THE EVOLUTION OF THE EXCRETORY SYSTEM IN CERTAIN GROUPS OF THE FURCOCERCOUS CERCARIAE.

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(Plates IX—XII.)

Within the last few years numerous workers have added very materially to the sum total of our knowledge of the detailed structure of a number of furcocercous cercariae and we are now in a position to attempt a systematic grouping of the various species based on the characteristics of their excretory systems.

In 1922 I attempted a classification of the furcocercous cercariae and created a number of groups in accordance with the number of flame-cells in the body and tail-stem. Since the publication of this paper, Miller (1926 and 1927) has attempted a further subdivision of certain of these groups and has created others to accommodate new species. This author now sub-divides the furcocercous cercariae into two main divisions according as a pharynx is present or absent. These two main divisions, Pharyngeal and Apharyngeal, are again split up into (*a*) those that possess long furcal rami, these being longer than one-half the length of the tail-stem, and this group he terms the Longifurcate group; and (*b*) those that have short furcal rami, the Brevifurcate group, the furcal rami in these instances being shorter than one-half the length of the tail-stem. This latter group, however, in the light of more recent discoveries requires modification, for, as Miller himself has shown in a recent paper (*vide infra*, p. 363), certain cercariae, that in all other characters agree with and belong to the Brevifurcate group, actually possess furcal rami that are slightly longer than half the tail-stem. Finally, a further subdivision of these groups is based on the presence or absence of an acetabulum; we thus have Monostome and Distome groups, but it must be borne in mind that the absence of an acetabulum in the larval stage may be due merely to a retarded development of this organ and does not necessarily imply that such a form will develope into a Monostome adult. We can thus recognise the following main divisions:—

- Pharyngeal
  - Brevifurcate
    - Distomes
    - Monostomes (no known representatives)
  - Longifurcate
    - Distomes
    - Monostomes
- Apharyngeal
  - Brevifurcate
    - Distomes
    - Monostomes
  - Longifurcate
    - Distomes
    - Monostomes

Each of these last sub-groups can be still further sudivided by the presence or absence of some other organ, such as eyes, by differences in the number or the staining reactions of the so-called Salivary or Penetration Gland cells, the character of the digestive system or by the different number and arrangement of the flame-cells in the excretory system. Miller himself (1926) in his classification of the Brevifurcate Distomes made use of the number of flame-cells present in the body and tail to distinguish between the various sub-groups; but I would here emphasise that a similar number of flame-cells in the body and tail does not necessarily indicate a close relationship. It is also necessary to know the exact manner in which the ducts unite with each other and with the anterior and posterior collecting tubules. As Cort and Brooks (1928, p. 203) have pointed out "The definite determination of the connections of each capillary becomes of the greatest importance in interpreting the pattern of the system", and only when the pattern of the whole system is identical are we justified in placing different species of cercariae in the same sub-group of the whole series. Faust (1926, pp. 106-107) in his study of the South African Larval Trematodes, and especially of those cercariae that belong to the Apharyngeal Brevifurcate Distome series, has reached the conclusion that "the essential differentiating features of the Apharyngeal fork-tailed Cercariae consisted not in the digestive, excretory or genital organs but in the number or micro-chemical reactions of the secretory cells." While agreeing that this is so, so far as the specific identification of cercariae *belonging to the same sub-group* is concerned, it must not be overlooked that there are several distinct sub-groups among the Apharyngeal Brevifurcate cercariae and that these sub-groups are distinguished from one another by the pattern and number of flame-cells in the excretory system.

In the following pages I have attempted to trace the evolution of the excretory system in certain groups of the furcocercous cercariae. It has not been possible to include all the known furcocercous cercariae in the schemes of evolution that I have drawn up; a case in point is *Cercaria indica* II, in which the anterior collecting tube receives capillaries from three flame-cells, while the posterior tubule is connected with seven flame-cells in the body and an eighth in the tail-stem, all of which, if my original observations were correct (*vide* Sewell, 1922, p. 271, pl. xxix, fig. 4), open separately; it is, however, possible that I was mistaken, and until further observations have been made the position of such a form must remain a matter of doubt. A similar case in point is *Cercaria bombayensis* No. 9 in which Soparkar (1921, p. 26, pl. iv, figs. 1, 3) has indicated the presence of an excretory system in which there are six flame-cells opening independently into the anterior collecting tubule and six into the posterior collecting tubule, two of these latter being situated within the tail-stem. *Cercaria gigas* Faust also appears to differ from most other cercariae of the Brevifurcate series by a similar independent connection of some of the flame-cells with the collecting tubules. In this species there are six flame-cells opening into the anterior and three into the posterior tubule, while, in addition, there is a single flame-cell that opens into the main collecting tube and another in the tail that is directly connected with the caudal excretory canal. Faust himself (1919, p. 331) remarks that so far as the excretory system is concerned this species appears to be unrelated to any of the other species with which he was dealing in the paper under consideration. The presence of flame-cells that are not in any way connected with the anterior or posterior collecting tubules but open either into the main collecting tube, as mentioned above, in *Cercaria gigas* or into the caudal excretory canal, as in *Cercaria gigas*, *C. allahabadii* Chatterjee and *Cercaria* sp. Hesse, seems to indicate that in certain cases the original primary connection of these flame-cells may be lost and secondary connections be established. The occurrence of isolated examples of this phenomenon does not, however, in any way invalidate the suggestion that the usual line of development occurs by and through the successive division of individual pairs of flame-cells.

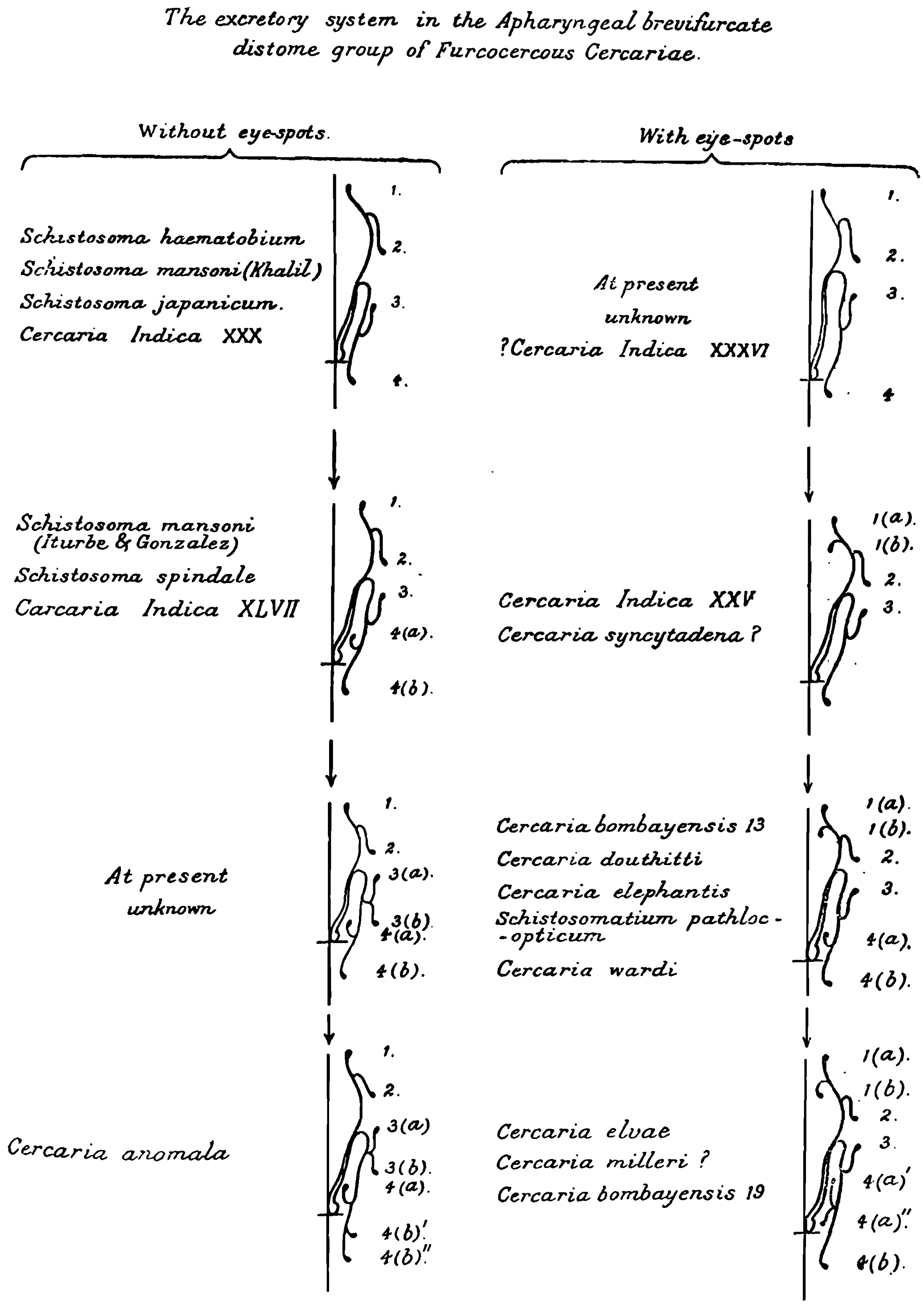
In all the series that I have examined we appear to start with a primitive form in which there are four flame-cells on each side of the body, three being in the distome body itself and the fourth in the tail-stem; these four cells are so arranged that two open into the anterior collecting tube and two into the posterior. Faust (1919) has attempted to represent graphically by means of letters the various systems present in certain groups of the cercariae; thus for the excretory system of the cercaria of *Schistosoma japonicum* Kats., in which the system is of the primitive type and consists of four pairs of flame-cells, two connected with each anterior collecting tube and two with the posterior, his formula is $\alpha+\beta$. In the same group he places *Cercaria douthitti* Cort and *Cercaria elephantis* Cort, in which the system is more elaborate. Each of these letters thus stands either for a pair of flame-cells or for a group of three, but whereas all the flame-cells connected with the anterior tubule are contained in the distome body, one of the posterior set lies outside the body in the tail-stem. For *Cercaria furcicauda* Faust gives the formula $\alpha+\beta+\gamma$, but here the pairs of flame-cells denoted by α and β respectively are connected with the anterior tubule and only the pair included under letter γ is connected with the posterior tubule. This method is thus inconsistent and, moreover, cannot be applied to show the gradual evolution of the excretory system by the successive division of certain flame-cells into two or more. Faust (*loc. cit.*, p. 333) remarks "present knowledge not only preponderates in favour of the view that the number of flame-cells in the species is constant, but establishes the belief also that the same basic number and arrangement of flame-cells exist within families and sub-families." In 1924 he deals with this subject more fully and emphasises the great importance of a study of the excretory system as a guide to the correct systematic position of any cercaria. He remarks (*loc. cit.*, p. 261) "it is not too much to state that all members of a natural adult group possess the same basic excretory pattern." He also gives (*loc. cit.*, Table II) a very extensive survey of the different groups of cercariae, showing the fundamental type of the excretory system in each group and the excretory formulae, derived from this fundamental type, in the various sub-groups. He does not, however, attempt to show how this fundamental pattern in each sub-group is reached; and yet if it can be shown, as I believe it can in many instances, that the flame-cell pattern in one sub-group can be derived by a simple process of fission in individual pairs of flame-cells in the fundamental or basic pattern of the group, we ought to be able to arrive at certain conclusions, that will, I anticipate, prove to be fairly trustworthy, regarding the process and mode of evolution. A study of the evolution and development of the system tends to show that every flame-cell pattern is reached by the division of an original single-pair flame-cell system. Such a system is, at present, only known in certain Miracidia belonging to the genera *Amphistomum, Azygia, Bunodera, Echinochasmus, Echinostomum, Fasciola, Gastrodiscus, Gorgodera, Hapalotrema* and *Sphaerostomum.* The next stage in evolution is represented by the excretory system of the Miracidia of the genera *Hemistomum, Holostomum, Notocotyle* and *Schistosoma,* in which the originally single flame-cell has divided into two, there thus being four flame-cells in all in the body. A further division of each of these flame-cells would give us a system in which there are four flame-cells on each side of the body, and it is such a system that seems to be the starting point in several different lines of evolution in the furcocercous cercariae. As La Rue (1926, p. 273) has pointed out this difference in the number of flame-cells in the excretory system of the Miracidium denotes a division of the Digenea into two main groups, those Miracidia with the excretory formula of (1+1) belonging to the group that includes the Strigeidae and the Schistosomatidae. Cort and Brooks (1928, p. 202) have called attention to the manner in which flame-cells divide into two as development proceeds. In comparing the two accounts of the excretory system in *Cercaria douglasi,* namely that originally given by Cort (1917, p. 53, fig. 2c) and that given by themselves (*loc. cit.*), they suggest that in all Holostome cercariae there is first established a primary fundamental excretory system having a pattern in which single flame-cells are found on each side of the body and tail at definite levels. The first stage of evolution or development of this system consists in the division into pairs of the flame-cells at a certain level; " This," they remark, " may occur in the cercaria stage in some species." One of the daughter-cells would become dorsal and the other ventral in position. They suggest that the primary pattern of the excretory system of *Cercaria marcianae* La Rue has three flame-cells connected with the anterior collecting tubule and a similar number with the posterior, one of these latter flame-cells being in the tail-stem. They point out that such a system has been shown by me to be present in *Cercaria indica* I, and starting with this system the subsequent stages are, according to these authors, represented firstly by Cort's earlier account of *Cercaria douglasi* and Mathias' account of the cercaria of *Strigea tarda,* while the second stage is represented by the condition found in the mature *Cercaria douglasi.* In this assumption they entirely ignore the presence of a cross-connection between the main excretory tubules of the two sides of the body in *Cercaria douglasi* and its absence in *Cercaria marcianae* and, as I hope to show, this is quite unjustified.

As I have already mentioned, in each evolutionary series we appear to commence with a simple system, such as is met with in the true Schistosomes, in which there are four pairs of flame-cells, three pairs being in the distome body and the fourth in the tail-stem, and of these two are connected with each collecting tube. These flame-cells I have numbered from 1 to 4 respectively, commencing from the most anterior. When any of these primary flame-cells divide to give rise to two daughter flame-cells, these are dénoted by 1*a* and 1*b*, 2*a* and 2*b*, etc., respectively. When any of the daughter cells undergo division the product are denoted by the addition of a comma (') or two (''), so that we should from flame-cell No. 1 get flame-cells 1*a* and 1*b* and from 1*a* get 1*a'* and 1*a.''* Finally those cells connected with the anterior and posterior collecting tubules are enclosed within round brackets, thus ( ), while those that are situated within the tail-stem are further enclosed in a square bracket [ ]. Both Miller (1927, p. 28) and Cort and Brooks (1928, p. 202) have pointed out that it is, in certain cases, difficult to be certain of the correct location of the flame-cells and Miller concludes that " it does not seem feasible to construct a classification of the furcocercous cercariae based only on the excretory system." While recognising the difficulty, I am convinced that the excretory system is the most important of all for the correct determination of the systematic position of any given species in the evolutionary series, and the possibility of faulty or incomplete observation does not seem to be an adequate reason for disregarding it ; further study may necessitate the transference of a species from one group to another but that is equally the case in any scheme of classification and with any class of animal.

The Apharyngeal Brevifurcate Distome Series.

Commencing with the Apharyngeal Brevifurcate Distomes, I have in text-fig. 1 traced the manner in which the excretory system appears to have been evolved in the two series of forms that are included in the main group, namely those that possess eyes and those in which these organs are absent. The former of these two series includes those cercariae that develop into the true Schistosomes, while the members of the second series probably all develop into closely allied forms, to one of which the generic name *Schistosomatium* has been given. In the *Schistosomatium* series, in which eyes are present, the primitive condition, namely that in which there are three flame-cells in the body and one in the tail-stem on each side, has not yet been definitely demonstrated in any species. No cercaria with this system is definitely known, but it seems probable that the form described by me under the name *Cercaria indica* XXXVI (Sewell, 1922, p. 263) may be such a form ; as I then pointed out, I could detect only three pairs of flame-cells in the body and one in the tail of this species. The formula would thus appear to be $2\times\ (1+2)+(3+[4])$. Commencing with an excretory system of this type, the first stage in the process of evolution appears to be the division of the most anterior flame-cell, No. 1, into two daughter-cells, so that we now get three flame-cells connected with each anterior collecting tubule and two with each posterior, the formula now being $2\times(1a+1b+2)+(3+[4])$; such a system has been shown to be present in *Cercaria indica* XXV Sewell and it is in all probability also present in *Cercaria syncytadena* Faust.

Progressing a stage further, we next find that the most posterior flame-cell, No. 4, which is situated within the tail-stem, has divided into



Text-fig. 1.

two, namely $4a$ and $4b$, and of these No. $4a$ apparently migrates into the distome body, while $4b$ remains within the tail-stem. This type of system is represented by the formula $2\times(1a+1b+2)+(3+4a+[4b])$. The next stage in the evolution of the system is again brought about by the division of one of the posterior flame-cells, namely the most posterior cell in the distome body, No. $4a$, as a result of which we get two daughter flame-cells, which I term Nos. $4a'$ and $4a''$; we thus get the formula $2\times(1a+1b+2)+(3+4a'+4a''+[4b])$. We thus appear to have a series of groups in which the number of flame-cells in the excretory system increases from three pairs in the body and one pair in the tail-stem to six pairs in the body and one in the tail. Miller (1926, p. 66) orginally recognised the two latter groups, with five and six pairs of flame-cells in the body respectively, as being separate and distinct and he named them Groups D and E in the Apharyngeal Brevifurcate Distome series. Subsequently, however, he (1927, p. 66) combined the two into a single " Elvae " group ; but in so doing I think he has made a mistake. In his account of this combined group he gives as one of the characters, " Large Apharyngeal *Longifurcate* distome Cercariae "[1] ; but in a foot-note he adds that " These cercariae, in four of which the furcae are only slightly greater than half the tail-stem length, are so much more like those of the brevifurcate groups that they are classed among them rather than with the longifurcates." Although the various species that Miller includes in this single group are closely related, differences in the excretory systems render it desirable, in my opinion, to retain the two groups. The first group, which Miller (1926) terms the " Bombayensis No. 13 " group and Faust (1924) the " Wardi " group, possesses five flame-cells in the body and one in the tail on each side, arranged according to the formula $2\times(1a+1b+2)+(3+4a+[4b])$; in this group we can place the following species :—

Cercaria bombayensis No. 13 Soparkar.
Cercaria douthitti Cort.
Cercaria elephantis Cort.
Cercaria tuckerensis Miller.
Cercaria variglandis Miller and Northup.
Cercaria wardi Miller,

and the Cercaria of *Schistosomatium pathlocopticum* Tanabe.

On the basis of certain differences in the penetration glands Miller (1926, p. 67) separates off from the others *Cercaria elephantis* and *Cercaria echinocauda* and places these two by themselves in a group which he terms Group G (*Elephantis*). Although the life-history of only a single example of this ' Bombayensis ' No. 13 group is known, namely that of *Schistosomatium pathlocopticum* Tanabe, it seems safe for us to assume that all the other forms in this group will ultimately be found to belong either to the same or to a very closely related genus.

In the second group " Elvae " (*sensu stricto*), in which there are six pairs of flame-cells in the body and one in the tail, arranged according to the formula $2\times(1a+1b+2)+(3+4a'+4a''+[4b])$, we can include the following species :—

Cercaria elvae Miller.
Cercaria bombayensis No. 19 Soparkar, and probably
Cercaria milleri Faust.

It seems probable that *Cercaria ocellata* La Val. also falls within this group ; Ssinitzin stated that it possesses seven flame-cells on each side and, as Miller (1927, p. 68) remarks, these are probably so arranged

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[1] The italics are mine. *R. B. S. S.*

that there are six pairs in the body and one in the tail-stem. Dubois (1929, p. 96, pl. ii, fig. 8) has recently redescribed the species and has figured the excretory system : in his figure he shows that there are three flame-cells connected with the anterior collecting tubule and four with the posterior, one of these four lying in the tail-stem ; unfortunately his figure does not show clearly the connection of the three most posterior flame-cells in the body, all three apparently being connected with capillaries that arise close together. Miller also included in his conjoint " Elvae " group the species *Cercaria macrosoma* Brown ; he declines to accept Brown's statement that this cercaria possesses a pharynx, and in a foot-note he remarks " In the case of *Cercaria gigantea* and *C. macrosoma* the assumption may be made that the alimentary canal of each is of the same type as that present in the other members of the group." Such an assumption is, I think, unwarranted. Moreover Miller ignores the fact that the caudal excretory canal in *C. macrosoma* opens on the sides of the furcal rami and not at the tips, as in all other members of the Brevifurcate series. Although the number of flame-cells in the excretory system is identical in *Cercaria elvae* and *C. macrosoma*, it seems probable that this number is reached in a different manner. In the " Elvae " group, as I have pointed out, it is flame-cell No. 4*a* that has undergone division into 4*a*′ and 4*a*″ ; but in *Cercaria macrosoma*, if we may judge from the figure given by Brown (1926, pl. iii, fig. 27) it is flame-cell 4*b* that has divided into 4*b*′ and 4*b*″, while No. 4*a* remains single (*vide infra* p. 374).

In the non-eyed Apharyngeal Brevifurcate Distome series, which appears to constitute the true *Schistosoma* series, we get a very similar process of evolution. Commencing again with the simplest system of four pairs of flame-cells, two in the anterior region of the body and two, of which one is in the tail-stem, in the posterior, we find that this type is characteristic of the human-infesting Schistosomes and occurs in the following species :—

The Cercaria of *Schistosoma haematobium*,
the Cercaria of *Schistosoma japonicum* and, according to Khalil,
the Cercaria of *Schistosoma mansoni*.

It is also found in *Cercaria indica* XXX, the adult stage of which is not yet known. In this group, which I (1922, p. 250) termed the " Japonicum " group and which Miller (1926, p. 64) calls Group A of the Apharyngeal Brevifurcate Distomes, the excretory formula is, as before, $2\times(1+2)+(3+[4])$. From this stage the first step in the evolution of the series is represented by my " Spindale " group and Miller's Group B ; this step is reached by the division of one pair of flame-cells, but in this instance it is not, as in the *Schistosomatium* series, the most anterior that divides first, but the most posterior, No. 4 giving rise to 4*a* and 4*b*, of which 4*a* apparently migrates into the distome body and only 4*b* remains in the tail-stem ; there are thus still two flame-cells connected with the anterior collecting tubule, but three with the posterior. The formula for this stage is thus represented by $2\times(1+2)+(3+4a+[4b])$. This type of excretory system has been shown by Soparkar to be present in the cercaria of *Schistosoma spindale* and by me in *Cercaria indica* XLVII ; Iturbe and

Gonzales (1919) claim that the cercaria of *Schistosoma mansoni*, which they investigated in Venezuela, also possesses this type of excretory system. It is possible that the cercariae investigated by Khalil and by Iturbe and Gonzales respectively, although in each case supposed to be that of *Schistosoma mansoni*, may in reality not have been identical; on the other hand, it is interesting to note that this latter stage in the evolution of the excretory system of this series agrees exactly with the condition found by Faust and Melleny (1924, p. 85, pl. v, fig. 23) in a very early stage of development, which they term stage B, of *Schistosoma japonicum* within its final host. These authors (*loc. cit.*, p. 49) have called attention to this additional flame-cell in the species of cercariae that I have included in the present group; they consider that "this supernumerary cell may be explained as a precocious development, anticipating the time when the caudal flame-cell is pinched off along with the tail and a new unit is formed by the division of the anterior unit of this group, thus producing the original symmetry of the system." It seems to me, however, that one should distinguish between the various stages in the process of evolution of the system in the various groups and the developmental changes that occur in any given type of excretory system as we pass from the larva to the adult. If ontogeny repeats phylogeny the processes should theoretically be the same but this additional flame-cell in the posterior end of the body in the larva of the "Spindale" group appears to arise by the division of the flame-cell No. 4 and not of No. 3. A similar though somewhat greater difference in the number of flame-cells has been noted in the excretory systems of the immature and mature examples of *Cercaria douglasi*. In the original description of the flame-cell pattern given by Cort (1917) it was stated that there were five flame-cells on each side in the body and two in the tail-stem, and of these three were connected with the anterior collecting tubule and four with the posterior; these cercariae were taken from crushed snails and Cort and Brooks (1928) now suggest that they were not quite mature. In the mature cercariae these latter authors give the number of flame-cells as eight in the body and two in the tail on each side; four of these are connected with the anterior collecting tube and six with the posterior. It thus seems clear that there may be a certain degree of development of the system in the larval stage, so that it is important for observers to make certain that the specimens under examination are fully developed and this can only be done by allowing the cercariae to complete their development and be set free naturally from their mollusc host.

The next stage of evolution in this series, following the "Spindale" group, is at present unknown, but it is probably represented by the formula $2\times(1+2)+(3a+3b+4a+[4b])$, flame-cell No. 3 now having undergone division.

Finally, we reach the type of system present in *Cercaria anomala* Rao (1929) in which the most posterior flame-cell, No. $4b$, has undergone division, giving rise to $4b'$ and $4b''$, both of which remain in the tail-stem. The formula thus becomes $2\times(1+2)+(3a+3b+4a+[4b'+4b''])$.

Since the first two groups in this series are known to belong to the true Schistosomes, it seems reasonable to conclude that the form discovered by Rao will eventually prove to belong to the same genus, *Schistosoma*, or to one very closely related to it.

The exact relationships of the Monostome Furcocercous cercariae to the Distome groups of the series is still a matter for speculation. In my account of the Indian cercariae (1922) I put forward the view that the Distomes had been evolved from the Monostomes; at that time the number of Monostome cercariae known to me were comparatively few and in all known cases presented a simple and primitive type of excretory system. The subsequent discovery of several Monostome forms with more complicated systems renders this view untenable. The occurrence among the Monostome larvae of both Longifurcate and Brevifurcate forms seems to indicate, as Miller (1926, p. 59 *et seq.*) has suggested, that these forms have been derived from the Distome series by the suppression of the acetabulum and the fact that the forms now known, while possessing excretory systems of varying degrees of complexity, can all be fitted into the same scheme of evolutionary development as the Distome cercariae, indicates that this suppression of the acetabulum has occurred on more than one occasion.

Dubois (1929, pp. 142, 144) has recently put forward the view that the "Lophocerca" Monostome group is not related to the Furcocercous cercariae, such similarities as exist between them being, in his opinion, due, in all probability, to the similarity of their life-histories. He apparently does not regard the similarity of their life-histories as being in itself, in all probability, evidence of their close relationship. Among the differences that he believes to exist between the two groups he cites :—

(1) The presence of a crest,
(2) The absence of an acetabulum,
(3) The differences in the excretory systems and
(4) The presence in the miracidia of the "Lophocerca" group, of only one pair of flame-cells, whereas there are two pairs in the Furcocercous Group.

In his "Lophocerca" group Lühe (1909) included two forms, *viz.*, *Cercaria cristata* La Val. and *C. microcristata* Ercol. and in 1919 I included in the group four additional species, namely *Cercariae indicae* IX, XIII, XXXIX and LV. In the previous year Soparkar (1921) published his description of *Cercaria bombayensis* No. 8; while exhibiting certain differences in structure, this cercaria is clearly closely related to the other Indian forms. A further species closely related to the Indian forms was described and figured by Faust (1926, p. 102, pl. vi, figs. 1*a-c*) from material sent to him from South Africa by Cawston; this species he has kindly named *Cercaria sewelli*. Finally, in the early part of last year McCoy (1929) published the account of yet another species that agrees closely with the Indian forms, *Cercaria brevifurca*. So far as it is possible to judge all these forms present the same salient features in the structure of the excretory system; there is a small excretory bladder at the posterior end of the body, from which arise two main tubules that pass forwards on each side of the body to about the middle of its length, where they bifurcate into anterior and posterior collecting tubules. Posteriorly there arises from the bladder a caudal excretory canal, that passes down the tail-stem and then bifurcates into two, one branch passing along each furcal ramus and opening at its tip. This much of the system has been traced in *Cercariae indicae* IX, XIII, XXXIX and LV, *Cercaria bombayensis* No. 8, *Cercaria sewelli* and *Cercaria brevifurca*. We know but little regarding the internal structure of either *Cercaria cristata* or *C. microcristata*, but Ercolani (1881, p. 275) describes the presence in the latter form of a small excretory bladder of a triangular form. As regards the number and distribution of the flame-cells most Indian forms, *Cercaria sewelli* and *Cercaria brevifurca*, agree in the possession of three pairs of such cells in the body, two being connected with the anterior collecting tubule and one with the posterior. *Cercaria bombayensis* No. 8 differs from these forms by the presence of an additional pair of flame-cells in the body and a pair at the base of the tail, there thus being two pairs of flame-cells connected with the anterior collecting tubule and three pairs with the posterior.

In 1922 Scheuring published his account of the life-history of *Sanguinicola inermis*, the cercaria of which closely resembles, but according to this author is probably not identical with *Cercaria cristata*, and in 1925 Ejsmont[1] described two other cercariae belonging to the same genus. In the account that he gives of the cercaria of *Sanguinicola inermis* Scheuring describes and figures the excretory system as possessing two independent canals that appear to commence at the anterior region of the body and run back through the whole length of the body and tail-stem, each eventually passing along the furcal ramus of the same side to open at the tip. Scheuring figures no excretory bladder and was apparently unable to locate any flame-cells. Dubois (1929) gives a brief description of an additional species that he names *Cercaria helvetica* XVI, but he confines himself almost entirely to the external characters and with the exception of the salivary or penetration gland cells he neither makes any mention of nor figures the internal anatomy. If the observations of Scheuring and Ejsmont are correct there is a marked difference between these two forms and the others that have been included in the " Lophocerca " group. In this connection Dubois remarks " Tout d'abord, nous devons constater que les observations de Sewell ne nous paraisent pas toujours très prècises et peut-être quelquefois subjectives : c'est ainsi que les résultats de l'étude anatomique des espèces du groupe ' Lophocerca ' ne correspondent pas aux données des spècialistes de ces formes Ejsmont et Scheuring." I may, perhaps, be allowed to take exception to this remark ; I will, however, merely point out that my studies are in complete accord with those of Soparkar, Faust and McCoy. In attempting to form an estimate of the value of this distinction in the characters of the excretory system it must be borne in mind that it has been definitely shown, *vide* the work of Johnson (1920) on the development of *Echinostomum revolutum* (Froelich), of Looss (1900) on *Cercaria distomatosa* Sons. and *Cercaria vivax* Sons., and of Faust and Mellany (1924) on the cercaria of *Schistosoma japonicum*, as well as the work of Ssinitzin (1911), that during the early

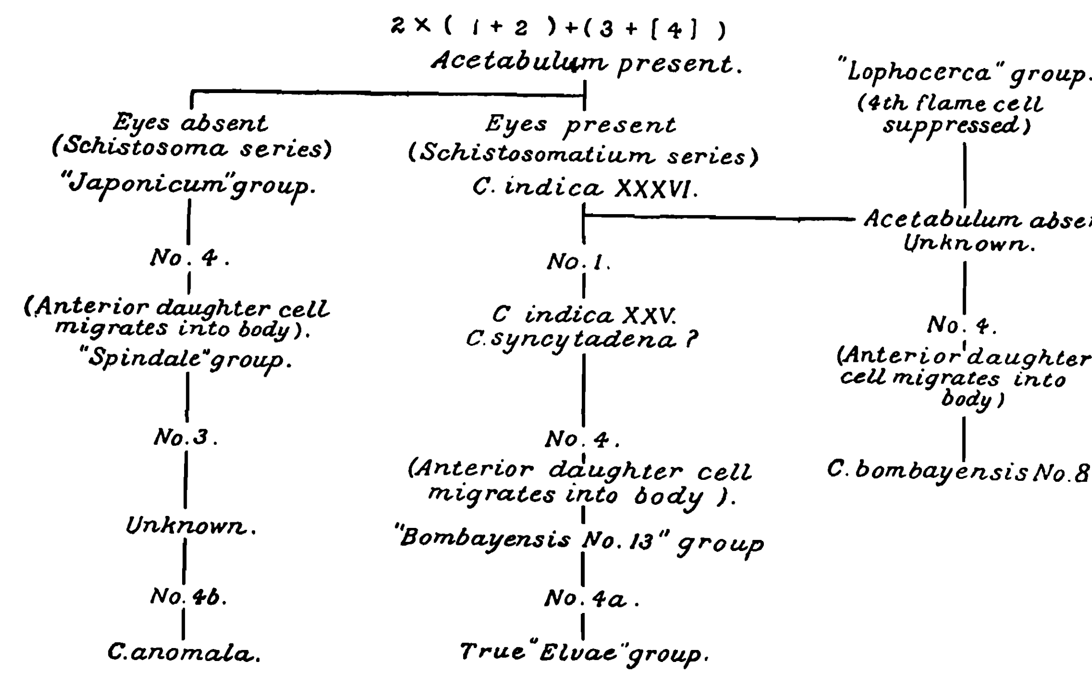
[1] I have not been able to refer to this paper. *Author.*

development of cercariae the excretory ducts of the two sides of the body are separate and that these ducts run independently down the length of the developing tail. The presence of two independent ducts in the tail-stem of the cercariae of the genus *Sanguinicola* may thus be due merely to the retention of an early developmental character.

Differences also exist between the various members of this group in the character of the alimentary canal. In no case have I been able to detect any oesophagus or intestinal caeca in the Indian forms that I have studied. Soparkar, however, in *Cercaria bombayensis* No. 8 describes this system as follows: "the alimentary system is simple, and, as in Schistosome cercariae, consists of a mouth which opens a little behind the anterior end, a long oesophagus passing through the oral sucker, and a dilated caecum which is situated about 80μ from the anterior end. There is no trace of any muscular pharynx." A similar digestive tract exists in *Cercaria brevifurca* McCoy; but Faust was unable to trace any intestine in *Cercaria sewelli.* Scheuring in the case of the cercaria of *Sanguinicola inermis* describes an oesophagus that terminates in a bulky 4-pointed gut; " der schlund fuhrt in einen plump 4-zipfeligen Darm." This latter he very obscurely figures as being situated about the junction of the anterior and middle thirds of the body length, in the region where one would except the brain mass to be (*vide* Sewell, 1922, pl. iv, fig. 5) and much more anterior than the position of the caecum in either *Cercaria bombayensis* No. 8 or *Cercaria brevifurca*, and I am inclined to wonder whether he was not mistaken in his interpretation. Another feature in which some of these species differ from others lies in the character of the Parthenita. In the majority of species development occurs in small oval or rounded sporocysts, that contain only a single mature cercaria; this type of development is found in *cercariae indicae* XIII, IX and LV, *Cercaria sewelli* Faust and the cercaria of *Sanguinicola inermis.* Others, however, develop in elongate and thread-like sporocysts, if we can trust the statement made by Ercolani (*vide* Sewell, 1922, p. 47). Finally, both *Cercaria bombayensis* No. 8 Soparkar and *Cercaria brevifurca* McCoy develop in rediae.

From the above it seems clear that the group " Lophocerca " is not strictly homogeneous and probably consists of several smaller sub-groups. The only reason for separating these forms completely from the other furcocercous forms might lie in the presence in the Miracidium of only two flame-cells, instead of two pairs, but here again we are ignorant of the miracidia of all the cercariae of this group except those of the genus *Sanguinicola*, and until we know more about the various forms I prefer to regard them as being the larval forms of either the genus *Sanguinicola* or nearly allied genera and together, with the exception of *Cercaria bombayensis* No. 8, constituting the group " Lophocerca."

I have previously (1922, pp. 45, 350-1) called attention to the great degree of similarity that exists between the " Lophocerca " group of the Brevifurcate Monostomes and the Schistosomes, but the presence of eyes in the members of this group seems to indicate that they are more nearly related to the *Schistosomatium* series. At the present day the known forms of the Brevifurcate Monostomes, with a single exception, fall within the limits of this single group, every member of which is characterised by the presence of eyes and in all probability by the possession of an excretory system that has only three pairs of flame-cells in the distome body and none at all in the tail-stem, similar to the condition shown by me to be present in *Cercariae indicae* IX and LV : a similar system has been shown to be present in *Cercaria brevifurca* McCoy. The formula for such a system can be represented by 2×(1+2)+(3) and it is probable that the group has been derived from the primitive Brevifurcate Distome form with an excretory system having the formula 2×(1+2)+(3+[4]) by the suppression of the acetabulum and the reduction of the fourth pair of flame-cells in the tail. The only Brevifurcate Monostome form that does not belong to the "Lophocerca" group, namely *Cercaria bombayensis* No. 8 Soparkar, appears to have been derived from the same primitive parent stock, in which the acetabulum has been suppressed but which possessed the full complement of flame-cells as expressed by the formula 2×(1+2)+(3+[4]). In the process of evolution flame-cell No. 4 has undergone division into two daughter-cells, Nos. 4*a* and 4*b*, and of these the most anterior has migrated into the distome body, leaving only a single flame-cell in the tail-stem ; the excretory formula, which is in complete agreement with the condition figured by Soparkar (1921) in this species, is thus 2×(1+2)+(3+4*a*+[4*b*]).



Text-fig. 2 showing the probable lines of evolution of the Brevifurcate Furcocercous Cercariae.

In the accompanying text-figure 2, I have attempted to show the manner in which the evolution of the two series of Apharyngeal Brevifurcate Distomes and the Brevifurcate Monostomes has been brought about. At the top I have given the primitive excretory formula from which all the others appear to have evolved and at each stage I have noted the flame-cell that undergoes division. Since the order in which the various flame-cells successively undergo division is different throughout the two series, *viz.*, the *Schistosoma* and *Schistosomatium* series, it seems probable that each series has been evolved by independent processes from the common ancestor that possessed the primitive excretory formula $2\times(1+2)+(3+[4])$ and further that the *Sanguinicola* series, *i.e.*, "Lophocerca" group of the Brevifurcate Monostomes, represents a branch line of evolution that has arisen from the *Schistomatium* series by the suppression of the acetabulum, followed by changes in the character of the excretory system.

The Pharyngeal Longifurcate Distome Series.

Evolutionary processes, very similar to those that I have just been discussing, can also be traced in the excretory systems of the Pharyngeal Longifurcate Distomes. There seems to be but little doubt that the cercariae of this division are the larval stages of the Holostomes; and they are all now regarded as being larval forms belonging to the family Strigeidae. Larvae of this type have been shown experimentally "to encyst (usually) and undergo metamorphosis into Strigeid larvae (Diplostomum, Tylodelphys, Tetracotyle and Codonocephalus)" (*vide* La Rue, 1928, pp. 269, 271). The cercariae can, however, be divided into two groups by the presence or absence of a transverse connection across the distome body, either just in front or just behind the acetabulum, uniting the main collecting tube of one side with that of the other. As I have already pointed out (*vide supra*, p. 360) Cort and Brooks (1928, p. 202) have called attention to the degree of similarity that exists in the excretory systems of certain of these Holostome larvae but they compare forms that possess this cross-connection with others in which it is absent, thus ignoring what I believe to be an important structural difference. That the two series are closely related is not questioned, but as we trace the probable course of evolution of the excretory system we find that, although the main line of evolution is identical in the two groups, the subsidiary lines appear to be different. Cort and Brooks (1928, p. 188) have called attention to the relationships that appear to exist between certain Holostome cercariae. In one group they place *Cercaria flexicauda*, *C. laruei*, *C. modicella*, "Cercaria C" Szidat, and tentatively *Cercaria* sp. Hesse and *C. chrysenterica* Miller. Of these forms *Cercaria flexicauda*, *C. laruei* and "Cercaria C" Szidat are known to penetrate into fish and become localised in the lens of the eyes, while the last named form developes ultimately into *Hemistomum spathaceum* Rud., which La Rue has made the type of his genus *Proalaria*. In the second group they place *Cercaria douglasi*, *Cercaria Strigeae tardae* Steenstrup; Mathias; *Cercaria indica* I and *Cercaria fissicauda* La Val.; Brown, and tentatively include *Cercaria tenuis* Miller, *Cercaria indica* XXII Sewell and *Cercaria marcianae* La Rue, though this latter species they regard as an aberrant form. Dubois (1929) added *Cercaria helvetica* XIII (possibly identical with *Cercaria* C. Szidat), and *C. helvetica* XV to the *Proalaria* group, and in addition described certain other forms that appear to provide connecting links in the general evolutionary series of the Longifurcate Furcocercous Distomes.

The "Tetis" and "Vivax" groups of Furcocercous cercariae (*vide* Sewell, 1922, pp. 280, 291) appear from their excretory systems to form a separate evolutionary series. Dubois (1929, p. 150) regards them as forming a transitional series between the " Monostome " and " Distome " Furcocercariae. As I have shown later Monostome forms appear to have been evolved on several occasions and from different sub-groups and at present we know too little of the connections of the flame-cells to enable us to form any opinion regarding the line of evolution of these aberrant forms.

Group I ; *The " Strigea " Series.* (Plate IX).

Taking first the series in which a cross-connection between the two main excretory tubes is present, the most primitive type of excretory system would appear to be composed, as in the series that we have been previously considering, of four pairs of flame-cells, two pairs connected with the anterior collecting tubule and the other two with the posterior, the most posterior pair of flame-cells being situated in the tail-stem. As we have seen, such a system has the formula $2\times(1+2)+(3+[4])$; but at present no cercaria belonging to this series has been discovered with this simple type of system. The first step in the process of evolution that appears to have taken place is the division of the most posterior flame-cell, No. 4, into two daughter-cells, Nos. $4a$ and $4b$, of which $4a$, as in the Brevifurcate series, migrates into the distome body and only $4b$ remains in the tail-stem. The formula thus becomes $2\times(1+2)+(3+4a+[4b])$, and this type of system is known to be present in *Cercaria hirsuta* Miller and is, possibly, also present in *C. granula* Miller, though in a few cases additional flame-cells were detected (*vide* Miller, 1927, p. 73).

At this stage it seems probable that there have been two lines of evolution, differing in the position of the flame-cell that next undergoes division. In one series the next cell to divide is the most anterior, namely No. 1. This would give rise to the formula $2\times(1a+1b+2)+(3+4a+[4b])$. At the present time there is no known cercaria with this system but a subsequent stage, that is reached by the division of the most posterior flame-cell in the distome body, namely No. $4a$, brings us to the formula $2\times(1a+1b+2)+(3+4a'+4a''+[4b])$ and this type of system is present in both *Cercaria bulbocauda* Miller and *C. absurda* Miller, two forms that possess a dilated tail-stem somewhat similar to that of *Cercaria anomala* Rao (1929). In spite of their abnormal type both these forms appear to belong to this series. In *Cercaria absurda* the furcal rami are remarkably short and more nearly resemble the condition present in the Brevifurcate series ; but *Cercaria bulbocauda* possesses long furcal rami. This condition of the excretory system is apparently followed by a further subdivision of the most posterior flame-cell, No. $4b$, the anterior daughter-cell, No. $4b'$, migrating into the distome body. This change gives rise to a system having the formula $2\times(1a+1b+2)+(3+4a'+4a''+4b'+[4b''])$, which agrees with the condition present in certain examples of *Cercaria fissicauda* La Val ; Brown. Brown (1926, p. 31) records that in certain examples of this species the number of flame-cells in the tail-stem was only one pair and it is probable that these examples were immature. In the majority of individuals, however, the system showed two pairs of flame-cells in the tail-stem; we thus would have a system represented by the formula $2\times(1a+1b+2)+(3+4a'+4a''+4b'+[4b''*+4b''**])$. This would appear to represent the excretory formula of the adult *Cercaria fissicauda* and has been reached from the immature stage by the subsequent division of the pair of flame-cells in the tail-stem, No. $4b''$

In an alternative route, the successive divisions of the two posterior pairs of flame-cells is reversed and in the first stage of evolution from the condition represented by the formula $2\times(1a+1b+2)+(3+4a+[4b])$ it is flame-cell No. $4b$ that divides into two, prior to the division of No. $4a$. At this stage the excretory system is represented by the formula $2\times(1a+1b+2)+(3+4a+[4b'+4b''])$. This formula is characteristic of the early or immature stage of development of *Cercaria douglasi*, as described originally by Cort (1917), and of the cercaria of *Strigea tarda* Streenstrup described by Mathias (1925). The subsequent division of flame-cell No. $4a$ would bring us to the condition represented by the formula $2\times(1a+1b+2)+(3+4a'+4a''+[4b'+4b''])$, which presents the same total number of flame-cells as in the immature *Cercaria fissicauda* Brown, but differs in having two flame-cells in the tail-stem; no form, however, is at present known with this type of system. The next intermediate stages appear to be brought about by the division of flame-cells Nos. 3 and 2 each into a pair, but at present we have no evidence as to which of the two is the first to undergo division. The final stage of evolution is represented by the formula $2\times(1a+1b+2a+2b)+(3a+3b+4a'+4a''+[4b'+4b''])$ and this is the condition present in the mature *Cercaria douglasi* Cort and *Cercaria sanjuanensis* Miller, and possibly also in Cercaria A (Szidat). A further stage in the evolutionary series is represented by *Cercaria helvetica* XIV Dubois. In this species there are twelve flame-cells on each side of the body, as in *Cercaria marcianae* La Rue, but in this latter form there is present a cross-connection between the main excretory tubes, which places it in the "Strigea" series. The actual connections of the flame-cells are not known, but it is probable that the excretory system is represented by the formula $2\times(1a'+1a''+1b'+1b''+2a+2b)+(3a+3b+4a'+4b''+[4b'+4b''])$ and that this condition is reached from that present in the mature *Cercaria douglasi* Cort and *Cercaria sanjuanensis* Miller by the division of flame-cells $1a$ and $1b$ each into two.

Cercaria burti Miller appears to be an aberrant member of the series under consideration and is closely related to *Cercaria hirsuta* Miller. In this species there are only two flame-cells connected with the anterior collecting tubule and five with the posterior; of these five, four are situated within the distome body and only one in the tail-stem. The manner in which this type of system has been evolved appears to have been from the formula, characteristic of *Cercaria hirsuta*, $2\times(1+2)+(3+4a+[4b])$ by the successive divisions of flame-cells Nos. $4a$ and 3, though which of the two is the first to divide cannot be stated, as no intermediate stage has as yet been discovered. The formula, representing the excretory system of *Cercaria burti*, is $2\times(1+2)+(3a+3b+4a'+4a''+[4b])$. So far as the distribution and connections of the flame-cells are concerned, an exactly similar excretory system is present in *Cercaria helvetica* XXXI Dubois (1929, pl. iv, fig. 14). In this latter species, however, instead of a single cross-connection between the main excretory canals there are two, one lying just behind the acetabulum, as in *C. burti*, while a second crosses the body a little in front of the bifurcation of the intestinal caeca. A further stage of development along this line of evolution is probably represented by *Cercaria helvetica* XXIX Dubois (1929) in which species there are 12 flame-cells on each side, ten pairs being in the distome body and two pairs in the tail-stem. Unfortunately Dubois was unable to trace the connections of the flame-cells with the collecting tubules : it is, therefore, impossible to give a definite formula, but the arrangement as shown by him points to its being as follows, $2\times(1a+1b+2a+2b)+(3a'+3a''+3b'+3b''+4a'+4a''+[4b'+4b''])$. This stage can be reached from the condition present in *Cercaria burti* by the division of flame-cells 4*b*, 3*a*, 3*b*, 2 and 1, but in what order these cells divide is unknown.

There seems to be little doubt that all the species of cercariae in this evolutionary series will ultimately be found to belong either to the genus *Strigea* or to a very closely related genus.

Group II ; *The "Proalaria" Series.* (Plate X.)

The second series of the Pharyngeal Longifurcate Distome Cercariae is characterised by the absence of any connecting vessel across the distome body between the two main collecting tubules. As in the previous series, the most primitive stage in the evolutionary series is as yet unknown, but it would almost certainly possess the same excretory formula, namely $2\times(1+2)+(3+[4])$, two flame-cells being connected with each of the collecting tubules and the most posterior flame-cells being situated within the tail-stem. Starting from this simple type, the first stage in evolution appears, as in the "Strigea" series, to be brought about by the division of the most posterior flame-cell, No. 4, into two daughter-cells, Nos. 4*a* and 4*b*. Two cercariae seem to exhibit this type of system, so far as the actual number of flame-cells is concerned, but they show, *inter se*, a very interesting difference. In one, namely, *Cercaria modicella* Cort and Brooks, both the daughter cells remain within the tail-stem, and this species thus possesses the formula $2\times(1+2)+(3+[4a+4b])$ and, so far as is at present known, evolution along this line has not proceeded further. I have placed *Cercaria modicella* Cort and Brooks here provisionally. In their account of this species these authors figure only three flame-cells in the body, which is all that they were able to detect with certainty ; they, however, in the text (1928, p. 188) state that "the digestive system, penetration glands and excretory system as far as it could be worked out offer no points of difference from *C. flexicauda* and *C. laruei*." It is possible, therefore, that *C. modicella* should be grouped with these latter forms, but until the complete system has been traced its position must remain doubtful. In the other case only the posterior daughter-cell remains within the tail-stem and the anterior apparently migrates into the distome body. The formula thus becomes $2\times(1+2)+(3+4a+[4b])$. This type of excretory system is found to be present in *Cercaria micromorpha* Brown.

From this latter stage the evolution of the excretory system may, apparently, proceed along one of two lines. In the first, which appears to be of the nature of a branch line, the first stage can only be conjectured, since there is no known form whose excretory system fits with the theoretical formula. In this line the flame-cell system of the anterior collecting tubule remains unaltered and consists of only two flame-cells on each side of the body; in the posterior system flame-cell No. 4*b* divides into 4*b*′ and 4*b*″, and of these the anterior daughter-cell migrates into the distome body. The formula thus becomes $2\times(1+2)+(3+4a+4b'+[4b''])$. The next stage, brought about by the division of flame-cell No. 4*b*″ in the tail-stem, brings us to the condition expressed by the formula $2\times(1+2)+(3+4a+4b'+[4b''*4b''**])$. In this way we ultimately get a condition in which there are five pairs of flame-cells within the distome body and two pairs in the tail-stem. This number agrees exactly with the condition present in the excretory system of *Cercaria tenuis* Miller. Miller (1927, p. 46, pl. vii, fig. 74) figures the flame-cells and their connections in this species but he remarks that their actual distribution is " not known beyond all possible question." The arrangement that he shows, however, agrees exactly with the formula given above, and, if this be correct, this line of evolution may be an alternative route by which the flame-cell system may have evolved to reach the condition found in *Cercaria chrysenterica* Miller, in which the excretory formula is $2\times(1a+1b+2)+(3+4a+4b'*+4b'**+[4b''*+4b''**])$, the necessary intermediate stages being brought about by the division of flame-cells Nos. 4*b*′ and 1.

In the second possible line of evolution and, so far as one can judge, the main line, the next stage of development following on the condition found in *Cercaria micromorpha*, is again similar to the corresponding change in the " Strigea " series, in which a cross-connection between the main collecting tubes is present; following the division of the posterior flame-cell, No. 4, the most anterior cell, No. 1, now divides into 1*a* and 1*b* so that in this line the third stage of evolution possesses the formula $2\times(1a+1b+2)+(3a+4a+[4b])$. This represents exactly the condition shown by me to be present in *Cercaria indica* I Sewell.

At this stage we again find that the course of evolution may take one of two directions. In both lines of evolution it is the most posterior flame-cell that divides, No. 4*b* giving rise to 4*b*′ and 4*b*″, and in one of the branches we find once again that the anterior of these two daughter-cells appears to migrate into the distome body, leaving only the most posterior cell in the tail-stem. The formula thus becomes $2\times(1a+1b+2)+(3+4a+4b'+[4b''])$, which is characteristic of *Cercaria macrosoma* Brown. As I have already mentioned (*vide supra*, p. 364) Miller has included this species in his " Elvae " group of the Apharyngeal Brevifurcate Distomes, but Brown describes and figures a perfectly definite pharynx, although he could detect no further trace of the alimentary canal, and it seems to me that the species fits, so far as the excretory system is concerned, much more naturally into the present series. The final known stage of evolution in this line is reached by the division of both the posterior flame-cells, Nos. 4*b*″ and 4*b*′, into two daughter-cells each, thus reaching the condition shown by the formula $2\times(1a+1b+2)+(3+4a+4b'*+4b'**+[4b''*+4b''**])$, which is again the exact expression of the excretory system present in *Cercaria chrysenterica* Miller.

In the second line of evolution both daughter-cells remain in the tail-stem, thus giving us the formula $2\times(1a+1b+2)+(3+4a+[4b'+4b''])$ and it is this type of excretory system that is found to be present in *Cercaria emarginatae* Cort. Exactly the same excretory formula is present in *Cercaria indica* XXII Sewell (1922, p. 276, pl. xxx, figs. 1-3). Although this latter species differs from most of the forms in this series, especially in the absence of any apparent pharyngeal bulb, it seems probable that, in reality, it should be grouped here with the pharyngeal forms. In *Cercaria indica* XXII, as I pointed out, there is a triangular dilatation of the oesophagus just behind the penetrating organ ; in *Cercaria allahabadii* Chatterjee (1930, p. 65) this dilatation takes the shape of " a bulbar enlargement of the oesophagus. Unlike that of other cercariae and adult Trematodes it is not provided with muscle fibres." Finally in *Cercaria* sp. Hesse (1923, p. 227) there is a cluster of cells opening into the oesophagus in the position of the pharynx and Hesse (*loc. cit.* pl. 1, fig. 8*a*) labels this organ the pharynx in his illustration. These three cercariae appear to form a branch line of evolution in which the flame-cells in the tail lose their original connection with the posterior collecting tubule and acquire a secondary connection with the central caudal canal. Chatterjee does not appear to have been acquainted with Hesse's paper ; but there can be little doubt that all three forms are closely related and probably form a progressive series. So far as the excretory system in *Cercaria indica* XXII is concerned, this, as mentioned above, agrees exactly with the condition present in *Cercaria emarginatae.* In *Cercaria allahabadii* Chatterjee there is an additional flame-cell in the distome body, produced, apparently, by the division of flame-cell 4*a*, and the formula for the whole system can be represented by $2\times(1a+1b+2)+(3+4a'+4a'')+[4b'+4b'']$; if Chatterjee's observations are correct, the two flame-cells on each side of the tail-stem, rerepresented, as before, in the formula by the figures in square brackets, have completely lost their original connection with the posterior collecting tubule and have acquired a secondary connection with the central caudal canal and this is indicated by the altered position of the brackets. The exact relationship of *Cercaria* sp. Hesse, unfortunately, cannot be definitely stated. The division of flame-cell No. 3 into two, *viz.*, 3*a* and 3*b*, would give us the theoretical formula $2\times(1a+1b+2)+(3a+3b+4a'+4a'')+[4b'+4b'']$, and according to this there would be in all seven flame-cells in the distome body, as in Hesse's species, but it is impossible from his figure to determine the connections of these cells with the collecting tubules. In the tail-stem, however, he definitely shows, as Chatterjee has shown in *Cercaria allahabadii,* two flame-cells connected directly, with the central caudal canal.

Two other cercariae, *viz., C. helvetica* XIII and *C. letifera* (Fuhrm.), which appear to be closely related to *C. emarginatae* Cort., have recently been described by Dubois (1929). In both instances the excretory system can be derived from the formula, characteristic of *C. emarginatae,* $2\times(1a+1b+2)+(3+4a+[4b'+4b''])$ by the division of a single flame-cell. In the case of the former species it appears to be flame-cell No. 3 that has divided, giving rise to the formula $2\times(1a+1b+2)(3a+3b+4a+[4b'+4b''])$, three flame-cells on each side of the body being connected with the anterior collecting tubule, and five, of which two are in the tail-stem, with the posterior. In *C. letifera* Fuhrm., although the total number of flame-cells is the same, namely 8 pairs, their arrangement is different. The condition in this species is reached from that present in *C. emarginatae* Cort by the division of flame-cell No. 2 thus giving the formula $2\times(1a+1b+2a+2b)+(3+4a+[4b'+4b''])$.

Turning back once again to the condition present in *Cercaria emarginatae* the next stage in the main line of evolution of the system is, apparently, brought about by the division of the most posterior flame-cell in the distome body, No. 4*a*, into two, thus giving us a type of excretory system represented by the formula $2\times(1a+1b+2)+(3+4a'+4a''+[4b'+4b''])$. This type of system is present in *Cercaria flexicauda* Cort and Brooks and *Cercaria laruei* Cort and Brooks, and possibly also in *C. modicella* Cort and Brooks (*vide supra*, p. 372). The next stage in the process is, unfortunately, again unknown, but assuming that the process follows the same course as in the preceding series, the division of flame-cell No. 3 into 3*a* and 3*b* would give us the formula $2\times(1a+1b+2)+(3a+3b+4a'+4a''+[4b'+4b''])$, a condition that at present has no known representative ; the number of flame-cells agrees with those present in *Cercaria* sp. Hesse, but differs from that species in having the flame-cells in the tail connected with the posterior collecting tubule and not with the central caudal canal. This stage may, however, represent an alternative route in the evolution of *Cercaria* sp. Hesse. A further stage in the evolution appears to be reached by the division of flame-cell No. 2 into two daughter-cells Nos. 2*a* and 2*b*. The formula thus becomes $2\times(1a+1b+2a+2b)+(3a+3b+4a'+4a''+[4b'+4b''])$, a condition that is characteristic of *Cercaria longifurca* Cort and Brooks. The final stage in the series, so far as our present knowledge extends, is reached by the division of both the two anterior cells, namely 1*a* and 1*b* into two, the final formula thus being $2\times(1a'+1a''+1b'+1b''+2a+2b)+(3a+3b+4a'+4a''+[4b'+4b''])$, which represents the system present in *Cercaria marcianae* La Rue.

In 1922 I pointed out that, corresponding to the Longifurcate Furcocercous Distomes, there was a Monostome form, represented by *Cercaria indica* XXVII Sewell ; and since then three additional Monostome forms related to the same series have been described, namely *Cercaria bessiae* Cort and Brooks, *Cercaria multicellulata* Miller and *Cercaria hamata* Miller. If, as seems probable, the Monostome Longifurcate Cercariae have been derived from the Distome series by the suppression of the acetabulum, it becomes a matter of some importance to try and discover whether the four species mentioned above represent a single line of evolution or whether the Monostome type has been evolved from the Distome series on more than one occasion, in which case the disappearance of the acetabulum must be attributed to convergence, or, as it is sometimes called, parallelism in evolution.

In this Monostome series we appear to start, as in the Distome series, with the simple excretory formula $2\times(1+2)+(3+[4])$ representing a system in which there are four flame-cells on each side of the body, the most posterior being situated in the tail-stem and two flame-cells being connected with the anterior and posterior collecting tubules respectively. Such a system has been shown by me to be present in *Cercaria indica*

XXVII Sewell. *Cercaria bessiae* Cort and Brooks possesses in all eight pairs of flame-cells, six on each side in the distome body and two in the tail-stem. The full connections of these flame-cells have not been worked out, but, so far as it is possible to judge from their positions as shown (*vide* Cort and Brooks, 1928, pl. xxvii, fig. 1), and the distribution of the capillaries, the formula for the whole system would appear to be $2\times(1a+1b+2)+(3+4a+4b'+[4b''*+4b''**])$. The condition represented by this formula is exactly intermediate between the condition present in the excretory system of *Cercaria macrosoma* Brown and *Cercaria chrysenterica* Miller on the one hand, and between that of *Cercaria tenuis* Miller and *Cercaria chrysenterica* Miller on the other, but the complete absence of an acetabulum indicates that this form represents a branch line in the process of evolution and cannot be regarded as a direct stage between either of the abovementioned forms. An excretory system of this type could be reached by a separate line of evolution commencing from the condition present in *Cercaria indica* I Sewell, in which, as noted above, the excretory formula is $2\times(1+2)+(3+[4])$. The first step in such a line of evolution would appear to be the division of flame-cell No. 4 into $4a$ and $4b$, the anterior daughter-cell $4a$ migrating into the body ; we should thus reach a Monostome form in which the excretory formula would be $2\times(1+2)+(3$ $4a+[4b])$, as in *Cercaria micromorpha* Brown, and by the subsequent division of (*a*) flame-cell $4b$, into $4b'$ and $4b''$, $4b''$ migrating into the body, (*b*) flame-cell $4b''$, both daughter-cells remaining in the tail-stem, and (*c*) flame-cell I, we arrive at the formula given above for *Cercaria bessiae*, but at the present time no monostome species with excretory systems corresponding to any of the intermediate stages have been discovered.

Two other Monostome forms, namely *Cercaria multicellulata* Miller and *Cercaria hamata* Miller, possess an excretory system that can be expressed by the formula $2\times(1a+1b+2a+2b)+(3a+3b+4a'+4a''+[4b'+4b''])$. They thus agree exactly with the condition present in *Cercaria longifurca* Cort and Brooks. Such a condition of the excretory system cannot be derived from that present in *Cercaria besiae* and it seems highly probable that both these forms have been evolved by the suppression of the acetabulum from a Distome ancestor that possessed this type of excretory system. Faust (1924, Table II) groups the " Rhabdocoela " and " Lophoides " groups together with the basic formula $2[(2)^n+2]$, and in the " Rhabdocoela " group he places together *Cercaria rhabdocoela*[1] and *C. multicellulata* Miller. While the total number of flame-cells is identical in these two species, their connections with the main excretory tubes are very different, and on this ground I think they should not be placed in the same sub-group. The evidence at our disposal thus certainly points to the monostome condition having arisen independently in the group of Holostome cercariae on three different occasions.

Group III. (Plate XI).

An additional line of evolution may possibly be represented by certain cercariae that Faust (1919, pp. 330-331, 336-339) described from Rome,

[1] The name of this species as given originally by Faust (1919, p. 338) is *C. rhabdocoela*.

Georgia and Urbana, Ill. in America. In this series Faust attributes to *Cercaria furcicauda* three basic groups of two flame-cells each, in *Cercaria quattuor-solenata* there are four such groups, and in *Cercaria rhabdocoeca*[1] there are five. A study of these forms shows clearly that they must be placed in different sub-groups but it also shows that the flame-cell system in each species and sub-group can be derived from a single fundamental 4 flame-cell system, such as we have seen to be present in the other groups of the Longifurcate Distome series, by the successive division of certain pairs of flame-cells, and, since there is no cross-connection between the main excretory tubes, the group would appear to be connected with the " Proalaria " series.

In this series we again start from the fundamental system of two flame-cells connected with both anterior and posterior collecting tubes, the most posterior flame-cell on each side being situated within the tail-stem; the formula is thus, as before, $2\times(1+2)+(3+[4])$. The next stage in evolution appears to be brought about by the division of the most anterior flame-cell, No. 1, into $1a$ and $1b$, thus giving a system having the formula $2\times(1a+1b+2)+(3+[4])$. At the present time no cercaria with this system is known but the next step in development, brought about by the division of flame-cell No. 2 into $2a$ and $2b$, gives us the formula $2\times(1a+1b+2a+2b)+(3+[4])$. It is possible that the order in which the successive divisions take place may be the reverse of that given above but the final state exactly represents the degree of development in *Cercaria furcicauda* Faust. From this stage it would appear that development may proceed along two lines. In the first the next flame-cell to divide is No. $1b$, giving the formula $2\times(1a+1b'+1b''+2a+2b)+(3+[4])$, which corresponds with the arrangement of the flame-cells, as given by Faust (1919, p. 329, fig. 7), in *Cercaria robusticauda* Faust. As Faust points out, the size of the anterior flame-cell in this species, which is considerably larger than the others, points to its undivided character or, as he expresses it, its " double nature ; " if this be the correct view, one would have expected the flame-cells in the posterior end of the body to be equally large, but this is not the case, if one may judge from Faust's figure, though the 2nd and 3rd pairs of flame-cells in the anterior end of the body seem to be intermediate in size between the 1st pair and those at the posterior end.

The second possible line of evolution proceeds from the condition present in *Cercaria furcicauda* Faust by the division of flame-cell No. 4 into $4a$ and $4b$, giving the formula $2\times(1a+1b+2a+2b)+(3+[4a+4b])$, both the daughter-cells remaining within the tail-stem; and then by the division of flame-cell No. 3 into two we reach the stage represented by $2\times(1a+1b+2a+2b)+(3a+3b+[4a+4b])$, which exactly expresses the condition of the excretory system in *Cercaria quattuor-solenata* Faust so far as the number of the flame-cells is concerned, but the character of the connections of these flame-cells is very different from those of other members of the series. As Faust (1919, p. 331) points out, in this species " the main collecting tubule has been shortened to a minimum,

[1] Faust (1924, Table II) refers to this species and the group in which he places it by the specific name *rhabdocoela*.

while the four secondary tubules have been lengthened accordingly." The resulting pattern is so different that one may be justified in doubting whether the species should rightly be included in the series. Finally, the successive divisions of flame-cells $1b$ and $1a$, each into two daughter-cells, gives us a system, expressed by the formula $2\times(1a'+1a''+1b'+1b''+2a+2b)+(3a+3b+[4a+4b])$, which closely corresponds with that in *Cercaria rhabdocoeca* Faust. In this species Faust (1919, p. 330) figures five pairs of flame-cells arising independently from the main excretory canal, *i.e.*, ten flame-cells on each side, and of these the posterior pair is situated in the tail-stem and the other 4 pairs in the Distome body. There is no actual division of the main excretory tube into anterior and posterior branches; the condition could, however, be reached if we suppose that the pair of flame-cells $(3a+3b)$ have shifted their position from their original point of origin from the posterior collecting tube to the anterior collecting tube—this would give a formula $2\times(1a'+1a''+1b'+1b''+2a+2b+3a+3b)+[4a+4b]$. At the same time in this species the acetabulum has been suppressed, and this and the characters of the alimentary canal show a resemblance to the "Lophoides" group, near which Faust classes it. Its exact position in the evolutionary series must, however, for the time being be left uncertain.

The order of division of the flame-cells in this series would thus appear to be Nos. 1, 2, 4, 3, $1b$ and $1a$, which is entirely different from the order in the other series of Longifurcate Distomes that we have studied.

In the accompanying Plate XII I have shown the probable course of evolution among the Pharyngeal Longifurcate Furcocercous Cercariae, both Distomes and Monostomes. As before I have started with the primitive ancestral form, possessing an excretory formula of $2\times(1+2)+(3+[4])$ and have noted the order in which the various flame-cells have undergone division. It will be seen that at the outset there was a division into two main lines of evolution, distinguished from one another by the presence or absence of a cross-connection between the main collecting tubules of opposite sides of the body. It is interesting to note that in two of the main lines of these evolutionary series, namely the Douglasi-helvetica XIV line of the " Strigea " and the Emarginatae-marcianae line of the " Proalaria " series, the order in which the flame-cells undergo division appears to be identically the same, namely Nos. 4, 1, $4b$, $4a$, 3, 2, $1b$ and $1a$. This suggests the possibility that this order of division had been impressed upon the ancestral series prior to the change that gave rise to the two sub-divisions, namely the development of the cross-connection between the collecting tubules.

Throughout both series there is a marked tendency for the more posterior flame-cells to undergo division before those that are situated more anteriorly and, as we have already noted in the Brevifurcate cercariae, there is also a tendency for the anterior daughter-cell produced by the division of the flame-cell in the tail-stem to migrate into the distome body.

Finally, it seems clear that the suppression of the acetabulum and the consequent production of a monostome form has occurred on more than one occasion and in different lines of evolution.

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