

PARTHENOGENESIS IN THE MOLLUSC
PALUDESTRINA JENKINSI.

PART I.

By GUY C. ROBSON, M.A.

(Published by permission of the Trustees of the British Museum.)

CONTENTS

	PAGE		PAGE
1. Introduction	65	4. Parthenogenesis	68
2. Relationships, etc.	66	5. History and Distribution	71
3. Ontogeny	67	6. References	78

I. Introduction.

THE Gastropod Mollusc *Paludestrina jenkinsi* (Smith) is found widely spread in England, Wales, and Ireland, and has been a familiar object of study among field-naturalists since it was first described in 1889. Its capricious distribution, sudden appearances and disappearances, and rapid invasion of fresh water has always excited much comment. Furthermore, in 1919, Boycott² stated that he had obtained experimental evidence that it was parthenogenetic, and that he had reared two successive generations without observing either a male or male reproductive elements. This result was confirmed by Quick.¹⁰

As two problems seemed to be involved which might have an interesting mutual relation, I undertook in May 1919 a more detailed investigation of the problem, and Dr Boycott handed over the cytological side of the study to Professor J. B. Gatenby. It was originally intended to publish the results together, but as Dr Gatenby's work has been delayed it has been thought advisable to announce the results of our work separately.

I am indebted to Dr A. E. Boycott, F.R.S., for continued advice and assistance, and to numerous collectors and members of the Malacological and Conchological Societies who kindly undertook to obtain material for me.

Guy C. Robson

2. Relationships, etc.

Paludestrina jenkinsi is a streptoneurous Gastropod of the suborder Tænioglossa. It is thus referable to the same group as *Paludina* and *Littorina*, and is usually placed in the same family as *Bithynia* and *Tanganyicia*. It is a small animal measuring some 5 to 6 mm. in length when fully grown, and is found on plants and submerged débris in fresh and brackish water. The genus is widely distributed and three other species are known in this country—*ulvæ*, *ventrosa* and *confusa*—all of which are estuarine or brackish water forms, while *ulvæ* is also found on the open coast. The structure of the genus is fairly well-known (Robson²¹), while that of *jenkinsi* has been already described (Robson¹⁸). It differs anatomically and conchologically from the other British species in several well-marked characters and seems to stand somewhat apart from them. Thus in the form of the radula *ulvæ*, *confusa*, and *ventrosa* seem to be united by several common features which are lacking in *jenkinsi*.

The recorded distribution of *jenkinsi* may be found in detail in the "Census of British Land and Freshwater Mollusca."²² It extends over nearly all England, over the north and south of Wales, and round the coast of Ireland and a considerable way inland. It is very sparsely distributed in Scotland, only two localities being recorded for it. It is also found in Denmark, Holland,* and on the Baltic littoral as far east as Warnemünde (Johansen⁹). Only the first of these continental localities has been verified by actual specimens, which were forwarded to me by Dr Johansen through the kind offices of Mr B. B. Woodward. Palæontological evidence on distribution is considered in another context (p. 71).

In this country *jenkinsi* is found in fresh, brackish, and tidal waters. In Denmark, Holland, and Germany it is apparently estuarine only, though it has a wide range at Randersfjord (Johansen⁹) of 1 to 20 promille. It is an important fact to

* After this paper was sent to the press, I received from Mme. T. van Benthem Jutting a copy of her paper *Flora en Fauna der Zuider Zee*, 1922 ("Zoet- en Brakwattmollusken"), in which the distribution in Holland is discussed. I venture to disagree (pp. 73-4) with Mme. Jutting's view that, in this case, parthenogenesis is an adaptation to life in fresh water.

Parthenogenesis in Mollusc *Paludestrina jenkinsi*

notice that the peculiar reproductive phenomena described herein occur in brackish as well as fresh water. The animal is able to stand sudden changes of salinity without exhibiting signs of distress. On several occasions I have transferred specimens from water of 17 promille, or over, to London tap-water, without observing either discomfort or interruption of reproductive activity. The behaviour of *P. ulvæ* and *ventrosa* may be compared (Robson¹⁹).

3. Ontogeny.

The cytological details of oögenesis will be described by Professor Gatenby. Certain comparative details and facts of ontogeny may, however, be described here.

Before leaving the ovary the eggs are irregular in shape, being compressed by each other and by the adjoining lobes of the hepatopancreas. Ova in all conditions of development are found during most periods of the year, and the various stages described (Robson²¹) for *P. ventrosa* were observed. The ripe oöcytes, as in *ventrosa* and *ulvæ*, are full of yolk spherules of various sizes, and transitional stages in the increase in the charge of yolk are to be found, the cells of the germinal epithelium and the primary oögonia having little or none. The oöcytes have a large, usually clear nucleus and a single large nucleolus within which, as in *Crepidula* (Conklin⁶), is found a densely staining body. This is frequently pressed out against the periphery of the nucleolus; but stages are found in which the latter is homogeneous and the above-mentioned inclusion is not seen. In the structure of the ovary and the various stages of oögenesis there is little to differentiate this phase of development from that found in *ulvæ* and *ventrosa*, though the number of eggs appears to be less in *jenkinsi* than in other forms.

From the ovary the eggs pass down the oviduct and find their way into the *brood-pouch*, where they undergo their further development and the definitive structure is attained. The embryos become covered by a hyaline capsule in which they are surrounded by a nutritive(?) fluid. It is not uncommon to find unsegmented eggs thus encapsuled in the brood-pouch. The later stages of embryonic development appeared to be

Guy C. Robson

interesting and in contradistinction to what occurs in *Paludina* (Erlanger⁸) and *Bithynia* (Sarsin²³). In these molluscs the embryos appear to depend for nutrition on the oviducal secretions. In *P. jenkinsi*, however, the embryo is usually found attached to large yolk-bearing macromeres, as in certain *Rachiglossa*. A normal full-grown individual usually contains 35 to 45 young in the brood-pouch, some of which will be found already freed from their capsules. The discharge of the young has already been noted (Boycott¹). In captivity the mother and brood tend to keep together for some time, the young crawling over the maternal shell on which some five or six may sometimes be found. This association has been shown by experiment to be accidental rather than an indication of maternal instinct.

I have definite evidence that more than one brood may be hatched out in the year. Several examples in my cultures had two broods, in March-April and September. This is not, however, an invariable rule as single annual broods have been observed in other cases. On the other hand, continuous brooding has never been observed in captivity.

An example born in April will attain about 2.0 mm. (or one-third of its total growth) by October; and as I have found example of 2.5 mm. with the ovary ripe, and examples at 3.0 mm. with embryos in the brood-pouch, it is highly probable that it is the rule for most individuals to become sexually mature in the year of birth. In captivity breeding is more frequent and (I think) more rich in offspring in the autumn months; though this is a point in need of verification.

4. Parthenogenesis.

The absence of a male in *jenkinsi* was first commented upon by F. Taylor.²⁵ Following on this hint, C. Oldham and A. E. Boycott made extensive searches with the same result. But until Boycott made his breeding experiments these searches were confined to the examination of the external appearance of the animal. Gravid females are always discernible by the white embryos which are visible through the shell of the body-whorl. The absence of any mature forms not containing young was regarded as suggestive, though it was admitted

Parthenogenesis in Mollusc *Paludestrina jenkinsi*

that this was not a final proof that males did not occur. The facts recorded by Boycott were highly significant; but again they did not offer overwhelming evidence, as no examination was made for a partly suppressed male phase or for dwarf males.

In May 1919, therefore, I instituted inquiries of an intensive and extensive nature. Specimens were obtained from twenty-three different localities in all the main areas of distribution in the British Isles and Denmark. Three of these were definitely tidal stations and three more were in brackish water. At the same time the other British species of the genus were examined, and the anatomy of *jenkinsi* and *ventrosa* was exhaustively described. It was found that *ulvæ*, *ventrosa*, and *confusa*, as well as *Amnicola taylori*, were all dioecious. It was found that *jenkinsi* differed from the others in the possession of a brood-pouch excavated in the pallial integument. The presence of a spermatheca in *jenkinsi* was commented upon (¹⁸ p. 430), and will be again considered.

Specimens from all the localities in question were examined according to the following plan:—

(A) All the individuals obtained from many widely separate localities were examined.

(B) Batches of specimens from certain localities were isolated and subjected to a routine examination every month for a year.

(C) Batches of young were isolated from birth and examined at intervals until a growth of 6 mm. was attained.

(D) Cultures were kept in water of (a) various salinity, (b) various temperature, (c) various degrees of organic pollution, and (d) with a reduced food supply. It may be remarked that the resistance to adverse conditions shown by this animal is very remarkable. They will live for years in water in which their fæces are allowed to accumulate, in which the oxygen supply is very much reduced, and in which a large accumulation of bacterial slime is formed. They will also resist desiccation for three or more days.

Examination was made of smears of the gonad and serial sections through various parts of the reproductive system. The sexes in the Hydrobiidæ are externally differentiated by the presence in the male of a large penis which is cephalic in

Guy C. Robson

position. But neither the absence of this organ in *jenkinsi* nor the presence of embryos in the brood-pouch was taken as adequate evidence as to sex.

The result of this inquiry was that from May 1919 to June 1923 no trace of a male or male reproductive elements was found. In all stages of growth, all localities, including the continental, and all degrees of salinity, etc., the material examined was exclusively female, and I am satisfied that in this period and in the material under investigation there were neither dwarf males nor a restricted male phase.

The spermatozoa of the allied species were examined and found to be highly characteristic, so that it is most unlikely that male reproductive elements have been overlooked in *jenkinsi*.

I have now upon record one case of five parthenogenetic generations and several of four. In such cases, of course, some compromise is necessary in order to carry out examination for spermatozoa. By starting with a large number one can afford to kill off a certain number for detailed examination. In such cases, of course, not every member is exhaustively examined for sex. As a general rule, I allowed about a half of each generation to arrive at full reproductive activity, killing off the rest at various stages between 1.5 mm. and 3.0 mm. There is thus no absolute certainty that the animals that reproduce themselves have not had a male phase; but there is a pretty strong presumptive case against it. Moreover, they were always killed and examined in detail after giving birth.

I have previously stated (p. 69) that the other species of this genus and *Amnicola taylori* are dioecious. Of the allied genera *Hypsobia*, *Bythinella*, and *Vitrella* are also dioecious, and the suborder Tænioglossa seems to be fairly uniformly characterised in this respect.

As is well known natural parthenogenesis has not been previously recorded in the Mollusca. Pelseneer¹⁶ has assembled a number of cases recorded among Pulmonata which he describes as "ponte sans fécondation préalable (parthénogénèse naturelle)." He remarks that the fact that it occurs in monœcious forms has led people to assume that these cases are of self-fertilisation, and adds that the only

Parthenogenesis in Mollusc *Paludestrina jenkinsi*

case "réellement observé de tentatives d'autofécondation est celui de *Limnæa auricularia* de von Baer." Such cases are obviously very difficult to employ as evidence. Nothing short of the passage of spermatozoa into the receptaculum seminis from the vas deferens in one and the same individual can be taken as actual proof of self-fertilisation. This has actually been witnessed in the case of *Arion* by Künkel,¹⁸ and the occurrence of modification of the reproductive organs by which it might be facilitated have been recorded by Kleiner¹⁰ for *Tachea* and by Ramanujam for *Veronicella*.¹⁷ On the other hand, in the cases recorded by Pelseneer the only convincing proof of parthenogenesis, *i.e.* absence of spermatozoa is entirely wanting. The cases cited by Pelseneer are therefore more likely to be ones of self-fertilisation, or at least to be regarded as "not proven" as parthenogenesis.

5. History and Distribution.

The distribution and history of this form are very remarkable, and no consideration of its parthenogenetic habit can be made without reference to them.

P. jenkinsi was first described in 1889 from specimens taken at Plumstead in the Thames Valley. This was not, however, its first appearance in this country. It seems to have been recognised in 1886 from specimens obtained between Deal and Sandwich (Woodward²⁰). Many years previously to this it had been taken and described under MS. names. Thus there is a *Hydrobia ferrusina* in the Jeffrey's collection from "Hampshire," and in 1859 G. B. Sowerby figured, but did not describe, a *Rissoa castanea* from Gravesend. This is very like *P. jenkinsi*, and specimens of the latter are to be found in the Norman collection, that were obtained by Mr Pickering, the original finder, and labelled as *H. castanea*, though they are not dated. Finally, Boycott records (* p. 266, footnote) the statement of A. W. Stelfox that specimens were collected in Lough Neagh in about 1837.

We therefore know that *P. jenkinsi* had been recognised in England some fifty years before its actual description.

Earlier still we have three records of it in a subfossil condition in the British Isles. One is at Blythborough

Guy C. Robson

(Suffolk) in surface deposits of mediæval age (*c.* 1500-1600). The second is at Barking in South Essex, a few miles from the Thames in a deposit which, according to Mr A. S. Kennard, is not more than two hundred years old. A third is at Limerick in an older alluvial deposit.

I am indebted to Mr Kennard for information concerning these deposits and for the loan of the actual specimens, and I have no doubt as to the correct determination of the specimens. Mr Woodward has informed me that he considers that the species extends back to early historic times but not beyond the late Roman period. It is absent in Messrs Kennard and Woodward's records from inland Pleistocene and early Holocene horizons.

In the "Census of British Land and Freshwater Mollusca,"²² the species is stated to have been "found originally in brackish water" and to have "spread into rivers, streams, and canals." This statement deserves careful consideration as it has been thought to afford a clue to the origin of the parthenogenesis.

The following is a record of the important occurrences:—

1. Bleach Lough, Limerick, near estuary of R. Shannon.
 2. Blythborough—on tidal river Blythe.
 3. Barking—a few miles from tidal part of R. Thames.
 4. Gravesend (1859), in ditches, near Thames estuary.
 5. Hampshire (?).
 6. E. Greenwich (1883), near Thames estuary.
 7. Deal, Sandwich (1886), coast.
 8. Plumstead and N. Woolwich (1889), near Thames estuary.
 9. Sandwich (1891), coast.
 10. Topsham (1892), estuary of R. Exe.
 11. Dudley (1893), the first inland record.
- } Subfossil.

From that date onward it was found in numerous inland localities.

IRELAND.

1. Lough Neagh (1837?), in fresh water but near coast.
 2. Port Stewart (1893), coastal.
 3. St Johnstone (1893-99)
 4. Carrigans (1893-99)
- } Tidal part of R. Foyle.

Parthenogenesis in Mollusc *Paludestrina jenkinsi*

5. Culmore (1893-99), coastal.
6. Kenmare (1893-99), estuarine.
7. Newry (1893-99), estuarine.
8. Mouth of R. Sixmilewater, Co. Antrim (1893-99).

After that date it has been found in more inland localities.

SCOTLAND.

Found only in estuarine waters (Perthshire) or water near the latter.

DENMARK AND GERMANY.

Estuarine.

All the English records after 1892-93 show that it was found in large quantities in inland places. What is more, it is usually recorded as a new addition to the local fauna, and comments are made on its abrupt appearance and prodigious numbers. The case recorded by Mr Morris¹⁸ of its first appearance near Lewes is most instructive, for he apparently never found it there before 1894, and yet in about three months after its first abrupt appearance it was obtained in enormous quantities. Its first occurrence at Droylsden, Lancs. (Taylor) and Mr J. N. Milne's evidence²⁴ are analogous cases.

As far as England is concerned, I think we may take it as certain that the scanty references previous to 1889 are indicative of the rare occurrence of the species. Numerous collectors were at work in all parts in the middle of last century and their work indicates careful and exhaustive search. Had *jenkinsi* been as plentiful then as it is now, it must have been found repeatedly and placed on record.

In the British Isles, then, we have ample reason for asserting that, with the exception of Lough Neagh and the vague Hampshire locality, all the records are either estuarine or within the immediate vicinity of estuarine waters.

I think we must conclude that originally an inhabitant of tidal or brackish waters about the last decade of the nineteenth century it became adapted to fresh water and spread rapidly inland. We obviously cannot accept Mr L. Adams' theory that it was imported with Baltic timber; nor is this theory relevant to our discussion.

Now there is no immediate causal connection between the

Guy C. Robson

parthenogenetic habit and this change in distribution. The former occurs in brackish water as well as in fresh. It was not, therefore, the change to a new environment that induced a change in the mode of reproduction. On the other hand, it may have been the development of the latter that facilitated the rapid and prolific dispersal in fresh water.

Boycott has pointed out that the chances of dispersal are increased by the adoption of this mode of reproduction, as a single individual is certain to reproduce itself if accidentally transferred to a new locality.

Boycott's views as to the relation between mode of reproduction and dispersal are set forth elsewhere,⁴ and the case he makes out is convincing. But to invoke it to account for the sudden multiplication of *jenkinsi* involves a serious difficulty. We would, in short, be compelled to assume that somewhere between 1890-1900 parthenogenesis was acquired simultaneously over wide areas of England, Wales, and Ireland. The following dates of new occurrences are significant:—

- 1892. Topsham (Devon).
- 1893. Dudley.
- 1894. Lewes.
- 1896. Ireland (rediscovery).
- 1898. Middlesboro'.
- 1899. Droylsden (Lancs.).
- 1898. Lough Neagh (reappearance).
- 1904. Barnstaple.
- 1905. Hoddesden (Herts.).
- Blisworth (Northants.).

It might be urged that the above records are merely the superficial indications of a more definitely orientated wave of invasion having a single centre of dispersal. I admit that they are not to be taken at their face value. But at the same time we should point out that there is not the least indication of a common centre of dispersal. The localities are widely separated on different sides of the British Isles and are dated within a few years of each other.

I do not therefore think that the advantage in dispersal and oësis provided by parthenogenesis is capable of explaining the sudden increase in numbers and the invasion of fresh water.

Parthenogenesis in Mollusc *Paludestrina jenkinsi*

Furthermore, there are numerous cases of analogous rapid invasion in which parthenogenesis cannot be invoked, e.g. *Crepidula fornicata* on British coasts, *Achatina fulica* in Ceylon and India, *Planorbis indicus* in India, and *Dreissensia polymorpha* in Europe generally.

Finally, as a proof that rapid extension of range is not an inevitable sequel to parthenogenesis, we may point out that in Scotland *P. jenkinsi* was first recorded in 1906, but has not spread from the Tay valley (Coates⁶).

I feel, therefore, that some additional factor or factors must be sought to explain the distributional history of *jenkinsi*. We have unfortunately no evidence at present as to how or when the parthenogenetic mode of reproduction manifested itself. To judge by the still unmodified spermatheca it should be fairly recent. We have no evidence that its incidence is not periodic.

But as the extraordinarily rapid extension of range from an estuarine habit is a remarkable thing in itself and may have been aided by the acquisition of the new mode of reproduction, it will be useful to suggest the other factors with which parthenogenesis may have co-operated.

There are five points to be noticed that have not been fully discussed anywhere yet.

(A) *P. jenkinsi* is singularly free from Trematode parasites which are so frequently found in the gonad and liver of fresh and brackish water Molluscs. *P. ventrosa* and *ulvæ* are often very heavily infected, and I have sometimes found 90 per cent. of the former in which the gonad is entirely destroyed. The effect of this castration is obvious, and more than one author has suggested it as an explanation of the capricious distribution of certain Molluscs. In brackish water *jenkinsi* from Oxwich (in which infected *ventrosa* and immune *jenkinsi* were found living side by side), St Olave and Randers Fjord I have never obtained an infected example.

(B) A consideration of the invasion of freshwater between the years 1889-1905 leaves one with the conclusion that the first areas to be invaded were either industrial districts or areas traversed by canalised waterways. Now it has been shown that *jenkinsi* is viviparous and therefore devoid of a

Guy C. Robson

larval stage. But, on the other hand, the newly-born young have extraordinary powers of adhesion and manage to withstand powerful currents of water siphoned over them as efficiently as the adults. Transport along newly-opened canals may therefore be a factor in distribution.

(C) There is no evidence that *jenkinsi* is associated in its distribution with any special plant. It is found on *Elodea*, *Lemna*, *Potamogeton*, etc., and appears to have no particular preference as far as can be experimentally ascertained. Dr Boycott and others have found it in roadside "trickles" of water without any plants at all. On the other hand, in 1919, I found it in the Brent (Middlesex) swarming on *Elodea canadensis*. A few months later the particular reach was cleared of the plant and *jenkinsi* vanished simultaneously. Such a single case is, however, insufficient as evidence. Nevertheless we should point out that the invasion of fresh water by *jenkinsi* does seem to have some relation with the equally remarkable invasion of England by *Elodea*. The latter made its first appearance in England in about 1845. Ten years later it was swarming in most inland waters, and it attained a maximum in about 1870, after which its mode of reproduction changed and it became more normal in its occurrence. It thus precedes *jenkinsi* as an invader by some thirty-five years; though in some cases (e.g. in Sussex) the interval is reduced to eighteen years. Bearing in mind the fact that *jenkinsi* apparently had a very long history as an estuarine form, its invasion of fresh water in the early "nineties" after that of *Elodea* suggests a connection between the two. It may of course be purely a matter of coincidence. The interval between the two invaders may seem extensive, but relatively to the long estuarine history of *jenkinsi* it is short. I do not suggest that the connection may be immediate. *Elodea* is not to-day a vital necessity of *jenkinsi*, but it is conceivable that it prepared the way for *jenkinsi* by contributing some factor to the food supply. I have already¹⁹ suggested an intimate connection between another member of this genus and associated plants.

We may here remark that though *jenkinsi* is found on plants it does not actually chew the leaf. From examination

Parthenogenesis in Mollusc *Paludestrina jenkinsi*

of the stomach contents it appears to browse on the micro-flora found on the plants and also on the decayed organic debris of the bottom.

(D) Apart from adhesion to inanimate objects the other means of dispersal of *jenkinsi* have not been made the subject of inquiry and experiment. Transport on weed carried by birds has been suggested, and some definite evidence is available (Peacock¹⁴; Coates⁵) that point in this direction. On the other hand it appears to have definite relations with certain fish (Dean⁷). Carp appear to eat it voraciously and perch to avoid it.

(E) Boycott⁸ has shown that it lives more commonly in running water with a fairly swift stream, and also that it is perhaps negatively rhæotropic. Following a suggestion of the same author, I have shown that there is some evidence that it is also negatively phototropic.²⁰

We thus see that the ascertained factors controlling the œcesis of *jenkinsi* are many and complex, and it seems that parthenogenesis must take its place as one of many such contributing factors in determining the invasion of fresh water. We have seen that in itself it is not enough to procure wide and rapid dispersal.

After a long period of residence in brackish and estuarine waters in insignificant numbers and with the same "patchy" and capricious distribution as *ventrosa*, due to periodic wholesale destruction through parasitic castration, it may have acquired immunity from such a limiting factor. Following upon this event may have occurred the development of parthenogenesis, and the two factors combined must have increased its chances of dispersal to an absolute certainty. But, as in Scotland and Denmark to-day, it still lacked other factors favouring a wide dispersal. Birds may have carried it inland without any fresh colonisation, as we may assume this factor is operative in Scotland. Finally, its chance distribution into an area prepared by the preceding invasion of *Elodea* may have completed the chain of favouring circumstances.

This sketch of the circumstances of distribution is not to be regarded as a final account of facts. It is intended to illustrate how factors ascertained by observation and experiment

Guy C. Robson

might combine to produce the known results. The long estuarine history, the abrupt change in distribution and numbers, the continued local occurrence in Scotland and on the Continent, and the details of its invasion of fresh water indicate a complex of factors, of which not all were operative at the same time and in the same locality.

6. References.

- ¹ Boycott, A. E. (1917), *Journ. Conch.*, **15** (5), 149.
- ² " (1919), *ibid.*, **16** (2), 54.
- ³ " (1919), *Trans. Herts. N. Hist. Soc.*, **17** (2), 35.
- ⁴ " (1921), *ibid.*, **17** (3), 266-270.
- ⁵ Coates, H., *Trans. Perthshire Soc. N. Sci.*, **7** (4), 42.
- ⁶ Conklin, E. G. (1902), *Journ. Acad. N. Sci.*, Philadelphia (2) **12** (1), 7.
- ⁷ Dean, J. D. (1904), *Journ. Conch.*, **11**, 15.
- ⁸ Erlanger, R. (1891), *Morph. Jahrb.*, **17**, 337.
- ⁹ Johansen, A. C. (1918), *Randers Fjords Naturhistorie* (Bløddyrene), **5**, 430.
- ¹⁰ Kleiner, E. (1912?), *Inaug. Dissert.*, Zurich.
- ¹¹ Korscheldt, E. (1891), *Sitzb. Nat. Freunde*, Berlin, **7**, 131.
- ¹² Künkel, E. (1912), *Verh. Ges. D. Ges. Naturf.*, Leipzig, No. 83, p. 437.
- ¹³ Morris, C. (1894), *Journ. Conch.*, **7**, 414.
- ¹⁴ Peacock, E. A. (1917), *Selbourne Magazine*, 331, **28**, 80.
- ¹⁵ Pelseener, P. (1920), Mem. in 8vo, *Ac. Roy. Belgique* (2) **5**, 243.
- ¹⁶ Quick, H. (1919), *Journ. Conch.*, **16** (3), 97.
- ¹⁷ Ramanujam, S. (1922), in *Nature*, 2740, **109**, 593.
- ¹⁸ Robson, G. C. (1920), *Ann. Mag. N. Hist.*, ser. 9, **5**, 425.
- ¹⁹ " (1920), *Ann. Mag. N. Hist.*, ser. 9, **6**, 525.
- ²⁰ " (1920), *Proc. Malac. Soc.*, **14**, 1.
- ²¹ " (1922), *Q.J.M.S.*, **68** (1), 159.
- ²² Roebuck, W. D. (1921), *Journ. Conch.*, **16** (6), 177.
- ²³ Sarasin, P. (1882), *Arch. Zool. Inst.*, Würzburg, **6**, 1.
- ²⁴ Stelfox, A. E. (1911), *Proc. R. Irish Ac.*, **29**, 118.
- ²⁵ Taylor, F. (1910), *Journ. Conch.*, **8**, 231.
- ²⁶ Woodward, B. B. (1898), *Proc. Malac. Soc.*, **8**, 297.