THE EFFECTIVENESS OF PASSIVE DISPERSAL IN HYDROBIA JENKINSI.

By

BENGT HUBENDICK.

(Riksmuseum, Stockholm.)

With 3 Maps.

Since a long time back observations and conclusions regarding the dispersal of gastropods have been published by different authors. In order to give a synopsis of all these KEW (1893) has compiled a great many facts, and BOYCOTT (1936) has contributed to KEW's work by furnishing supplementary material. In a previous paper (1947) I have myself had occasion to form an opinion on the effectiveness of passive dispersal. I based my opinion on the actual situations of distribution, whereas KEW and BOYCOTT based theirs to a vast extent on direct observation of migrating individuals. Starting from all this I got the idea that passive dispersal, *i. e.* that part of the dispersal which is independent of the activity of the animal itself, may greatly contribute to the distribution of a fresh-water gastropod. This my opinion was, however, merely inductive. To have it confirmed I thought it useful to follow the actual process of dispersal in a single species. Strictly speaking, this can only be done by reconstruction, *i. e.* by reconstruction supported by a good deal of probability. To name some examples of molluscs that, in recent time, have spread over a fairly vast geographical area and the spreading of which has been observed, I refer to *Dreissena polymorpha* (Pallas), *Petricola pholadiformis* Lamarck (*cf.* HESSLAND 1944), *Achatina fulica* Férussac (*cf.* ABBOTT 1949), and *Hydrobia jenkinsi* Smith.[1] It is only the dispersal of the last-mentioned species over the area around the North Sea and in the Baltic that will be dealt with here more closely. However, before entering on its history of dispersal, it is necessary to touch on the origin and on the earliest European occurrence of the species as well as on its systematic identity.

Hydrobia jenkinsi was originally described by SMITH (1889) on material from Plumstead in the Thames district. This species was, however, figured as *Rissoa castanea* by SOWERBY as early as 1859. In addition to this, a

[1] = *Paludestrina j.*, *Potamopyrgus j.*, and *Potamopyrgus crystallinus carinatus* Marshall in the literature.

few finds of the species made at earlier dates than 1889 have been pointed out in collections. A find reported from Ireland in 1837 (*cf.* STELFOX, 1927) has not been established with full certainty. In connection with the first occurrence of the species in Europe and the problems relating to its origin, its systematic position was discussed a great deal. Some authors have thought it possible or have taken it for certain that the species belongs to the genus *Potamopyrgus* (PILSBRY & BEQUAERT, 1927; THIELE, 1928; BOETTGER, 1931), inhabiting mainly the southern hemisphere. The shell-features are almost identical, but beyond that no morphological proof has as yet been advanced to support this opinion. The presumed relationship of the species to *Potamopyrgus* has been the strongest reason for its having been regarded as recently introduced into Europe. In opposition to this, STEUSLOFF (1927) assumes *jenkensi* to be "eine kürzlich (um 1880) in England neu entstandene, mit starkem Expansionsvermögen ausgestattete Art."

BOETTGER (1931) supposes the European species to be a recently immigrated and mutated form of the West-Indian species *Potamopyrgus crystallinus* Pfeiffer. However, *Hydrobia jenkinsi* has been found as subfossil in holocene clay in the London district (KENNARD & WOODWARD, 1899; KENNARD, 1923; STEUSLOFF, 1909). The earliest specimens are supposed to originate from 1500—1600 A. D. These finds have reversed ADAMS' theory on the origin of the British occurrence of the species (1893, 1897). ADAMS assumes the species to have been introduced together with timber imported from the Baltic area. Actually, however, this is not conceivable, as *Hydrobia jenkinsi* did not inhabit the Baltic area before 1900. The only report of its occurring there earlier has been published by SCHLESCH (1927). He reports the species as a fossil in Littorina deposits in Estonia. BOETTGER (1934) has doubted this statement. He supposes the find to have actually represented *Hydrobia ulvae* (Pennant) or *H. ventrosa* (Montagu). These two species are known from quarternary deposits in the Baltic area and it has even been possible to determine the former species on the basis of the radula (FELIKSIAK 1938). In view of the vastness of quarternary geological researches in the Baltic area SCHLESCH's determination must be considered most doubtful. In the British Isles, too, the quarternary and especially the recent mollusc fauna has been examined most thoroughly and has been an object of constant observation for a long time. Disregarding the problems of systematic position and those concerning the geographical origin of *Hydrobia jenkinsi*, it may be almost taken for certain that before 1900 the species had not had a considerable range either in Europe or on the British Isles.

One would not make a serious mistake by trying to reconstruct the process of dispersal of *H. jenkinsi* on basis of the reports published on the

finds of this species. Many reports indicate with a precision of up to one or a few years the first appearance of the species in a locality. In most cases, however, the find-reports only give the last immigration date of the species for the respective locality. BOYCOTT (1917) claims that the species is prone to die out after a few years, which would mean that the appearance of the species constitutes a reliable item of registration as to the process of dispersal. This, however, does not apply to geographic conditions, for which the first occurrence within a region is of decisive importance. Furthermore, the life-time of the large populations certainly varies greatly. The attempt made in the following lines to reconstruct the dispersal of the species within western Europe can therefore only lead to approximate results. Still, the fairly regular process of dispersal that will be described may indicate that the material has been satisfactory.

The first reliable find of living *Hydrobia jenkinsi* in Europe was made in 1859 in brackish water in the Thames estuary (Fig. 1, 2). An obvious dispersal of the species does not seem to have started earlier than in the eighties. Probably even at that time, and certainly not later than 1893, it had already immigrated into the fresh waters of the Thames district. About the nineties the species suddenly appeared in several brackish water localities along the British South and East coast and in Ireland. Its first find in Ireland, however, was made in fresh water. During the first decade of 1900 the species spread over a great part of the fresh waters of South England and of the Midlands and also in Ireland, where it has extended particularly its northern range. The species further occurs in new localities of brackish water, especially so on the English West coast and in Scotland. It continued to expand its range successively in the British Isles and gradually made its appearance in the brackish waters of northern Scotland and of the Orkneys and in fresh water on the Hebrides and on Jersey in the Channel. The reconstruction in Fig. 2 is based upon the about hundred dated finds shown in Fig. 1.

It is difficult to find out in how many localities *H. jenkinsi* has immigrated from brackish water into fresh water. The way in which the range of the species has increased in England gives the impression that it may have been the result of merely a few immigrations or of an immigration only into the Thames district, *i. e.* from one centre of distribution only. But considering all occurrences of the species on the British Isles there can hardly be any doubt that it has immigrated several times from brackish into fresh water. This is likely to have happened not only in the Thames district, but also at any rate in the Edinburgh area, on the Orkneys and in Ireland, within the latter region probably in two localities. In addition to this, independant immigration into fresh water may have taken place at Barmouth in the Merioneth district and possibly also in

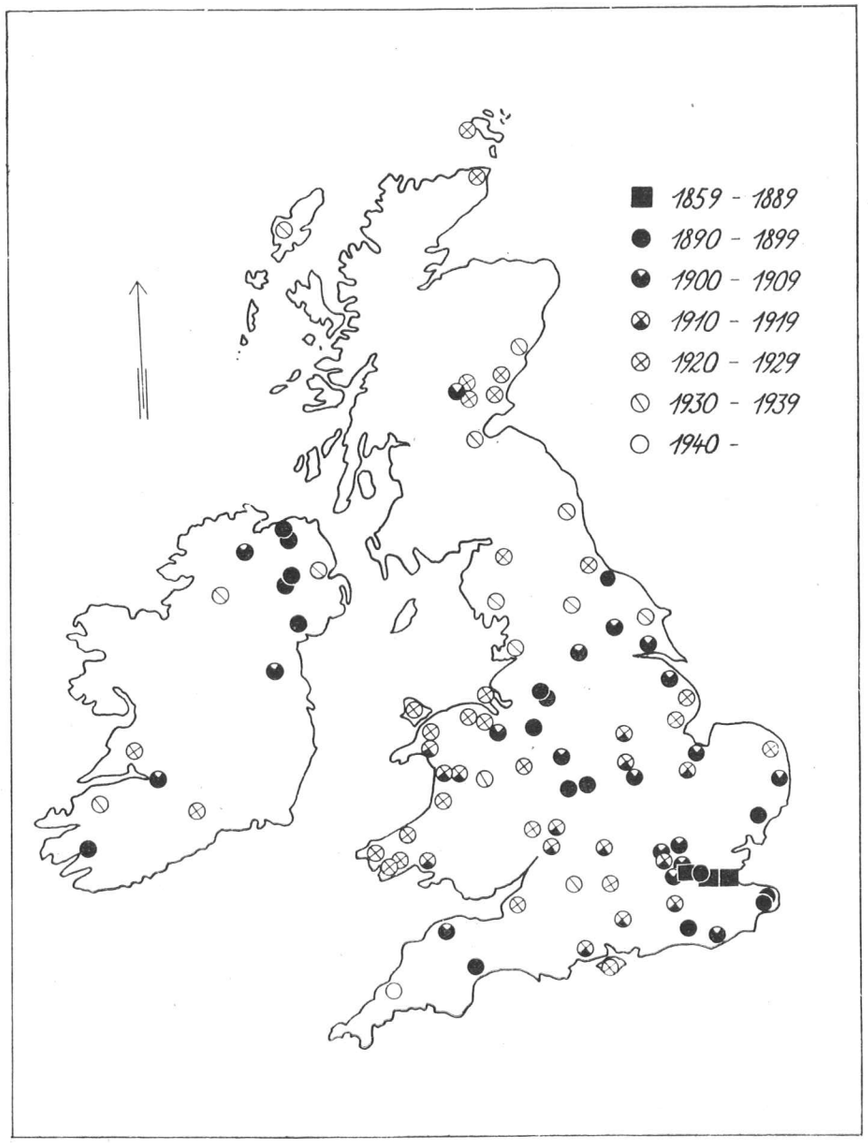

Fig. 1. Dated finds of *Hydrobia jenkinsi* in the British Isles.

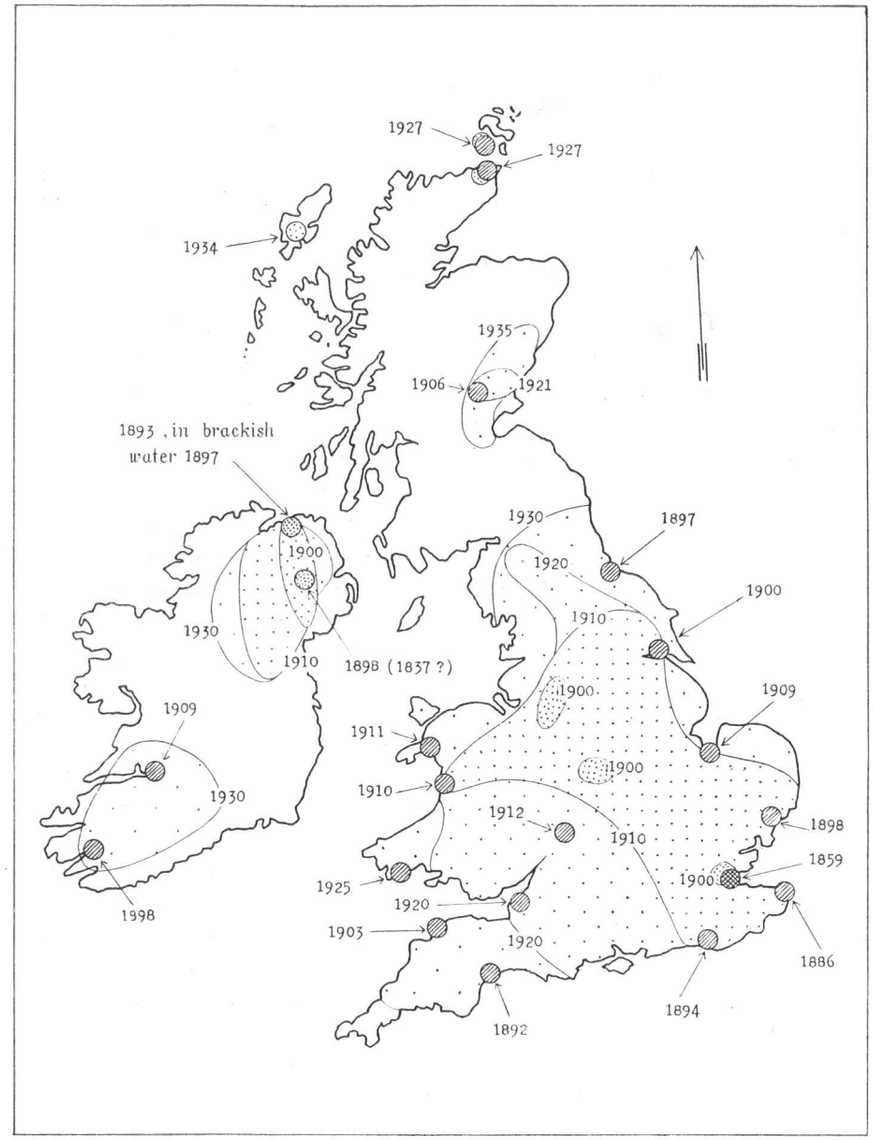

Fig. 2. Dispersal of *Hydrobia jenkinsi* in the British Isles. The hatched rings mark the localities of the first finds in brackish water within the respective regions; dotted rings correspond to finds in fresh water. The dotted areas mark schematically the probable range at various dates. The map is based on the finds in Fig. 1.

the following areas[1]: Sussex East, Pembroke, Lincoln North, Durham and Caithness. It may finally be added that the relatively successive character of progression in each area of distribution is illustrated by the character of the isorithms, which, on the whole, are concentric (*cf.* Fig. 2). In Ireland the process of distribution seems to be slower than in England.

A successive course of dispersal is still more conspicuous in the Baltic region (Fig. 3). *H. jenkinsi* was first noticed there near the Kiel canal in 1900. From there it probably spread to northern Jutland, where it was first observed in 1915, and over all the Baltic up to the innermost portion of the Gulf of Bothnia, where the species was observed in 1945. The opinion that the species has penetrated gradually through the Baltic region is not based on more than 16 reports, which relate to the first finds of the species in different places. Considering the possible lapse of time between the date at which the animal was noted and that at which the species actually arrived at the various localities, the number of observations may seem too small to allow of a conclusion as to successive immigration. Primarily the map illustrates the history of discovery of the species. But the nearly complete geographical successiveness represented by the finds in addition to the extent of the immigration during at least 35 or possibly 45 years makes such a conclusion a relatively certain one. Probably the map also, at least approximately, illustrates the history of migration.

H. jenkinsi has also spread into Holland and Belgium (Fig. 3). Within this area as well as in various parts of northern Germany and in Jutland the species has immigrated into fresh water.

The process of dispersal described here admits of some reflections on the method of dispersal. But to be able to judge of their validity from a wider point of view it is necessary to note the special qualifications for dispersal in *Hydrobia jenkinsi*. The mobility of the species is only slight, and at any rate its ability of active dispersal is not great enough to be of any importance geographically. Its passive dispersal is facilitated by the species being able to live in brackish as well as in fresh water. According to Benthem Jutting (1923), the species is oligohalinophilous and prefers a Cl-standard of 0.1—1.0 g per litre (corresponding to a salinity of 0.2—1.6 $^0/_{00}$). According to Adam (1942), it can live under certain conditions in a salinity of 20—22 $^0/_{00}$ after having been transferred directly from fresh water, and it is able to live for a limited time in a salinity of 32 $^0/_{00}$ if the latter has been gradually reached. Spontaneously, however, the species only lives in water having a salinity between 0 and, at the utmost, 20 $^0/_{00}$ (Ellis, 1932). It probably thrives best in water with a low salinity, *i. e.*

[1] Regarding the division of the British Isles into faunistic districts, *cf. J. of Conch., 10, pl. 5* (1902).

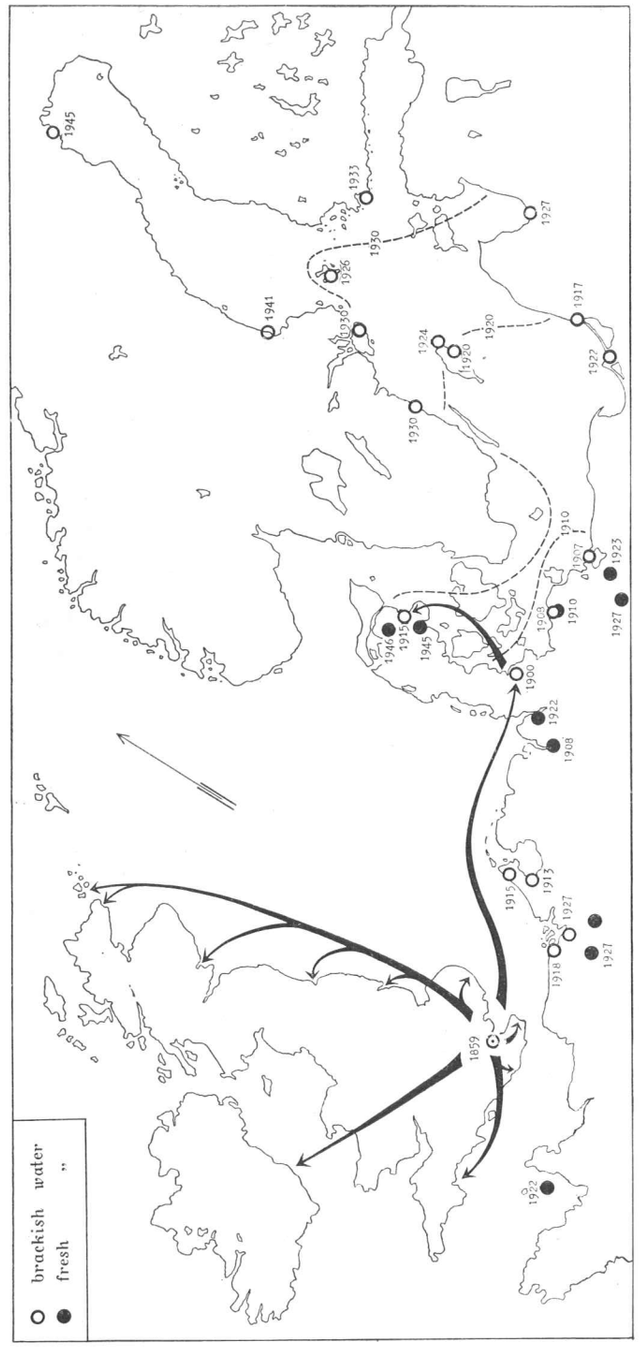

Fig. 3. Dispersal of *Hydrobia jenkinsi* in brackish water and its occurrences in fresh water on the Continent. The arrows indicate schematically the dispersal towards localities of brackish water. The isorithms in the area of the Baltic mark the hypothetical but presumable fronts of dispersal at various dates. Only the localities of the earliest finds of the species are marked there. The number of find-localities has considerably increased later on.

3—10 ‰. Boycott (1936) considers *H. jenkinsi* to be resistent to lack of calcium carbonate, *i. e.* to be what he calls a "soft-water species".

In this connection the conditions of reproduction in the species are of special importance. Several authors had observed the lack of males (Taylor, 1910; Boycott, 1919; Quick, 1920) until Robson (1923) pointed out the occurrence of parthenogenesis. He examined smears of the gonad and serial sections through various parts of the reproductive system. *H. jenkinsi* not only shows a parthenogenetic development but it is also viviparous or ovoviviparous. Krull (1935) has observed eggs as well as sperms in the gonad, and he consequently considered the species to be hermaphroditic and reproductive by self-fertilization. His opinion has hitherto not been confirmed by other zoologists, but has, on the contrary, been critisized by Sanderson (1940). This author and also Rhein (1935) have shown the pathenogenesis to be diploid. However, there seems to be no difference between the influence of parthenogenesis and that of self-fertilization on the effectiveness of the passive dispersal. Sanderson (1940) suggests that there may be two races: a dipoid one on the continent and a tetraploid one in Britain. However, the diploid form has been observed in one locality only. Further facts are desirable to elucidate this problem.

The foregoing survey of reports relating to the dispersal of *Hydrobia jenkinsi* shows with great evidence a high capacity of or disposition for passive dispersal in the species. The influence of this capacity, if exercised for a long time, may become very important biogeographically. But it may only be of general importance under a certain presupposition, *i. e.* if the dispersal is not synanthropic. And in *H. jenkinsi* such a method of dispersal does not seem wholly excluded. It is, above all, probable that human transport means have contributed to the transference of the species from the British Isles to the Kiel Canal. The dispersal in the British Isles is probably not synanthropic. British malacologists have often expressed their astonishment at the rapid dispersal of the species and have asked themselves how it may be explained. Yet they have not referred to a synanthropic method of dispersal. Boycott (1921), however, assumes the canalization system to have facilitated the dispersal of the species in the inland waters of the southern and midland districts of England. At any rate a synanthropic method of dispersal in the Baltic region seems unlikely because of the probably successive course of the dispersal. As to dispersal by shipping in the Baltic, such can hardly be expected to be in conformity to the scheme which actually seems to exist; though of course theoretically such a possibility cannot be rejected. It is, at any rate, impossible to decide how the dispersal has actually come about. There is, in many cases, no other possibility of explaining the often very efficient dispersal of fresh water gastropods than by the agency of birds or other

flying animals, a method of dispersal which, therefore, is also conceivable for *Hydrobia jenkinsi*. Schwarz (1929) has observed one more type of passive dispersal in Hydrobiids; he says that "unter besonderen Verhältnissen (Windstille, Sonnenbestralung, Ebbe, Austrocknen, ruhig auflaufende Flut) für gewisse sehr leichte Gehäusetiere infolge der physikalischen Eigenschaften der Wasseroberfläche die Möglichkeit der Ausbreitung über sehr weite Flächen, bzw. der fast ausschliesslichen Anhäufung unversehrter Gehäuse gegeben ist". Changes of level by tide water may, of course, be substituted, *e. g.* by such caused by variations in atmospheric pressure, which are common in the Baltic area.

The dispersal of *H. jenkinsi* in western Europe and especially in the Baltic area is a concrete example of the great possibilities of the passive distribution for small-sized gastropods belonging to the fresh-water or the brackish-water fauna. From a biogeographic point of view so great a capacity of dispersal is of the greatest importance. In *H. jenkinsi*, however, this capacity may partly be due to the parthenogenetic reproduction (or self-fertilization) and in addition it may be favoured by the ability of the species to live in brackish as well as in fresh water.

Acknowledgements.

I am anxious to express my gratitude to Mr. R. Winckworth, London, and to Mrs. N. F. Macmillan, Bromborough, England, for their assistance in procuring reports from literature not available in Sweden. I am, further, exceedingly obliged to Mr. G. Mandahl-Barth, Charlottenlund, Denmark, for his reports on the occurrence of *H. jenkinsi* in fresh water in Jutland.

Literature.

Abbott, R. T., 1949. Nat. Hist., 58: 68. New York.
Adam, W., 1942. Bull. Mus. roy. Hist. nat. Belg., 18 no. 23. Brussels.
Adams, L. E., 1893. J. of. Conch., 7: 148.
——, 1894. Id., 7: 390.
——, 1897. Irish Nat., 6: 234. Dublin.
——, 1898. J. of Conch., 9: 15.
——, 1898. Id., 9: 114.
——, 1930. Proc. I. Wight Nat. Hist. Arch. Soc., 1: 694. Newport.
Bacchus, D., 1922. J. of Conch., 16: 262.
Beeston, H. and Wright, C. E., 1904. Id., 11: 72.
Benthem Jutting, T. van, 1922. Flora en Fauna der Zuiderzee, p. 391. Helder.
——, 1923. Arch. Moll., 55: 199.
Boettger, C. R., 1931. Arch. Zool. Ital., 16: 250. Torino.
——, 1934. Arch. Moll., 66: 52.
Booth, F., 1909. Naturalist London, 1909: 204.
Boycott, A. E., 1917. J. of Conch., 15: 216.
——, 1919. Id., 16: 54.
——, 1921. Trans. Hertfords. Nat. Hist. Soc., 17: 263. London.
——, 1936. J. Anim. Ecol., 5: 116. London.
Carpenter, G. D. H., 1945. J. of Conch., 22: 146.
Carpenter, G. D. H. and Cooper, J. E., 1908. Id., 12: 190.
Carter, C. S., 1923. Naturalist London, 1923: 286.
Cooper, J. E., 1911. J. of Conch., 13: 138.
——, 1918. Id., 15: 275.
Crapper, E., 1924. Id., 17: 98.
——, 1924. Id., 17: 104.
——, 1924. Id., 17: 137.
Crouch, W., 1890. Essex Nat., 4: 213. Buckhurst Hill.
Daniel, A. T., 1894. Rep. N. Stafforts. Field Cl., 28: 94. Stafford.
——, 1894. J. of Conch., 7: 325.
Dupuis, P., 1927. Ann. Soc. Roy. Zool. Belg., 58: 31. Brussels.
Ellis, A. E., 1932. Proc. Malac. Soc. London, 20: 11.
Feliksiak, S., 1938. Zool. Anz., 122: 186.
Goddard, T. R., 1926. Trans. Nat. Hist. Soc. Northumberl. Newcastle. 6: 238. London.
Grensted, L. W., 1923. Lancashire Ches. Nat., 15: 163. Manchester.
Gumley, E. M., 1927. Irish Nat., 1: 175. Belfast.
Hann, A., 1898. J. of Conch., 9: 89.
Hessland, I., 1944. Fauna Flora, p. 15. Uppsala.
Hollis, W. H., 1920. Northamps. Nat. Hist. Soc. Field Cl., 20: 200. Northampton.
Holzfuss, E., 1927. Abh. Ber. Pommerschen Naturf. Ges., 8: 87. Stettin.
Horsley, J. W., 1905. J. of Conch., 7: 200.

Hubendick, B., 1947. Zool. Bidr. Uppsala, 24: 419.
Humphreys, G., 1911. J. of Conch., 13: 254.
Jaeckel, S., 1927. Arch. Moll., 59: 255.
——, 1940. Sitzungsb. Ges. naturf. Fr. Berlin, p. 114.
Johansen, A. C., 1918. Forh. 16 Skand. Naturf. möte, p. 633. Kristiania.
——, 1918. Randers Fjords Naturhistorie, p. 430. Copenhagen.
Kennard, A. S., 1923. Proc. Malac. Soc. London, 15: 241.
Kennard, A. S. and Woodward, B. B., 1899. Id., 3: 297.
——, 1901. Essex Nat., 11: 288. Buckhurst Hill.
Kew, H. W., 1893. Int. Sci. Series, 75. London.
Krull, H., 1935. Zool. Jahrb. Anat., 60: 399. Jena.
Luther, A., 1933. Mem. Soc. Fauna Flora Fenn., 10: 11. Helsingfors.
MacDonald, R., 1932. J. of Conch., 19: 263.
Marshall, J. T., 1889. Id., 6: 140.
Mayfield, A., 1909. Id., 12: 269.
McMillan, N. F., 1942. Proc. Liverpool Nat. Field Cl., p. 11.
——, 1943. North Western Nat., 18: 320. Arbroath.
McMillan, N. F. and Henderson, M., 1945. Proc. Liverpool Nat. Field Cl., 1944, p. 10.
Morris, C. H., 1894. J. of Conch., 7: 414.
Odhner, N. Hj., 1921. Fauna Flora, 16: 85. Uppsala.
Oldham, C., 1892. J. of Conch., 7: 108.
——, 1901. Id., 10: 42.
——, 1912. Id., 13: 340.
——, 1914. Id., 14: 160.
——, 1916. Id., 15: 86.
——, 1926. Id., 18: 17.
——, 1927. Id., 18: 70.
——, 1928. Id., 18: 272.
Overton, H., 1894. Id., 7: 414.
——, 1905. J. of Malac., 1: 15. Birmingham.
Petch, T., 1901. Trans. Hull. Sci. Field Nat. Cl., 1 (4): 236. Hull.
Phillips, R. A., 1909. Irish Nat., 18: 143. Dublin.
Pilsbry, H. A. and Bequaert, J., 1927. Bull. Amer. Mus. Nat. Hist., 53: 69. New York.
Quick, H. E., 1920. J. of Conch., 16: 97.
Recorder's Report in J. of Conch. 1912, 13: 317; 1922, 16: 273; 1923, 17: 27; 1924, 17: 122; 1925, 17: 222; 1926, 18: 28; 1929, 18: 299; 1931, 19: 123; 1931, 19: 184; 1933, 19: 344; 1935, 20: 156; 1935: 20: 187; 1937, 20: 313.
Rhein, A., 1935. Naturwissenschaften, 23: 100. Berlin.
Robson, G. C., 1920. Ann. Mag. Nat. Hist., 5: 425.
——, 1923, Brit. J. Exp. Biol., 1: 65.
——, 1926. Id., 3: 149.
Roebuck, W. D., 1912. J. of Conch., 13: 349.
——, 1913. Id., 14: 81, 310.
——, 1916. Id., 15: 91, 190, 276.
——, 1920. Id., 16: 101.
Sanderson, A. R., 1940. Proc. Zool. Soc. London, 110: 11.
Schlesch, H., 1927. Arch. Moll., 59: 69.
——, 1927. J. de Conch., 71: 80.

Scholten, J., 1919. Bijdr. Dierkunde, 21: 67. Leiden.
Schwarz, A., 1929. Natur und Museum, 59: 50. Frankfurt a. M.
Shrubsole, G., 1935. J. of Conch., 20: 130.
——, 1936. Trans. Eastbourne Nat. Hist. Soc., 11 (3): 36.
——, 1941. J. of Conch., 21: 256.
Smith, E. A., 1889. Id., 6: 142.
Stelfox, A. W., 1927. Irish Nat. J., 1: 174. Belfast.
Steusloff, U., 1924. Arch. Mecklenburg Naturf., 1 (2): 7. Rostock.
——, 1909. Arch. Fr. Naturg. Mecklenburg, 63: 82. Güstrow.
——, 1927. Verh. Int. Ver. theor. angew. Limn., 3: 455. Stuttgart.
——, 1939. Arch. Moll., 71: 82.
Stubbs, A. G., 1902. J. of Conch., 10: 284.
——, 1905. Id., 11: 211.
Taylor, F., 1900. Id., 9: 340.
——, 1910. Id., 8: 231.
——, 1918. Lancashire Nat., 11: 19. Darwen.
Thiele, J., 1928. Zool. Jahrb. Syst., 55: 351. Jena.
Tomlin, J. R. le B., 1904. J. of Conch., 11: 11.
Wallis, H., 1902. Naturalist London, 1902: 270.
Vaughan, J. W., 1914. J. of Conch., 14: 220.
——, 1926. Id., 18: 64.
Weaver, G. H., 1910. Id., 13: 47.
Welch, R. J., 1913. Naturalist London, 1913: 288.
——, 1923. Id., 1923: 347.
——, 1926. Irish Nat. J., 1: 135. Belfast.
——, 1927. Id., 1: 175.
——, 1931. Id., 3: 197.
Whitehead, H., 1935. J. Anim. Ecol., 4: 58. London.
Woodward, B. B., 1892. Ann. Mag. Nat. Hist., 9: 376.