Mantelrand des erwachsenen Thieres aber konnte ich diese Drüsen nicht mehr auffinden, so dass es den Anschein hat, als ob sie zugleich mit den Mantelfortsätzen verschwänden." Speyer's thesis (160) is mainly anatomical, but the author included a general description of the mantle, and distinguished in it the cells which secrete the pigment and the shell; the structure of the cells is very imperfectly described and the exact limits of the shell gland were not distinguished. He did not distinguish the mantle ridge or the groove in the margin of the mantle, and in the description of the embryos made no reference to the processes on the mantle margin. Bouchard-Chantereaux (12) and Moquin-Tandon (118, 119) referred to the mantle of the adult *Viviparus* only casually, and, like the authors mentioned above, did not distinguish the mantle ridge or the groove; they also make no reference to the shell gland area of the mantle.

Moynier de Villepoix (122) in his criticism of Longe & Mer's paper (107) referred to the mantle of *Viviparus,* and remarked that the ridge and furrow along the mantle margin of *Helix,* which he had named " bandelette *or* glande palléale " and " gouttière palléale " res-

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[1] Swammerdam's work on *Viviparus* was completed about 1670, though *Biblia Naturae* was not published till 1737, 67 years after his death. The species of *Viviparus,* so far as can be judged from the figures in his work, and which are reversed in reproduction, was *V. fasciatus* (Müller).

pectively in his earlier papers (120, 121) are also similarly developed in the mantle margin of *V viviparus.*

Sewell (154) described the condition of the mantle in the adult *V bengalensis*, the common Indian Banded Pond-snail, and found that traces of the embryonic processes of the mantle can be recognised even in the fully developed adults. Of the processes, the one opposite the commencement of the gill is specially marked, while yellow pigment splashes on the mantle margin, according to the author, " possibly denote the former positions of the others that have since disappeared." The mantle ridge or the " bandelette palléale," he called the shell-gland, but did not, in view of the detailed paper by Annandale (1), which immediately followed his own, describe the structure of the mantle margin. Annandale in the paper cited published a detailed histological account of the margin of the mantle, and devoted a great deal of attention to the glands which secrete the shell and the mantle processes ; these latter are discussed separately (p. 264). His account is, unfortunately, incorrect in many details and I have thought it best to include here extracts from the author's summary rather than offer a summary of my own. On the dorsal surface of the margin of the mantle he designated the so-called " white-band " of earlier authors by the more appropriate name of " supramarginal ridge." This structure in other Gastropods, as remarked already, has been called " bandelette palléale " by French and " Drüsenpolster " by German authors. In front of and running parallel to the supramarginal ridge he found a groove which he labelled " supramarginal groove." This groove is the " sillon palléal " " gouttière palléale " or " Mantelfurche " of other Gastropods. In passing he noted the distribution of the ciliated and non-ciliated epithelium on the upper and the lower surfaces of the mantle, and described the musculature of the marginal region in detail. He included a few remarks about the connective tissue part of the mantle. He did not describe the cells or glands which secrete the nacreous layer but believed that this is " probably affected by unicellular glands scattered over the whole of the upper part of the mantle." Regarding the other glands which secrete the periostracum and the main calcareous part of the shell, he distinguished two types, (i) the periostracal, and (ii) the calciferous glands. The structure of the periostracal glands is summed up by him as follows :—" true multicellular glands of a vermiform shape, consisting of contorted tubules and opening to the surface by ducts with cellular walls. They lie some distance below the external surface in a transverse series along the extreme margin, for the most part beneath (*i.e.* distad of) the calciferous glands and with the main axis of each gland at right angles to the margin. Their ducts open into the supramarginal groove." I have carefully examined large series of sections of both embryos and adults of different species preserved in various fixatives during different periods of their activity, but have failed to find glands of the type described by Annandale. Further, no such glands are known in the mantle region of any other family of Gastropods. There are no multicellular glands in the region of the mantle-groove, and, so far as I can see, the author must have mistaken some parts of the calciferous glands for the structures he described. The calciferous glands, according to the author, are " much more bulky and differ considerably in structure. They occupy the supramarginal ridge and as a rule extend slightly beyond it both above and below, lying only a short distance beneath, or actually on, the surface and having no cellular ducts. Like the periostracal glands they form a transverse series, though the main axis of each gland is at right angles to the margin. Each gland is at first an elongate cylindrical tubule of gland cells forming a large number of closely and adpressed loops in the external margin of connective tissue. The cells are large and do not appear to have any intimate organic connection *inter se*. The lumen of the tubule has no special lining. At this stage ducts, perhaps of a temporary nature, can be detected in sections, but they form mere gaps in the epithelium, leading out from ill-defined spaces beneath it (fig. 2, Pl. iii). Later the gland cells become greatly enlarged and elongate and open direct on the external surface ; while the tubular character of the glands disappears." This description of the structure of the glands is not accurate ; the author apparently did not understand their true nature, *i.e.*, that they are composed of unicellular gland cells.

Herfs (71) published an account of the histological structure of the mantle of *V viviparus* about the same time as the paper by Annandale and apparently without having seen it. His object in studying these structures was to decide the origin of the gland cells of the mantle-ridge and he does not deal with the rest of the mantle in any detail. The cells when fully developed appear subepithelial, but Herfs from his study of sections of the young of *V viviparus* concluded that they are true epithelial cells which sink down into the subepithelial region, and added that in sections one can actually follow the gradual passage of the cells from the epithelial to the subepithelial region. Moynier de Villepoix had previously (121) arrived at the same conclusions for *Helix*. He further attempted to homologize the glandular areas in the mantle of *Viviparus* with those of *Helix* and other Gastropods. According to him it is hard to distinguish definitely the various areas which secrete the different layers of the shell, and he had no observations to offer on the subject. By analogy, however, he distinguished with Moynier de Villepoix (121) and Biedermann (6) the periostracal gland region in the mantle-groove and possibly also in the marginal zone of the mantle in front of it. For the calciferous gland he referred to the uncertainty expressed by Simroth (159) regarding the main glandular area in the Prosobranchs being homologous with that of forms like *Helix*, but still was of opinion that the gland-region in *V viviparus* is quite like the " bandelette palléale " or " Drüsenpolster " of *Helix aspersa*, and probably here also forms the region by which the main calcareous part of the shell is secreted. His description of the cells though not sufficiently detailed is accurate. He further observed that the gland cells in the white-band area of the mantle are only seen in young individuals and are confined to the regions in which the shell is being secreted. In the adults on the other hand there are no deep-seated glands and the tall epithelial cells lie entirely in level with the other cells of the epithelial band.

II. *The Processes of the Mantle Margin.*

Bouchard-Chantereaux (12) was the first author to observe the development of processes on the margin of the mantle of the fully formed embryos of *Viviparus viviparus*. He described the processes as " trois petites lobes triangulaires du bord du manteau, qui ont environ un millimètre de longueur, et sont toujours renversés sur la coquille ; ils sont situés à la place où seront plus tard les trois bandes noires qui ornent ce manteau, et dont une seule commence à se former, les deux autres n'étant encore annoncées que par des petites taches grisatres plus ou moins eloignées les unes des autres, mais rangées sur une meme ligne." He further noticed that with the growth of the embryos these processes, which form the hairs (poils) on the surface of the three carinae of the embryonic shell, became gradually reduced and finally disappeared. In some cases the processes persisted, and in the adult animals could be distinguished as minute papillae opposite the colour bands of the mantle.

Moquin-Tandon (118) further extended the work of Bouchard-Chantereaux, and correctly described the position of the processes on the right side of the mantle margin. He hinted at a possible connection between the colour bands of the mantle and those of the shell and also between the mantle processes and the ridges on the shell. He further remarked that in exotic species of the genus *Viviparus* with a multicarinate shell, the mantle processes do not differ very much in number or size from those in *V viviparus.* To the left of the three processes, noted above, he found on the margin seven small, irregular, teeth-like processes. In a later work Moquin-Tandon (119) gave a good summary of the previous work, but apparently in ignorance of the work of Leydig (102) to which he makes no reference, and added that the processes are found in the embryos of *V contectus* (Millet)= *V. fasciatus* (Müll.) ; he does not make any remarks on the condition in the embryos of *V viviparus.* He published a figure of the mantle margin, and stated that the processes were hollow, and had each an open channel in the mid-dorsal line.

Leydig (102), apparently independently of the works of the authors noted above, described the presence of three processes on the mantle margin of the fully formed embryo. According to him the embryo, while still in the uterus and enclosed in the egg membrane, develops along the right side of the mantle margin three wart-like processes ; these later elongate and become finger-shaped. The processes were further found to be contractile, and Leydig definitely connected the processes with the formation of the hairy ridges on the embryonic shell.

Erlanger (43), in his detailed account of the embryology of the same species, did not refer to the processes of the mantle in the body of the paper, but in fig. 9 (Pl. xxii), which represents a fairly advanced embryo, he showed four almost equally developed processes arising from the right side of the mantle margin ; these he called " fingerförmige Ausstülpungen des rechten Mantelrandes " or the finger-shaped evaginations of the right side of the mantle border. Lankester (100), Bütschli (23), Drummond (40), Tönniges (168) and Otto and Tönniges (126) do not refer to the processes in their account of the embryology of *V viviparus.*

Annandale (1), who in connection with the development of the sculpture of the shell studied the structure of the mantle in the Viviparidae, noted that the processes of the mantle are present in a large number of species of the family belonging to a number of distinct genera found in different parts of Asia. Regarding the common European species *V viviparus* and *V. fasciatus,* he does not say anything as to the condition in the former beyond referring to Leydig's figure, but in the case of *V. fasciatus* [1] he found that the processes are as well developed as they are in any of the Asiatic species. He gave an admirable account of the gross structure of the processes, and designated the three processes first noticed by Bouchard-Chantereaux, the " Primary Processes." He also found other similar processes developed in between and to the left of the primary processes, and called these " Secondary " and " Tertiary " processes. The outermost primary process on the left side he distinguished as the " Peripheral," while the other two were simply designated first and second. The peri-

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[1] This species is referred to as *V. contecta* (Millet) in Annandale's paper.

pheral process, which is usually the most prominent, was according to Annandale morphologically the youngest, but played the most important part in the orientation of the shell sculpture. He further remarked that the processes " are not mere projections of the margin but organs with a definite form, position and function." In the mid-dorsal line of the processes he described a groove—the marginal groove—which was found to be connected with the supramarginal groove of the mantle margin. In his second paper Annandale (2) published further details about the primary and secondary processes in highly sculptured species of the Burmese Viviparid, *Taia* Annandale. The details were based on a study of living material, and as a result he was able definitely to assign the function of moulding of " the chaetae which ornament the shell in spiral rows, at any rate in the younger stages of its growth " to the processes of the mantle. In full grown shells of the sculptured species of *Taia* he considered them to correspond in position to the three main spiral ridges, but owing to their small size he did not think that they had any real influence in moulding the actual ridges. As to the processes in the embryos of the Viviparidae as a whole he now qualified his view of their occurrence in all the Viviparidae with the remark " which in a few species are perhaps alone present."

III. *The Structure of the Mantle Margin of the Viviparidae.*

(*a*) *Terminology.*

To make the terminology employed clear and to avoid repetition, I will preface the account of the structure of the mantle margin with a description of the terms I have used. In the following account I have adopted most of the terms proposed by Annandale (1), but in some cases it has been necessary to introduce fresh names. In place of the expression Marginal Region of the Mantle or its abbreviation Marginal Region suggested by Annandale, I use Mantle Margin for the anterior free edge of the roof of the pallial cavity. The term Supramarginal Ridge (Pl. xx, fig. 1, *S. R.*) is used for the thickened, glandular, band-shaped area which runs parallel to and at a short distance from the free edge of the mantle in its upper or dorsal part; it is usually of a different colour from the rest of the mantle. As in other Gastropods, the mantle, in this family also, forms a more or less complete envelope round the anterior part of the animal. In most species the ventral portion of the mantle consists of only a narrow pigmented band. In this region the area corresponding to the supramarginal ridge is continuous with the free margin and there is no trace of the groove in front of it. Immediately in front of the supramarginal ridge is a shallow canal—the Supramarginal Groove of Annandale (Pl. xx, fig. 1, *S. G.*)—running all along the mantle margin. The mantle margin of the embryos, and in some cases of the adults also, is produced into wartlike or finger-shaped projections; these are designated as the Marginal Processes (Pl. xx, fig. 1, *M. P.*). As has been remarked already Annandale distinguished these processes as Primary, Secondary or Tertiary, according to the probable sequence of their origin, and the degree of their development. The primary processes from their positions on the right half of the mantle margin I distinguish as the Sutural, Median and Peripheral respectively. Of these the sutural is the outermost process on the right side and lies near the suture of the shell, the peripheral lies opposite the periphery of the bodywhorl of the shell and more or less marks the dividing line between the right and the left half of the upper part of the mantle, while the median lies between these two processes. The processes are channelled in the mid-dorsal line, and this shallow channel or groove, Annandale's Marginal Groove, I term the Groove of the Processes. It begins in the supramarginal groove posteriorly and anteriorly ends freely near the mantle margin.

(*b*) *Macroscopic Structure.*

In the following account I propose to deal with the structures in the various subgenera of the family separately, and shall also, where possible, include notes on the mantle margin of the embryos of different stages.

Viviparus Montfort.—In the description of the different forms of this heterogeneous subgenus I will give a detailed account of the mantle margin of the common Indian Banded Pond-Snail—*Viviparus bengalensis* (Lam.)—and indicate the main differences in the various groups of this subgenus.

In fairly young embryos of *V bengalensis* while still enclosed within the egg envelope, the mantle margin shows the three primary processes on the right side (Pl. xxi, fig. 1) traces of two or three secondary processes are also to be seen on the left side. The edge has a very narrow band of black pigment interrupted in the region of the processes ; it is shown as a black line in the figure. The supramarginal ridge, which is very prominent, is, at this stage, very broad and appears of a creamy colour. The supramarginal groove is very narrow and hard to distinguish ; its position is indicated in the drawing by a thin line. It is, however, easily to be seen where the grooves of the processes originate from it. The three dark pigmented bands on the region of the mantle lying posterior to the supramarginal ridge on the right side of the mantle of preserved specimens appear as if they alternate with the primary processes. This is, however, a result of fixation, for in the living specimens they are seen to lie opposite the processes and underneath the colour bands of the shells.

In a specimen the shell of which is about half an inch in length, the mantle margin in front of the supramarginal ridge is much broader than the ridge itself. It appears uniformly dark, and only the grooves of the processes in this region are seen as white lines. The supramarginal groove and the ridge (Pl. xxi, fig. 2) are both quite distinct, and the ridge is seen to be rather narrower laterally. In preserved specimens no distinct colour bands can be distinguished on the posterior region of the mantle, and the pigment appears to be uniformly suffused. Some specimens, however, show slight differences in the intensity of the pigment in different regions and the mantle appears banded. The three primary processes, of which the peripheral is usually the best developed at this stage, are quite prominent, and a number of secondary and tertiary processes are also to be seen.

In a full-grown specimen, as has been described by Annandale (1) and Sewell (154), the marginal processes are indicated by the wavy margin of the mantle and the different colouration of the areas corresponding to the processes. The supramarginal ridge and the groove are both distinct, but the former is not so distinct as it is in the earlier stages. Its development further varies with the degree of activity of the shell secreting areas and the state of preservation of the specimens, but I have not come across any specimen in which the two structures had entirely disappeared.

In *V sumatrensis* (Dunker) the mantle margin is similar to that of *V bengalensis*, except that in the adult the margin shows a number of distinct processes, and the supramarginal ridge and groove are more clearly indicated.

In *V viviparus* (Linn.) the embryos show the primary processes for a short period of their embryonic life, but they are then very minute (Pl. xxi, figs. 3, 4). This apparently is the reason of their having been overlooked by most of the recent workers on the embryology of this mollusc. In fully developed embryos traces of the processes are sometimes to be distinguished by the remains of the grooves of the processes, but the processes as such disappear before birth. In the adult mantle margin even the traces of the grooves are no longer visible, but otherwise the structure is similar to that of *V bengalensis* described above. In species of the group of *V fasciatus* (Müll.) and allied forms the primary processes are well developed and are distinctly finger-shaped. The mantle margin of an embryo of *V pyramidalis* (Jan.) Rossm. is figured (Pl. xxi, fig. 5), and the condition in *V fasciatus* and *V duboisiana* (Mousson) is very similar to it. The mantle margin of the adults of all these species is similar to that of *V viviparus,* but the supramarginal ridge and groove are better developed, and in some young specimens traces of the grooves of the processes also remain.

Viviparae Dissimiles Group.—The embryonic mantle margin of *V dissimilis* (Müll.) has been described by Annandale (1), who in living specimens found four secondary and a number of tertiary processes in addition to the three primary ones ; the situations of the processes were observed to correspond to the ridges on the embryonic shells. In a preserved very young embryo (Pl. xxi, fig. 13), I found the three primary processes on the right half of the mantle, and two secondary ones on the left half. In older specimens the condition resembled that described by Annandale, and remains of some of the processes were to be distinguished on the mantle margin of the adults as well (Pl. xxi, fig. 14). In *V quadratus* (Benson), *V delavayana* (Heude), *V sclateri* (Frauenfeld), *V javanica* (v. d. Busch) and *V. laevigatus* (Bavay) the structures are similar to those of *V dissimilis,* and the only difference to be noticed is in the degree of development of the processes. In strongly ridged species like *V quadratus* (Pl. xxi, fig. 15) and *V sclateri* the primary processes are all equally well developed and are distinctly finger-shaped. In *V delavayana* (Pl. xxi, fig. 12), which has many rather feeble and almost equally developed ridges, only the peripheral primary ridge is well developed, but a number of secondary ridges and the sutural and the median are indicated by their grooves.

Viviparae Unicolorae Group.—The two species of this group, *V unicolor* (Olivier) and *V sambesiensis* Sturany, which I have examined, are similar to *V dissimilis.* In a very young embryo of *V sambesiensis* (Pl. xxi, fig. 28) the three wart-like primary processes are developed on the right side. I, unfortunately, had no older embryos of this species, but embryos of *V unicolor* were almost identical with those of *V dissimilis* referred to above. In the adult of *V unicolor* also the condition is similar to that of *V dissimilis,* but in the case of *V sambesiensis* (Pl. xxi, fig. 29) which has a large number of feebly developed, low ridges on the shell, there are numerous subequal processes to be seen all along the margin.

Cipangopaludina Hannibal.—I have examined spirit material of a number of species of this subgenus from such widely separated area as India, China, Amur Basin and Japan, and find that the conditions are very uniform in all the species. In young embryos (Pl. xxi, figs. 9-11) the three primary processes are strongly developed. In older embryos, however, only the peripheral (Pl. xxi, fig. 8) remains as a distinct process, while the others, which are probably less functional, are indicated only by the remains of their grooves; traces of some secondary and tertiary processes are also to be seen on the left half of the margin. The supramarginal ridge and groove are, however, better developed than in *Viviparus*. The adult mantle margin is very similar to that of the fully grown embryos, but the peripheral process also becomes much less distinct and is apparently functionless.

Neothauma Smith.—In young embryos the mantle margin (Pl. xxi, fig. 30) shows the three primary processes. The median is rather feebly developed, and traces of some secondary processes are also to be distinguished. The adult mantle margin, in the specimen examined, did not show any processes, but remains of some as grooves were to be seen. Corresponding to the well developed sutural and peripheral ridges of the shell there are distinct longitudinal thickenings of the mantle such as are found in the case of *Dactylochlamys* described in detail below.

Dactylochlamys Rao.—The shells of this subgenus are highly specialised in that they are ornamented with spiral, continuous ridges. The ridges vary in the degree of their development, being only low ridges, or fairly raised structures channelled out throughout their extent, or they are quite solid. The mantle margin of the adults of the various members of this subgenus is correspondingly specialised, though probably it would be more correct to describe it as having retained its embryonic characteristics much more than is the case with any other members of the family.

In *D. oxytropis* (Benson), a species with well developed, hollow ridges on the shell, even the very young embryos (Pl. xxi, fig. 19) show the three finger-shaped primary processes, and traces of a number of secondary and probably tertiary processes, indicated by their grooves, on both the right and left half of the mantle margin. In addition to the processes there are three rather low ridges corresponding to the primary processes and running backward from them on the surface of the mantle; these apparently serve as the moulds for the hollow primary ridges of the shell. In the adult (Pl. xxi, fig. 20), the primary processes remain as definite processes, and some of the secondary and tertiary processes also persist, though from preserved material only it is not possible to lay down exactly the positions of those which remain as definite structures throughout the life of the animal. Of the longitudinal ridges on the surface of the mantle the sutural persists as a definite structure, but the others are only faintly indicated.

D. tricostatus (Lesson), *D. burroughiana* (Lea.), and *D. ussuriensis* (Gerstfeldt) are similar to *D. oxytropis*, and only differ in the degree to which the processes persist in the adult. All the three species are at a lower grade of evolution regarding the development of the ridges than *D. oxytropis*, and corresponding to the feebly developed ridges on the shells of these species the processes of the mantle margin and the ridges on the surface of the mantle are also less well developed.

In *D. costatus* (Quoy and Gaimard) the embryonic mantle margin (Pl. xxi, fig. 26) shows three well developed finger-shaped primary processes. The adult mantle margin (Pl. xxi fig. 27), corresponding to the many low, almost equally developed and not very channelled ridges of the shell, has a large number of subequal processes. In the poorly preserved material before me it is not possible to distinguish the primary processes except by their position. The edge is, as shown in the figure, distinctly furrowed, and this appears to correspond to the channels of the shell.

In *D. lanaonis* (Bartsch) var. *iota* (Bartsch) the structures are similar to those in *D. oxytropis,* but the processes, both in the embryos and in the adults, are not so well developed. In a young embryo of the typical form of *D. lanaonis,* which has a more ridged shell than that of var. *iota,* the embryonic mantle margin (Pl. xxi, fig. 21) shows three distinct primary processes (1-3), and continued backwards from these on the surface of the mantle are three ridge-like thickenings (*R*) corresponding to the hollow ridges of the shell. In var. *theta* (Bartsch) the processes and the ridges are both less strongly developed (Pl. xxi, fig. 23). The mantle margin of the typical form of *D. lanaonis* (Bartsch) shows in the case of the adult specimens (Pl. xxi, fig. 22) the highly contracted primary processes and remains of some other processes, while the ridges on the surface of the mantle, corresponding to the well developed ridges of the shell, are strongly marked. In the embryos and adults of *D. pagodula* (Bartsch) the conditions are similar (Pl. xxi, figs. 24, 25), except that the ridges are better developed, and the peripheral is the most prominent of all.

Margarya Nevill.—I have had only a portion of the mantle margin of an adult of *M. melanoides* Nevill in a poor state of preservation, and am, therefore, unable to describe in detail the condition in this subgenus. The arrangement of the supramarginal groove and ridges is similar to that in other members of the family, and traces of processes indicated as grooves could also be distinguished.

Taia Annandale.—The conditions in both living and preserved material of various species of this subgenus have been admirably described by Annandale (1, 2), and I have nothing to add to his account except to confirm it in all details.

Tulotoma Haldeman.—The mantle margin of the embryo (Pl. xxi, fig. 32) shows three primary and a number of secondary and tertiary processes. Corresponding to the strong development of the median ridge in this subgenus the median process is better developed, and the peripheral lies further to the left and below the periphery of the shell; this latter process is also less strongly developed. In the adult mantle margin (Pl. xxi, fig. 33) the processes are only feebly indicated in preserved specimens, but the ridges on the mantle surface running backwards from the processes are well developed; in the figure only the sutural and the median are shown.

In the poorly preserved material of the North American types *Campeloma* Rafinesque and *Lioplax* Troschel, I have not been able satisfactorily to make out the processes in the adults. Unfortunately none of the specimens before me are gravid, and I am, therefore, unable to add anything about the conditions during the embryonic life. The arrangements of the supramarginal ridge and groove in these forms are similar to those in other Viviparidae. Traces of grooves were made out in the adult mantle margin in some specimens, which would indicate that probably they also, like other members of the family, develop processes on the mantle margin during the embryonic stages.

Rivularia Heude.—I had no spirit material of this interesting subgenus, but a dry animal aken out of the shell and softened in spirit-glycerine showed the same arrangement of the supramarginal ridge and groove as other members of the family.

Cleopatra Troschel.—In the material at my disposal there are no gravid individuals, and my notes on this genus are very fragmentary. The structures in the mantle margin of the adult are arranged in the same way as in other members of the family. In some whole mounts and sections of the mantle margin grooves, probably corresponding to the processes of the margin, were distinguished.

Summary.—From the above account of the macroscopic structure of the mantle margin of both embryos and adults of different members of the family Viviparidae, it is clear that the arrangement of the shell secreting areas, the supramarginal ridge and groove, and the general surface of the mantle, is more or less uniform. It corresponds exactly to that of the various other Gastropods in which it has been investigated, and the only important difference lies in the development of special processes on the margin of the embryos, some of which also persist in the adults. The embryonic mantle margin develops three primary and a number of secondary and tertiary processes, which are channelled in the mid-dorsal line, and communicate through this groove with the supramarginal groove of the mantle margin. The processes correspond to the ridges or the sculpture on the shells of these snails, and either disappear entirely during or after the embryonic life, or persist in varying grades of development in different members of the family. In addition to the processes special thickened ridges are developed on the mantle surface of some of the sculptured forms, corresponding to the hollow ridges of the shells, and apparently serving as moulds for them.

(c) *Histological Structure.*

As this paper is mainly concerned with the shell-secreting areas of the animal the histological account will also be confined to the tissues which take part in the secretion and formation of the shell in the Viviparidae.

I have investigated the mantle margin of a large number of species of the family, and find that the general structure in all of them is uniform. The main difference is with reference to the areas occupied by the supramarginal ridge, the relative development of its glandular cells, and of the supramarginal groove. In the following pages I give a detailed account of the structures in *V viviparus* and *V. fasciatus,* and refer only to the differences observed in other forms.

It may also be noted that in spite of the very large numbers of specimens of different species of all ages which I have examined macroscopically and by sections, I did not come across any individuals in which the supramarginal ridge had become fully degenerate, and resembled the condition mentioned by Herfs (71) for *V viviparus* or as has been described by Moynier de Villepoix (121), Burckhardt (22) and other authors for *Helix.* This may be due to the animal and the shell not having reached the stage of maximum growth, and I believe that in Viviparidae, at least, this stage is not reached till very late in life. Animals of *V sclateri* (Frauenfeld) for example, the shells of which were 48 mm. in length, still had a distinct supramarginal ridge, and the cells constituting it were as clearly differentiated as they are in the individual in which the shell is still to be secreted.

The structures as they are seen in the embryos taken out of the uterus of the gravid females will be described first and then as they are in the adults.

Supramarginal Groove.—In a young veliger even before the formation of the pallial cavity, the mantle fold develops a distinct groove on its dorsal surface behind the edge; this is the beginning of the supramarginal groove, and was given the name ' Schalenfalz " by Erlanger (43). As is seen in a vertical section of the embryonic mantle margin (Pl. xxiii, fig. 1), the groove is fairly deep and is lined by columnar epithelial cells. At this stage the groove is much more extensive than the supramarginal groove of the adult, and its cells gradually pass into those of the edge of the mantle on the one side and those of the supramarginal ridge on the other. In the younger stages the great extent of the area of the groove is correlated with the great activity in the formation of the periostracal shell. Later with the active development of the supramarginal ridge the area of the groove is encroached on and greatly reduced (Pl. xxii, figs. 1, 2). I am unable to state definitely whether any of the cells of the groove also are modified to form the ridge, but it appears as if they take part in its development. This would be quite in accordance with the facts when one remembers that there is no differentiation of the different areas in the early stages of the embryo, and that all the structures—the mantle, its margin, the supramarginal ridge and the groove—are differentiated from the everted embryonic shell-gland (*vide infra*, pp. 308, 309).

In the fully formed embryos the groove consists of a moderately deep channel (Pl. xx, fig. 2, *S. G.*), lined by rather narrow elongate columnar cells, in which the nucleus of the cells lies near the base of the cells. The cells pass gradually into the elongate cells of the supramarginal ridge on the inner side and the less elongate ones of the margin on the outer. The conditions are similar in the embryos of *V. fasciatus* (Pl. xx, fig. 6), *D. oxytropis* (Pl. xx, fig. 9), *Tulotoma magnifica* (Pl. xx, fig. 16), *Taia*, *Cipangopaludina* and other forms. In the adult the groove is much shallower, and varies in depth and in the depth of its constituent cells with the stage of activity of the cells. In individuals in a more or less active state of secretion, the cells (Pl. xx, fig. 3, *G. C.*) are elongated, being as much as 90μ in length, and the lower inner ends of the cells are slightly swollen. The nucleus is ovoid, and in a number of cells in which it was measured, it was $13\mu \times 5\mu$. There is a large nucleolus and a number of small chromatin granules irregularly distributed in the nuclear substance. The nucleus usually lies near the base of the cells, but in some of the younger unmodified cells which do not reach the basement membrane, it appears to lie about the middle of the layer. The protoplasmic contents seen in sections are reticulate and contain large numbers of minute granules. There are no pigment granules in any of those cells. The cells of the groove, whether along its outer or inner edge, are not ciliated, as was stated by Annandale (1); the region of ciliated cells, marked *C. E.* in the drawings on Plate xx, begins along the outer margin of the groove. In a specimen of *V. fasciatus* the cells of the groove (Pl. xx, fig. 7) were not so columnar, and resembled those of the mantle surface. The same was the case with *Tulotoma magnifica* (Pl. xx, fig. 17), but the material of this species was not sufficiently well preserved for critical work; in the embryonic mantle of this species the cells are more elongate (Pl. xx, fig. 16). In *V delavayana* (Pl. xx, fig. 8, Pl. xxiii, fig. 3), *Taia intha* (Pl. xx, fig. 14, Pl. xxiii, fig. 3), *Margarya melanoides* (Pl. xx, fig. 15, Pl. xxiii, fig. 6) and other forms the cells lining the groove are not very different from those in *V viviparus.*

The cells of the groove described above secrete the periostracum in the Viviparidae, and there are no other periostracal glands of the type described by Annandale (1).

Marginal Processes.—In embryos of *V. fasciatus*, as seen in the microphotographs (Pl. xxii, figs. 1, 2, *G. M. P.*), and as was confirmed by examination of various series of sections, the processes are projections of the mantle margin, and their grooves are only extensions of the supramarginal groove. The cells lining the grooves are intermediate in character between those of the supramarginal groove and the free edge of the mantle. They are narrower and not so deep as the cells of the groove, their nucleus is comparatively smaller and more rounded, while the protoplasm is not so rich in granules. None of them, like the cells of the supramarginal groove, are ciliated. They probably secrete mucus, but in view of the scarcity of granules in them, I am of opinion that the cells of the grooves do not take any part in the formation of the periostracum of the shells. In half-grown individuals of *V. bengalensis*, in which the marginal processes were still present, it was found that in sections parallel to the mantle margin (Pl. xx, fig. 4) the grooves of the processes differ in depth according as they belong to the primary, secondary or tertiary series of processes. The grooves are lined by epithelial cells, which are columnar but less deep than those of the mantle, and differ in having no flask-shaped unicellular glands between them. The structure of the processes of various members of *Dactylochlamys* and other forms, in which only the grooves of the processes are found in the adults, was found to be identical with that of *V bengalensis.*

Supramarginal Ridge.—In young embryos of *V viviparus*, such as that figured on Pl. xx, fig. 2, it is clearly seen that the cells of the supramarginal ridge are only slightly modified epithelial cells. They increase gradually in size from the outer to the inner margin, and are the largest about the middle of the area, where they extend deepest into the connective tissue. Further from this area they again become smaller and gradually pass into the cells which form the outer covering of the mantle. In older embryos of *V fasciatus* (Pl. xx, fig. 6), the cells on the right are the least modified, while those on the left are much deeper and resemble the less modified cells of the adult. Most of them are arranged in separate bundles, and the cells are curved in their lower halves ; as a result different sections show different parts, but in continuous series of sections it is possible to follow the cells throughout their entire extent. A slightly more advanced stage is reproduced as figure 2 (Pl. xxii), the gland cells are much deeper, and owing to lack of space are pushed sideways into the connective tissue. The supramarginal ridge does not occupy as much space on the surface as it does in the earlier stages. The embryonic mantle of *Tulotoma magnifica* (Pl. xx, fig. 16) represents a less advanced stage than that of *V fasciatus* referred to above, while that of *D. oxytropis* (Pl. xx, fig. 9) is of about the same age.

From the above series it is clear that the gland cells of the supramarginal ridge are the highly modified cells of the epithelial covering of the mantle, and that in the earlier stages they differ only slightly from the cells which line the adjacent areas. Later they become greatly modified, but even in adults there is a continuous modification of the adjacent cells to replace those which degenerate. This is clearly shown in Herfs's figure (71), and in the adult of *V. fasciatus* (Pl. xxii, fig. 5), in which the area marked *X* does not represent the supramarginal groove but some of the cells of the supramarginal ridge which are not fully modified.

The general arrangement of the structures in the mantle margin of the adult is shown in fig. 4 (Pl. xxii). The supramarginal groove (*S. G.*) is a shallow canal a little way from the edge on the dorsal surface, while next to it is the area marked *X* in the figure, shown more highly magnified in fig. 5. The supramarginal ridge (*S. R.*) lies next to the groove as a raised area, and the glandular cells (*G. C.*) forming it are seen as the darker mass in the upper part of the section. Examined with a higher power of the microscope the dark mass is seen to be formed of cells, which are somewhat flask-shaped and are 270-280μ in length. They do not lie quite straight, but as was well expressed by Herfs (71) the principle of the economy of space results in the cells becoming crowded together and curving sideways in the subjacent connective tissue. The inner ends of the cells are somewhat swollen, but the outlines are often irregular. The lower swollen part of the cells contains a rounded to ovoidal nucleus which is about 15μ in maximum diameter. As is seen in the figures (Pl. xx, fig. 5 and Pl. xxii, figs. 6, 7) the nucleus has a prominent central nucleolus and a large number of chromatin granules scattered round it. The protoplasm is granular and somewhat vacuolated ; it stains deeply with plasmatic stains like eosin, and with specific mucin stains like Methylene Blue, Mucicarmine, Thionin and Toluidin Blue. There are no pigment granules in the cells, but masses of them are often found between the bases of the cells in the connective tissue. The groups of cells are sometimes separated into indefinite bundles by connective tissue and muscle fibres.

Near the bases of cells there are usually large masses of shining yellowish rounded globular structures (*G.C.* in figures on Plates xx, xxii), which are not stained with haematoxylin or plasma stains, but which, as was determined by micro-chemical reactions, are calcareous in nature. The calcareous particles, as is discussed further on (p. 291), consist of a double organic salt of calcium, and from the connective tissue probably pass into the gland cells of the supramarginal ridge. In the cells themselves they are represented by the minute granules mentioned above.

In various members of the family, as is to be seen from the figures on Plates xx, xxii and xxiii, the gland cells (*G.C.*) differ in length and thickness, but the general form is similar, and I have failed to distinguish any specific differences. The cell contents differ according to the stage of activity of the cells, and the form of the cells is correlated with it. An extensive area of undifferentiated cells is found on the two sides of the supramarginal ridge, and these cells apparently become modified and replace the cells which degenerate.

It is not possible to be definite about these gland cells of the supramarginal ridge, but I agree with the various authors mentioned already that they probably secrete the ostracal layers of the shell.

Outer Covering of the Mantle.—The general covering of the mantle on the dorsal surface consists of cylindrical or cubical cells. In the part next to the supramarginal ridge they are elongate, but gradually become shorter as the distance from the margin increases. As is to be seen in fig. 11 (Pl. xx), the cells of the region next to the supramarginal ridge are rather elongate and narrow ; they have an ovoidal nucleus without any distinct nucleolus but are rich in chromatin material, and the plasma is full of minute granules (Pl. xxiii, fig. 2, *M.E.*). There are no flask-shaped unicellular gland cells, Schulze's "Becherzellen," in between the epithelial cells, and none of them are ciliated. In the regions of the pigmented bands on the mantle, the epithelial cells contain large numbers of pigment granules confined to the upper third to half of the cells.

Though I have failed to distinguish calcareous granules in these cells, I have no doubt that they are responsible for the secretion of the hypostracal layers of the shell. They show the same reactions with Thionin, Toluidin Blue and Methylene Blue as the gland cells of the supramarginal ridge, and it may be assumed by analogy that they are similarly concerned in the secretion of some layers of the shell.

The cells which cover the margin of the mantle anterior to the supramarginal groove differ from the ones described above in being ciliated, and in having large numbers of unicellular gland cells between them. They apparently play no part in the secretion of the shell.

The structure of the spiral ridges on the surface of the mantle of some of the Viviparidae, corresponding to the ridges on the shell, is of no special interest. Their outer epithelial covering does not differ from that of the rest of the mantle, while the thickened area of the ridge is filled on the inside by specially well developed connective tissue and muscle fibres in these regions.

Pigment.—In earlier stages pigment is found in the mantle of the Viviparidae in definite cells, which, following Distaso,[1] I call chromatophores. These cells are ovoidal in outline, and have a large rounded nucleus (Pl. xx, fig. 13). The plasma of the cells contains numerous minute granules of a darker colour, varying in number and quantity in the different cells. I have not been able to trace their origin in the nucleus, as Distaso was able to demonstrate in the case of *Helix* and other Gastropods, but from the comparative poverty of chromatin material in the nuclei of chromatophores with comparatively large numbers of pigment granules (see, for example, the ones in Pl. xx, fig. 13 and Pl. xxiii, fig. 10, *P.C.*), I am inclined to agree with Distaso as to their nuclear derivation. As has been mentioned already, pigment granules are not found in the gland cells of the supramarginal ridge, but are present in large quantities in the epithelial cells of the upper surface of the mantle ; they are particularly numerous in the cells from the areas of the colour-bands. Apparently from the chromatophores the granules are passed out, and for a time lie freely in the connective tissue near the basal ends of the cells covering the upper surface of the mantle, and, as is shown in fig. 12 (Pl. xx), they eventually pass into the epithelial cells. In the cells they are later found to lie in the upper third to half of the cells.

It is not clear as to how the secretions are passed out from the different types of gland cells, but there are no definite ducts of the type suggested by Nalepa (124) and Annandale (1). The secretion of the cells must be poured out directly on the surface, but what the exact mechanism is I am unable to say.

Summary.—The mantle of the Viviparidae and the structures constituting it are all formed from the everted shell-gland of the embryo, and the various types of cells lining the supramarginal groove and the ridge result from the modification of the original undifferentiated epithelial covering of this structure. The cells which secrete the various layers of the shell are all more or less modified unicellular glands, and apparently pour out their secretion separately and directly to the outer surface of the cells. The connective tissue is not directly concerned in the secretion of the shell substance, but the calcareous

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[1] Distaso, A.—*Biol. Centralbl.* XXVIII, pp. 120-129 (1908). A detailed discussion of the production of pigment in the Gastropods is included in this paper.

material in the earlier stages is stored in it, and after undergoing various modifications is passed into the variously modified unicellular gland cells (*vide infra* pp. 290, 291). The pigment is originally found in special cells—chromatophores—in the connective tissue, and following Distaso, I believe that it is derived from the nuclear material of the cells themselves. From the chromatophores the pigment is passed into the connective tissue, and is later found in the cells which form the outer covering of the mantle.

5. HISTORICAL ACCOUNT OF THE STRUCTURE OF THE SHELL.

I. *General.*

The earliest work on the structure of the shell to be considered is that of Bournon (13). He regarded the shell as resulting from the crystallization of calcium carbonate and corresponding in shape with the surface of the animal over which it is formed. According to Bournon the shell consists of two parts, an outer organic covering and an inner calcareous region consisting of three zones of thin plates. The plates in turn are formed of rhombic crystals. The disposition of the plates in the outer zone is different from that in the two lower zones, and the appearance differs according as the plates are viewed from the side or the surface.

Gray (64) distinguished two kinds of shells, one in which the calcareous particles are crystallized and the other in which they are granular, and he considered these to correspond to Hatchett's (67) porcellaneous and nacreous types. In the crystalline shells he described three layers of calcareous matter consisting of thin lamellae arranged one over the other and formed of narrow, rhombic crystals. In the alternate lamellae the lines of cleavage of the crystals were observed to follow the same direction, while in succeeding lamellae they cross each other at right angles. The lamellae of the middle layer are described as running at right angles to the lines of growth of the shell, while those of the outer and inner layers cross those of the middle layer at right angles and run more or less in line with an axis drawn from the apex to the mouth of the shell. The granular shells in which the structure was found to be more or less uniform were stated to consist of numerous rather thin laminae with a number of thin plates of animal matter lying between the various plates. The shells in the various Molluscs may have either a crystalline or a granular structure, but in most of the crystalline shells the inner and anterior part of the shell is covered with a laminar granular layer.

Bowerbank (18) and Carpenter (25) considered the shell to be cellular in structure and to originate from a cellular basis. Bowerbank found that the calcareous parts of the shell consisted of three strata " uniform in the nature of their structure, but alternating in the mode of their disposition. Each stratum is formed of innumerable plates, composed of elongated, prismatic, cellular structure ; each plate consisting of a single series of cells parallel to each other." The plates are described as disposed alternately so that some of them are parallel to the lines of growth of the shell, while others are at right angles to them. In *Cypraea*, *Cassis*, *Ampullaria* and *Buliminus* the plates of the outer and inner strata were found to be arranged parallel to the lines of growth while those of the middle layer were at right angles to them ; in *Conus*, *Pyrula*, *Oliva* and *Voluta* the arrangement was the reverse. The prismatic cells of the various plates are described as intersecting those of the neighbouring plates at right angles. Carpenter fully agreed with Bowerbank regarding the minute structure of Gastropod shells.

Rose (142), as a result of his studies of sections of shells, came to the conclusion that the general arrangement of the layers is more or less similar in various Gastropods. He distinguished three calcareous layers in the shell, which consist of similar elements disposed in different directions. In each layer he distinguished thin, calcareous leaflets (Blättchen) which are arranged along their narrow margins and lie in the same directions in the outer and inner layers but are at right angles to those of the central layer. The leaflets, he stated, were formed of thin prisms arranged parallel to one another along their lateral surfaces. In two successive layers the directions of the prisms are at right angles to one another. He also published an ideal section illustrating his scheme of the structure of the Gastropod shell.

In the shells of *Neritina fluviatilis*, Claparède (27) designated the outer periostracum of the shell as the " Oberhaut," and described its cellular constitution in which, however, he was not able to discover any nuclei. The calcareous part of the shell he divided into two zones, an outer pigmented and an inner colourless. He did not describe the minute structure of the zones.

Leydig (103) distinguished three layers in the shell, (1) a homogeneous cuticle, (2) a calcareous crystalline layer, and (3) a homogeneous membranous calcareous layer. Longe & Mer (107) similarly distinguished three zones and added that the first calcareous pigmented zone consists of more or less vertical prisms, while the second zone is of many layers with the prisms of each layer arranged horizontally and at right angles to those of the upper zone.

Nathusius-Königsborn (125) concluded that the shell is an independent living structure which grows and develops without any relation to the animal. This part of his work has been severely criticised by Ehrenbaum (42) and Stempell (162), and need not be discussed here. His account of the structure of the Gastropod shell is useful and I include here an abstract of his summary. The structure of the shell is fibrillar, the fibrils being united to form plates which are arranged at right angles to the surface of the shell. The axes of the fibrils lie at angles of 45° to the shell surface, but in successive plates they lie in opposite directions and cross each other. The disposition of the plates is different, and those of the upper and lower zones lie at right angles to each other.

Tullberg (169) described the structure of the shell of *Buccinum* in detail and added a few comparative notes on the shells of *Strombus* and *Trochus*. He distinguished the organic cuticular covering of the shell or the periostracum, and in the calcareous part found three to four layers. In the various calcareous layers he described the arrangement of column-like structures and added that the disposition of the columns changes according as the sections of the shells are taken parallel to the margin of the aperture or at right angles to it. As to the constituents of the layers he agreed with Rose that they are formed of long, narrow plates or prisms arranged in rows. In two successive rows the prisms lie at right angles to each other. Dakin (32), following Tullberg, distinguished four calcareous layers under the periostracum. He stated that the shell may be divided into " two layers, an outer and an inner, the latter with three subsidiary strata built up in the same way, but as the geologists say, unconformable." The outer layer he distinguished as having more organic substance than the other layers and consisting of irregular crystals. He described the other layers as being built up of plates which present different views according to the planes in which they are cut in the sections.

Nalepa (123) described in the shell of *Zonites* an outer deep brown cuticle which is the only pigmented area in the shell, the calcareous layers underneath being quite colourless. In the calcareous layers he distinguished an outer prismatic layer and a lamellar zone consisting of many layers. He did not describe the finer constituents of the various layers.

Garnault (60) considered the shell of *Cyclostoma* to be composed of calcium carbonate and to consist of three calcareous zones, an external pigmented zone of many successive layers, a middle crystalline zone and the innermost stratified zone similar to the outermost part of the shell under the periostracum. The minute structure of the various layers was not described.

In *Amphidromus* Jacobi (79) described three zones in the calcareous part of the shell. The outer and the inner layers are similar and consist of oblique stripes crossing each other, while the middle layer is prismatic.

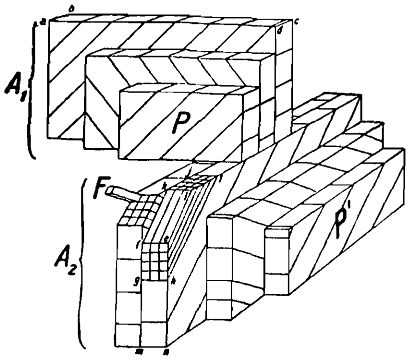
Thiele (167) discussed the structure of the shells of Chitons in detail and referred to the structures in other molluscs. For all classes of molluscs he distinguished in the shell three layers, an outer cuticular periostracum, the outer calcareous layer or ostracum and the inner calcareous layer or hypostracum. The periostracum he considered to be the basis for the crystallization of the calcareous part of the shell, and referred to the varying development of the other two calcareous layers in the different species. Simroth (159) accepted this division even though he did not agree with Thiele in regard to the areas of the animal which secrete the various layers. In most of the recent works authors have attempted to define the regions of the shell according to this division.

Linden (105) designated the three layers in the shell as cuticle, the prismatic calcareous layer and the porcellaneous calcareous layer or hypostracum, but did not give a detailed description.

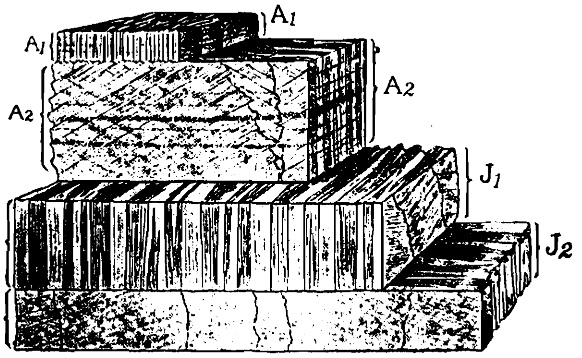
In *Trochus* Robert (140), following Thiele, distinguished the periostracum, the ostracum consisting of an outer pigmented porcellaneous zone and an inner lamellar mother-of-pearl zone, and the hypostracum. Frank (57), who investigated the shells of a number of Trochidae, found that the hypostracum is not always present, and that it is possible to distinguish three separate strata in the ostracum.

Biedermann (6) studied the structure of the shells of molluscs in great detail and to him we owe a really clear account of the highly complicated structure of the shell. He concluded that, leaving aside the periostracum, the shells of all Gastropods, whether land, freshwater or marine forms, have a "leaf-like (blätterige) or lamellar structure, which results from the shell in its entire thickness consisting of many systems of thin calcareous plates disposed one over the other like the leaves of a book ; in all layers the plates lie along their narrow edges and as a result their surfaces are always at right angles to the shell surface. In adjacent plates the long axes of the plates are at right angles to one another, and in no case is the surface of any plate flush with the surface of the shell. Each plate in its turn is formed of a very large number of thin calcareous threads whose axes cross at right angles in adjacent threads." In *Helix*, however, he had distinguished an outer calcareous zone with the appearance of a stalactite structure, but he believed that these stalactites in view of their appearance and their polarising properties are also constituted of fibres similar to those of the lamellae of the inner zone.

Flössner (51) published a very detailed and well illustrated account of the structure of the shell of *Helix pomatia*, which included instructive ideal sections of the scheme of formation of Gastropod shells in general.



Text-fig. 1.—Scheme to illustrate the principle of the formation of the structure of the Gastropod shell. A_1, A_2, two layers lying one above the other, and formed of plates P, P ; e, f, g, h, i, k, l, bundles formed of smaller bundles or fibrillae labelled F. After Flössner (51).



Text-fig. 2.—Ideal section of the shell from the bodywhorl of *Helix pomatia* reconstructed by Flössner (51). A_1, A_2, First and second outer layers, J_1, J_2, First and second inner layers.

He confirmed Biedermann's work, and showed that the so-called stalactite layer in the shell of *Helix* is constituted similarly to the inner lamellar layer, and that there is no difference whatsoever between the common snail and the marine mollusc regarding this zone of the shell. He divides the calcareous shell into two zones owing to the plates of the two strata running at right angles to each other. Each of the two zones is again divisible into two regions and the plates forming these also run at right angles to each other. The plates which constitute the layers in the various zones are formed in their turn of very fine fibrillae. He added that there are no true prismatic structures in any Gastropod shell and that the so-called prisms of the earlier authors are only the fibrillae united in bundles. The angle between the adjacent fibrillae is much less than a right angle.

Schumann (151) for the shells of *Gadinia*, Kleinstuber (85) for *Trochita* and *Janacus*, Beck (5) for *Buliminus*, Eckhardt (41) for *Vitrina* and Wille (174) for *Stenogyra* have described the three layers in the sense of Thiele, but their accounts are not of sufficient importance to be reviewed in detail.

Hammersten and Runnström (68) in their paper on the embryology of *Acanthochiton discrepans* describe in detail the development and structure of this mollusc and include interesting remarks about the homologies of the areas which secrete the various shell layers in the chitons with those of the Gastropods and Pelecypods.

II. *Shell Sculpture.*

Bournon (13), from his studies of the shell structure of *Strombus gigas* and *Cassis cornuta,* believed that the tubercles on the surface of these shells represent hollow protuberances of the embryonic shell produced by special processes of the animal over which the first shell was modelled. Later the processes of the animal were withdrawn and the hollow regions of the shell filled up by calcareous matter.

Bouchard-Chantereaux (12) and Moquin-Tandon (118, 119) definitely ascribed the secretion of the periostracal hairs on the embryonic shells of *Viviparus viviparus* to the three finger-like processes of the mantle margin on its right side. In view of the observations of these authors that with the disappearance of the processes the three carinae or the ridges of the shell also disappear, it may be inferred that the formation of the carinae was also considered by them as being dependent on the mantle processes. Leydig (102), independently of the work of Bouchard-Chantereaux, discovered and described the three mantle processes in *V. viviparus* and connected them with the secretion of the shell and in particular with the three rows of periostracal hairs on the embryonic shell. Leydig is not quite definite as to whether in the region of the hairs the shell is secreted separately or the basal parts of the hairs form the shell, but in view of his criticism of Siebold (155), who considered the processes to be the projections of the " epidermal covering " of the embryonic shell, and his comparing them to the hollow processes which are found on the outer lip of the mouth of shells of *Strombus*, *Pterocera* and *Murex*, it may be inferred that Leydig regarded the hairs as projections of the shell itself. Leydig further suggested that the nature of the shell sculpture is indicated in the form of the shell-secreting zone of the mantle margin, or in other words the protuberances on the outer surfaces of the shells result from corresponding processes of the mantle. This was also well expressed in a general way for shells of all molluscs by Johnston (82), according to whom " the shell of every class is moulded on the mantle of the animal," and further " whenever the edge of the mantle is furnished with any fold or protuberance, with processes or beards, corresponding processes on the shell declare the fact ; and these processes are cast in the form of cases for the protection of the fleshy part they represent." This was to some extent elaborated by Bronn (20), who considered the shell to be a more or less exact reproduction of the form and structure of the mantle, as a result of the later deposition of shell substance on the inside the uneven inner surface becomes smooth but the sculpture persists on the outside of the shell. As an elaboration of this view von Martens (111) stated that the transverse or vertical ridges on the surface of the shells are produced by periodic secretion of shell substance by the entire mantle margin, while the longitudinal ribs result from regular continuous secretion of definite points only. The sculpture may, purely physiologically, be pre-indicated (präformiert) in the mantle margin.

Gräfin von Linden (105) found that in *Trochus turbinatus, Murex trunculus* and to a limited extent in *Helix pomatia* the situation and arrangement of the mantle furrows corresponds exactly with the sculpture on the shells. She stated that it was possible to correlate all protuberances on the shells with increased secretion of calcareous substance at corresponding points on the upper surface of the mantle. In these areas, as a result of the ridges and furrows on the mantle surface, the shell-secreting areas are correspondingly increased, and Linden, who did not distinguish any definite shell-glands, added that the height of the mantle epithelium corresponds directly to the thickness of the shell over it. The tubercles or spines on the surface of the shell were also supposed by Linden to be due to correspondingly arranged areas of the mantle epithelium.

Simroth (157), from his studies of the Gastropods of the Plankton Expedition, concluded that the first foundation of the larval shell or the Prosopoconcha is a structureless, membranous covering of conchiolin, which is later strengthened by the deposit of shell-substance and develops hairs, ridges, etc. Hairs or chaetae, with which he also included comparatively feebly developed tubercles of conchiolin, are the first to appear. These result from indefinite irregularities of certain cells of the mantle margin which secrete the cuticle more actively than others. The tubercles at this stage are irregularly distributed over the surface of the shell. In the following stages the changes in the structure of the shell are due to mechanical influences (mechanischen Forderung) as a result of which the actively secreting cells become arranged at definite intervals, and the tubercles resulting from their secretions are also formed in definite rows or spirals. Larger secretions of closely grouped cells accumulate and are deposited on the surface of the shells as chaetae, while secretions from definite areas, which do not increase the thickness of the shell-membrane as a whole, form folded, wavy, longitudinal ridges. The regular wavy projections of the ridges form the bases for the protuberances, knobs and other processes which may be later developed. All these different types of protuberances on the surface of the shells are, according to Simroth, direct products of the mantle, but he does not distinguish any special areas which lead to their formation. In a later work Simroth (158) stated that the protuberances of the Gastropod shell are a result of mechanical influences, and are arranged in spirals at right angles to the mantle margin, while on the Pelecypod shell they are arranged parallel to the edge of the mantle ; in the latter case they are not due to mechanical influences but result from rhythmic secretions of the shell.

Stempell (162) did not deal in detail with the sculpture of the Gastropod shell. He, however, considered the formation of the sculpture as being connected with permanently formed structures of the mantle margin rather than with special processes which are developed afresh at regular intervals for the secretion of each tubercle.

From the results of experiments on the regeneration of the shell of Helicids by Techow (166) and a general summary of his work by Korschelt (87), it is clear that the regenerated shell in the regions away from the influence of the mantle margin is quite different in structure from the normal shell. The yellowish grey pigment of the normal shell is replaced, by a whitish grey pigment, and in place of the characteristic low ridges on the outer surface of the normal shell only a fine granulation is to be seen. The structure of the regenerated peristome or of other areas of the shell where the margin of the mantle can take part in its regeneration is the same as the normally secreted shell. It is clear from these observations that the margin of the mantle is responsible for the production of the shell sculpture.

Biedermann (7) was of opinion that the formation of the sculpture of the molluscan shells is probably connected with the structure of the mantle margin through the epithelium on its surface, which at least for a time is directly in contact with the outermost shell layers.

Annandale (1) studied the sculpture and its origin in the Viviparidae in great detail. He found that the sculpture of the shells is partly periostracal and partly impressed on the outer calcareous layers ; this latter he called " test-sculpture." In the embryonic shell both types of sculpture are present, but the periostracal sculpture is comparatively more predominant. The periostracal sculpture of the embryonic shell, he stated, is not secreted but moulded by the marginal processes of the mantle. The primary spiral rows of chaetae on the shell are thus formed by the three primary mantle processes, while other rows of chaetae result from secondary processes. The fine vertical lines of the shell are due to deposition of horny matter direct from the supra-marginal groove on the shell surface, and he considered each line to be " a separate act of secretion." The underlying test-sculpture corresponds with the periostracal which is considered to be a mould for it. The uninterrupted hollow ridges on the surfaces of the shells of certain species are explained as being due to " greatly hypertrophied marginal processes, the mere presence of which on the internal surface of the shell while the calcareous matter was soft is sufficient to account for their presence." The solid continuous ridges are similarly believed to result from slight hypertrophy of the calcareous glands in corresponding areas of the mantle. In the case of more highly sculptured types of shells " the projections are formed owing to periodical hypertrophy of the calciferous glands in the part of the mantle that lies immediately beneath the ridge on the shell, and moulded into shape by temporary lobes of the mantle edge." Annandale in a second paper (2) slightly modified his earlier views. The marginal processes, he stated, correspond in position to the spiral ridges of the shells but are " far too small to mould them," and only represent points " at which the products of secretion of the calciferous cells are liable to accumulate " In the highly sculptured *Taia intha* he observed in the living animals opposite the ridges of the shell " broad, shallow almost semicircular projections on the edge of the mantle with a marginal process on the tip of each. These projections are in no way differentiated in structure from the remainder of the mantle edge and are not at all thickened in their natural state ; they merely represent an increased area of secreting surface. In their natural condition and when in a state of active secretion, however, they become periodically convex above and concave below, thus forming a mould for the nodules or scales." The rows of tubercles are explained as being due to more or less rhythmic prolongations of the processes for the secretion of the projections. The smooth ridges of the shells result from continuous secretions of corresponding processes of the mantle throughout the period of growth, while in smooth shells the mantle edge is evenly convex and its secretions also regular all over. Annandale's views are essentially similar to those of Bournon, von Martens and Simroth, but in addition to attributing shell secretion to glands distributed over special areas he attached greater weight to the mechanical influence of specially developed regions of the mantle margin in moulding the different types of sculpture.

6. STRUCTURE OF THE SHELL OF THE VIVIPARIDAE.

The shell of the Viviparidae, as indeed of all Gastropods, is divisible into two constituent parts, an outer membranous organic periostracum and the thick inner calcareous layers, which are distinguished into two zones according to the arrangement of the plates constituting them and the different regions of the mantle by which they are secreted.

In this section of the paper I will deal with the structure of the shell as it is seen in sections ; the constitution of the shell, the reactions of the various substances forming it and the secretion of the different layers will be discussed separately below.

Periostracum.—The periostracum of the young embryonic shell soon after its secretion consists almost entirely of organic material, and is thin and membranous. Examined under a fairly high magnification (Pl. xxiii, fig. 7) it is seen to be formed of more or less parallel bands separated from one another by slightly rugose lines, which mark the areas of junctions of the bands and, apparently, correspond to the separate acts of secretion of the periostracal substance. Each band in its turn is seen to consist of a large number of elongated somewhat curved blocks arranged almost parallel to one another. The longer axes of the blocks run roughly at right angles to the long axes of the bands and to the margin of the aperture, while the bands themselves lie parallel to it. The periostracum of adult shells, examined after the removal of the calcareous layers, either by peeling or by the action of dilute acids, appears as a more or less homogeneous membrane, and does not show any traces of either the bands or the blocks mentioned above. In external surface view or seen as a transparent object, the periostracum exhibits faint marks of the lines of growth, while on the inner surface the impressions of the calcareous plates in the form of wavy lines arranged in a sort of network can be distinguished. In sections of the periostracum prepared after decalcification of the shell or even those prepared by grinding the shells, I have failed to distinguish any definite layers in it corresponding to those mentioned by Flössner (51) for the shells of *Helix.* The outer regions are somewhat darker and brownish, while the inner are lighter and more yellowish, but this is probably due to the outer surfaceb eing exposed to the action of light, water, etc., and does not seem to be correlated with the different times of the secretion. With age and gradual drying, as probably also through the action of the atmosphere and water in which the aquatic snails live, the periostracum becomes a more or less homogeneous membrane, and the various elements forming it at the time of its secretion become intimately fused with one another, while by stretching over the calcareous layers and by rubbing against other objects the lines of demarcation between the constituent elements disappear. Beyond the yellowish or brownish pigment, which is inherent in the periostracum, no other pigment is present in it. The ground colour of the shells is due to the colour of the periostracum, but the prominent colour bands of the shells of some of the members of the Viviparidae lie deeper in the calcareous layers, and are seen through the semi-transparent periostracum.

Calcareous Layers.—In the large number of species of the family, the shells of which I have investigated, I have been able to find only two main zones of the calcareous layers. The two layers correspond to the outer and inner layers of Biedermann (6) and Flössner (51). In the shells of the Viviparidae, however, I have failed to find any division of each of these two zones into an outer and inner region, distinguished by the arrangement of the plates constituting them, such as is so well shown in Flössner's figures and described in his excellent account of the shell of *Helix.* In the Viviparidae it may therefore be concluded that there are only two main zones in the calcareous part of the shell, and these, following Thiele (167), I distinguish as the ostracum and the hypostracum. The two zones are both formed of a large number of elements which, following Flössner, I call plates; they are arranged in various layers like the leaves of a book. These main plates of the ostracum and the hypostracum lie at right angles to each other, those of the ostracum running in the direction of the windings of the shell or at right angles to the margin of the aperture, while the hypostracal plates run parallel to the latter. The plates are formed of large numbers of bundles of fibrils, which lie at an angle to the main axes of the plates, and in adjacent bundles cross each other at right angles. The final elements in the structure of the shells, which can only be distinguished under high magnifications, are called the fibrils. They are arranged parallel to each other and unite to form the bundles ; they apparently represent the minute elements which are formed by the solidifying of the calcareous secretions of the gland cells of the supramarginal ridge and the general mantle epithelium.

Ostracum.— Seen in a surface view, the ostracum (Pl. xxiv, fig. 8, *O.*) appears like a meshwork, the plates constituting it appear alternately light and dark, and run more or less parallel to each other, and, as has been noted above, at right angles to the margin of the aperture. The various plates are not absolutely straight, and differ in thickness in various parts of their course. They often branch at the two ends, and their forked ends unite with those of the neighbouring plates. Lateral branches running in the direction of the long axes of the plates are also given off, and these connect the various plates in the same way as the branches at the ends. The alternating light and dark appearance of the plates under the microscope appears to be due to the plates lying at different levels, and is probably to be correlated with the different times at which the secretions have become set. The appearance resembles the figures of the outer layers of the shells of *Helix* in Biedermann's and Flössner's papers.

Hypostracum.—The apperance of the hypostracum in a surface view is quite different from that of the ostracum. The plates, as seen in the microphotograph (Pl. xxiv, fig. 9, *H*), are almost uniform in thickness, do not branch to any extent, and are arranged with great regularity. They run parallel to one another, and at right angles to those of the ostracal plates, and show the same light and dark arrangement. This appearance is very different from that of the inner layer of *Helix* figured by Flössner, but apparently the difference is one of degree rather than of the type of arrangement.

Having dealt in general with the structure of the shell of the Viviparidae, I will now describe the sections of those shells which exhibit special features. As a general point, however, it may be noted that the appearance of the layers of plates varies according to the direction in which the sections are prepared. In sections of the shell taken parallel to the margin of the aperture, *i.e.*, parallel to the lines of growth of the shell, the ostracal plates, which are cut at an angle, appear as a series of lines crossing one another almost at right angles, while each of the plates forms an acute angle with the surface of the shell. The hypostracal plates on the other hand are cut more or less parallel to their lateral margins, and in the sections appear as vertical columns arranged more or less parallel to one another and with their axes at right angles to the shell surface. In a section taken at right angles to the one described above, the axes, along which the plates are cut in the two zones, are reversed, and the section presents an almost reversed arrangement of the plates of the ostracum and the hypostracum to that in a section parallel to the margin. The condition described above is quite the opposite to that figured and described by Flössner for the shells of *Helix,* but as will be clear from the microphotographs accompanying this paper (Plates xxiii, xxiv) this is the arrangement seen in the shells of the Viviparidae, and I am unable to account for the discrepancy in the two accounts.

In the following description I will deal only with the structure of the shells as they are seen with low magnifications, not exceeding 200 diameters, as the finer elements or the fibrillae composing the plates are identical in all cases, and I have nothing to add about their structure in the family. In the account I use the words *margin* and *surface* for the margin of the aperture and the external surface of the shell respectively.

The structure of (1) the more or less smooth-shelled forms like *Viviparus* and *Cipangopaludina,* (2) the solid ridged species of *Viviparus* like *V boettgeri* Kobelt, (3) the hollow-ridged species of *Dactylochlamys,* (4) the semi-sculptured forms like *Neothauma* and *Rivularia* on the one hand and (5) the tuberculated types like *Taia, Margarya* and *Tulotoma* on the other, are all separately dealt with.

Smooth-shelled Forms.—Of this type I have investigated the shells of *Viviparus viviparus* (Linn.), *V bengalensis* (Lam.), *Cipangopaludina lecythis* (Benson) and *C. chinensis* (Gray). The structure is uniform in all the species, and it is only necessary to describe one case in detail. The periostracum during the preparation of the sections often peels off and is very seldom left intact. In a section of the shell of *C. lecythis* (Pl. xxiii, fig. 12 *P*) it is seen to consist of a rather narrow band of darkish colour overlying the calcareous zones.

The relative thickness of ostracum and hypostracum is usually maintained in the same species, but varies in different regions of the same shell so that in sections of shells taken in different directions the thickness appears to vary greatly.

The ostracal plates in a section parallel to the margin (Pl. xxiii, figs. 10, 12) are seen to run almost parallel to one another and at acute angles to the surface. The plates of the different layers, which lie one above the other, cross one another at right angles ; this is well seen in the middle of the field in the photograph of the shell of *C. lecythis* (Pl. xxiii, fig. 12). In some places the plates fork at their lower ends over the hypostracal plates, and become intertwined with the plates of the latter zone. In sections at right angles to the margin (Pl. xxiii, figs. 11, 13), the cut surfaces of the bundles constituting the plates are arranged in almost vertical pillars, which in photographs and under the microscope appear alternately light and dark. In the pillars which appear as dark bands, the bundles of fibrils run from above downwards and at acute angles to the surface. In the light bands, on the other hand, the bundles lie flat one over the other and almost parallel to the surface.

The plates of the hypostracum are arranged similarly to those of the ostracum, but the direction of their axes differs from that of the ostracal plates. As a result, in sections parallel to the margin (Pl. xxiii, figs. 10, 12), the cut ends of the plates appear as vertical pillars, while in sections at right angles to the margin they run (Pl. xxiii, figs. 11, 13) parallel to one another, and cross those of the adjacent plates at right angles. This is well seen in fig. 11, in which, as a result of unequal etching, series of plates of the various layers are seen to run in opposite directions and cross each other at right angles. The same figure also shows the parallel arrangement of the ostracal plates and the way in which their lower ends become intertwined between the forked ends of the hypostracal plates.

Solid ridged Forms.—From amongst species of this type I prepared sections of the shells of *V boettgeri* Kobelt ; the section parallel to the margin passed through a number of the ridges, while the one at right angles was taken through one of the grooves. The arrangement of the plates and the bundles in the plates of both the ostracum and the hypostracum in this species is similar to that of the smooth-shelled forms described above. The interesting point about this form is the almost straight surface of the shell below the ridge (Pl. xxiv, fig. 1), there being no trace of any groove on the inner surface corresponding to the outer ridge. The ostracum as compared to the hypostracum is very thick, but in the region of the groove (Pl. xxiv, fig. 2) the difference in the respective thickness of the two zones is not so marked.

Hollow-ridged Forms.—Of this type I have investigated the shells of *Dactylochlamys oxytropis* (Benson), *D. lanaonis* (Bartsch) and *D. persculptus* (P. & F. Sarasin) ; in the last species the shell is very thick, and appears to be covered with almost solid ridges. The sections parallel to the margin were all taken through the ridges while those at right angles were mostly through the intermediate areas. The periostracum in these forms is specially well developed, and is very closely applied to the ostracum lying below it. I have examined various preparations of it made from adult shells, but have not been able to distinguish any structure in them. In the region of the ridges on the shell the periostracum follows the outline of the ridge in the sections, and plays an important part in the formation of the ridges (*vide infra* pp. 293-297).

In sections of the shell parallel to the margin, the inner outline of the sections of the grooves is concave, but the concavity varies in different species. It is most marked in *D. oxytropis* (Pl. xxiii, fig. 14), while in *D. lanaonis* (Pl. xxiii, fig. 16) and *D. persculptus* (Pl. xxiv, fig. 5) it is less pronounced. In all these cases the concavity is reduced by the extra hypostracal plates which fill up the hollow grooves on the inner surface. The structure in all the three species investigated is uniform, and I will include only short notes on the sections, which are reproduced in the plates accompanying this paper.

In sections parallel to the margin the ostracum is seen to be very well developed in the region of the ridges. The plates of this zone, as in a section of *D. persculptus* (Pl. xxiv, fig. 5), run crosswise from side to side and almost parallel to the surface. About the middle of the ridge, or the groove as it should be termed when viewed from the inner surface of the shell, the plates curve upwards to fill the concavity. In sections at right angles to the margin the ostracal plates are seen to be arranged in columns, which appear alternately light and dark and, as is clearly shown in a section of the shell of *D. oxytropis* (Pl. xxiii, fig. 15), the plates often fork above and below, become connected with one another and bound up with the plates of the hypostracal layers.

The hypostracum in all the species in sections parallel to the margin is seen to be formed of vertical columns of plates. The columns are not quite vertical to the surface in the region of the ridges, but curve outwards along the sides, and about the centre their number is greatly increased by the forking of the plates (Pl. xxiv, fig. 5). The same section shows the lines of growth of the shell in this zone as somewhat arched horizontal lines. In sections at right angles to the margin the plates and bundles forming them run at acute angles to the surface, and cross at right angles the plates of the subjacent layers (Pl. xxiii, fig. 17). In *D. persculptus* (Pl. xxiv, fig. 6) the hypostracal layers appear to be arranged in vertical columns, but this is due to the section being a little oblique. This section enables one to understand the different appearances which are produced by the plates and the bundles forming them, according to the planes along which the sections are made. The same section, as also that of *D. lanaonis* (Pl. xxiii, fig. 17), shows the basal part of the hypostracal layer as having a different arrangement from the rest; this is due to the plates being inclined at slightly different angles, and having been cut along different planes from the rest.

Semi-sculptured Forms.—Of this type I have investigated the shells of *Neothauma tanganyicense* (Smith) and *Rivularia auriculata* (von Martens) var. *bicarinata* Kobelt. In both the species sub-solid ridges are found on the shells in the regions corresponding to the sutural and the peripheral primary ridges of the embryonic shell. I figure sections of the latter. The periostracum is well developed, but does not show any special structure. The ostracum is very much thicker than the hypostracum, and shows a number of lines of growth (Pl. xxiv, fig. 3). In sections parallel to the margin the ostracal plates are arranged in vertical columns, most of which fork irregularly, send out lateral branches, and often do not extend through the entire length of the ostracal zone. In the lighter columns, which alternate with the darker ones, the bundles are arranged parallel to the surface, while those of the darker bundles are not so obliquely arranged. In a section at right angles to the margin and passing through the peripheral ridge, the different parts of the ridge are seen to be unequally thickened (Pl. xxiv, fig. 4). The bundles of the plates are arranged in the same way as in other members of the family. The hypostracal zone is not well shown in the section parallel to the margin (Pl. xxiv, fig. 3) and its component elements are not easy to distinguish in the photograph, but the lines of growth are seen as darker lines; these latter appear as lighter lines in sections at right angles to the margin (Pl. xxiv, fig. 4). In sections at right angles to the margin the column-like arrangement of the plates is clearly shown, and it was observed that in *Rivularia* the hypostracal plates are more closely arranged than in other members of the family.

Tuberculated Forms.—I have examined the shells of a number of species of *Taia*, *Margarya melanoides* Nevill, and *Tulotoma magnifica* (Conrad). In all these forms, whether provided with tubercles or elongated scales, the structure of the shells is similar, and it will suffice to deal with one of the forms in detail. I reproduce photographs of the ostracal and hypostracal plates magnified about 200 times as seen in sections at right angles to the margin, to show the structure of the bundles in *T. crassicallosa* Annandale & Rao. The periostracum is not seen in the photograph of a section of *Taia naticoides* (Theobald) parallel to the margin (Pl. xxiv, fig. 8). In other sections, however, it was found to form a thin membranous covering over the ostracum; its relations to the tubercles are considered separately below. The ostracum, as in *V boettgeri* or the semi-sculptured species like *Neothauma* and *Rivularia,* is very thick and forms the greater part of the calcareous region of the shell.

The plates constituting it in the region of the ridges (Pl. xxiv, fig. 8) or the tubercles (Pl. xxiv, fig. 10), as seen in a section parallel to the margin, are arranged at acute angles to the surface and cross those of the subjacent layers at right angles. In the region of the tubercles, where the concave cavity on the inside is filled by the ostracal plates, the plates are arranged in the same way as in the hollow-ridged species described above. In sections at right angles to the margin, the plates are found to be arranged vertically in columns, which show the usual alternating dark and light appearance. The tubercles are formed entirely by the ostracal layer and a thin covering of periostracum both above and below the calcareous part (Pl. xxiv, figs. 9, 11). The section of the shell of *T crassicallosa*, referred to above, shows two consecutive scales formed one next to the other, and illustrates the way the plates curve to fill up the hollow tubercular areas in these regions. The same section distinctly shows the lines of growth in both the ostracal and hypostracal zones.

In a more highly magnified photograph (Pl. xxiv, fig. 12) of the ostracal plates, as seen in a section at right angles to the margin, the bundles of fibrils in the darker columns are seen to run obliquely at different angles to the surface, while in the lighter ones they run more or less parallel to the surface. It also shows the forking of the plates over those of the hypostracum and the manner in which the plates of the two zones unite with one another. The plates of the hypostracum are arranged similarly to those in the shells of other members of the family, and it is only necessary to note the peculiarities of the sections figured. The shell of *Taia naticoides* cut parallel to the margin (Pl. xxiv, fig. 8) shows the plates arranged in vertical columns, while in a section at right angles to the margin (Pl. xxiv, fig. 9) the plates, which are cut a little obliquely, exhibit the forking and branching and their connectiont with the ostracal plates lying above them. In a more highly magnified section, examined as a transparent object, the bundles of the plates of the lower layers are seen through those of the upper layer crossing each other at right angles (Pl. xxiv, figs. 12, 13). Underneath the ridges and the tubercles the outline of the hypostracal region (Pl. xxiv, fig. 10) is somewhat concave in the same way as it is in the hollow-ridged forms.

Reference may also be made to the manner in which the succeeding whorls become connected with the previous ones. As is seen in a section of *D. persculptus* (Pl. xxiv, fig. 7) through the penultimate and a part of the bodywhorl taken parallel to the margin, the periostracum persists between the calcareous layers of the two whorls and forms the foundation on which the thick ostracal layers of the following whorl become attached uniting the two shell whorls. The plates in this region branch more extensively and are more closely placed so as to follow the outlines of the preceding whorl.

Summary.—The shells of the Viviparidae consist of an outer thin organic covering—the periostracum—and the thick inner calcareous region, which is divisible into an outer ostracum and an inner hypostracum. The periostracum of the adult shell is a homogeneous membrane, without any special structure, but that of the embryonic shell shows an almost exact reproduction of the cellular elements of the supramarginal groove by which it is secreted. In both the smooth and the sculptured types the mould for the deposits of the calcareous part of the shell is formed by the periostracal covering. For the discontinuous tubercles or the scale-like projections of the shells also the first mould is apparently formed by the periostracum, the separate structures being due to discontinuous secretion of the periostracum and later of the calcareous layers.

The ostracum and the hypostracum in the calcareous part of the shell are identical in structure, and the different appearance of the elements in the sections is due to the different planes along which they are cut during sectioning. Each of the zones is formed of a large number of strata or layers which are arranged parallel to one another in each zone, but the layers of the ostracum lie at right angles to those of the hypostracum. Each layer in its turn is formed of numerous plates, arranged parallel to one another. The plates consist of large numbers of bundles of fibrils, which in adjacent plates run at right angles to one another. The fibrils are the final elements, which can be distinguished by means of the microscope. In smooth-shelled forms the ostracum and the hypostracum are of almost equal thickness, but in forms with sculptured shells the ostracum forms the greater part of the thickened ridges, the tubercles and the scaly projections.

7. SECRETION, COMPOSITION AND THE FORMATION OF THE SCULPTURE ON THE SHELL OF THE VIVIPARIDAE.

As a result of the work of the various authors reviewed already and my observations on the Viviparidae, there can be no doubt that the secretion of the shell is entirely due to the mantle. The periostracum and the ostracal calcareous zone is secreted by the mantle margin, while the general epithelial covering of the mantle behind the supramarginal ridge forms the hypostracal calcareous zone.

From a study of the structure of the periostracum and the contents of the modified epithelial cells of the 'gouttière palléale' Moynier de Villepoix (121) concluded that in *Helix* this area forms the periostracum. In *H. aspersa* some of the cells at the base of the pallial groove were further found to be specially modified to form a 'glande globuligéne,' which was believed to be responsible for the secretion of the periostracum. Moynier de Villepoix considered the secretion of the periostracum as unique in molluscs, and described it as being of the nature of an endogenous formation. According to him a small vacuole appears in the granular protoplasm of the cells, it gradually grows at the expense of the protoplasm until it appears as a single or a number of globules, which occupy the greater part of the cell. The globules are supposed to be extruded from the cells by the bursting of the cell wall, and Moynier de Villepoix suggested that probably the muscles below the cells help in the extrusion of the granules. This gland was not found by Moynier de Villepoix in *H. hispida* in which the periostracum is specially well developed and is furnished with hairy projections, and no corresponding gland has been found in the large number of Gastropods the mantle margin of which has since been investigated. Biedermann (6) did not remark on the endogenous formation of the periostracum, but stated that it consists of polygonal structures which directly correspond to and present exact impressions of the cells by which they are secreted. The periostracum is formed by the hardening of the secretion of the cells of the supramarginal groove. Biedermann compared the periostracum to the chitinous covering of the Arthropods, and considered it to be a true cuticular formation. This view, however, it may be noted, is quite different from that of Bowerbank (18) and Carpenter (25), who considered the shell to have a cellular constitution. Annandale (1) did not correctly identify the periostracal glands, but rightly suggested that the periostracal substance 'is poured in a liquid condition into the supramarginal groove,' and passing through the grooves of the processes is deposited on the edge of the lip of the shell.

As has been mentioned above there is no 'glande globuligène' in the Viviparidae, and I am of opinion that the periostracum in this family, as indeed in all Gastropods, is secreted in the form of a solution by the cells of the supramarginal groove. In young embryos and even later when the shell is being actively secreted, the margin of the shell is embedded in the supramarginal groove and is intimately connected with its cells. In sections of an embryo of *V viviparus* in this condition it was found that the area of attachment consists of the undifferentiated periostracal secretion in the form of a series of elongated pillar-like masses, which lie parallel to one another, and correspond exactly both in number and arrangement to the cells of the supramarginal groove by which, apparently, they are secreted (Pl. xxiii, fig. 1, *P.S.*). The young periostracum of the embryonic shells, as has been described already, shows the same structure, and a similar appearance has been figured by Biedermann (6, pl. v, fig. 30) for the young shell of *Helix*. These pillar-like structures result from the hardening of the plastic secretions of the cells of the supramarginal groove, and each of them probably corresponds to a single act of secretion.

The periostracum when freshly secreted, and even for some time afterwards, is positive to the Biuret Reaction. Small pieces of it after treatment with copper sulphate solution became deep violet after washing and on being placed in a solution of sodium or potassium hydroxide. This positive reaction of the periostracum in the earlier stages, as was also found by Biedermann (6) in the case of *Helix*, shows that the substances forming it are of the nature of proteins. Later, however, the periostracum of the older shells is negative to the Biuret Reaction. The sclero-protein constituting it at this stage and resulting from slight changes in the constitution of the original proteins was given the name Conchiolin by Fremy.[1] He studied the constitution in great detail and found that Conchiolin is insoluble in water, alcohol or ether, and does not dissolve even in concentrated alkaline or acid solutions. It may, therefore, be inferred that the periostracal substance is of a protein nature. I have not studied its chemical composition, but am able to confirm Fremy's results for the periostracum of the Viviparidae.

As to the first sculpture of the shells in the form of hairs or ridges Moynier de Villepoix was right in considering it as entirely periostracal. The hairs on the shells of *Helix hispida*, as I can confirm from my own observations, are entirely periostracal structures, and the calcareous layers do not take any part in their formation as was believed by Leydig (103). In the case of the Viviparidae the embryonic sculpture whether in the form of hairs or ridges is, as Annandale (1) rightly noted, periostracal, but in the adults the ostracum fills up the grooves on the inner surfaces of the ridges, and all forms of sculpture on the adult shells are produced by both the periostracum and the calcareous layers of the shell.

The first calcareous layers of the shell were believed by Longe & Mer (107) to be already fully formed as rounded discs, and lying in the cells of the epithelial organ (=supramarginal ridge of the present account), whence they are deposited on the inner surface of the periostracum. Moynier de Villepoix (121) suggested that probably an organic substance of

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[1] Fremy, E.—*Ann. Chemie e. Physique* (3) XLIII, p. 96 (1855).

an albuminous nature is secreted with the calcium in the form of calcium carbonate. The mucus-like secretion is deposited on the inner surface of the periostracum, and the further process may best be stated in the words of the author ' la cristallisation du calcaire ne serait plus qu'une question de séparation moléculaire : la dissociation du bicarbonate en dissolution dans le liquide devant forcément amener la cristallisation du carbonate en mélange avec l'albumine à l'état de calcosphérites de formes variables.' Biedermann (6) as a result of extensive experiments is of opinion that the secretion consists of a solution of calcium phosphate, most of which after crystallization is transformed into calcium carbonate. Later,[1] however, he was of opinion that there may be some calcium carbonate also mixed with the calcium phosphate, but his remark that ' die primär abgelagerte Phosphatschicht später unter dem Einfluss der lebenden Zellen wieder gelöst und mit neuem Sekret von anderer Zusammensetzung gemischt, eine zur bildung der " Stalaktiten " geeignete Lösung liefert ' is difficult to understand. Annandale (1) is not definite as to whether the secretion is in the form of a solution or solid particles.

I am inclined to agree with Biedermann and earlier authors that the calcium is taken with the food by the animal, and that from the alimentary canal it passes into the liver, as was supposed by Barfurth[2] and has been confirmed by Biedermann & Moritz.[3] From here the calcium passes with the blood stream to various tissues as was noticed by Annandale (1), and I can confirm from my observations that this calcium, in the form of calcosphaerites, is then deposited in the connective tissue. The calcosphaerites become deeply stained with borax carmine or Delafield's haematoxylin, and disappear after being treated with dilute acids. In micro-chemical tests they were found to be positive to all reagents mentioned in Zill's work (179) for identifying calcareous particles, while the production of gas bubbles on the addition of acids shows that they consist of calcium carbonate. A certain amount of protein material is, however, mixed with them, as even after the sections are left for twenty four to forty eight hours in dilute acids a matrix remains in place of the calcosphaerites. The calcosphaerites must hereafter undergo some changes in their composition, for during the next stage in which they are found lying close to the bases of the gland cells of the supramarginal ridge, they do not show the characteristic form of the calcosphaerites, nor do they stain in the same way. They consist of small rounded or ovoid globules of a shining light yellowish colour. They are not affected by acids, but form the characteristic octahedral crystals of calcium oxalate on being treated with a solution of ammonium oxalate. I have not studied their chemical composition, but from the work of Biedermann on *Helix* it may be assumed by analogy that they are probably calcium phosphate masses with a certain amount of protein material mixed with them. The probability of their being of the nature of a double organic salt should not be ignored. The globules are then found in the gland cells of the supramarginal ridge, where they appear as minute granules in the glandular secretion.

As to the deposition of the calcareous material on the lower surface of the periostracum, Moynier de Villepoix (121), following the line suggested by Harting's[4] experiments on the

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[1] Biedermann, W.—*Zeitschr. allg. Physiol.* I, pp. 154-208, pls. iii-vi (1902).

[2] Barfurth, D.—*Archiv Mikrosk. Anat.* XXII, pp. 473-524, pl. xx (1883).

[3] Biedermann, W. & Moritz, P.—*Archiv ges. Physiol.* LXXV, pp. 1-86, pls. i-iii, (1899).

[4] Harting, P.—*Verhandl. kon. Akad. Wetensch. Amsterdam*, XIV, pp. 1-84, pls. i-iv (1873).

artificial production of calcosphaerites by precipitating calcium carbonate ($CaCl_2+K_2CO_3=CaCO_3+2KCl$) in a liquid containing organic substances like albumin, gelatin, etc., found that it was possible to obtain bodies similar to the calcosphaerites by mixing precipitated chalk dissolved in soda water with egg albumin. He further found that on varying the proportions of the calcareous and the albumin solutions it was possible to vary the size and numbers of the calcosphaerites. Steinmann,[1] who carried out further experiments in this direction, concluded that the deposition of the calcium is due to an extra-cellular crystallisation process, and that the most important part in this process is played by the interaction of calcium carbonate on an organic albuminous substance. This view of the explanation of the structure of the shell on purely physico-chemical lines was adopted in a slightly modified form by Simroth (159). Stempell (162) in addition to the above brought in the influence of the so-called ' Sekretionkomplexe ' for explaining the formation of the structural elements of the shell. These secretion complexes, as Biedermann rightly remarked, are purely of the nature of hypotheses for which there is no support either in the structure of the soft parts or of the shell. Biedermann's account (6) is undoubtedly the clearest exposition of the present state of our knowledge of the subject, and I agree with him as to the general principles. According to him ' ohne allen Zweifel jeder durch eine besondere Strukture ausgezeichneten Schalenschicht auch eine besonders geartetes, von besonderen Zellen bereitetes Sekret entspricht, aus dem sich unter Bedingungen, die zur Zeit noch nicht hinlänglich klargestellt erscheinen, aber jedenfalls nichts mit einer durch Fäulnis bewirkten Eiweisszersetzung zu tun haben, jene charakteristischen Formen ausscheiden.' The only points about which I differ from him are that, as has been shown already, the structure of both the ostracal and the hypostracal zones is similar, and that the same influences are at work in the formation of the two zones ; further, though the influence of the organic substances found in the mucus-like secretion is not quite as was suggested by Harting, Moynier de Villepoix, Steinmann and others, there can be no doubt that it plays an important part in the deposition of the calcareous part of the shell.

Reference may here be made to the analyses of the shells of various species of Asiatic Viviparidae by Fowler and Malandkar.[2] According to these authors the calcium in the shells is in the form of carbonate.

In order to decide whether the calcium carbonate in the shells of the Viviparidae is in the form of calcite or aragonite, I used the methods suggested by Schmidt.[3] Powdered shells on being boiled for about half a minute in a concentrated solution of cobalt nitrate (Meign's Reaction), or on treatment with a concentrated solution of Mohr's Salt, gave different results for different species. Thick-shelled forms like *Margarya* or *Tulotoma,* which gave positive reactions, appear to consist entirely of aragonite, while in the case of the thin shelled species results were mostly negative, and apparently in these shells calcium is deposited in the form of calcite. In some cases as *Rivularia* and *Neothauma* some of the powdered part of the shell showed a positive reaction, while the rest was negative, and it appears, therefore, that in these shells the various layers are differently constituted.

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[1] Steinmann, G.—*Ber. naturfor. Ges. Freiburg,* V, XI (1889, 1899). I have not been able to consult Steinmann's papers, and my remarks are based on the excellent summary of the works in Stempell (162) and Biedermann (6).

[2] Fowler, G. J. & Malandkar, M. A.—*Journ. Ind. Inst. Sci.* VI, p. 190 (1923).

[3] Schmidt, W. J.—*Die Bausteine des Tierkörpers in Polarisierten Lichte,* pp. 67, 68 (Bonn, 1924).

Many thin sections of the shells of various Viviparidae have been examined with polarised light, but owing to the minuteness of the fibrils it was not possible to arrive at any definite results as to whether any given layer was composed of calcite or aragonite.

The secretion of the smooth or almost smooth shells with only a few very low ridges or with purely periostracal sculpture may be considered first. In these forms the embryonic shell of all the species has three low ridges ornamented with periostracal chaetae. The three rows of chaetae and the ridges correspond to the three primary marginal processes in position, and as Bouchard-Chantereaux (12), Moquin-Tandon (118, 119), Leydig (102) and Annandale (1, 2) rightly concluded, they are directly due to the marginal processes of the mantle. This was further confirmed by Annandale's observations on the presence of secondary and tertiary series of marginal processes corresponding to similar ridges on the shells of some Viviparidae. My examination of the soft-parts of the adults and embryos of large numbers of forms of the family fully confirms the views of the earlier authors, and I am of opinion that, in the smooth-shelled species, the periostracal chaetae found on the shells of various species and the low ostracal ridges on which the chaetae are found are directly due to the influence of the marginal processes. In some species the processes still exist, but there are no corresponding ridges, as for example in *V bengalensis* and still more so in *V dissimilis*, but the processes are greatly reduced, and the only possible explanation seems to be their degeneration.

In the secretion of the shell the periostracal secretion is deposited along the margin of the shell from the supramarginal groove, and in the case of the marginal processes the secretion is conveyed along the grooves of the processes and is moulded over the processes themselves. Where the processes are reduced the shell area produced over them does not differ from the rest of the shell deposited by the other parts of the margin, but where the processes are well developed they form periostracal projections on the shell. The latter is the case in the embryos of almost all the species, and becomes specially important in the production of the well developed projections of different types on the adult shells of various species. The secretion of the first calcareous layers or the ostracum results from the glandular supramarginal ridge, while the hypostracum continues to be secreted later on the inner surface of the ostracum by the general epithelial covering of the mantle and thus the shell increases in thickness.

As to the formation of the sculpture of the shells there can be no doubt that it is due to the specially developed marginal processes, which persist in the adults of various species, The opinions of the various authors like Bournon, Johnston, Bronn, Leydig, von Martens von Linden, Annandale and others have already been reviewed, and it is only necessary to refer to the suggestion of the Sarasins, a communication from whom has been included by Biedermann in his valuable work (7). These authors affirm that the processes of the mantle margin form the projections on the shell, particularly during the periods of growth. They referred to the processes on the mantle of *Physa*, which, however, they could not explain in view of the shell of this form being smooth. Similar projections are found on the mantle margin of the Melaniidae, but the processes are solid and have no mid-dorsal groove of the type found in the Viviparidae, and are certainly not correlated with the projections of the shell in the same way as those of the Viviparidae. Probably the same explanation will be found to serve for the mantle processes of *Physa,* but at the present time I have no opportunity of confirming it.

My views on the subject of the production of the sculpture of the shells are based on the different development of the marginal processes of the mantle in the embryos of the different species of the family, and still more on the degree to which all or some of them persist in the adults. I differ from the previous observers in attaching special importance to the marginal processes in connection with the deposition and moulding of the periostracal secretions, and in this connection I consider the rôle of the grooves of the processes to be of considerable importance. The secretion in the supramarginal groove is conveyed along the grooves of the processes not only from the cells directly opposite them but also from the adjacent areas, and this large amount of secretion is moulded on the processes themselves. The secretion, as has already been noted, is purely organic in nature, and forms the periostracal covering on the inner surface of which the ostracal calcareous material is later deposited. It follows, therefore, that the calcareous projections will resemble both in form and size the periostracal moulds in which they are formed.

In forms like *Dactylochlamys,* in which the shells are provided with continuous hollow ridges, it has been observed that the marginal processes are specially developed, or as Annandale aptly stated " hypertrophied." They persist throughout life, and regulate the intermittent deposit of the periostracal secretion along the lines already laid and mould it in the form of hollow channels. The hollow ridges of the shells, as seen from the outer surface, correspond exactly in number, arrangement and position to the marginal processes and apparently the periostracal secretion conveyed by the latter through their grooves is laid along the margin of the shell in line with the already existing ridges, and moulded into form with them. In this connection the purely mechanical influence of the ridges on the mantle behind the supramarginal ridge, such as are found in *Dactylochlamys lanaonis, D. pagodula,* and even in forms like *Tulotoma, Neothauma* and others, probably both in embryos and adults can not be ignored. The epithelium on the surface of the mantle behind the supramarginal ridge secretes the hypostracum, and in these forms the spirally placed ridges of the mantle would help in keeping the ridges of the shells hollow. This mechanical influence is further demonstrated by the fact that in the earlier whorls of the shells, which are occupied by the visceral mass and where there are no ridges on the surface of the animal, the grooves gradually become shallower by being filled up with the hypostracal secretions. The same condition in a less marked degree is found in the penultimate and the first part of the bodywhorl, where the mantle ridges gradually become less prominent.

I have had no opportunity of examining the animals of the forms with semi-solid or solid continuous ridges on the shell, but the structure of the shells, as for example of *V boettgeri* and still more of D. *persculptus,* shows that the ridges are originally hollow, and in the earlier stages appear as hollow concave channels on the inner surface of the shells. At this stage they resemble the hollow-shelled forms of the subgenus *Dactylochlamys,* and consist of the outer periostracum and the inner ostracum only. Later, as probably there are no ridges on the surface of the mantle to influence the form in which the hypostracum is deposited, the grooves are filled by an increased quantity of calcareous secretion. Various grades ranging from almost flat to concave inner surfaces of the grooves are found in different species and even in different parts of the same shell.

In both the cases referred to above the material deposited in each period of secretion of the shell must follow the lines of the parts of the shell already formed, and during succeeding periods also must start from where it had stopped at the end of the preceding period. In this connection the marginal processes play a very important part.

The last type to be considered is that in which the shells are ornamented with separate and almost discontinuous tubercles, knobs or scale-like projections. Two points, which seem to have escaped the attention of all previous workers, must be considered first. The tubercles, of whatever form, are developed on continuous spiral ridges corresponding to the primary, secondary or tertiary ridges of the embryonic shells, and represent only specially developed areas of the ridges themselves. The sculpture of the shells, leaving aside that of the whorls corresponding to the embryonic shell, is best developed on the earlier whorls, particularly in the sculptured forms of the Viviparidae.

In the various species of the remarkable Burmese subgenus *Taia* Annandale, the tubercles on all the ridges are best marked on the penultimate whorl. All the rows of tubercles are almost equally developed, but in some cases, varying with species and age, the sculpture is almost equally developed on the whorl previous to the penultimate and on the first part of the bodywhorl. On the bodywhorl itself, however, the tubercles of the peripheral ridge alone are well developed, while those of the other primary and secondary ridges are greatly reduced, and the ridges appear to be uniformly developed.[1] In the case of *Margarya* Nevill this is still better marked. The tuberculated ridges are much better developed in the young shells and on the earlier whorls of the older shells. The bodywhorl of full grown individuals has very few tubercles and the ridges also are less strongly developed. Conditions are very similar in *Tulotoma* Haldeman, and it may, therefore, be concluded that with age the production of the sculpture becomes greatly reduced. It is clear; therefore, that the origin of the sculpture of the shell of the Viviparidae, as Annandale rightly pointed out, is to be looked for in the marginal processes of the mantle which undoubtedly become reduced with age. As with the continuous ridges on the shells, so the different types of discontinuous sculpture are due to successive intermittent secretions of uneven amounts of periostracum followed by similar and more pronounced secretions of the ostracal shell layers. The periostracal secretion conveyed through the grooves of the processes is moulded on the processes in the form of scales or tubercles, and later this is strengthened by the increased secretion of the ostracal layers by the specially developed " cushion-like thickenings " of the supramarginal ridge which are developed opposite the marginal processes of the mantle and correspond to the ridges of the shell. These thickenings were first observed by Annandale (1) in preserved material of some species of *Taia*, and later (2) their presence was confirmed by the same author from examination of living individuals of different species of the same subgenus. I have found them in preserved material of *Taia*, and similar structures are also recognizable in the mantle margin of *Tulotoma*. It is thus clear that the increased secretion of the ostracal substance in special regions combined with the intermit-

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[1] For figures of the different species of *Taia* reference may be made to the excellant plates in Annandale's paper (*Rec. Ind. Mus.* XIV, pls. xv-xviii (1918)).

tent discontinuous secretion of the periostracum, which is indicated by the presence of periostracal covering on both the upper and lower surfaces of the scaly tubercles of *Taia* and *Margarya* (*antea*, p. 288) is responsible for the formation of the tubercles. Each tubercle must be completed during one period of secretion of the shell, and the shell margin starting from it, with the next period of activity, is continued originally as an ordinary ridged area, and later with specially increased secretion the next tubercle is formed in line with the previous one. In some cases (Pl. xxiv, fig. 11), owing probably to suspension of secretion during the same period of secretion, two tubercles lying one above the other may be formed.

To sum up, it may be noted that the cushion-like thickenings secrete more calcareous matter than the adjacent parts of the supramarginal ridge, and that this helps in the formation of the specially developed sculpture on the shells in the areas corresponding to the thickenings. As long as the calcareous matter is evenly secreted sculpture in the form of even ridges is formed in the already moulded periostracal structures, but with increased activity in the secretion of the ostracal zone followed by a period of relaxation, the periostracal secretion is transformed into a scaly or tubercular protuberance strengthened by the calcareous ostracal matter and greatly raised from the adjacent area of the shell. The next periostracal part of the shell starts below this protuberance instead of from its margin. As to what determines the periodic increased activity it is impossible to be certain, but there is no evidence of secretion complexes in the sense of Stempell (162).

It is not possible to offer any explanation as to why the marginal processes are better developed in the embryos of some species than in others, or why they persist in some and degenerate or altogether disappear in the adults of others. A general reduction with age is, however, indicated by the reduction of the sculpture on the older whorls of the shells, and this points to the processes being of the nature of primitive structures which persist in certain forms and lead to highly sculptured shells, while in others they disappear or become reduced, and the resulting shells are correspondingly smooth or only slightly sculptured. Annandale (2) was probably right in considering the sculpture as being due to evolution of a particular structure, in this case the marginal processes, and with it the hypertrophied region of the supramarginal ridge, and further to the inheritance of one kind of acquired character. Evolution of similar types of sculptured shells due to the similar structure of the respective animals, as I have discussed elsewhere, is, however, due to parallel evolution, and does not imply any genetic relationship between the various forms.

Annandale (1) remarked that in the shells of the Viviparidae the " colour-pattern is periostracal in origin, though the calcareous matter may be slightly stained." Flössner (51) in the case of the *Helix* shells considered the pigment to be confined to the outer calcareous zone. In order to decide this point definitely the periostracum was removed from the shells of a number of banded species of the Viviparidae, and it was found that the colour-bands, as already noted, are situated in the calcareous part. On removing the various layers of the calcareous part by gradual decalcification, it was found that the pigment is confined to the area between the ostracum and the hypostracum, and is secreted apparently with the hypostracal layers.

The development of the shell sculpture is directly associated with the grooved marginal processes of the mantle. The processes are not the organs of secretion, but act as mechanical moulds over which the continuous ridges, whether hollow or solid, or the separate protuberances of the shell are formed ; they also act as guides for the deposition of the shell along regular lines. The sculpture of the embryonic shell is entirely periostracal, while that of the adult shell is formed by the periostracum and the ostracum ; the hypostracal layers are only secondarily concerned in it. In all cases, however, the sculpture is performed by the periostracal secretion moulded over the specially developed marginal processes.

The sculpture becomes less pronounced on the later whorls of the shells, and this is correlated with the gradual reduction and atrophy of the marginal processes of the mantle. It is not possible to determine the causes for the different development of the marginal processes both in the embryos and the adults of the various members of the family Viviparidae, but Annandale's explanation of the evolution and inheritance of certain acquired characters appears to be the most probable. Similar types of sculpture on shells of species found in widely separated areas are examples of parallel evolution and do not indicate genetic relationship between the different forms.

In addition to the inherent pigment in the periostracum the colour-bands of the shells of the Viviparidae lie in between the ostracal and the hypostracal layers.

Summary.—The periostracum is entirely organic and consists of modified scleroproteins, which have been given the name of Conchiolin. It is secreted by the cells of the supramarginal groove in the form of a solution.

The calcareous material for the formation of the shell is probably taken in the form of carbonate with food and passes from the alimentary canal into the liver. From the liver it is carried with the blood stream, and is stored in the connective tissue of the mantle, and probably also in other areas, in the form of calcosphaerites. The chemical reactions of the calcosphaerites show that they do not consist entirely of calcium carbonate, but also have an organic matrix. The calcosphaerites later undergo some chemical change and become transformed into a double organic salt with the calcium in the form of a phosphate, and are found as shining rounded globules lying near the bases of the gland cells of the supramarginal ridge. From here they pass into the gland cells and are secreted with the mucus-like secretion of the cells. The deposition of the calcareous layers of the shell in the form of fibrillae appears to be due to the interaction of an organic albuminous substance on the calcareous material, both of which are found in the secretion of the cells, but, with our present knowledge, it is not possible to determine the influences which are at work. The calcium carbonate in the adult shells of the Viviparidae results from the transformation of the calcium phosphate material which is secreted by the gland cells. It is deposited either as calcite or aragonite, and the different layers of the shells consist of either calcite or aragonite, both of which in some form are found in the same shell. The ostracal layers of the shell are secreted by the gland cells of the supramarginal ridge, while the hypostracal part is secreted by the general epithelium which covers the outer surface of the mantle.

8. REVIEW OF THE LITERATURE ON THE EMBRYONIC SHELL-GLAND AND ASSOCIATED STRUCTURES IN MOLLUSCA.

I proposed working out the development of the embryonic shell gland the mantle and the shell-gland region of the adult of *Viviparus viviparus* (Linn.), and with this end in view had collected and preserved embryos of various stages, and written up the following review of the literature on the subject, when I came across Andersen's paper[1] on the development of the identical areas in the same species. This masterly work together with the earlier ones of Erlanger (43) and Otto and Tönniges (126) makes it unnecessary to go over the same ground again. In view of the great importance of the embryonic shell-gland, and as no detailed summary of the previous work is available, I include here a review of the literature dealing with the gland in all classes of molluscs excluding the Cephalopoda. References to practically all important contributions on the subject are included, but preliminary and incomplete papers are not reviewed. The accounts of Balfour (3) and Korschelt and Heider (88) are incomplete and out of date, while Heschler (73) and Macbride (109) refer only to the shell-gland in the forms the embryology of which they include in their works.

The work on the Viviparidae and some of the general papers are considered separately in the beginning. Following Pelseneer's classification (128) the review of the literature for the different classes of Mollusca is treated under the following heads :—

(1) Amphineura, (2) Gastropoda under the divisions Aspidobranchia, Pectinibranchia, Opisthobranchia and Pulmonata, (3) Scaphopoda, and (4) Lamellibranchia under the orders Protobranchia, Filibranchia and Eulamellibranchia. The literature is treated chronologically, but papers dealing with nearly related forms are discussed together.

Viviparidae and General.—Leydig (102) was the first to describe the development of the mantle of *Viviparus viviparus.* He referred to the mantle in its connection with the secretion of the shell, but did not find the shell-gland of the embryo or of the adult. In his account of the mantle without recognizing their true nature he, however, described the cells which later form the supramarginal ridge of the mantle of the adult. Lereboullet (101) gave good figures of various stages in the development of the larval shell-gland of *Limnaea,* but did not understand its significance and considering it to be connected with the anal invagination called it the " tube rectal." Ganin (59) appears to be the first who understood the connection of this area with the shell-gland of the embryo and its relation with the mantle. It was not, however, till Lankester (95) discovered the structure in the centre of the aboral pole of the embryo of *Aplysia* that its true nature was understood. He called it the " shell-gland," but made no remarks about its relation to the shell-gland of the adult. In the following year Lankester (96) recorded the gland in the embryos of other molluscs, and this was followed by a detailed paper (98) in which he described and figured the " existence of a specially differentiated patch of epidermal cells at the aboral pole, which develops a deep furrow, groove, or pit in the centre, almost amounting to a sac-like cavity opening to the exterior. The first (chitinous) rudiment of the shell appears as a disk on the surface of this gland, but also in some cases the cavity or groove is filled by a chitinous plug." He further suggested the homology of the gland which secretes the internal shell or the " pen " of the Cephalopods with the embryonic shell-gland of the Gastropods and Lamellibranchs. This theme was elaborated in two other papers (97, 99), but from his studies of the fossil forms he now concluded that the two structures are

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[1] Andersen, K.—*Morphologisch. Jahrb.* LIII, pp. 211-258, pl. vii (1924).

different. Leaving aside the Cephalopods he had so far found the shell-gland in the embryos of the molluscs *Aplysia, Neritina, Limnaea* and *Pisidium,* but in two contributions (99, 100) he described a similar shell-gland in the embryos of *V viviparus.* The structure of the gland was not described nor its later development followed. He, however, noted that even after the shell assumes a dome-like shape " the pit of the shell-gland is still in existence and is filled by a chitinous knob of the shell."

The work of Fol (52-56), though it does not deal with the development of *Viviparus,* should be referred to here. Fol is the only author who, so far as I can find from the literature, distinguished between the shell-gland of the embryo and that of the adult, and gave detailed descriptions of the structures concerned. In his paper on the development of the Pteropods (53) he included a good summary of the earlier literature on the development of the shell and its relation to the mantle in all classes of molluscs. In Pteropods, Heteropods and pulmonate Gastropods, Fol found the embryonic shell-gland to develop on the aboral pole from a thickening of the ectodermal cells. This area later becomes invaginated and forms a definite pit (l'invagination coquillèire ou préconchylienne), which was found to be filled with a trabecular secretion ; this latter in some forms was seen to spread on the surface of the embryo and harden into a shell. The fate of the invagination was found to be different in various molluscs, it either disappeared entirely or persisted in part and marked the region from which the mantle develops. Fol distinguished the larval shell (la coquille larvaire) from the shell of the adult (la coquille définitive). The larval shell was found either to persist and form the first part of the adult shell or to disappear in part or altogether. The adult shell, he concluded, was secreted by the mantle margin, while its inner surface, in most forms, was strengthened by the deposition of shelly secretions from the general epithelial covering of the whole mantle. Agreeing with Lankester he considered the embryonic shell-gland to be the same structure in Lamellibranchs and Gastropods, and homologous with the pit which secrets the internal shell of Cephalopods. In his paper on the pulmonate Gastropods (56, c) he figured a transverse section of *Limnaea palustris* (p. 152, fig. 4) and a sagittal section of *L. stagnalis* (p. 153, fig. 5). In the first figure he called the mantle margin the shell-band (le bourrelet coquillèire), while in the second he simply designated it as the mantle margin. In the second figure, which is a section of an advanced embryo, he represented the flask-shaped *anlagen* of the unicellular shell-glands of the adult without recognising their true significance.

Bütschli (23) confirmed Lankester's observations regarding the development of the shell-gland in the embryo of *V viviparus,* and described the formation of a chitinous plug (Conchyolinpfropf) in the invaginated gland, the appearance of which, according to Bütschli, marks the beginning of the growth of the larval shell and probably also of the allied mantle structures. He further found that soon after the completion of the development of the shell-gland the invagination disappears and its cells become flattened. In his account he confused the margin of the mantle, which is separated about the same time, with the shell-gland of the embryo.

Blochmann (9) noticed in embryos of *V viviparus* in the gastrula stage the separation of the shell-gland on the aboral pole. The ectoderm in this region is thickened and consists of tall, narrow cells.

Erlanger (43) in his classical work on the embryology of *V viviparus* included a few remarks on the origin and the development of various stages of the shell-gland. The youngest embryo in which he saw the beginning of the shell-gland was 0·09 mm. in length, it had a well developed velum, but the mesoderm had not yet been differentiated. The shell-gland at this stage consists only of a thickened patch of ectodermal cells on the dorsal surface of the embryo. In somewhat older embryos with spindle-shaped mesodermal cells, the shell-gland becomes separated and extends from the velum to the anus. It is now a rounded plate formed of tall, cylindrical cells. He did not describe the invagination of the larval shell-gland, its transformation, and the appearance of the *anlagen* of the shell-gland of the adult. He, however, described in an embryo of 0·64 mm. the embryonic shell as membranous and added that its margins are embedded in a furrow just above the thickened mantle margin, which he considered to be responsible for the further secretion of the shell and called it the shell-groove (Schalenfalz). In the second part of his paper he gave a good figure of the invaginated shell-gland (Pl. xxxii, fig. 1) with its chitinous plug (Schalenknopf). In another figure of a fully grown embryo he showed a large number of glands in the mantle lying just behind the margin, and labelled these the glands of the mantle margin (Drüsen des Mantlerandes) ; these glands, the true nature of which was not understood by Erlanger, are functional even at this stage of the embryonic life and ultimately become the shell-glands of the adult.

Drummond's remarks about the embryonic shell-gland and its ultimate fate are very incomplete and inaccurate in her otherwise excellent paper (40). In the youngest embryo observed she found the shell-gland to consist of a deep pit widely open to the exterior. In the second stage the shell-gland is " partially evaginated, and begins to form the visceral hump" Whatever the fate of the embryonic shell-gland may be it certainly never forms the visceral hump either of the embryo or of the adult. Drummond casually referred to the development of the mantle and the mantle fold, but did not recognise the *anlagen* of the shell-gland of the adult in it.

Tönniges (168) included a few notes about the development of the shell-gland and the changes undergone by it during its transformation into the shell-gland of the adult. He described the shell-gland as a thickening of the ectoderm on the dorsal surface extending from the velum to the anus of the embryo in the trochophore stage. In the next stage the gland was found to become invaginated and compressed against the dorsal wall of the primary gut. The invagination later becomes more marked and is filled by a chitinous plug (Bütschli's Conchyolinpfropf). At a slightly later stage, when the mantle is beginning to be differentiated, the shell-gland cells become much flatter and a thin membranous shell begins to appear. The shell is supported somewhat later along its free margins in the mantle-groove. Good figures of the shell-gland and associated structures are also included in the paper. Otto and Tönniges (126) further extended the observations of Tönniges referred to above. Their account of the earlier stages is a confirmation of the earlier work of Tönniges, but they also described the fate of the embryonic shell-gland, the chitinous plug and the relation of the shell to the mantle and the mantle groove. They considered the great development and the height of the cells of the embryonic shell-gland in its earlier stages as being due to the great activity of the cells for the secretion of the embryonic shell.

The stage after the invagination of the shell-gland is described in detail, and it was found by the authors that after this stage the tall epithelial cells of the shell-gland, in conformity with the great activity in the development of the other organs of the embryo, become quite flat. The membranous shell at this stage spreads itself over the dorsal surface of the embryo and the first trace of the mantle-fold begins to appear. The further development of the mantle-furrow is also described. Anderson, in the paper cited, has given a very detailed and complete account of the changes undergone by the embryonic shell-gland, the development of the mantle, the pallial cavity and their relations to the general form of the embryo. He does not give any details of the histological structure, but these will be found in the works of Otto and Tönniges.

Amphineura.—Kowalevsky (89) did not correlate the conditions in the Chitonidae with those in other molluscs, and it is not clear from his account that any thickening of the shell-gland area takes place in the early embryo, and whether there is an invagination and later evagination of the shell-secreting areas. The shell-secreting area is divided into seven grooves corresponding to the seven calcareous plates of the shell (the eighth plate is not secreted till later in embryonic life), but as was pointed out by Korschelt (88) its development is otherwise similar to that of the shell-gland in other molluscs. In the formation of the shell the tegumentum is first secreted and the articulamentum is laid under it later on. Heath (70), who studied the cell-lineage in *Ischnochiton,* found that the shell-secreting areas are derived from the ectomeres and apparently three quartettes take part in the formation of the various shell-patches and the mantle. In Solenogastres the only account is the short paper on the development of *Dondersia* (*Myxomenia*) *banyulensia* by Pruvot (133). The shell-gland and its development in this form are not described by the author, but seven rows of plates are shown to develop on the dorsal surface of the embryo. These rows of calcareous plates, as was pointed out by Heschler (73), recall the seven shell-valves of Chiton, and it is possible that in the embryos of Solenogastres the plates are secreted by glands similar to those of Chiton.

Gastropods.—A good general review of the shell-gland for some Gastropods was published by Pelseneer (129) but a great deal of the earlier work is not reviewed in his masterly memoir.

Aspidobranchia.—In *Patella coerulea* Patten (127) found that the shell-gland begins to be differentiated on the aboral pole posterior to the velum shortly before the closure of the blastopore. It consists of a flat plate of tall, columnar ectodermal cells, which begin to extend at its outer margins. In the middle of its external surface is formed a large depression or invagination which becomes very extensive and appears Y-shaped. According to Patten it seems to " exert modifying influence upon the processes which take place within the interior of the embryo". Later with the flattening and evagination of the gland the lateral and posterior extensions are reduced, and the area, except along its margins, which are thick and later develop into the mantle, consists of flattened cells. The membranous shell is secreted during the invaginated stage of the gland and is later strengthened by the secretion of calcareous matter. Wilson (175) does not definitely state the cells from which the shell-gland in *Patella* is derived, but he observed its formation as a thickened plate of ectodermal cells on the dorsal surface behind the prototroch.

In *Haliotis* Boutan (15) did not describe the earlier stages, but noted the formation of an invaginated shell-gland. According to him the shell is secreted by this gland, and in the earlier stages is coiled like that of other Gastropoda. Later Boutan (17) also referred to the formation of the shell-gland in *Haliotis, Acmaea, Fissurella* and other Aspidobranchs, but did not go into details.

In *Neritina* Claparède (27) saw the shell at an early stage, but did not detect the shell-gland, nor did he describe the secretion of the embryonic shell and the development of the mantle. He, however, connected the further secretion of the shell with the mantle, but did not distinguish any shell-gland region in it. Lankester (98) described the invaginated gland filled with a chitinous plug, but did not deal with the various stages in its development. Blochmann (8) did not give a detailed account of the embryonic shell-gland in *Neritina,* but in the oldest embryo observed by him he figured the shell-gland as a somewhat concave plate with a shallow invagination in its centre.

Boutan (14) studied the embryology of a number of species of the genus *Fissurella.* In all these species the embryonic shell-gland was found to arise on the aboral pole and soon became invaginated, and the first rudiment of the shell was secreted. The invaginated area later flattened out and the mantle originated from its margins. The formation of the shell, which in the earlier stages is coiled like that of other Gastropods, and its transformation into a cup-shaped shell are also described in detail.

Robert (141) in the case of *Trochus* agreed with Conklin (28) that the shell-gland was a derivative of the *2d* cell of the developing egg.

Pectinibranchia.—In *Ampullaria* Semper (153) did not detect the earlier stages in the development of the shell-gland. In the first stage described by him the shell-secreting area is in the form of an oval plate of flat, polygonal cells, which apparently represents the stage after the evagination and flattening of the cells of the shell-gland. In an older embryo he noted the shifting of the shell-secreting area to the place where the mantle originates. The development of the shell was also described but its secretion was not definitely connected with any glands in the mantle or elsewhere.

Bobretzky (10) saw a circular invagination in the young embryos of *Nassa mutabilis* which he described as the " Schalengrube" Later the gland became everted and a cuticular shell was secreted over it. He noted that the shell grows along the margins in the thickened marginal zone of the shell-gland, which he distinguished as the " Anlage des Mantels" After its evagination the shell-gland is lined by flattened cells which become still thinner. In *Fusus* and *Natica* the development of the shell-gland was found to be similar to that in *Nassa.*

In *Calyptraea sinensis* Salensky (143) noticed an invagination on the dorsal surface of the embryo in the middle of the Mantel-Anlage and covered by a plate-like rudiment of the shell, which is free in the middle but embedded in the mantle thickening along the margins. He, however, did not recognize in this invagination the shell-gland of the embryo and did not describe its further development.

Sarasin (146) described the development of the embryonic shell-gland in *Bithynia tentaculata.* His account is not very clear and in the earlier stages he appears to have confused the invagination of the shell-gland with the blastopore. The later stages are not described in detail, but good figures illustrating the everted gland and, in still older embryos, its flattened cells covering the visceral mass accompany his paper. He described the development of the mantle from the marginal region of the shell-gland, and without recognizing their true nature figured the anlage of the shell-glands of the adult in the mantle margin. Erlanger (44) gave a detailed and accurate account of the shell-gland in the same species. The shell-gland was found to appear soon after gastrulation as an ectodermal thickening on the dorsal surface in the post-velar area. Later it shifts to the left and lying opposite the oral invagination produces the first signs of asymmetry in the developing embryo. In the next stage the gland is invaginated and a thin cuticular shell is secreted over it. The evagination, flattening and spreading of the gland cells and the development of the shell-furrow and the mantle ridge are also described. He does not give any account of the development of the shell-gland of the adult, but from his text and figures it appears that he saw the gland-anlage in the mantle-furrow.

Salensky (145) described the shell-gland in *Vermetus* as the " glands préconchylienne" It was distinguished on the dorsal surface of the embryo as an insignificant invagination lined by tall ectodermal cells. Salensky casually referred to its connection with the secretion of the shell and the development of the mantle, and added that its further history is the same as in other molluscs.

McMurrich (110) remarked that the " shell-area " in *Fulgur* is formed in the same way as in other molluscs. He saw the invagination of the gland but considered it to be of unknown significance. Conklin (29) gave a detailed account of the shell-gland in *Fulgur*. He described the shell-gland as one of the earliest and largest of the developing organs and the one most instrumental in shaping the form of the embryo. It was found to develop as an aggregation of ectodermal cells in the mid-dorsal plane posterior to the apical pole. The cells forming it are probably derived from the ectomere *2d* and by an increase in their numbers cause a saucer-shaped depression in this area. The depression becomes deeper and subsequently evaginates. The thickened margin forms the mantle-ridge, while the central part, which is formed of a layer of flat ectoderm cells, is covered by a thin cuticular shell. Conklin had previously (28) described the shell-gland of *Crepidula* in detail. In this Gastropod the shell-gland arises from the cell *2d*, the first somatoblast, also called *X* by many authors. He also noted that the development of this area seems to be similar in the various forms which have been studied, and that it gives rise to the first shell, the mantle-edge and fold, and the layer of cells which covers the yolk under the shell.

Delsman (36) described the various stages in the development of the shell-gland and the mantle in *Littorina obtusata*. The development is similar to that in other Gastropods noted above and the gland arises in the same way. The author did not recognize in the mantle the anlage of the shell-gland of the adult.

The work of Fol (56, b) on Heteropods has already been referred to but a few notes may be included here to make this summary complete. In these forms simultaneously with the closing of the blastopore the shell-gland is formed as an invaginated pit on the aboral pole. Later it becomes everted and an embryonic shell is secreted in all forms whether they are with or without a shell in the adult. The embryonic shell is completely lost in *Pterotrachea*, *Firoloidea* and allied forms, and exists as a rudimentary structure in

Carinaria. The mantle is developed from the margins of the gland, but in forms without a shell in the adult it degenerates later.

Opisthobranchia.—The first discovery of the shell-gland in *Aplysia* by Lankester (95) and his detailed account of the gland in two species (98) has already been referred to. Blochmann (9) described the earlier stages in the development of *Aplysia limacina*, and noted that the earlier rudiments of the shell-gland described and figured by Lankester do not represent the shell-gland but only an ectodermal cell aggregate ; the true gland-anlage being situated higher up towards the animal pole. He traced the stages from a flat plate of columnar cells to a fairly deep pit formed by invagination on the aboral pole diammetrically opposite the oesophageal invagination. The cells of the pit were later found to spread outwards and become flatter in the greater part of the gland, while the marginal area remained thick and formed the mantle. Mazzarelli (113) gave good figures and described the various stages in the development of a number of species of Aplysiidae, and fully confirmed the account of Blochmann. Georgevitch (62) studied the embryology of *Aplysia* paying special attention to cell-lineage, and though his account of some of the earlier stages and the formation of the mesoderm has been criticised by Carazzi (24), his paper fully confirms the earlier work of Blochmann and others. It is also the best connected account of the formation of the shell-gland in this Opisthobranch.

Rho (139) did not enter into details of the development of the shell-gland, but described and figured most of the stages in *Chromodoris*. Heymons (74) did not describe the history of the shell-gland in *Umbrella mediterranea* in detail, but referred to its appearance close to the " anal cells." In a figure of a 24 days embryo he shows the gland as a pit. In a 31 days embryo the first rudiment of the shell is figured over the evaginated pit of the gland, and the mantle is beginning to be differentiated. In a 34 days embryo the shell-fold of the mantle can be distinguished, while the greatly flattened cells of the gland are spread over the surface of the embryonic visceral mass. Lacaze-Duthiers and Pruvot (94) described the various stages in the formation of the shell-gland or the preconconchylian invagination on the aboral pole of the embryo of *Philine*. The later stages in the evagination of the gland, the flattening of the cells and the formation of the mantle are also described. Viguier (170) did not trace the earlier stages in the development of the shell-gland in *Tethys*, but figured and described the invaginated gland, and referred to the role of the mantle in the secretion of the shell in the later stages. Casteel (26) carefully described all the earlier stages in *Fiona*. He found that at quite an early stage there is great activity in the area between the posterior limb of the " cross " and the blastopore, and the cells on the posterior and upper surface of the gastrula are specially high. The centre of the area is then invaginated and the lower wall of this pit pushes the enteron below it. With the growth of the lower part of the invagination its margins become greatly constricted above and are distinguished by a ring of large granular cells. Shortly afterwards the invaginated area opens outwards and forms a thick-celled cap on the posterior surface of the veliger larva. The gland also spreads with the growing larva and its cells become much flatter, while the shell appears on its surface. The cells along the margin of the area, which are specially concerned with the secretion of the shell, are marked by their large size and apparently represent the mantle-anlage. He found that from a very early stage the shell-gland is displaced slightly to the left of the body, and with its growth the lack of bilateral symmetry becomes marked in the developing larva.

Fol's work (56a) on Pteropods, noticed already, may be briefly reviewed here. He observed that the shell-gland is formed as a pit on the aboral pole of the embryo. Later the pit is everted and its cells become flattened except along the margins where they form the mantle. The shell is secreted shortly before the evagination of the pit and is supported by the thickened mantle zone. In all Pteropods a shell is secreted in the embryonic stage even though it is absent in many forms in later life.

Pulmonata.—Gegenbaur (61) did not describe the earlier stages in the development of the shell-gland, but gave a good account of the later stages in *Limax* and *Clausilia.* In the earlier stages the shell in both genera is enclosed in a sac. In *Limax,* which has an internal shell throughout its life, the sac remains closed, but in *Clausilia* Gegenbaur found that the shell becomes external by the disappearance of the dorsal wall of the shell-sac and the mantle which lie over it. Heider (88) explained this peculiarity of an internal shell in *Clausilia* by supposing that a small opening, not noticed by Gegenbaur, probably persists in the roof of the shell-sac, thereby implying that the sac is not fully closed at any time of its development, and added that in this case the shell-gland does not evaginate till late in life. Schmidt (150) investigated the development of *Limax, Clausilia* and *Succinea* and, though he did not deal with the very early stages, was able fully to confirm Gegenbaur's work. In *Clausilia* and *Succinea* he found that the shell-gland soon after its invagination is separated from the outer ectoderm as a closed sac lying between the outer mantle-covering and the dorsal wall of the intestine. He described the various stages in the development of the closed shell sac and found that the first shell is secreted inside it as a thin cuticular membrane. Later the dorsal wall of the sac fuses with the mantle wall over it, and in this fused membrane an opening appears. The shell protrudes through this aperture and gradually becomes an external structure. Schmidt inferred from these observations that probably in all Stylommatophora the first shell is formed in a closed sac, and that in those with an internal shell the gland throughout life remains a closed sac. In *Limax* Kofoid (86) described only the first appearance of the shell-gland as an area of ectodermal cells which are specially marked by their large size. Meisenheimer (115a, b) gave a detailed account of the shell-gland in *Limax.* He confirmed the work of Schmidt and stated that the earlier details in the development of the closed shell-gland of *Limax* are similar to those of other Gastropoda.

Jhering (80), in his paper on the embryology of *Helix,* strongly criticised Lankester's account of the structure which the latter author described as the shell-gland in the embryos of some molluscs and stated that the structure was the mantle-anlage. He described the embryonic shell, but did not specify the region by which it is secreted. Later (81) he corrected his mistake about the shell-gland and added that the area represents the shell-gland and the mantle-anlage.

Joyeux-Laffuie (83) described in *Oncidium* the " invagination coquillière " on the aboral pole of the embryo, but did not deal with the earlier stages in its development. He included an account of the formation of the mantle and the secretion of a coiled shell like that of other Gastropoda, which is thrown off during the embryonic period.

The work of Lereboullet (101), Ganin (59), Lankester (96, 98) and Fol (56, c) on freshwater Pulmonates has already been reviewed. Rabl (134) studied various freshwater genera, *Physa, Planorbis, Limnaea* and *Ancylus*, but gave a detailed account of the development only in *Physa*. Like many other authors he confused the invagination of the shell-gland with the anal invagination, but in his later paper on *Planorbis* (136) he correctly interpreted the structures and, agreeing with Lankester, Fol and Bobretzky, called the aboral invagination the shell-gland. He, however, remarked that it was impossible to understand the physiological significance of the early appearance of this structure. Wolfson (177) gave a lucid account of the formation of the shell-gland and the mantle in *Limnaea stagnalis*. He found that the shell-gland is differentiated in the gastrula stage on the aboral pole of the embryo as a flattening of the ectoderm, which later becomes invaginated. With the growth of the foot the invagination shifts towards the head-end. In older embryos the invagination everts and forms a watchglass-shaped structure which is the anlage of the shell-gland and the mantle. Holmes (75) studied the cell-lineage of *Planorbis*. He found that the shell-gland first appears on the aboral pole a short distance behind the tip of the posterior arm of the " cross " in the region of the cells of the second quartette soon after the closure of the blastopore. He added that the gland is doubtless formed by the derivatives of the cells *2d* $^{1\cdot2}$ and *2d* $^{2\cdot1}$. Wierzejski (173) did not deal with the formation of the shell-gland in *Physa* in detail, though he noted that it is derived from the *2d* cell. From his excellent figures it is clear that the later development of the shell-gland in *Physa* does not differ from that in other Gastropoda.

Scaphopoda.—Kowalevsky (90) described the larva of *Dentalium* as similar to the trochophore larva of the Annelida. The larva at an early stage develops the shell-gland on its dorsal surface as a thickening of the ectoderm. This plate-like thickening of ectoderm cells becomes invaginated and forms a cup-shaped cavity. Later, as in other molluscs, the cavity evaginates and spreads to form a saddle-shaped structure resembling the shell-gland of Lamellibranchs at this stage. A saddle-shaped shell is secreted by this gland, and the tubular shell of the adult results by the fusion of the ventral margins of the growing shell, as was previously described by Lacaze-Duthiers (93). The mantle originates from the margins of the saddle-shaped gland as in Lamellibranchs. Wilson (175) confirmed the work of Kowalevsky and from his account of the cell-lineage in *Dentalium* it is clear that the gland arises from the region of the posterior arm of the " cross," and from descendants of the somatoblast corresponding to *2d* in other molluscs.

Lammellibranchia. Protobranchia.—Drew (37) described in embryos of *Yoldia limatula* an unpaired shell-gland on the dorsal surface. Later the area is invaginated, but soon afterwards the sides arch upwards preparatory to protruding laterally to form the mantle. In older embryos the gland becomes localized at the edges where the cells remain large and granular, while further upwards they are flat like the cells of the mantle. The next stage shows the two valves of the shell secreted by the gland. In *Nucula delphinodonta*, according to Drew (38), the shell-gland is formed quite early on the dorsal side of the embryo near the head. Later the gland flattens slightly, but the edges remain raised and separated from the test, and at no stage it is really invaginated. In older embryos the gland, owing to the multiplication and flattening of its cells, arches upwards and comes to lie close to the test, while a space appears between it and the archenteron. The saddle-shaped structure which results from these changes begins to secrete the two valves of the shell on the two sides, and the mantle-folds are formed laterally by the growth of the lower edges of the saddle-shaped gland.

Filibranchia.—Barrois (4) shortly described the development of the shell-gland and the mantle in *Mytilus edulis,* and this species was also investigated by Wilson (176) without reference to Barrois's work. He described the shell-gland " as a distinctively refractive body near the velum " which has been often confused with the blastopore. He did not describe the later changes in detail, but noted that the gland soon assumes a bilateral form. Delsman (35) does not go into details about the shell-gland, but a more detailed account has since been published by Field (45).

Fullarton (58) referred to the shell-gland in *Pecten opercularis* as the preconchylian gland, but did not trace the earlier history. Drew (39) described the unpaired shell-gland anlage in *Pecten tenuicostatus,* and stated that its development is not different from that of other Lamellibranchs. The shell-gland is differentiated on the future dorsal surface and lies diammetrically opposite the stomodaeal invagination. In the invaginated stage the inner wall of the gland lies close to the upper wall of the archenteron, and later the gland begins to spread, evaginates and grows down on the two sides laterally to form the mantle.

Eulamellibranchs.—In the embryos of *Cyclas* or *Sphaerium* Stepanoff (163) correctly figured the shell-gland, but did not recognize its true nature for he called it the anlage of the mantle. Ganin (59) and Lankester (95, 98) independently worked out the true significance of the structure in *Sphaerium* and *Pisidium,* and connected it with the secretion of the embryonic shell and the formation of the mantle. Jhering (81) also correctly described the shell-gland in *Sphaerium,* but the most detailed account was published by Ziegler (178). According to Ziegler the gland is separated as a saddle-shaped invagination of the ectoderm on the dorsal surface of the embryo behind the head-rudiment. The invagination proceeds until its upper margins meet in the middle and then begins to evaginate and spread out. The first shell is now secreted, and Ziegler suggested that it is probably secreted by only the outer marginal cells of the area. He described the development of the mantle from the lateral margins of the gland and referred to its connection with the secretion of the two valves of the adult shell. He further remarked that the shell-gland of all Gastropoda and Lamellibranchia is similar in form and position.

Flemming (47) did not recognize the shell-gland in the early stages of the Unionidae, but later (48) considered the dark macromeres as probably representing the shell-gland. Rabl (135) confused the invagination of the shell-gland with the blastopore. Schierholz (148) confused the shell-gland with the invagination of the intestine, but later (149) described the unpaired shell-gland in the Unionidae and connected it with the secretion of the first shell and the formation of the mantle. Goette (63) critically reviewed the earlier work on the development of the Unionidae, and described the various stages from the thickening of the shell-gland plate, its invagination, evagination and flattening to form a saddle-shaped structure, which scretes the two shell-valves and forms the mantle on the two sides. Lillie (104), who studied the cell-lineage of the Unionidae, found that the shell-gland is derived from d^2 or the ectomere X, which he called the protoblast of the shell-gland. The shell-gland is formed as a plate of columnar cells by the repeated divisions of the ectomere, and its later development is the same as described by Goette.

Davaine (33) and Lacaze-Duthiers (92) noticed in the embryos of *Ostrea* a pit (*echancrure* or depression), which is the shell-gland, but did not understand its significance. Salensky (144) stated, and Fol (56, a) repeated that the shell-gland in *Ostrea* shows only a feeble excavation of the thickened epiblast and does not form a true invagination. Brooks (21) in *Ostrea virginica* confused the early stages of the invagination of the shell-gland with the blastopore, but correctly described the later stages. Horst (76, 77) gave a correct account of the shell-gland in *Ostrea edulis.* He found that the gland is formed on the animal pole as an invagination of the ectoderm. Later it is evaginated and is transformed into a saddle-shaped thickening. The first shell is unpaired and the mantle develops from the lateral extensions of the area. Meisenheimer (116) remarked that from a study of Horst's figures and descriptions that in some of the very early stages Horst, like the earlier authors, had confused the shell-gland and the midgut. Kent (84) figured some of the later stages in the development of the Australian rock-oyster (*O. glomerata*) but did not give details. Macbride (108) in the Canadian oyster referred to the development of the shell-gland which first appears on the back of the embryo as a pit and then flattens out and becomes saddle-shaped at the sides of which the first shell is formed as two calcareous particles. Stafford (161) gave a good summary of the previous work and confirmed the work of Horst to some extent. He, however, rightly added that most of the details about the shell and the shell-glands still remain to be worked out.

Hatschek (69) described in *Teredo* embryos a shell-gland in the preoral area, the development of which in the earlier stages is, according to the author, similar to that of Gastropods. The shell-gland is originally a flat plate, but later invaginates and forms a shallow sac which later evaginates and flattens out to form the mantle, and secretes the two shell-valves. In the earlier stages, as Meisenheimer (116) correctly pointed out, Hatschek had confused the anlage of the shell-gland with that of the midgut.

Meisenheimer (116) gave a detailed account of the development of the shell-gland in *Dreissensia polymorpha.* He found that as in the Unionidae and other Molluscs the shell-gland is derived from the first somatoblast *X*. It passes through the invagination and evagination stages similar to those of other bivalves and is unpaired in the young embryos. Its further development and the formation of the mantle proceed as in other Lamellibranchs.

Summary.—In all classes of molluscs, except the Cephalopods, the so-called shell-gland is differentiated shortly after gastrulation on the dorsal surface of the developing embryo. In various molluscs the cell-lineage of which has been followed, the gland is developed from the descendants of the first somatoblast or what is designated *2d* or *X* by different authors, and it may, therefore, be assumed that probably in all molluscs it is formed from the same region of the developing egg. The area of its appearance lies behind the velum near the end of the posterior limb of the "Molluscan Cross", and is formed of tall, cylindrical, probably glandular cells. At this stage the cells of this region are actively dividing, and as a result of this activity the central part of the area becomes concave and later invaginated as a cup-shaped structure.

The invagination is probably due to physical causes only. The cells in the area have greatly increased in numbers and must either spread over the adjoining regions or the plate bé invaginated as a cup. Space being available between it and the dorsal wall of the archenteron the latter course is adopted.

With the continued division of the cells, however, the invaginated part becomes too large for the available space, and evaginates forming a flattened plate over the postero-dorsal surface of the developing embryo. As a result of continued division most of the cells of the plate have by this time become thin and flattened, and only the marginal cells retain their original glandular character.[1] A thin cuticular shell has meanwhile been secreted over the area ; it is separated from the plate of cells in the greater part of its surface but is embedded along the margins in the thick marginal zone. There is no general agreement as to the region which secretes the first rudiment of the shell. Lankester, Fol, Bütschli and Erlanger have in *Viviparus*, *Aplysia* and some Pteropods and Heteropods described a chitinous plug filling up the cup of the invaginated gland. Fol in some of the Heteropods definitely described this chitinous structure as spreading over the invaginated pit, and forming the first shell. No such structure has, however, been described in the large majority of other molluscs, the embryology of which has been carefully investigated, and it seems doubtful whether the formation of the first rediment of the shell takes place in the way suggested by Fol. In *Sphaerium*, Ziegler was of opinion that probably only the marginal zone, which also forms the shell-secreting zone of the adult, secretes the first shell. This view seems to be more in accord with the general conditions and is the one suggested by the accounts of several of the more recent workers.

The main part of the area, *viz.*, the central part consisting of thin flattened cells, form the outer covering of the visceral mass of the adult in the Gastropods, and the upper part of the mantle-flaps in the Lamellibranchs and Scaphopods. The marginal zone consisting of the tall, glandular cells is transformed into the mantle and is mainly responsible for the production of the adult shell.

The two names usually employed for this embryonic structure *Shell-gland* (Lankester) and *l'invagination préconchylienne* (Fol) are in view of the above conclusion quite inappropriate.

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[1] The condition of a fully closed sac-like gland in the Stylommatophora is secondary and is not considered here.

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10. REFERENCE LETTERING.

The following reference lettering is the same for all the plates. *B. W.*, Body-whorl of the shell ; *C. C.*, Calcareous particles in the connective tissue ; *C. E.*, Ciliated epithelium ; *C. S.*, Calcosphaerites ; *C. T.*, Connective tissue ; *G. C.*, Gland cells of the supramarginal ridge ; *G. M. P.*, Groove of the marginal processes of the mantle as seen in sections ; *G. P.*, Groove of the marginal processes ; *H.*, Hypostracum ; *M.*, Muscle fibres ; *M.E.*, Epithelial covering of the dorsal surface of the mantle ; *M. P.*, Marginal process of the mantle ; *N.*, Nucleus ; *O.*, Ostracum ; *P.*, Periostracum ; *Pi.*, Pigment granules ; *P. S.*, The first periostracal elements of the shell ; *R.*, The longitudinal spiral ridges of the mantle surface ; *S.G.*, Supramarginal groove ; *S. P.*, Secondary processes of the mantle margin ; *S.R.*, Supramarginal ridge ; *X.*, The undifferentiated epithelial region of the supramarginal ridge ; 1—3, The three primary processes of the mantle margin.

EXPLANATION OF PLATE XX.

Fig. 1. *Viviparus bengalensis* (Lam.), from Calcutta. A part of the mantle margin of a full-grown individual from the right half, seen as a transparent object. It shows the well developed primary process and the remains of a number of secondary marginal processes. × 5.

Fig. 2. *V. viviparus* (Linn.), from near Manchester. A vertical section of the mantle margin of a young embryo showing the supramarginal ridge and the groove. × 300.

Fig. 3. *V. viviparus* (Linn.). The region of the supramarginal ridge and groove as seen in a vertical section of an adult. It shows the structure of the gland cells of the groove, the more highly modified gland cells of the supramarginal ridge, the calcareous globules lying near the bases of the gland cells in the connective tissue and the arrangement of the muscle fibres in the connective tissue. × 240.

Fig. 4. *V. bengalensis* (Lam.). A vertical longitudinal section of the margin of a half-grown individual parallel to the margin showing the grooves of the marginal processes as seen in a transverse section. × 50.

Fig. 5. *V. viviparus* (Linn.). The gland cells of the supramarginal ridge as seen in a vertical longitudinal section. Some of the less differentiated cells on the sides of the gland cells are also shown; they apparently later replace the degenerated gland cells. × 550.

Fig. 6. *V. fasciatus* (Müll.), from near Manchester. A vertic[illegible] the corresponding region of the mantle margin of an embryo to that in figure 3, t[illegible] manner in which the undifferentiated cells of the embryonic supramarginal ridge [illegible] formed into the gland cells of the region. × 240.

Fig. 7. *V. fasciatus* (Müll.). A vertical section of the mantle margin of the adult in the region corresponding to that in figure 2, to show the structure of the gland cells and the arrangement of the muscle fibres. × 240.

Fig. 8. *V. delavayana* (Heude), from Saifu, China. A vertical section of the mantle margin of an adult in the region corresponding to that in figure 3, and showing the supramarginal ridge and groove, the calcareous globules and the connective tissue. × 240.

Fig. 9. *Dactylochlamys oxytropis* (Benson), from Loktak Lake, Manipur. A vertical section of the mantle margin of an embryo showing the more extensive region of the gland cells of the supramarginal ridge than is the case with *Viviparus s. s.*; the basal parts of some of the cells from the neighbouring areas are arranged in separate masses. × 300.

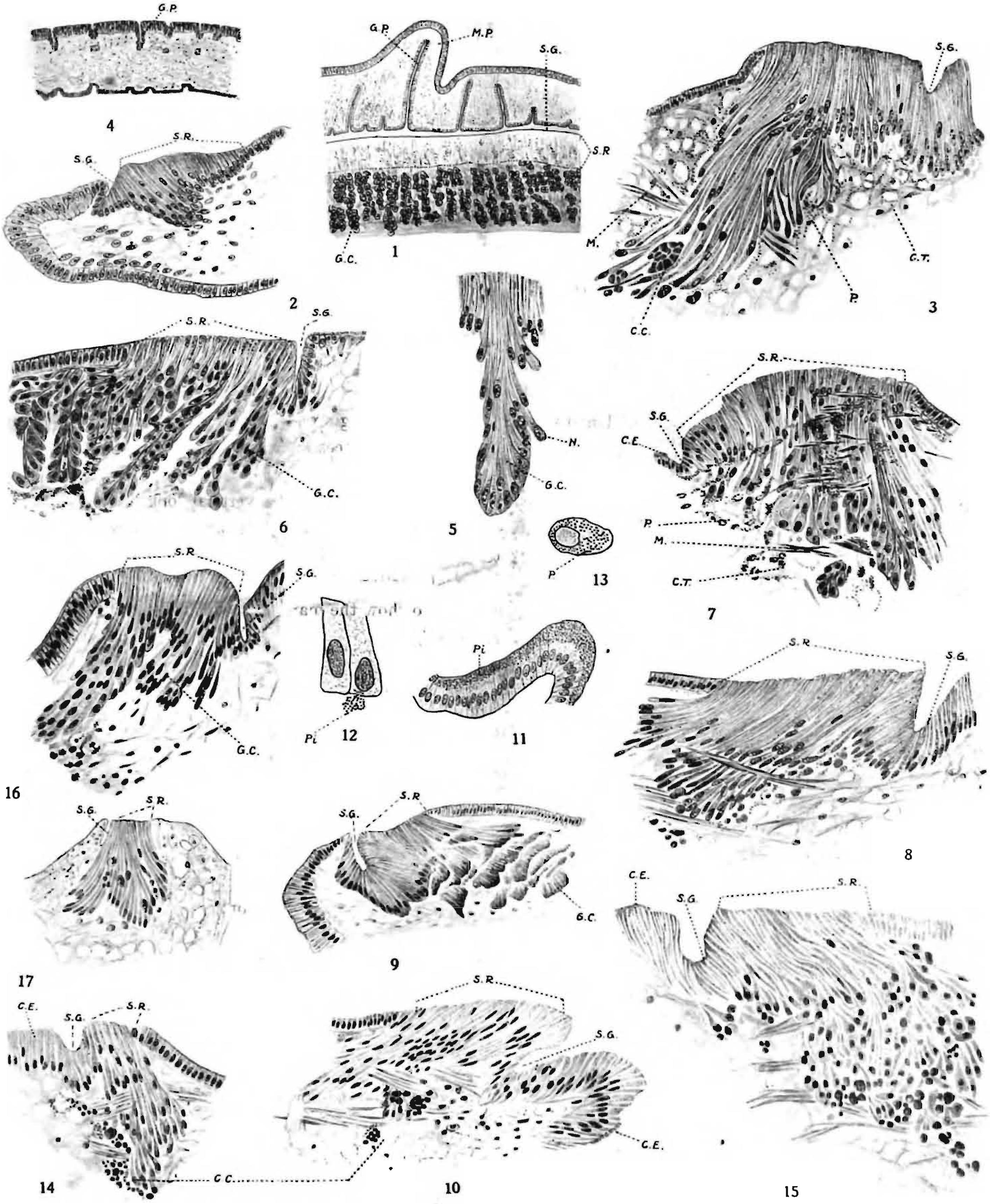
Fig. 10. *D. oxytropis* (Benson). A vertical section of the mantle margin of the adult to illustrate the structure of the area corresponding to that shown in figure 3. × 2[illegible]0.

Fig. 11. *D. lanaonis* (Bartsch) var. *theta* (Bartsch), from Lake Lanao, Philippin[illegible] The dorsal epithelial covering of the mantle surface from the region of the colour-ba[illegible] showing the pigment granules in the upper third to half of the cells. × 250.

Fig. 12. *D. lanaonis* (Bartsch) var. *theta* (Bartsch). Two of the cells of the dorsal epithelial covering of the mantle more highly magnified, and showing the passage of the pigment granules from the connective tissue into one of the cells. × *ca.* 750.

Fig. 13. *D. lanaonis* (Bartsch) var. *theta* (Bartsch). A chromatophore with its nucleus containing only a few feebly staining chromatin particles and the plasma with numerous pigment granules. × *ca.* 750.

Fig. 14. *Taia intha* Annandale, from Inlé Lake, S. Shan States. A vertical section of the mantle margin of an adult in the region corresponding to that shown in figure 3. × 240.



MANTLE OF VIVIPARIDAE.

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EXPLANATION OF PLATE XX—*continued.*

Fig. 15. *Margarya melanoides* Nevill, from Lake Tali, Yunnan. A vertical section of the mantle margin of an adult showing the very elongated gland cells of the supramarginal ridge, the large numbers of the calcareous globules lying near their bases, and the cells of the supramarginal groove. The nuclei of the cells lining the supramarginal groove could not be distinguished. × 240.

Fig. 16. *Tulotoma magnifica* (Conrad), from Coosa River, Alabama. A vertical section of the mantle margin of an embryo showing the supramarginal groove, the extensive supramarginal ridge and its elongated gland cells. × 240.

Fig. 17. *T. magnifica* (Conrad). A vertical section of the mantle margin of an adult showing the supramarginal groove ; the outlines of the cells lining it could not be made out in the sections. The gland cells of the supramarginal ridge are also somewhat degenerate. × 240.

EXPLANATION OF PLATE XXI.

Fig. 1. *Viviparus bengalensis* (Lam.). The last or the body-whorl part of the animal of a young embryo showing the three primary processes of the right side of the mantle margin, corresponding in position to the sutural, median and the peripheral ridges of the shell. × 20.

Fig. 2. *V. bengalensis* (Lam.). The mantle margin of a half-grown individual showing the three primary and four secondary processes; the latter are indicated by their grooves. × 6.

Fig. 3. *V. viviparus* (Linn.). The mantle margin of a young embryo showing the grooves of the three primary processes. × 10.

Fig. 4. *V. viviparus* (Linn.). The mantle margin of an older embryo than the one shown in the previous figure. It shows the well developed peripheral process, and traces of the first and second primary processes and the groove of a secondary. × 10.

Fig. 5. *V. pyramidalis* (Jan.) Rossmässler. The mantle margin of an embryo showing three finger-like primary processes. The condition in *V. fasciatus* (Müll.) and *V. duboisiana* (Mousson) is similar. × 10.

Figs. 6, 7. *V. javanica* (v. d. Busch). The mantle margins of an embryo (× 20), and an adult (× 10), showing a large number of primary, secondary and tertiary processes or their grooves; the latter are indicated as light lines between the dark areas. In the adult the peripheral process is the best developed, and lies about the middle of the field.

Fig. 8. *Cipangopaludina lecythis* (Benson). The mantle margin of a full-grown embryo showing the well developed peripheral process, and grooves of the other primary and secondary processes. × 10.

Fig. 9. *C. chinensis* (Gray). The mantle margin of a young embryo showing the three well developed primary processes. × 20.

Fig. 10. *C. chinensis* (Gray) var. *fluminalis* (Heude). The corresponding region of an embryo of about the same age as the one shown in figure 9. × 20.

Fig. 11. *C. chinensis* (Gray) var. *diminuta* (Heude). The corresponding region of an embryo of about the same age as the ones in figures 9, 10. × 20.

Fig. 12. *V. delavayana* (Heude). The mantle margin of a full-grown embryo showing the well developed primary processes and grooves of some secondary ones. × 10.

Fig. 13. *V. dissimilis* (Müll.). The mantle margin of a young embryo showing three well developed primary processes of the right side, and two secondary ones of the left. × 10.

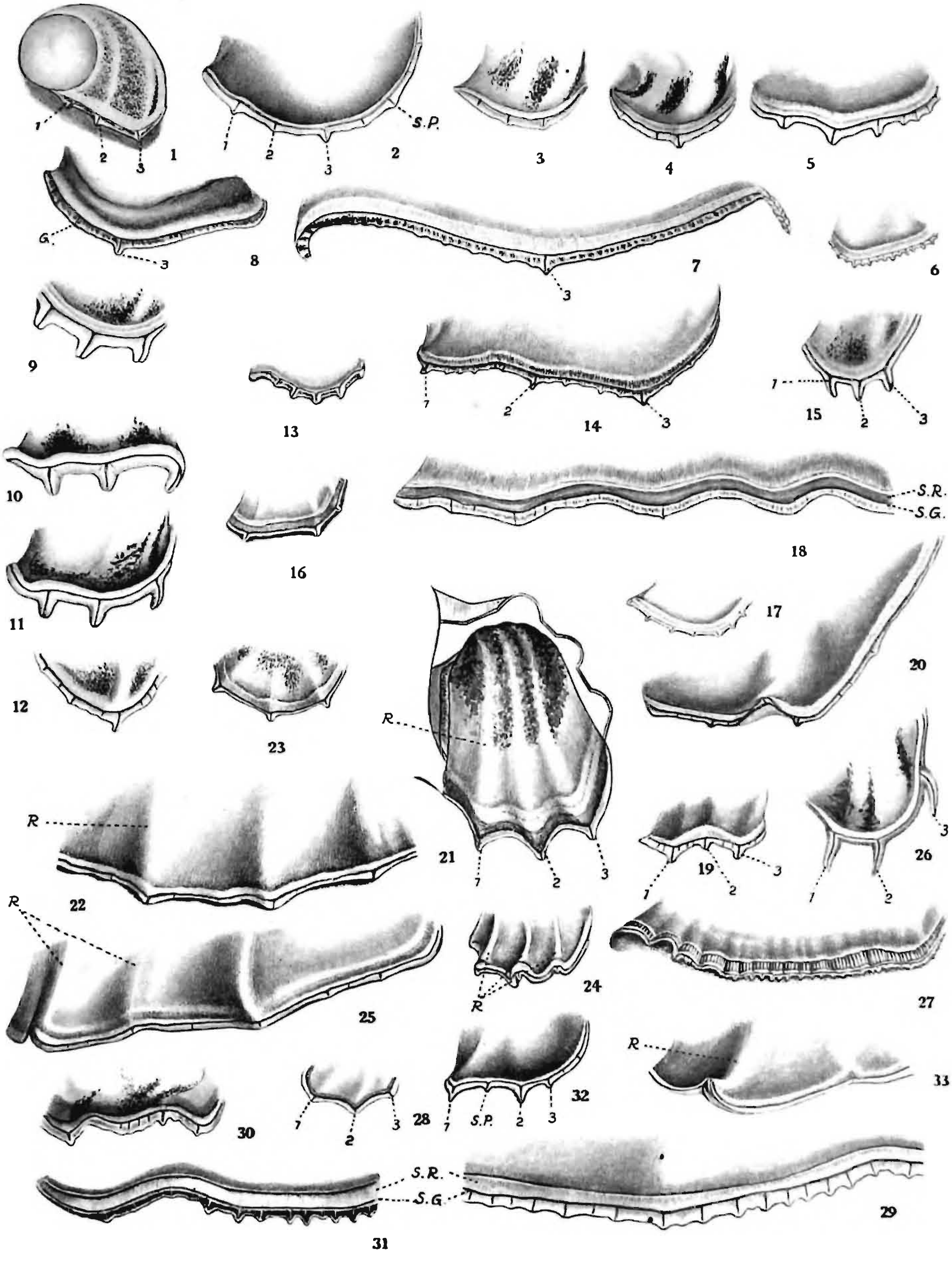
Fig. 14. *V. dissimilis* (Müll.). The mantle margin of a half-grown individual showing three well developed primary processes, and a number of secondary ones both to the right and the left of the peripheral. × 8.

Fig. 15. *V. quadratus* (Benson). The mantle margin of an embryo with well developed primary processes. × 20.

Fig. 16. *Taia crassicallosa* Annandale & Rao. The right half of the mantle margin of a young embryo with the three primary processes. As a result of contraction the peripheral appears to be the smallest of the three primary processes. × 20.

Fig. 17. *T. intha* Annandale. Embryonic mantle margin showing a number of processes along the edge. × 20.

Fig. 18. *T. intha* Annandale. The mantle margin of an adult showing the greatly contracted primary processes indicated by their grooves, and some secondary processes. × 10.



MANTLE OF VIVIPARIDAE.

LICHTDRUCK VON J. B. OBERNETTER, MÜNCHEN

EXPLANATION OF PLATE XXI—*continued.*

Fig. 19. *Dactylochlamys oxytropis* (Benson). The mantle margin of a full-grown embryo showing the three finger-like primary processes of the right side; the median or the second is a little contracted. × 10.

Fig. 20. *D. oxytropis* (Benson). The mantle margin of an adult showing three contracted primary processes of the right side, and traces of two of the left side. × 8.

Fig. 21. *D. lanaonis* (Bartsch). The mantle and the aperture area of the shell of an embryo showing the three hollow channels corresponding to the spiral ridges on the mantle; the latter are directly continued from the three primary processes. × 10.

Fig. 22. *D. lanaonis* (Bartsch). The right half of the mantle of an adult showing the contracted primary processes on the margin, the supramarginal ridge, the groove and its connections with the grooves of the processes. × 8.

Fig. 23. *D. lanaonis* (Bartsch) var. *theta* (Bartsch). The mantle margin of an embryo showing the three primary processes; the ridges in connection with these are also indicated on the mantle surface. × 10.

Fig. 24. *D. pagodula* (Bartsch). The mantle margin of a young embryo showing three well developed spiral ridges on the mantle surface in continuation of the primary processes of the margin; the latter are somewhat contracted. × 10.

Fig. 25. *D. pagodula* (Bartsch). The mantle margin of an adult showing the highly developed spiral ridges of the mantle surface and the contracted primary processes; traces of two secondary processes of the left side are also seen. × 8.

Fig. 26. *D. costatus* (Quoy and Gaimard). The mantle margin of a young embryo showing three well developed primary processes of the right side. × 20.

Fig. 27. *D. costatus* (Quoy and Gaimard). The mantle margin of an adult showing its greatly pleated or ridged surface, and traces of a large number of processes. × 8.

Fig. 28. *V. sambesiensis* Sturany. The mantle margin of a very young embryo showing the first indications of the three primary processes. × 20.

Fig. 29. *V. sambesiensis* Sturany. The mantle margin of an adult, which, owing to the large number of almost equally developed processes all along the margin, appears crenated. × 8.

Fig. 30. *Neothauma tanganyicense* (Smith). The right half of the mantle margin of a young embryo showing three primary processes, and traces of some secondary ones. × 20.

Fig. 31. *N. tanganyicense* (Smith). The mantle margin of an adult showing the rudiments of some processes of the right side, and a number of processes of the left side. × 8.

Fig. 32. *Tulotoma magnifica* (Conrad). The mantle margin of an embryo showing the three primary and a secondary process of the right, and traces of others of the left side. The ridges corresponding to the sutural and median ridge of the shell are also seen. × 20.

Fig. 33. *T. magnifica* (Conrad). The mantle margin of an adult showing traces of the primary processes and the spiral ridges corresponding to the sutural and median ridges of the shell. × 8.

EXPLANATION OF PLATE XXII.

Fig. 1. *Viviparus fasciatus* (Müll.). A vertical longitudinal section of a full-grown embryo to show the relationships of the mantle to the other structures of the animal. × 23.

Fig. 2. *V. fasciatus* (Müll.). The mantle margin in the same section as in figure 1 more highly magnified to show the relationships of the supramarginal ridge and its gland cells, the supramarginal groove and its connection with the groove of the marginal process. × 260.

Fig. 3. *V. fasciatus* (Müll.). A vertical section of the mantle margin of an embryo next to the region of a primary process. × 170.

Fig. 4. *V. fasciatus* (Müll.). A vertical section of the mantle margin of an adult showing the modified gland cells and the undifferentiated area of cells of the supramarginal ridge, the groove and the connective tissue. × 40.

Fig. 5. *V. fasciatus* (Müll.). The area of the supramarginal region in fig. 4 more highly magnified to show the arrangement of the gland cells, the undifferentiated cells, and the connective tissue with its inclusions. × 380.

Figs. 6, 7. *V. faiscatus* (Müll.). The basal parts of the gland cells in fig. 5 more highly magnified to show the structure of the gland cells; the structure of the connective tissue elements in this region is also to be seen. × 760.

Fig. 8. *V. fasciatus* (Müll.). The area near the basal parts of the gland cells showing the masses of calcareous globules in the connective tissue. × 1140.

Fig. 9. *V. viviparus* (Linn.). The region corresponding to that shown in fig. 8, and showing the calcareous globules. × 1140.

Fig. 10. *V. viviparus* (Linn.). A part of the section shown in fig. 9, showing the structure of the connective tissue, chromatophores and pigment granules. × 1140.

Fig. 11. *V. viviparus* (Linn.). A vertical section of the mantle margin of an adult showing the supramarginal ridge, the groove and the gland cells; the section is somewhat torn in the region of the groove. × 380.

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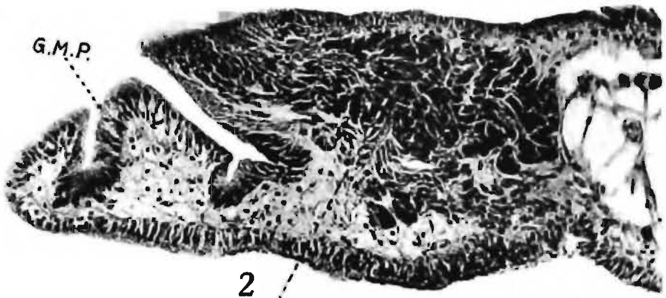

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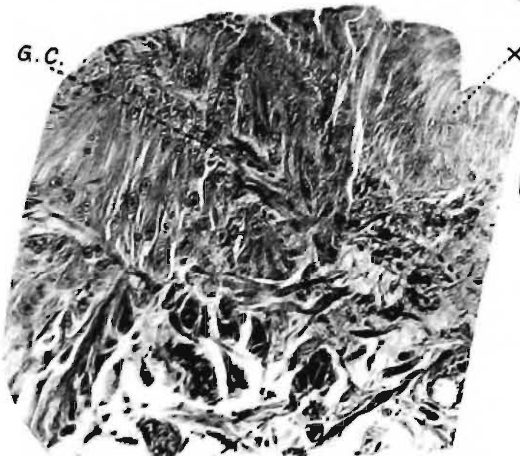

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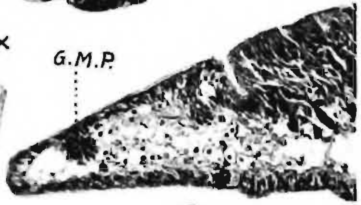

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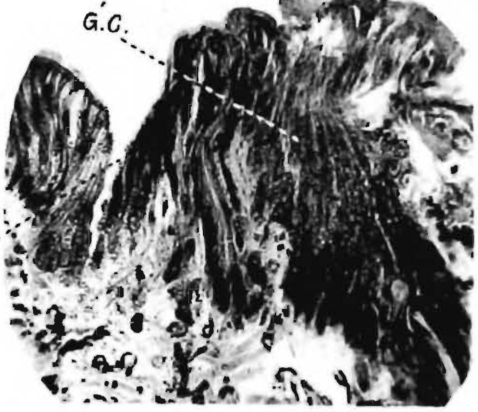

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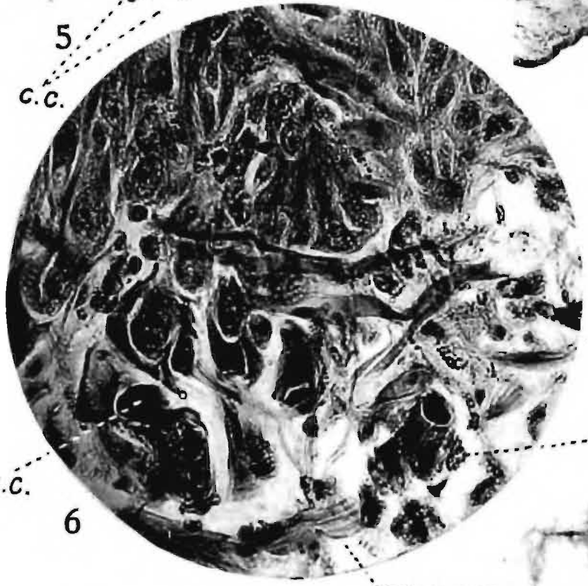

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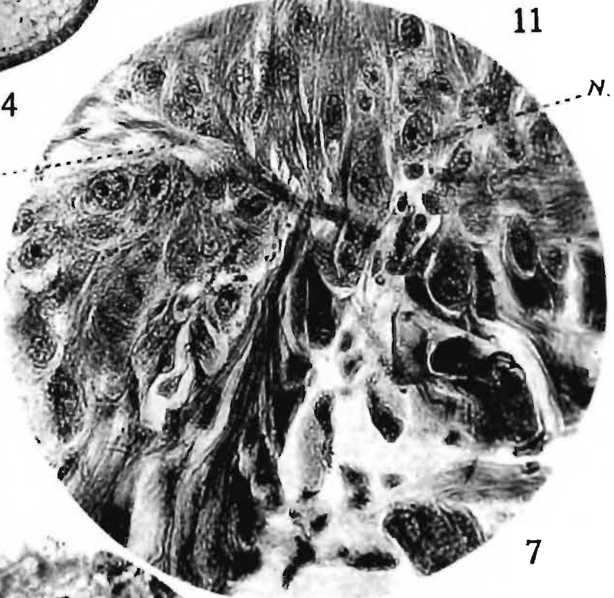

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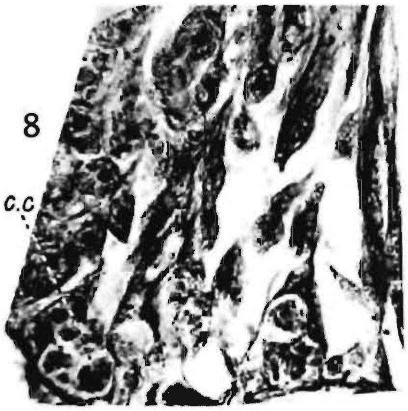

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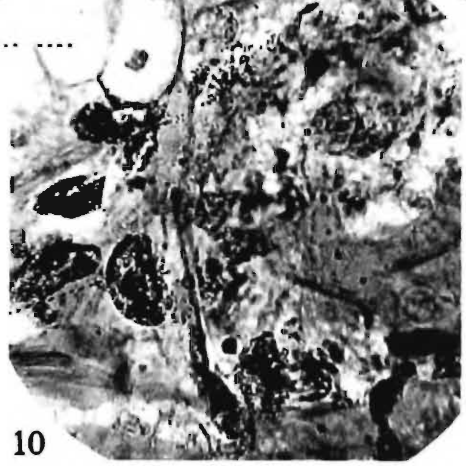

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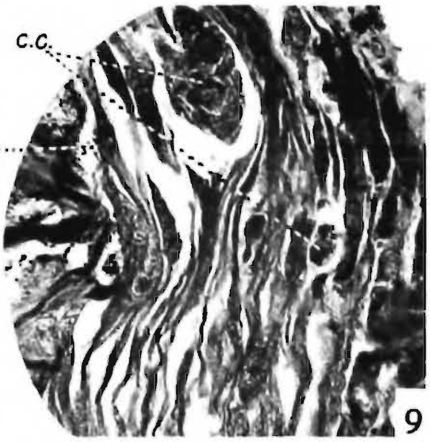

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MANTLE OF VIVIPARIDAE.

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EXPLANATION OF PLATE XXIII.

Fig. 1. *Viviparus viviparus* (Linn.). A vertical section of the mantle margin of a young embryo showing the extensive embryonic supramarginal groove, and the first secreted elements of the periostracal shell. × 760.

Fig. 2. *Dactylochlamys lanaonis* (Bartsch) var. *theta* (Bartsch). A vertical section of the mantle margin of an adult showing the basal parts of the gland cells of the supramarginal ridge, the calcareous globules, pigment granules, connective tissue, muscle fibres and the epithelial covering of the dorsal surface of the mantle. × 380.

Fig. 3. *V. delavayana* (Heude). A vertical section of the mantle margin of an adult showing the regions of the supramarginal ridge, the groove and the adjacent areas. × 380.

Fig. 4. *Taia intha* Annandale. A vertical section of the corresponding region of the mantle margin to that shown in fig. 3. × 380.

Fig. 5. *Cipangopaludina lecythis* (Benson). A vertical section of the mantle margin of an adult. The section is not complete and the areas of the supramarginal ridge and groove are not clearly defined, but it shows the extensive area occupied by the gland cells of the supramarginal ridge, and the calcosphaerites in the connective tissue. The arrangement of the muscle fibres is also clearly seen. × 210.

Fig. 6. *Margarya melanoides* Nevill. A vertical section of the mantle margin of an adult showing the supramarginal ridge, the groove and the extensive area occupied by the gland cells of the former. × 210.

Fig. 7. *V. viviparus* (Linn.). A drawing of a part of the periostracum of an embryonic shell showing the arrangement of the elements by which it is formed. × 250.

Fig. 8. *V. viviparus* (Linn.). A photograph of the ostracum of the shell from above, showing the arrangement of its plates; these run at right angles to the margin of the aperture. × 50.

Fig. 9. *V. viviparus* (Linn.). A photograph of the hypostracum of an adult shell seen from above, showing the arrangement of its plates; these run almost parallel to the margin of the aperture. × 50.

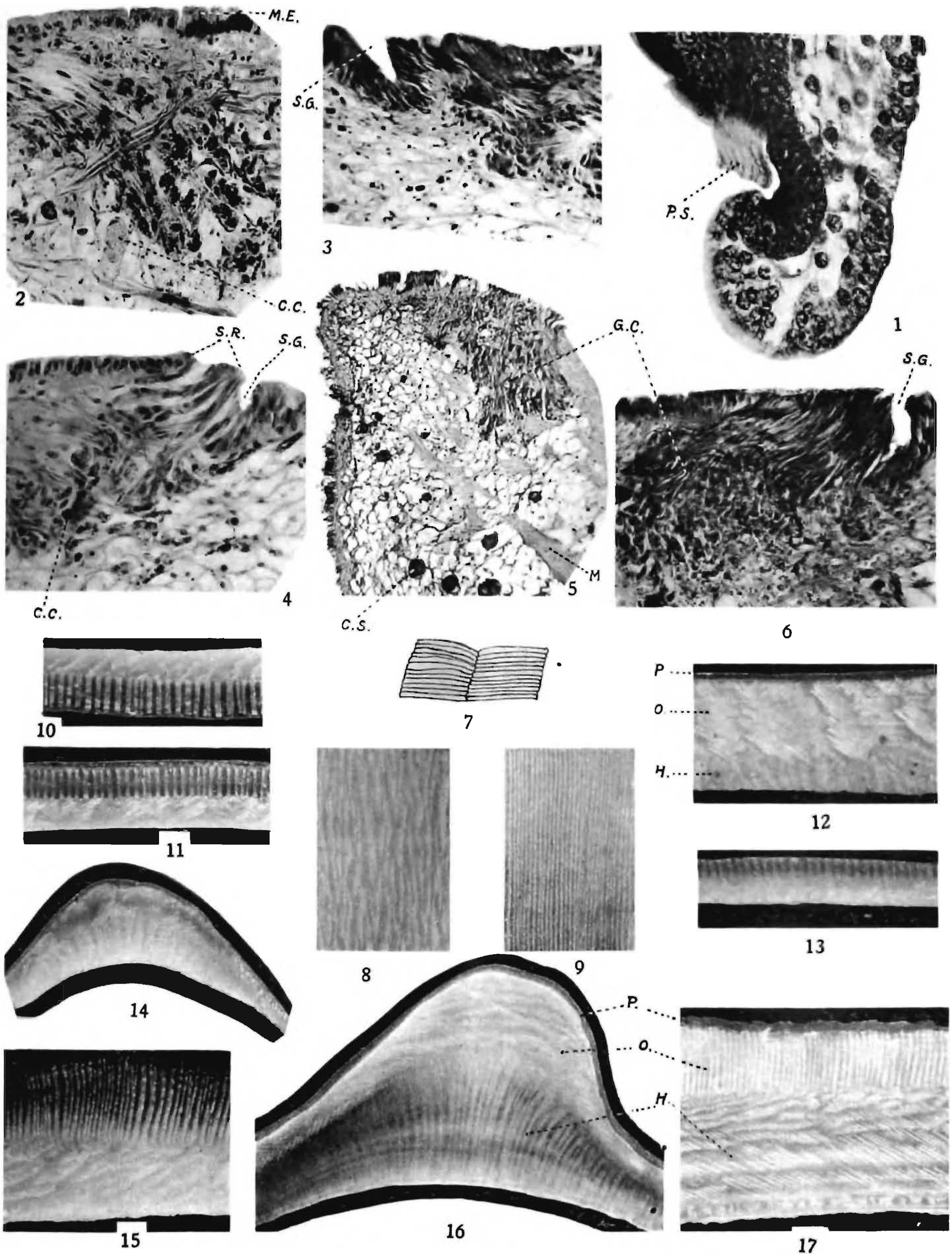
Fig. 10. *V. bengalensis* (Lam.). A section of the shell parallel to the margin of the aperture showing the ostracal plates running at acute angles to the surface of the shell, and those of the hypostracum arranged in almost vertical pillars. The periostracal layer is not preserved in the section. × 50.

Fig. 11. *V. bengalensis* (Lam.). A section of the shell at right angles to the margin of the aperture, show ing the ostracal and hypostracal zones. The arrangement of the plates in the two zones presents an almost reversed picture of that seen in the section parallel to the margin, in figure 10. × 50.

Figs. 12, 13. *Cipangopaludina lecythis* (Benson). Sections of the shell parallel to and at right angels to the margin of the aperture of the shell, and corresponding to those reproduced in figs. 10, 11. × 50.

Figs. 14, 15. *Dactylochlamys oxytropis* (Benson). Sections of the shell in planes corresponding to those of figs. 10, 11. Figure 14 shows a hollow ridge markedly concave on the inner surface of the shell while the section in fig. 15 was taken through the area between the sutural and the median ridges. × 50.

Figs. 16, 17. *D. lanaonis* (Bartsch). Sections of the shell in planes corresponding to those of the sections in figs. 10, 11. Figure 16 shows the arched ostracal plates filling up the greater part of the concavity of the hollow ridge. The forking of the hypostracal plates at their upper ends is also well seen in the same figure. The thick periostracal layer and the arrangement of the plates of both the ostracal and the hypostracal zones are very clearly seen in fig. 17. × 50.



MANTLE AND SHELL OF VIVIPARIDAE.

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EXPLANATION OF PLATE XXIV.

Fig. 1. *Viviparus boettgeri* Kobelt. A section of the shell parallel to the margin of the aperture showing the periostracum, the very thick ostracal zone and the rather feebly developed hypostracum as seen in the regions of the solid ridges of the shell of this species. The inner surface of the shell in the region of the solid ridges also is almost flat and not concave as in the case of the hollow-ridged species like those figured on plate xxiii. × 50.

Fig. 2. *V. boettgeri* Kobelt. Section of the shell at right angles to the margin of the aperture. The section is through one of the spaces between the solid ridges; the relative difference in the thickness of the ostracal and hypostracal zones is not so marked in these areas. × 50.

Figs. 3, 4. *Rivularia auriculata* (von Martens) var. *bicarinata* Kobelt. Sections of the shell in planes corresponding to those of the sections in figs. 1, 2. The greatly branching ostracal plates arranged in almost vertical pillars, and alternately appearing light and dark, owing to the arrangement of the bundles of fibrils, are clearly seen in fig. 3. × 50.

Figs. 5, 6. *Dacylochlamys persculptus* (P. and F. Sarasin). Sections of the shell parallel to and at right angles to the margin of the aperture of the shell; the second section is slightly oblique, and helps in interpreting the different appearance of the plates of the two zones in sections along different planes. Figure 5 shows the structure of the semi-solid ridges on the shells of this species, and the important part played by the ostracal zone in the formation of the ridges. × 50.

Fig. 7. *D. persculptus* (P. and F. Sarasin). Section of the shell through the penultimate and the body-whorl parallel to the margin of the aperture; the section is a little oblique. It shows the periostracum between the two whorls, and the arrangement of the plates of the various layers of the two zones. In the case of the body-whorl only a part of the section is shown in the figure. × 50.

Figs. 8, 9. *Taia naticoides* (Theobald). Sections of the shell in planes corresponding to those of sections in figs. 1, 2. The section in fig. 9 is through one of the scaly tubercles of the shell, and shows that it is formed by the periostracum and the ostracum; the periostracal layer on the inner surface of the tubercle shows the manner in which the secretion of the shell becomes connected with the already secreted regions of the shell in successive periods of activity. × 50.

Figs. 10, 11. *T. crassicallosa* Annandale and Rao.Sections of the shell in planes corresponding to those of sections in figs. 1, 2. The section in fig. 11 shows two scaly tubercles lying immediately one above the other, and the periostracal layer on the lower surfaces of the scales. The section in fig. 10 is in front of one of the tubercles, and a part of the ostracal zone in it is peeled off. × 50.

Figs. 12, 13. *T. crassicallosa* Annandale and Rao. The ostracal and hypostracal plates in fig. 11 more highly magnified, and showing the arrangements of the plates of the two zones and their connections with one another, as seen in a thin section by transmitted light. × 180.

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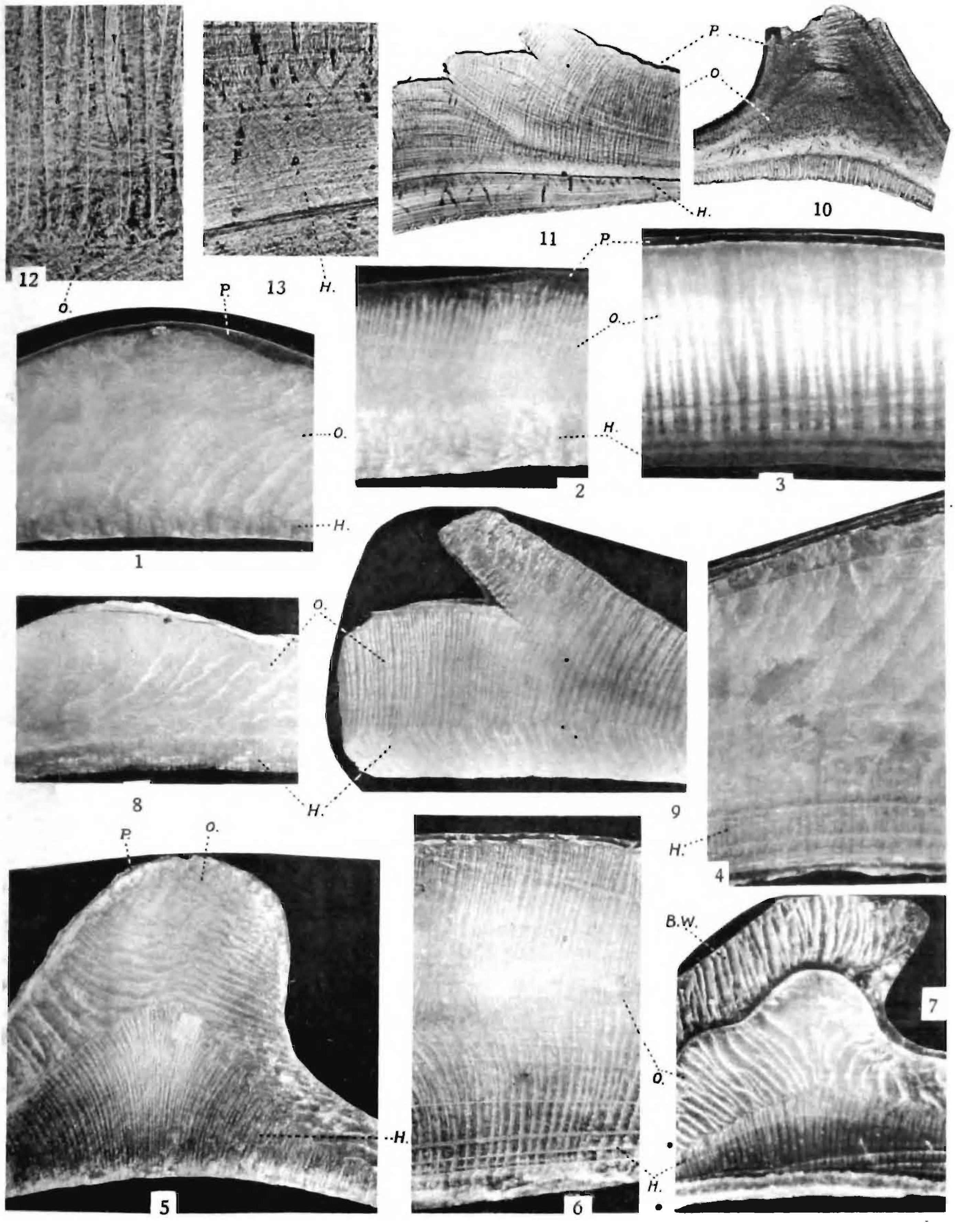

SHELL OF VIVIPARIDAE.

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