

A Form of Dimorphism and Asexual Reproduction in *Ptychodera capensis* (Hemichordata). By J. D. F. GILCHRIST, M.A., D.Sc., F.L.S., Professor of Zoology in the University of Cape Town.

(With 7 Text-figures.)

[Read 7th June, 1923.]

THE Hemichordata, considered as including the three groups represented by *Cephalodiscus*, *Balanoglossus*, and *Phoronis*, are of such importance as possible connecting links between the great groups of Vertebrates and Invertebrates that any new facts bearing on their relationship to each other or to other phyla of the animal kingdom are of particular importance. The following observations on a species of Balanoglossid, which exhibits a form of dimorphism, associated with sexual and asexual reproduction, may therefore be of special interest.

There appear to be at least four different species of "*Balanoglossus*" in S. Africa: three, which I have already described (Trans. Phil. Soc. S. Afr. vol. xvii. pt. 2, p. 151, 1908, and Ann. S. African Museum, vol. vi. pt. 2, p. 207, 1908), *Ptychodera capensis*, *P. proliferans*, *P. natalensis*, and an undescribed species, of which only a single imperfect specimen has as yet been found. The first and second were found in a tidal sandy pool in False Bay, the third in the muddy mangrove-bordered flats of Durban Bay, the fourth in a crevice of a rock at low-water mark in False Bay. The first two are obviously different from the third and from the fourth, which does not belong to the genus *Ptychodera*. The first two also seem to be quite distinct from each other, but their constant association in the same pool, their anatomical resemblance in all but the posterior regions of the body, and the fact that there is a normal process of asexual multiplication in one of them, gave rise to the suspicion that they might represent sexual and asexual forms of the same species.

Both species belong to the genus *Ptychodera*, the *Tauroglossus* of Spengel, and there appears to be no specific difference in size, shape, or structure of the proboscis and collar region. The size, shape, colour, and position of the genital wings immediately behind the collar are also similar. The differences in the posterior part of the body are, however, well marked, for (1) in *P. proliferans* (fig. 2) there are no hepatic cæca, either external or internal; (2) the caudal region is not clearly marked off from the branchio-genital region, and the bright yellow gonads seem to be continued into this region as two narrow streaks on either side of the intestine, which is never filled with sand as in *P. capensis*; (3) asexual reproduction takes place by

successive fragmentations or proliferations at the extremity of the tail ; (4) a further difference is that, though the two species were found in the same locality and under the same conditions, they do not usually occur at the same season, *P. capensis* being found chiefly, often exclusively, in the winter months, *P. proliferans* in the summer months, a fact which may, however, indicate a possible relation between the two species. To determine this point extensive collections were made at various seasons, but no indication of any

FIG. 1.

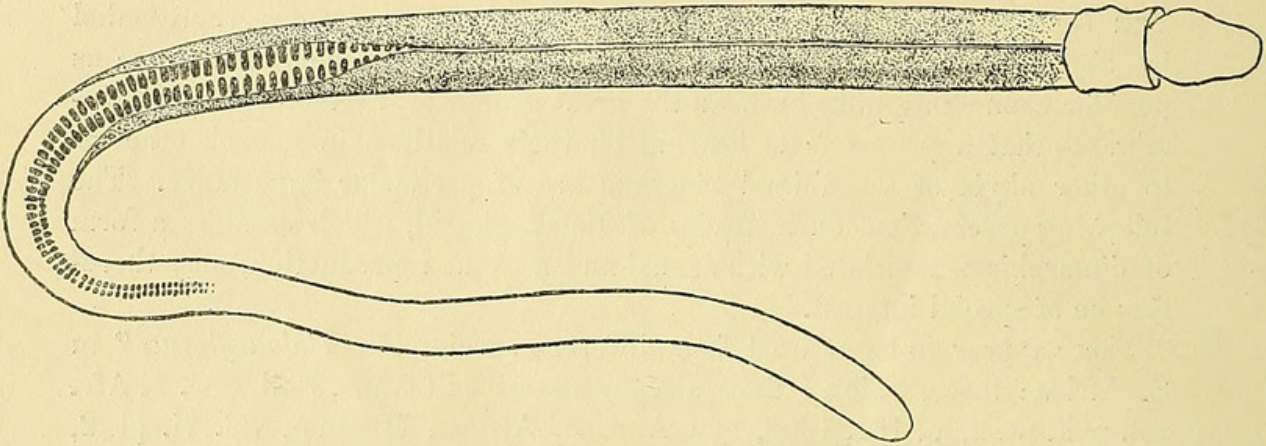
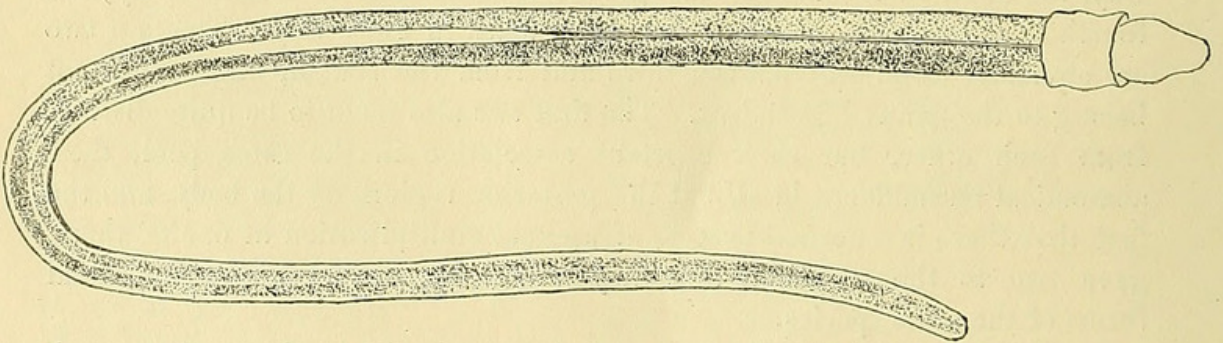
*Ptychodera capensis.*

FIG. 2.

*Ptychodera proliferans.*

transition from one form to the other was observed. The external differences between the two are shown diagrammatically by figs. 1 and 2, in which the bright yellow gonads are indicated by stippled shading and the hepatic caeca by black. Figs. 3 and 4 represent regenerating fragments, two and four weeks respectively after breaking off from the parent.

As both species are hardy animals, thriving fairly well in captivity when supplied with abundant pure sea-water, a number were kept in small glass tanks partly filled with sand, and were examined from time to time. The

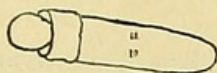
process of asexual reproduction was continuous in the summer months, but not rapid. In the case of half-a-dozen *P. proliferans*, kept in a separate vessel, about four to six small fragments were given off every week. For a time these remained in close proximity to the parent, but many of them were subsequently found free on the surface of the sand, and were readily moved about by any commotion of the water—probably a means of dispersal. Some of these fragments were isolated and examined from time to time. They moved about freely, a proboscis and traces of a collar appeared, and for three weeks seemed to be developing into a form like their parent *P. proliferans*, but, about the end of this period, some of them were seen to be developing hepatic cæca and genital wings, while still retaining the bright yellow colour and narrow intestine of the parent. Finally, after about a month, they had the general characteristics of *P. capensis*, with a few well-marked cæca and whitish caudal region, now containing a few grains of sand. The bright yellow colour had entirely disappeared even from the branchio-genital region, and they could not be distinguished from small *P. capensis* at a stage in which the gonads are not yet developed.

FIG. 3.



Proliferated part 14 days after
separation.

FIG. 4.



Proliferated part 25 days after
separation.

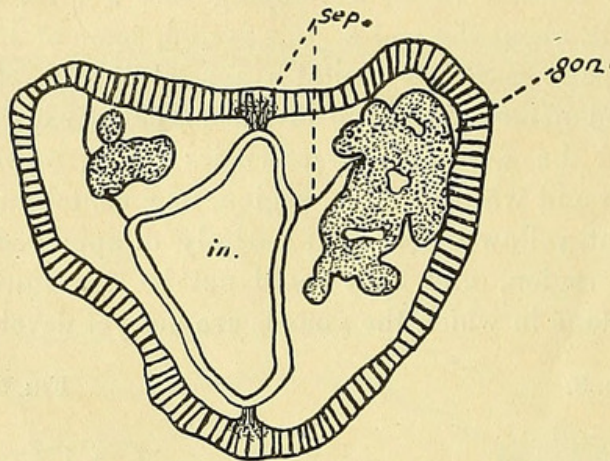
In order to ascertain further details of the transformation of the one form into the other, various stages were examined by sectioning. Sections of the tail region of *P. proliferans* show that the lateral septa are well developed throughout its length, and are in intimate connection with the gonads, which contain eosinophil globules, and, in some cases, one or two ova. The same condition is of course, found in the segments which break off from its posterior extremity, and this is maintained until the stage when the proboscis with notochord, &c., have appeared.

Figs. 5 and 6 show the conditions in a segment in which the proboscis is clearly shown, but not the collar region, and the gonads occur, not as a continuous streak, but at intervals, so that in some sections (fig. 5) the gonads still occupy a large part of the body cavity, but a few sections further on (fig. 6) they are almost entirely absent, though the lateral septa are still present. Sections of the same region at a later stage (about 4 weeks) (fig. 7) show an entire absence of gonads and no trace of lateral septa. Fragments of food-material—diatoms, protozoa, and flocculent organic matter—may now be seen in the intestine.

Evidently, therefore, the two species are identical, *P. proliferans* being capable of giving rise asexually to *P. capensis*. The question then arises as

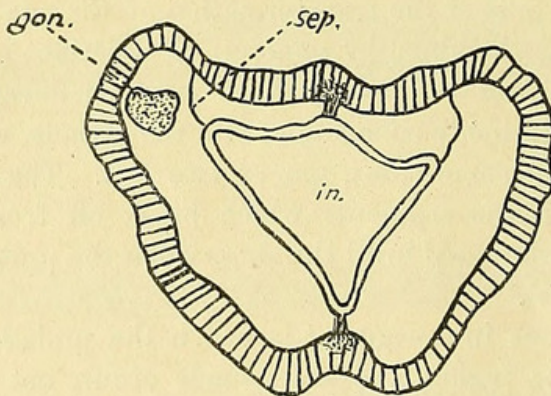
to whether this is a case of alternation of generations, *P. capensis* being the sexual form. To ascertain this the genital pleuræ of *P. proliferans* were examined by teasing, sectioning, and compression, the last-named method being the most suitable for examining a large number of individuals, as the ova are fairly large (.12 mm.) and conspicuous. The results of the examination were not consistent, some having apparently no ova, some only a few, and some a fair number.

FIG. 5.



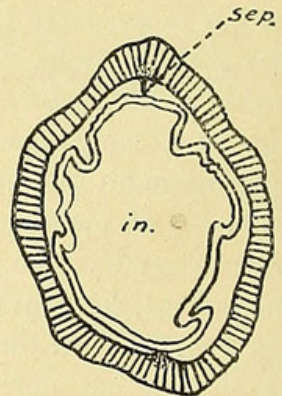
Transverse section of caudal region of the stage shown in fig. 3.
gon. = gonads; in. = intestine; sep. = septum.

FIG. 6



Another section of caudal region
further back than that shown
in fig. 5.

FIG. 7.



Transverse section of
caudal region at the
stage shown in fig. 4.

Towards the end of the summer (May) the six *P. proliferans* kept under observation had become considerably reduced in size, and a change was observed. The posterior region of the body became of a paler colour, the yellow streaks being reduced to a few scattered patches, and the intestine

contained a few grains of sand. At a later date hepatic cæca appeared about the middle of the body, and subsequently all were transformed into typical *P. capensis*, with fairly well-developed gonads, in which, however, there were no ova. Thus both the parent and its proliferated parts ultimately assumed the form of *P. capensis*.

Ptychodera proliferans would seem, however, to be capable of reproducing sexually, as the gonads contain well-developed ova. The facts, however, that (1) ova may occur in the proliferated part, and be used up like the granules in the growth of the body, and (2) that the ova ultimately disappear in the reduced adult, seem to indicate that there is no sexual reproduction in this form. There can be little doubt that *P. capensis*, into which both buds and parent are transformed, reproduces sexually, so that the whole process looks like a modified form of alternation of generations. There is evidence, however, which seems to indicate that *P. proliferans* arises from *P. capensis* by a division of the latter in front of or at the hepatic region, and subsequent prolongation and proliferation of the genital region, followed finally by regeneration of the lost hepatic and caudal region.

The nutritive eosinophil globules or granules evidently play an important part in the life-history of the animal, and their relation to the sexual elements may therefore be further enquired into.

They have been noted in many other Enteropneusta, but their origin and function remain in doubt. Spengel found that, in *P. minuta*, they were contained in cells in which no nuclei were seen. In *P. flava* Willey found no normal nuclei, and believed that the nuclei of the cells undergo a process of degeneration analogous to fatty degeneration. They were found to be present when the germ-cells were fully developed, but both authors found that they disappeared at the period of complete sexual maturity in the species they examined. As to their functions, Spengel could come to no definite conclusion; Willey suggested that they are partly for the nutrition of the growing germ-cells, but principally for providing an albuminous covering to protect the germ-cells during maturation.

In *P. capensis* they are absent only in the young stages. They are present from the time the germ-cells begin to develop and increase in numbers with them, and are present when the animals are fully developed. They do not disappear at complete sexual maturity, though the sexual elements then preponderate, and they subsequently (towards the end of the winter, when exceptionally large specimens were found) appear to increase in number, their bulk greatly exceeding that of the remaining germ-cells.

In *P. proliferans* stage they constitute the main mass of the gonads. These are greatly attenuated posteriorly and occur, as already stated, as two narrow streaks of a bright yellow colour in the elongated posterior region of the body, which is rounded and without pleural ridges in the living animal. The relative abundance of ova and globules was ascertained by the methods

already stated, and it was found that the well-developed gonads consisted mostly of globules alone, the eggs being only present, and in diminished numbers, in some cases.

The functions of globules in this case seem obvious, namely, the sustenance and growth of the non-feeding *P. proliferans*, and of the buds, till they reached the feeding stage.

The origin of globules and ova may best be studied in sections of *P. capensis* at a stage when the gonads are beginning to appear as small yellow streaks in the genital wings, and their early stages may be seen at the extremities of their lobate ramifications. The gonads are surrounded with a layer of cells with elongate nuclei. The developing ova occur just within this layer. They are of irregular amoeboid shape, and the germinal vesicle is already well marked. Alongside of the ova, and apparently arising from the same peripheral epithelium, are other cells, the outlines of which are not well marked, containing lenticular nuclei like those of the outer layer, and numerous small globules. In the older parts of the gonads the globules constitute a solid mass, sometimes with many scattered and disintegrated nuclei, and, in still later stages, only a mass of globules, some small and some comparatively large, the latter being most probably formed by confluence of the smaller. No globules were seen in the body of the ovum, which, when mature, is surrounded by a zone of clear tissue with radiating lines. It appears to be a reasonable inference that the granules are produced by modified germ-cells.

Though no such process of asexual reproduction has apparently been observed in other members of the Enteropneusta, the tendency of some species to fragmentation and regeneration is well known, and, if their life-histories could be followed out, it might be found that reproduction by fission is not an unusual process of multiplication, and is associated with the great abundance of eosinophil globules, which otherwise seem so difficult to account for.

The presence or absence of hepatic cæca, as well as the extent of their development, has not been found of any great systematic value in the Enteropneusta, and this case may indicate that other species may at different times assume different forms, in which these structures may be absent, or in various stages of development as in *P. proliferans*.

Some ten years ago it was noted as a remarkable fact by Korschelt and Heider that, while asexual reproduction was such a characteristic feature of *Cephalodiscus*, it was entirely absent in the closely-allied *Balanoglossus* and in *Phoronis*. Since that date it has been shown by Harmer that it is a normal process in a species of *Phoronis*, so that this distinction between the Pterobranchia, Enteropneusta, and Phoronidea disappears.



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