The Habitats of Fresh-Water Mollusca in Britain
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THE HABITATS OF FRESH-WATER MOLLUSCA IN BRITAIN[1]

BY A. E. BOYCOTT

Ask now the beasts, and they shall teach thee. Job xii. 7

(*With* 63 *Figures in the Text*)

CONTENTS

1. INTRODUCTION

WE have 62 fresh-water species, 26 bivalves and 36 gastropods, 10 of which are operculates and breathe by gills while the rest are pulmonates which normally breathe air. There are also 4 operculates (*Assiminea grayana*, *Paludestrina stagnalis* (*ulvae*), *P. ventrosa*, *Amnicola confusa*) and 2 pulmonates (*Ovatella bidentata*, *Phytia myosotis*) which affect the junction between fresh and salt water, but I know little about their habitats and shall not consider them further.

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Fresh-water differ from terrestrial habitats in two important particulars. (*a*) The environment is much more uniform from place to place than on land and less variable in any one place from time to time. Hence there is less difference between the inhabitants of various loci: no two watery habitats which are at all favourable to Mollusca will have such diverse contents as, for example, an old acid woodland and a chalk down. It follows too that transplantations, natural or deliberate, should be more likely to succeed than with land Mollusca, and that experimentation under controlled conditions is relatively easy, though it needs far more exploration than it has received from those who like keeping aquaria. (*b*) The habitats are mostly divided into discrete units and are definitely limited in size: some of them are presumably infinitely large from the molluscs' point of view, but others are so small and circumscribed that it seems likely that questions of roominess must arise, almost or quite unknown on land.

For descriptive purposes we may distinguish several groups of habitats classified by common human usage, though these do not of course necessarily correspond with the essential categories of molluscan ecology: they naturally grade into one another and it would be waste of time to try to define them too closely:

Rivers.

Streams.

Springs and the streamlets and trickles which come from them.

Canals.

Ditches.

Lakes, i.e. bodies of water large enough for the wind to raise significant waves and generally too deep in the middle parts for phanerogamic vegetation.

Ponds, of $\frac{1}{2}$ acre downwards and mostly of the order of 400 sq. yd. ($\frac{1}{12}$ acre) or less.

Marshes.

Ponds and, less often, lakes and marshes have to be further distinguished into (1) those through which a stream of water runs either perennially or in the winter and which are thus in communication with the river systems ("running"), and (2) those without any direct connection with another watery habitat ("closed"). We also have to note whether any of the smaller habitats always contain water or whether they dry up in the average summer ("drying") or in exceptional droughts. Ditches include permanent draining ditches connected with marshes, often of considerable size, and ditches made to keep land dry in wet weather which contain no water for most of the year.

The nomenclature is confused in a variety of ways. Thus what would be called a pond in lowland country may be dignified as a tarn, loch, lough or llyn in the hills. A "lake" in many parts of England may be a stream; a "pool" may be a pond, a good-sized lake or a slow-flowing piece of a river; a "ditch" in Ireland sometimes means a fence or bank

(**259**), and you may either fall into a "dyke" or climb over it; "spring" may mean a wood, and the dialect dictionary would no doubt reveal many other possibilities of perplexity, most of which would, as I hope to show, be solved by a knowledge of the Mollusca present.

It is evident that man has had a good deal to do with many of these habitats, and his influence on our water Mollusca is perhaps hardly less than on the land species. Canals, ditches, marl pits and brick diggings are entirely human and so are most ponds: they provide habitats of which there are few or no natural replicas. Man's interest has always been to get rid of marshes, drain river valleys and generally to make as clear a distinction as he can between dry land and water. In the result most of the places in which we collect, especially in the southern two-thirds of England, are more or less unnatural.

2. General biology

(*a*) *Food*

The bivalves feed at random by sucking in water and entangling any particles it may contain in their intestinal mucus "with catholic impartiality" (**256**), though Allen (**192**) thinks that the labial palps can exercise a certain amount of discrimination. They are therefore dependent on the Algae, etc., which happen to be present, which they filter out quickly and very efficiently, as Dodgson (**20**) has shown in his work on the cleansing of *Mytilus* from bacterial contamination. Allen found that a 200-gm. *Lampsilus* passed through 35 litres (10 gallons) a day; Dodgson got 53 litres (15 gallons) for *Mytilus* 3 in. long. Algologists would find the intestines of mussels worth study: Latter (**1**, p. 174) gives a list of the things found in *Anodonta*, and Prof. E. J. Salisbury got some rare Algae in some we caught in the Elstree reservoir. Except *Dreissena*, the bivalves live mostly on the bottom, though *Sphaerium corneum*, *S. lacustre* and some *Pisidium* often climb up plants, and sand or mud in some form seems to be a necessity: *Sphaerium* and *Pisidium* do no good in aquaria without it. But whether this substratum is needed to grow their microscopic food or to give them something to burrow in, I do not know: it may be useful in both ways.

The gastropods are more mobile, can fix themselves anywhere with their adhesive feet, and have the same type of rasping apparatus as the land Mollusca, so that selection is possible. They feed on the decayed remains of water plants and especially on Algae which they scrape off the leaves of the plants, the mud, stones and other surfaces (e.g. floating logs), as may be well seen as they crawl over the glass of an aquarium. In some loci (e.g. mountain lakes, or cement tanks), where there is little or no obvious vegetation it seems quite clear that the normal food of the *Limnaea peregra* and *Ancylus fluviatilis*, which may be abundant, is the algal slime on the stones. As with land Mollusca, it is most exceptional to see any evidence in the field that they eat the green leaves of the higher plants among and on which they live: I have seen it only once when an exceptional crowd of *Limnaea stagnalis* had eaten a bed of *Helosciadium* to pieces. Nor do they commonly do so in captivity, even when their rate of growth is seriously diminished by overcrowding and one may reasonably suppose that they are short of food. On the other hand, as slugs and snails do, they will eat cultivated plants such as cabbage and lettuce, though more readily when they are partly decayed. Warrington's (**2**) record that *Limnaea stagnalis* eats *Valisneria* greedily in aquaria I regard as exceptional rather than regular, also R. Welch's (**3**) note of "rare water-lily leaves" being destroyed by the same species and *Planorbis corneus*. At times they may be carnivorous and will eat meat, dead fish, etc.: as curiosities we may note that *Pl. corneus* has been caught eating the egg capsules of *Pl. vortex* (Sherborn (**4**)) and live *Limnaea peregra* (Cockerell (**5**)), and Webster (**237**) says it does best in aquaria with meat. They show the same liking as land snails for newsprint (**173**), cardboard, etc., and what they eat depends no doubt on what is available and on how hungry they are.

Limnaea peregra from any place where there is fine gritty silt will have some, often a great deal, in their stomachs; *Ancylus fluviatilis* is the same (**261**). Aquarium experience shows that *Limnaea* get on quite well without this mechanical aid to digestion, though Colton (**207**) found that *L. columella* grew better if silt was provided. The operculate *Goniobasis* gets rid of its sand in captivity in about 14 days (**208**).

The well-known experiments of Semper showing a direct relationship between the volume of water in an aquarium and the rate of growth of *Limnaea stagnalis* have been carefully worked over again with *L. peregra* by F. M. Turner (**6**), who concluded that the main if not the only factor was the food supply. He found, for example, that the rate of growth of snails brought up in standard jars was a function of their number, and that a single snail could be grown to its full adult size in 10 or 15 c.c. of water if it were fed well enough. The bad, and in the end fatal, effect of overcrowding young snails in aquaria is obvious enough, and it seems quite possible therefore that the abundance of a mollusc in a locus of limited size may depend on the food supply, though whether the occurrence of any species is so determined is problematical. Shortly before his death Turner had been feeding *L. peregra* on pure cultures of green Algae and had obtained some evidence of selective preferences, but *I know of no reasons for thinking that in nature any species of snail has any direct relation to any particular plant.* Snails like a good supply of green plants because these, while alive, oxygenate the water and provide surfaces for algal growth, but the specific associations which can easily be seen are, as with the land Mollusca, due to the plant and the snail both happening to flourish in the same kind of locus. In my study of the Aldenham ponds (**7**), for instance, I worked out several statistical specific concurrences between snails and plants (e.g. *Planorbis fontanus* with *Lemna trisulca*), but I do not suggest that there is any more intimate connection between them than there is between calcicole land Mollusca and beech trees. Similarly, a good many Mollusca will generally be found (in England) with water-lilies or with *Potamogeton crispus*, because these plants usually grow in places which are on other grounds favourable for them, and incidentally the large flat lily leaves provide a convenient and profuse growth of Algae. But the snails can get on quite well without the plants and there is no essential biological connection between them.

(*b*) *Life histories*

Reproduction. The larger mussels (*Anodonta*, *Unio*) are generally described as unisexual and there is commonly a considerable excess of females: Bloomer (**10**), however, finds a good many hermaphrodites in *Anodonta cygnea*, and it seems pretty clear that individuals change their sex: each female produces about half a million glochidia. *Sphaerium* and *Pisidium* are hermaphrodite and evacuate well-grown young, naturally in small numbers. Crowther (**277**) finds usually 6 or 7 in *Sphaerium corneum* but up to 30: Thiel (**182**) has shown at Hamburg that it has two generations a year with free lives from October to August and August to October, producing about 10 young each time, so that the annual increase is about 100. *Paludina* (unisexual) is also viviparous with about 50 young, as is *Paludestrina jenkinsi* (parthenogenetic) with broods of 20 or 30. The other operculates lay eggs, but no one seems to know how many. The pulmonates are all hermaphrodite and lay eggs. *Limnaea peregra*, *L. auricularia*, *L. stagnalis*, *L. palustris* and some *Physa Planorbis* (**217**) and *Ancylus* are known to self-fertilise quite readily (**13**), and they can probably all do so if need arises though they prefer cross-fertilisation. How many eggs are laid in nature is not clearly known, and our information about what happens in aquaria is very imperfect: in some of the accounts (e.g. Rimmer (294)) there is complete confusion between the number of eggs laid and the number per capsule, though I suspect that the two figures are proportionate to one another since both depend on the size of the parent. In captivity some races of *Limnaea peregra* average about 500 and can achieve as many as 3000 (**11**); other smaller races produce 200 or so. Correspondingly Oldham's data (**12**) suggest about 1000 for *Planorbis corneus* while *Pl. nautileus* has about 30 young. Interesting details about egg laying are given for the Indian *Limnaea luteola* by Sechaiya (**215**) and for the American *L. columella* by Baily (**216**).

Length of life. The larger mussels develop slowly and live for many years: if the lines of growth represent annual increments, 10 or 15 years is a common age and 70 has been suggested. Hence destruction of the adults may seriously diminish the population, as has happened with *Unio margaritifer* in the Scotch pearl fishery (**14**) and in Ireland. *Sphaerium* and *Pisidium* appear to be annuals. *Paludina* lives for several years but probably not as long in nature as in captivity, where Oldham (**15**) has kept female *P. contecta* for 5 years and the males (which are smaller) for at least $3\frac{1}{2}$ years. Cleave and Lederer (**22**) say of *P. contectoides* in America that the wild males live about a year and the females up to 3 years, and Annandale and Sewell (**147**) found the same for *P. bengalensis* in India: it has been known since Spallanzani that one impregnation will suffice for more than the current year. *Bithinia tentaculata* often has such well-defined growth marks and *Neritina fluviatilis* is sometimes so thick and encrusted ("gerontic") that it seems probable that they may live 2 or 3 years, but the rest of the operculates are presumptive annuals as *Paludestrina jenkinsi* certainly is. All the pulmonates are annuals with a natural duration of life of 9–15 months or less, except *Planorbis corneus*, which lives and goes on growing for 2 or 3 years and breeds correspondingly often (**12**, **21**); Oldham has kept it in captivity up to 6 years. In hot summers *Limnaea peregra* may get through 2 generations in one season, as it may easily be induced to do in captivity (**11**, p. 57), and it has been found spawning in November in the underground water which comes out at Malham Cove at 46–48° F. all the year round (Percival MS.). Wild *L. truncatula* in Wales (**197**) normally have 2 or even 3 generations in a summer. This may explain why the largest specimens are found early in the spring and in Scotland. In America *L. columella* breeds a new generation about every 2 months in the laboratory (**23**).

I do not understand the statements that in central Europe (**16**, p. 39) and in north America (**17**, p. 51; **18**, vol. 1, p. 412) such species as *L. stagnalis* need 2 or even 3 years to reach maturity. It may possibly be true for places where a severe winter stops growth for several months, but it certainly does not apply to this country where the annual cycle can be clearly seen in wild *L. stagnalis, L. auricularia, L. peregra, Planorbis complanatus,* etc.

Parasitism, etc. In their early stages the large mussels are obligatory "parasites" on fish. Some American species can apparently pass through their metamorphosis in the parent's brood pouch (**214**), and for one the amphibian *Necturus* makes a good host: the claim (**213**) that they can be reared in simple nutrient solutions needs confirmation. In America, too, where a good deal of attention has been paid to mussels for the sake of pearl buttons, there is some (but not much) evidence that certain species have specific relationships with particular fish (**240**, summary and literature in **18**). In Britain, however, I know of nothing to suggest that fish can be dispensed with or that the kind of fish matters very much. Wilson (in **19**) notes the curious point that parasitic Copepods may so occupy the gills as to prevent the attachment of glochidia. No other fresh-water molluscs are dependent for development or in any other way on another animal.

It occurred to me at one time that the widespread discontinuous distribution of some uncommon species might be due to something queer in their life histories, possibly a parasitic phase. But I have bred the three most conspicuous instances—*Segmentina nitida* (from Lewes), *Amphipeplea glutinosa* (Co. Kildare) and *Limnaea glabra* (Leeds, Scotland) to maturity under conditions which excluded fairly satisfactorily the intervention of another animal or any special plant.

(c) *Mortality*

Enemies and parasites. Fresh-water Mollusca have many enemies. Domestic and domesticated ducks are the worst, and they can completely destroy all the Mollusca in a pond or ornamental water, though this drastic effect may be due as much to the putrefactive fouling of the water as to actual eating. I know of no instance where under natural conditions an enemy may be reasonably accused of exterminating any established species: the great majority of animals which prey on snails are more or less omnivorous, and when a snail population is reduced beyond a certain point they turn their attention to other foods which are easier to find: trout, for example, as Pentelow (**33**) and Slack (**34**) have shown, eat what they can get. Rats (**24**, **181**, **244**), water-shrews (**255**) and otters (**155**) eat mussels and snails. Herons and other birds no doubt kill a good many. Peacock (**222**) has occasionally found *Limnaea auricularia* and *Dreissena* on thrush stones, and Carter (**25**) has seen a thrush pick out *Limnaea stagnalis*, smash and eat it: I have watched a blackbird fish out *Planorbis corneus* from a tank in my garden several times, but no attempt was made to eat them. Bellamy (**26**, p. 246) says that in Devon crows pick mussels out of the rivers and drop them on rocks to smash them as gulls do cockles (**63**), and they have been seen eating *Anodonta cygnea* and *Unio pictorum* (**262**) and *Dreissena* (Oldham), which tufted duck will also dive for and then be robbed by gulls (**263**). Thompson (**264**) mentions a grey wagtail full of *Ancylus fluviatilis*. By general consent fish are very fond of snails which are highly esteemed as fish food in trout hatcheries and also for coarse fish: Hall (**27**) specially commends *Planorbis corneus*, *Limnaea peregra*, *L. stagnalis* and *L. auricularia*, and says that the newly hatched young "seem to be the most acceptable of any food to fresh-water fish". Fishing clubs in Yorkshire buy *L. peregra* in quantity for fish food (**30**), and various large species (including even *Dreissena* (**181**)) seem to be moved about a good deal to rivers and lakes where they do not rightly belong. But the interest of fish is not restricted to the fleshy sorts: several observers (**28**, **29**) have found large numbers of *Valvata piscinalis* in trout's stomachs which must be more shell than meat, as must *Paludestrina jenkinsi* (**253**); in the north of Scotland the contents of the trouts' stomachs are often made up almost entirely of *Pisidium* (Oldham), and Burnett discovered *Limnaea burnetti* because he had the curiosity to see what a trout from L. Skene had inside it. In aquaria Krull (**232**), Henson (**245**) and I have found leeches extremely destructive, and gastropods are said to be the natural food of *Glossosiphonia* and *Helobdella* (**31**, **253**), as they are of the rare bug *Aphelocheirus aestivalis* (**265**). Various carnivorous larvae such as *Hydrophilus* (**188**) and beetles such as *Dytiscus* eat eggs and young snails as may caddis worms (**12**); glowworm larvae readily eat *Limnaea* if they get the chance (**266**). The rotifer *Proales gigantea* is parasitic in the eggs of *Limnaea* (**267**). *Limnaea* frequently harbours the larvae of trematode worms, often in immense numbers, and *L. truncatula* is well known as the usual intermediate host of the sheep fluke, but whether these parasites do the snails much harm seems doubtful unless they are present in great excess (**198**): *Valvata* and *Pisidium* may also be infected. In India and Portugal *Bilharzia* larvae definitely injure and kill their *Planorbis* hosts (**199**). Pelsencer (**268**) gives a long list of parasites. The common *Chaetogaster* is probably immaterial.

Mortality in the young. Whatever the precise destructive agents, field experience suggests strongly that those which are effective in keeping the snail populations within reasonable bounds act on the infants: the killing of adults is generally of no great moment and the eggs[1] seem to be fairly safe. One sees a pond, for instance, with vast numbers of capsules of *Limnaea peregra* or *Planorbis complanatus*, and on searching through them one finds that the eggs are developing in a healthy way almost without exception. Yet in two or three weeks' time it may be quite difficult to find the young snails, and it is exceptional to find young ones much more numerous than adults will be later on: the weeding out seems to occur very soon after birth, and the viviparous species are relatively immune. Similarly, if a reservoir goes dry and one can obtain a view of the mussels, the young ones do not seem to be more than enough to maintain the adult population. This infant susceptibility also applies to adverse physical and chemical conditions: eggs are resistant and can be moved about from one sort of water to another with impunity, and those of *Limnaea stagnalis* will develop normally either in distilled water or 5 % salt solution (**32**). But newly born snails have to be treated with a good deal of care, and they are easily killed by a sudden move to different water which older ones do not seem to notice. In nature, therefore, there is an immense "infant mortality". This does not occur if the changes and chances of wild life are excluded, for the whole of a brood of several hundred *L. peregra* may be safely reared in aquaria if they are given room and food enough. The intensity of selection obviously varies greatly in different species: a population of *Anodonta* would be maintained by the survival of less than 1 in a million of the young; *Limnaea peregra* needs perhaps 1 in 500, *Sphaerium* 1 in 10.

(*d*) *Dispersal*

It is possible for many water Mollusca to spread a long way by continuity of their habitats. A map dated 1870 included in the report of the Canal Commission (1909) shows 215 catchment basins in England and Wales: many of them are small coastal areas, but the Thames includes about 8 % of the whole, the Severn 7·5 %, and the Trent 7 %. The canals which were built between 1760 and 1810 joined together all the larger river systems, and the whole canal basin occupies about half of England and Wales (**8**, Fig. 63 and below, p. 173). Similarly in Ireland the Shannon drains 14 % of the country and in Scotland the Tay covers 8 %. *Planorbis acronicus* (**204**), recent and fossil, is found only

[1] In *Neritina* one embryo in each capsule of about 50 eggs eats the others before hatching.

in the Thames drainage: none of our other species is restricted to a single basin, nor does the natural arrangement of the rivers appear to exercise any decisive influence on their geographical distribution.

There are, however, a number of "closed"[1] habitats, i.e. restricted loci separated by land from any other water, and the occurrence of snails in such places depends on their being able to reach them as well as on their ability to live in them. Small coastal streams and springs belong to this group, and the common cattle ponds of the midlands and south of England provide such places in immense numbers: in the 6114 acres of the parish of Aldenham in Hertfordshire there are or have been about 170. The dew ponds[2] of the chalk downs are a rather dramatic type of the same thing. They are mostly from 5 to 30 yd. across, seldom more than 2 or 3 ft. deep; they receive water only from the rain or dew which falls in the immediate neighbourhood or which seeps through the soil, and lose it only by evaporation or percolation. These ponds have either been made *de novo* or made out of existing marshy places to which they would all gradually evolve and ultimately become dry land if they were not from time to time cleaned up and dug out. In the form of ponds with free water they have therefore a limited life and the conditions in them are constantly slowly changing. Some of them are derived from primaeval loci; the new ones presumably date from the keeping of cattle in enclosed fields or the extension of sheep farming on the downs and are about 300 years old or younger. Like the flora (**236**) their fauna depends to some extent on their age.

Many of these closed ponds contain an abundant molluscan fauna: it is indeed, I think, true to say that something will be found in all in which a collector would on inspection expect to get Mollusca and in a fair proportion of those which look unpromising. More than 100 years ago Montagu (**35**, p. 90) was impressed at finding *Sphaerium lacustre* "and 1 or 2 others" in a remote closed pond in Wilts., but it was Reid (**36**), in his classical paper "On the natural history of isolated ponds", who first drew attention to the interest and significance of the facts which make it quite clear that many species are carried overland without much difficulty. *Limnaea peregra*, *L. stagnalis*, *Sphaerium lacustre* and *Pisidium* spp. seem to be the species most commonly found in downland dew ponds (**281**) which are often a long way from one

[1] "Closed" was perhaps rather an unfortunate choice, but the obvious alternative "isolated" implies remote from other water which many of the loci in question are not. In the present connection, "closed" means that nothing can get into them without coming overland. In botanical ecology, the word has been in common use to indicate habitats which are full, i.e. in which a new-comer can find no room. It may be that some small ponds are "closed" also in this sense, but the evidence is suggestive rather than conclusive (below, p. 127). Perhaps "discontinuous" habitats would be better.

[2] A great deal of unnecessary mystery has been made about dew ponds. They do not easily dry up because (*a*) they are watertight, (*b*) rainfall is nearly always considerably in excess of evaporation from a free-water surface, (*c*) there is seldom any standing vegetation to increase the water loss by transpiration.

another or any other water: in the majority of those which I have looked at in Wiltshire I could find no Mollusca. The cattle ponds in the parish of Aldenham (**7**, **9**) are much closer together and near other loci which are rich in snails. In 1915, 69 of the 84 closed ponds which survived till 1925 contained Mollusca of 18 species, the total occurrences being 173; the number of sorts per pond varied from 0 to 8 with an average of 2·1. The most frequent species were *Planorbis nautileus* (32 ponds), *Limnaea peregra* (26), *Ancylus lacustris* (18), *Sphaerium corneum* (15), *Sph. lacustre* (15), and *Planorbis fontanus* (12); *Limnaea palustris* (2), *L. stagnalis* (6), *Planorbis albus* (8), *Pl. complanatus* (3), *Pl. vortex* (3), *Pl. spirorbis* (3), *Pisidium cinereum* (2), *P. milium* (9), *P. nitidum* (3), *P. obtusale* (5), *P. personatum* (7) and *P. subtruncatum* (4) were also present. Figures such as these do no more than systematise the experience of all collectors and they represent the accumulation of many years of dispersal.

A re-examination of the same ponds in 1925 gives us perhaps some idea of what is going on now. Only 65 of them yielded Mollusca; there were 64 disappearances and 93 fresh appearances (mostly *Planorbis nautileus*, *Pl. fontanus* and *Ancylus lacustris*), so that the total number of occurrences had risen to 202. Making some allowance for the imperfections of collecting, these data indicate that transport overland is going on at a considerable rate: on the average each pond got one new species every 9 years.[1] Other evidence comes from *Paludestrina jenkinsi* (below, p. 140), which in the last 40 years has invaded the fresh waters of this country from its original estuarine habitats and is now a common inland species. It hardly occurs in stagnant water, and theoretically it might have reached most of its loci by crawling up the rivers, streams and canals. But it is frequent in little springs and trickles on the coasts, e.g. of Devon and Cornwall, which are in effect as isolated and "closed" as a dew pond, and it has reached the islands of Skokholm and Skomer (**37**, **228**) off the Pembroke coast, Orkney (**38**) and North Uist (A. R. Waterston), as well as remote districts in the west of Ireland. *Elodea* is also a useful analogue, for in this country it spreads by the dispersal of pieces of the plant. Introduced about 1847, it got all over England in the next 25 or 30 years (see the map in **39**, p. 393) and is not uncommon in closed ponds. It is easily killed by drying—more easily than most snails—and one cannot doubt that the agent which spreads it would be equally effective in dispersing Mollusca.

This evidence all goes to show that certain species at any rate are easily and freely dispersed. Unfortunately many interesting kinds are seldom or never found in closed ponds, nor can they live there if they are put in, so that one cannot tell whether they are easily transported or not. For *Planorbis corneus* we have definite evidence (**8**, **40**) that transport is difficult though it is not very easy to see why. Laver (**41**) round Colchester noticed the paradox that though it was naturally confined to the river system the largest specimens he had seen were in a water butt. It is roughly true that the species "never"

[1] Nelson (**224**) describes the addition of 6 species to a pond fauna of 4 in about 20 years.

occurs spontaneously in small closed ponds, though it has been successfully introduced into a good many by aquarists in England and Ireland (**116**), especially in its decorative albino form (**183**). It was certainly absent from the Aldenham ponds until I introduced it into a number in 1917, since when it has flourished and still abounds, without any further, spontaneous spread from these secondary loci: Welch (**179**) notes similarly that it has not spread from a locus in Sligo to which it was introduced 30 years ago. It is evident in this instance that there is little difficulty about oecesis if transport can be achieved. Reid noticed that the operculates were not found in closed ponds and this is nearly true. As Prashad (**269**) and Thomasson (**239**) point out, it is hard to see how *Paludina* could be carried about, and it never occurs in closed ponds unless it has been put there by man, e.g. in the King Lane pond at Leeds or in the Manchester pits (**84**) or in a garden pond at Hereford (**28**). But there is no obvious difficulty in the transport of young *Bithinia* or *Valvata*, and *Bithinia tentaculata* does occasionally occur in marl pits in Cheshire (**85**) and Kent. *Anodonta* and *Unio pictorum* rarely live in closed loci: where they do they were probably introduced as glochidia on fish (generally carp) with which many ponds were stocked when the standard of life was lower and people were glad to eat such tasteless food.

The *means of transport* were very fully discussed by Kew in 1893 (**73**), and I do not think anything has been seen since which adds anything really new to his survey, though various fresh examples of snails in transit have been observed. There is also much interesting information in Ridley's book (**127**) on the dispersal of plants, and in Arber (**166**) and Peacock (**231**). The chief agents are, I believe, birds and especially wild duck, which may have bivalves nipped on their toes or gastropods sitting on their legs or any small snails in mud on their feet or beaks or in wisps of weed round their necks. Insects may also play a part over short distances, and if whirlwinds can produce showers of fish (**165**) they can no doubt distribute snails as well. Stelfox (**80**, **241**) thinks that more consideration should be given to the possibility of snails and small mussels crawling overland through wet vegetation.

(*e*) *Competition*

As I pointed out in my previous paper (**132**) there is little or no evidence that interspecific competition is a factor of any importance in determining the occurrence of land Mollusca. With the fresh-water species the position is rather different: there are facts which suggest competition though they are not conclusive.

(*a*) It is, I think, true that other things (water, climate, etc.) being equal, a large habitat is likely to contain more species than a small one, and going from one locus to another one gets the impression that, for example, a cattle pond 10 yd. across may be "full" in the sense that there is no room for fresh species, the delicate young of which would presumably be more sensitive to crowding than the established population. There may of course be other reasons for this than competition: a large locus contains a greater variety of subhabitats than a small one and the visits of transporting agents are probably more numerous, i.e. there is more prospect of a snail reaching the larger place and of finding congenial conditions when he gets there. But facts such as the following are suggestive. In 1915–25 there were in the Aldenham ponds 18 species which might, as far as one could judge, each have occurred in any one of 40 small closed ponds of a favourable complexion: but in 1925 the distribution was as follows:

Kinds of Mollusca	...	1	2	3	4	5	6	7	8
Number of ponds	...	2	9	6	9	6	4	3	1

The most abundant species were *Planorbis nautileus* (26 ponds), *Pl. fontanus* (24), *Ancylus lacustris* (19), *Limnaea peregra* (17) and *Sphaerium corneum* (17). From this we may judge that such a pond becomes fairly "full" when it contains 5 or 6 of the species which are available in the immediate neighbourhood and able to live in such places. It also seems significant that 20 ponds which in 1915 had one or two sorts each had by 1925 made a net gain of 37 occurrences, whereas 11 ponds which started with 4 or more species per pond showed a net loss of 3. Two larger loci near-by—a reservoir and a backwater of the Colne—each showed 13 of the pond species as well as their own special kinds. Apart from size, both of them are in general more favourable places for Mollusca than the cattle ponds, and we have to bear in mind the general rule that competition is more likely to be effective under indifferent or bad conditions. Large loci of a good kind (below, p. 171) may contain nearly but never quite all the possible species, and it would perhaps be unreasonable to expect a complete galaxy. As J. C. Bellamy (**26**, p. 315) said as long ago as 1839, in a pioneer work on animal ecology which deserves to be better known, "I believe no instance can be adduced where the Fauna of a locality accords so precisely with its physical conditions as to include all those creatures generally found in such spots, and to exclude those generally absent from the same", and Elton (**42**, p. 22) has emphasised the same truth.

(*b*) Some one species, generally *Limnaea stagnalis* or *L. peregra*, sometimes occurs in such profusion in a small locus that it seems hardly credible that there can be enough room and food for many other species, especially those with much the same habits: bottom dwellers with different food requirements such as *Sphaerium* and *Pisidium* are presumably less affected. After all, food shortage can be very obvious in an aquarium: a water volume of 2 litres with a good stock of *Elodea* is just enough for the full growth of one or perhaps two *Limnaea peregra* and does not suffice for even one *L. stagnalis*, *L. auricularia* or *Planorbis corneus*. A small pond of 200,000 litres or so may therefore be presumed to have its limiting capacity, though I do not think that it is often reached. Stelfox, Welch and others (**100**, **103**) have commented on the disappearance of other species when *Paludestrina jenkinsi* appears in and overruns a locality.

(*c*) The land snails which occur in the bad loci which contain only a few sorts flourish equally in the best places which have many: with the possible exception of the calcifuge *Zonitoides excavatus* there is no evidence that any species is excluded from desirable loci by the "pressure of competition". This is also true in the main for the water Mollusca, but there appear to be several species which are driven to live in "oecological slums" with few or no companions and which are absent or rare in good places. The particular variety of slum is that provided by ponds, pondlets and ditches which hold water only in the winter and spring and go dry in any but the wettest summers: *a priori*, and by demonstration, these are not acceptable to most Mollusca, and they are deficient in plants and so in humus (**9**); they are "bad" places in the sense of being inadequate, not poisonous.

Limnaea glabra. Since the times of Müller (**43**, p. 136) who says, "in pratis humidis, ubi aquae vere stagnant", and of Montagu (**35**, pp. 396, 590), who found it only "in a splashy place by the road side, half way between Fowey and Looe in Cornwall", it has been generally recognised that *L. glabra* characteristically occurs in mean places where few if any other Mollusca care to live—shallow grassy ditches and ponds which usually dry in the summer, sometimes in marshes. It is often, probably generally, the only gastropod present: the available records are unfortunately very imperfect as regards *Pisidium*, and I imagine that some of these (*cinereum*, *personatum*, *obtusale*) would frequently be present. It is never found with a rich or even a respectable snail fauna, and the flora seldom goes beyond *Glyceria*. If other snails are present, they are restricted to the few species which can tolerate the conditions, i.e. *Limnaea peregra*, *L. palustris*, *Planorbis spirorbis*, *Physa hypnorum* and the *Pisidium* I have mentioned, less commonly *Planorbis nautileus* and *Sphaerium lacustre*. Thus Nelson (**44**), in some interesting papers on its occurrence round Birmingham and in Yorkshire, gives the following companions (neglecting *Pisidium*): (*a*) *Planorbis spirorbis*, (*b*) *Pl. spirorbis* and *Physa hypnorum*, (*c*) *Planorbis spirorbis* and *Limnaea peregra*, (*d*) *Planorbis spirorbis*, *Limnaea peregra* and *L. palustris*, (*e*) *Planorbis spirorbis*, *Physa hypnorum* and *Limnaea palustris*, and finally (*f*), which this experienced collector says is unique in his experience, with *L. peregra*, *Planorbis complanatus* and *Pl. contortus*. Common repute associates it particularly with *Physa hypnorum* and *Planorbis spirorbis*, as e.g. Morehouse found (**270**) but without, I fancy, taking sufficient account of the frequency with which it occurs alone. Richardson (**271**) found it with *Limnaea peregra*, *Planorbis nautileus*, *Pl. spirorbis*, *Sphaerium lacustre* and *Pisidium* sp., Hey (**272**) with *Limnaea peregra* and (which is rare) *Sphaerium corneum*, Blackburn (**160**) with *Planorbis spirorbis* and *Pisidium personatum*; Alkins (**50**), Adams (**64**) and Evans (**251**) note its concurrence with *Sphaerium lacustre* and Alkins says that generally *Pisidium personatum* is its only companion. I also have notes of its occurrence, without any other snails, with *P. cinereum* (**45**), with *P. cinereum* and *P. personatum*, with *P. obtusale* and *P. personatum* and with *P. personatum* (**46**). Geographically (Fig. 56) it occurs in a few places in Scotland as far north as Perth (**47**), in one place in Ireland and fairly generally in the northern half of England, in some parts of which (e.g. the Cheshire plain and parts of north Staffs.) it is not uncommon. In the southern half it is generally very rare though rather frequent in the New Forest in shallow ponds and temporary running ditches: mean ditches and drying ponds are common enough everywhere, so there must be some other factors to make a place suitable beyond a propensity to go dry in summer. Though it does not extend far north it has been found at considerable altitudes: 1100 ft. in Stafford by Alkins (**46**), 900 ft. in Edinburgh by Evans (in **47**) and 900 ft. on Breidden Hill in Montgomery by Oldham with *Limnaea peregra*, *Planorbis spirorbis* and *Pisidium personatum*.

Nelson had the impression that it is particularly frequent on commons, past and present, and if I were trying to summarise the characters of the places in which it is found I should say that it affects areas where the ground is harsh and poor, where the neighbouring vegetation is not luxuriant, where few land Mollusca will be found and where arable farming is at a minimum, i.e. the places which have longest been left as waste or common land because they have been little worth cultivation. Correspondingly, roadside ponds are rather common habitats which are in undisturbed and therefore well-leached soil. Laver (**41**) for Essex says "especially on gravelly soils" on which he never found *Limnaea stagnalis*. And, though it is not found in moorlands, it may be surmised from this that the water would be found deficient in salts: the only analysis I have (from Boscastle in Cornwall) showed very soft water (7 mg. calcium per litre), and I know of no natural occurrence in water which might be presumed to be hard. Butcher (**229**) says the New Forest streams are poor in mineral salts, and Ashford (**60**) comments on the erosion and decollation of *Bithinia tentaculata* there. The shell of *Limnaea glabra* is often decollated, and Beeston (**128**) suggests that they eat one another's shells for want of lime.

Experimentally in aquaria I have bred *Limnaea glabra* without any difficulty in both hard and soft water. Some from Leeds (which I owe to H. W. Haywood) were carried on for 2 generations in water with 6, 30, 60 and 100 mg. calcium per litre without any obvious difference, the figures representing the range from very soft natural waters to the exceptionally hard London supply. Other examples from Edinburgh (from A. R. Waterston) went on for 5 generations in Radlett water (calcium 60). But I am doubtful whether such experiments are conclusive except to show that it can live in hard water and that summer drying is no necessity as it is with some Crustacea or the seeds of *Alisma*. As others have noted (**59**, p. 135) it is fond of climbing out of the water in aquaria and often stops out till it dies. In nature, as might be expected, it breeds when its habitats contain water, i.e. in February or March.

Planorbis spirorbis belongs to the same group and has a distinct addiction to drying ponds, marshes and other bad places. It is far commoner than

Limnaea glabra and extends throughout Britain (Fig. 8). The data for the Aldenham loci seem to be characteristic and instructive. In 1915 out of 98 ponds which contained Mollusca it was found in 5, all of which went dry each summer: its companions were *L. peregra* (thrice), *Pisidium obtusale* (twice), and *P. personatum* (once). One pond was soon afterwards destroyed; *spirorbis* disappeared from another in 1916, from another in 1917 and from another in 1919, though in this last it had been so abundant that I took 620 specimens in one sweep of a small scoop. In 1921 it could be found in only one pond in the parish. However, in 1925, it was found sparsely (with *P. milium*) in another pond from which it had gone in 1926, and between 1923 and 1926 it appeared in 3 others, in 2 by itself, in the other with *Limnaea peregra*, *Planorbis nautileus* and *Pisidium obtusale*: from one of these it had gone by 1927 and from the 2 others by 1932. So that at the present time (1934) it again occurs in only one locus—a shallow trampled cattle pond 6 yd. across with *Glyceria* and *Juncus* which dries on the least provocation and in which *Planorbis spirorbis* and *Pisidium obtusale* have been abundant since 1915. It seems evident from this narrative that *spirorbis* is moved about from one place to another without much difficulty, and that it is far from happy in many of the loci to which it gains entry. Now during this period of 19 years there have been within about 1½ miles of the 9 *spirorbis* loci, all of which were drying ponds, at least 51 ponds which did not dry out even in 1921 or 1933 and which contained such a number of Mollusca (above, p. 125) that one could not doubt that they were fairly good habitats: but *spirorbis* has not been found in one of them. It is difficult to resist the conclusion that it lives in these bad places because it is excluded from the better habitats by the competition of other Mollusca. This fits in well with the fact that when we pass to roomier loci than cattle ponds we find *spirorbis* again and often in company with many other species. Thus in my own neighbourhood it lives freely in a large reservoir with 16 other species and it is not uncommon in such places, in canals, draining ditches, quiet river loci and the like, which have quite rich faunas. Thus Wood (**48**) found it in 3 of 11 midland lakes with such characteristic running water species as *Bithinia tentaculata* and *Physa fontinalis*. Like *Limnaea glabra*, it does not occur in the average good small pond, but unlike that species it can live with other species if the locus is large enough.

Pisidium personatum also prefers bad places. It is a widespread and common species in miserable loci and sometimes in wet places on land, and frequently occurs by itself. As Stelfox (**49**) points out it is not often found in good habitats, and Alkins (**50**) in his survey of the Oakamoor district found that it was restricted to ditches and marshes and was most frequent in those which dried in the summer; Favre (**51**) finds the same in Switzerland. And, particularly interesting, it lives in the depths of Rostherne Mere, Lake Windermere (C. Oldham) and the Lake of Geneva (**51**), to which only *P. conventus* of the other species of the genus and only *Limnaea peregra* of the other Mollusca

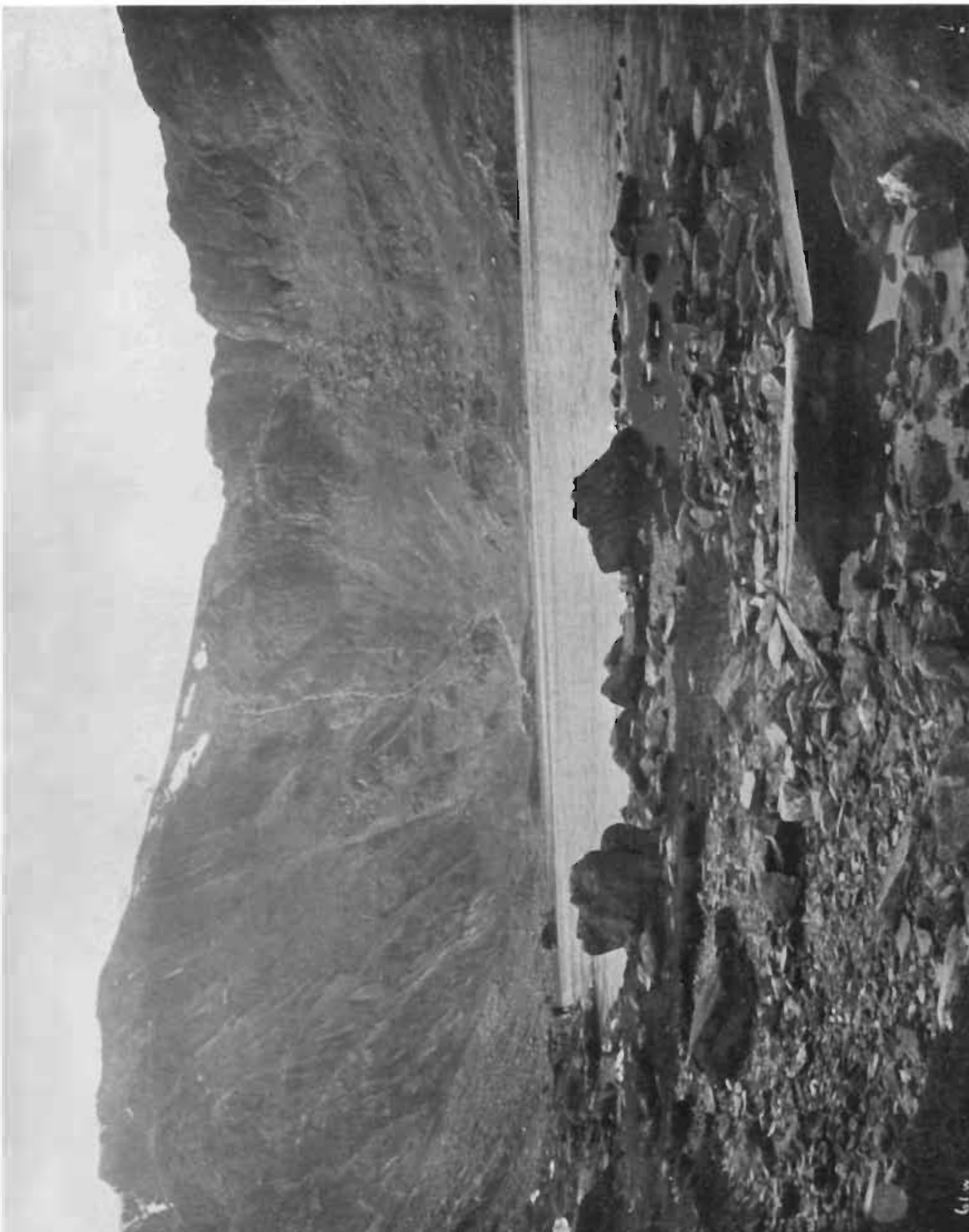


Photo. Abraham, Keswick

Phot. 1. Llyn Idwal, Carnarvonshire. A characteristic soft water lake, calcium 3 mg. per litre; 1223 ft. above sea level; relatively sheltered, the surrounding country rising to more than 3000 ft. Mollusca: *Limnaea peregra*, *Ancylus fluviatilis*, *Pisidium cinereum* and *P. lilljeborgii*. Above and to the right is the patch of calcareous ground where *Helix nemoralis*, *Clausilia rugosa* and other mollusca live with calcicole plants at 1800 feet (**132**, p. 10).

which live in this large water penetrate. It may be that *Pisidium obtusale* should go in the same category: it lives in poor loci, often by itself though seldom with *P. personatum* (below, p. 138), but its requirements are difficult to specify and its status remains indeterminate.

Physa hypnorum. To *Limnaea glabra*, *Planorbis spirorbis* and *Pisidium personatum* common opinion would add *Physa hypnorum*, but it seems doubtful whether it is really a slum dweller. It is quite true that it often occurs in shallow grassy drying pools[1] (including ponds among sand dunes (**219**)), temporary spring flashes, etc., and frequently with *Planorbis spirorbis* and sometimes *Limnaea glabra*, and Jenyns (**52**) remarked long ago on its curious habit of suddenly appearing and disappearing: it has these same habits throughout its extensive palaearctic range, in which, in Siberia, it lives nearer the Pole than any other pulmonate. Though it has been recorded at one time or another for all except 5 of the English counties, it cannot be called common, and many collectors would be hard put to it to lay their hands on live specimens on demand. But I feel uncertain about its having an actual preference for bad loci or an intolerance of companions, for examples to the contrary are easy to find. It lived for a while in a draining ditch near Watford with *Limnaea palustris*, *Planorbis corneus*, *Pl. complanatus*, *Pl. vortex*, *Pl. spirorbis* and *Bithinia tentaculata*; Stelfox (**54**) records it in Arland's Lough, Donegal, with *Limnaea peregra*, *L. auricularia*, *Planorbis nautileus*, *Pl. spirorbis* and *Pl. glaber*; Ellis (**55**) in Saddington Reservoir, Leicester, with *Limnaea peregra*, *L. stagnalis*, *Planorbis fontanus*, *Bithinia tentaculata* and *Sphaerium lacustre*. These would all count as "large" loci, but in two Lancashire ponds Davies (**56**) found it with *Limnaea peregra*, *L. stagnalis*, *Planorbis fontanus* and *Pl. nautileus* and Jackson (**57**) with *Limnaea palustris*, *Planorbis carinatus*, *Pl. vortex* and *Pl. spirorbis*. I suspect therefore that *Physa hypnorum* may not be an example of competitive seclusion but may more properly be classed with the next group which contains 4 species which are notoriously apt to be found in inferior loci because they happen to be able to tolerate the conditions and which are as common or commoner in good places with plenty of companions. The occurrence, for instance, of *Sphaerium lacustre* in dried ponds has often been commented on, and it has been stated (**59**) that the valves fit particularly closely though according to my own experiments it is no more resistant to drying in air than *Sph. corneum*; Collinge (**58**) says that it burrows exceptionally deeply (10–14 in.) in the mud. But the idea that it prefers such places is illusory and arises I think from our tendency to remember the dramatic discovery of many little mussels in a dried-up dew pond on the downs and to forget the occurrence of the same species in more conventional loci. In fact *Sph. lacustre* is quite common in many good places—ponds, rivers, canals—as well as in bad ones, and there is no evidence that it is driven into drying

[1] Dr K. B. Blackburn tells me that it is fond of the alga *Tribonema* (which other snails are not) and eats it freely.

ponds by competition. Similarly, *Planorbis nautileus* is frequently found in drying ponds especially if they are examined in spring when they contain water. But in our local ponds it occurred in 26 of 42 ponds which did not dry and in only 14 of 42 drying ponds[1] and this is in accord with general experience. *Limnaea palustris* is another species which lives sometimes in surprisingly dry places; Adams (**59**), for instance, calls it "amphibious", Ashford (**60**) says it may "lead an aerial life during summer", and Kew (**61**) mentions it in temporary winter water. In Aldenham I have watched it for 17 years (including the 1921 drought) living in thick grass by the roadside, where it got no more water than ran off the road: it was always plentiful until the place was destroyed in building operations. But its toleration of these conditions is in no way compulsory, for it is definitely more common in a variety of good habitats. The same appears to be true of *Pisidium cinereum* which can tolerate drying loci but is much more frequent in better places.

Of these 9 species which can put up with drying ponds, none is restricted to such places as are *Planorbis umbilicatellus* and *Pl. campestris* in northern Canada (Mozley), where melting snow produces ephemeral ponds each year in the same place in which *Limnaea palustris* and *Physa hypnorum* are frequent with *Sphaerium occidentale*, analogous to *Sph. lacustre* (**17**, **18**). Mozley (**250**) gives a good account of the flora and fauna (including 7 molluscs) of a Canadian pond which held water for less than 3 months in each year.

3. The habitats of the various species[2]

(*a*) *Bivalves*

The four large mussels—**Anodonta cygnea* (Fig. 36), **A. anatina* (Fig. 37), **Unio pictorum* (Fig. 45), **U. tumidus* (Fig. 46)—live in slow rivers, canals, large draining ditches, lowland lakes, reservoirs and large ponds, mostly running habitats though *Anodonta cygnea* and *Unio pictorum* live in some closed marl pits in Kent and *Anodonta cygnea* in marl pits near Manchester (**175**). The deliberate introduction of fish for angling or in times past for food probably explains why *Anodonta* and *Unio pictorum* are so common in reservoirs and ornamental waters, though they are sometimes put in for their own sakes (**174**) and were at one time eaten in Ireland (**181**; **247**, p. 31) and in the Fens (**243**). Thomasson (**239**) attaches special importance to sticklebacks on which he finds the glochidia. Only *cygnea* lives in Ireland, and in Great Britain it has been recorded as far north as Banff; *anatina* extends as far as Caithness, and the two *Unio* are restricted to England. This distribution is probably due in part to the relative rarity of suitable habitats in the north and west as well as to historical and climatic factors. Their essential needs are fish on which they can pass their early parasitic phase and incidentally travel about and a firm muddy bottom in which they can imbed themselves. Why they spend so much of their time two-thirds sunk in the mud I do not know: it seems an extravagant precaution against being swept away by any ordinary current. But a bottom suited to such a life is obligatory. They will not

[1] The corresponding figures for *Sphaerium lacustre* are 15 and 2 but I doubt whether these are really representative.

[2] In the following catalogue the species which are able to live in quite soft water are marked †, calcicole species ** and those which appear to need at least a moderate amount of lime *: the evidence is discussed in more detail below (p. 148).

live either on a hard stony or gravelly bottom or on one which is covered with a thick layer of soft humus in which they would have to disappear before they found firm ground: hence most closed ponds are unsuitable. The four species have similar tastes and may all occur together. *Anodonta anatina* seems to have rather more preference for rivers than *A. cygnea*, and *Unio tumidus* is distinctly the least common and has the most restricted geographical range: it needs fresher, cleaner water than the others and may be a river species which has extended into canals: Lowe (**243**) failed to get it to live in captivity, though *Unio pictorum* did well. *Anodonta cygnea* with or without *Unio pictorum* sometimes abounds in lakes without any pulmonates or operculates (**273**), which illustrates the dependence of the bivalves on the bottom and of the other groups on the water and vegetation.

**Pseudanodonta rothomagensis* (Fig. 61) (if that be really the correct specific name of the English form) is a river species occurring in the Thames and Severn basins and in some of the midland and Yorkshire canals.

The pearl mussel †*Unio margaritifer* (Fig. 14) lives in a well-defined river habitat, though it is a little difficult to specify the essential qualities. As Adams (**59**) points out it occurs only to the north and west of a line from Scarborough to Beer Head,[1] and a full account of its history and distribution is given by Jackson (**71**). It lives in the R. Exe, and passing thence east and north along the coast its next locus is the Whitby Esk in Yorkshire: travelling the other way it is found in Cornwall, all up the west coast and generally in Scotland north of Stirling, in Shetland, Lewis, Isle of Man and generally in Ireland, except in the central limestone plain and the Shannon basin. It is absent from the whole of the midlands and south-east of England. A typical locus is a quick running river up to 3 or 4 ft. deep with a mixture of boulders, stones and sand; it can burrow in fine gravel and particularly likes the sand which accumulates behind large stones: it also lives in the lakes (e.g. L. Earn) through which such rivers flow. Most of its habitats are places in which fishermen would expect to get trout and hope for salmon, though it occasionally (**194**) occurs in meagre streams. As it happens, most of the characteristic rivers contain soft water, and the areas in England and Ireland where it does not occur have hard water. Hence the belief, which I have advocated more than once (**7**, **133**), that soft water is the main factor in determining its occurrence.

There is no doubt that the great majority of its habitats contain soft water, and the following list[2] contains such recent analyses as I have been able to get. It is unrepresentative because I have neglected such districts as the west of Scotland (where all the rivers north of the Clyde must surely be soft) and gone out of my way to get samples from known habitats of the mussel in calcareous and dubious districts:

Glengarriff R. (Cork)	1	R. Teign (Devon)	3
R. Spey (Inverness)	2	R. Derwent (Westmorland)	6*
R. Dee (Bala)	2–4	R. Esk (Yorks.)	6
R. Irt (Westmorland)	2*	L. Leane and rivers (Kerry)	7–11
R. Conway (N. Wales)	3	R. Exe (Devon)	10
L. Lubnaig (Perth)	3	R. Taw (Devon)	11

* By the kindness of Dr W. H. Pearsall (see **291**).

[1] "If a line be drawn from Hull to Gloucester and then on to Plymouth, it can be said roughly that all the country to the east and south of it was for Parliament, and everything to the west and north for Charles." *Wales*, by W. H. Davies, 1925, p. 170.

[2] The figures are milligrammes of calcium per litre, i.e. parts per million, which I have always determined by the method given by Thresh and Beale (**148**). Divided by 4, they give approximately the total hardness expressed on the customary scale of parts of $CaCO_3$ per 100,000, and to have a uniform terminology I have converted the hardness figures of the literature to the calcium scale by the same factor, making the necessary correction if they are given in the older scale of grains per gallon (=parts per 70,000). But what is meant by "hardness" or "lime" is not always clear.

R. Tamar (Cornwall)	14	R. Lune (Lancs.)	30
R. Blackwater (Cork)	15†	R. Rede (Northumberland)	32
R. Ithon (Radnor)	17	R. Usk (Monmouth)	49, 51‡
R. Teme (Clun)	19	R. Nore (Queen's Co.)	79
R. Wye (Hereford)	15–33		

† From E. O'Mahony and A. W. Stelfox.
‡ From Dr H. W. Catto: a third sample higher up 12 years later gave 30.

In contrast with these I give a few figures I have collected which seem to be representative of the rivers in the south of England draining from calcareous strata which do not contain the pearl mussel:

R. Granta (Cambridge)	113	R. Avon (Salisbury)	85
R. Kennett (Suffolk)	115	R. Test (Hants.)	89
R. Gade (Herts.)	104	R. Frome (Dorchester)	70
R. Colne (Herts.)	107	R. Piddle (Weatherbury)	90
R. Thames (Staines)	90	R. Stour (Blandford)	85

West and north the hardness becomes rather less, e.g. R. Axe (Devon) 47, R. Otter (Devon), 37, R. Tees 32 and R. Tyne 34–36: none contain *U. margaritifer*.

The significance of soft water is also supported by the facts: (*a*) it occurs in the upper part of the Dee, above Corwen, where the water is soft (Ca 4) and not in the lower parts where it becomes as hard as 28 (Shrubsole, **65**, **148**); (*b*) similarly in the Teme it lives at Clun, where a sample gave 19, but not below near Ludlow where the hardness rises to 29–35; (*c*) it is common in the Herefordshire Wye (about 20) but not in its tributaries Lug (49), Arrow (41) or Monnow (37). Frierson (**66**) says that it does not occur in calcareous waters in the United States and Geyer (**67**) that it affects soft water in Germany. Further evidence in the same direction was given by McKean (**68**), who found that specimens from the R. Don in Scotland soon died when they were put into the chalky R. Wandle in Surrey, and by Haas (**69**) who says that his specimens died at once when they were transferred from soft to hard water.

The case for soft water is up to a point impressive, but it is difficult to put on one side the instances of the Usk and the Nore or to agree with Phillips (**70**) that the well-grown thick shells from the latter place are a new species. When too I tried Haas' experiment with specimens from the Wye[1] I found (**71**) that they lived happily in various hard waters with calcium 50–130 and finally in the Herts. Colne (Ca about 100) for several months till the winter floods carried them off. It is thus almost equally easy to argue that the thing that is requisite and necessary is a quick-flowing cool river with clean water and the right kind of bottom, and that it is as it were a physiographical accident that such rivers are nearly always soft, though I should have judged by the look of them that such southern calcareous rivers as the Test, Itchen or Otter would have been agreeable to *margaritifer*. It can hardly be the high summer temperature which excludes it from the south-east of England, for it is equally absent from the Shannon basin which is as cool as Wales or Cornwall. The natural host for the glochidia, which are very small and attach themselves to the gills, is the trout (**109**), which is common enough throughout Britain in both hard and soft water: minnows (**110**) also do well and are generally available except in the north of Scotland and parts of Ireland (**72**). Perhaps the solution of this very interesting question may come when someone discovers where the young mussels live after they fall off the fish till they are about 2 in. long—a matter of several years: at present this is quite unknown.

Dreissena polymorpha (Fig. 44) is closely connected with commerce and is found in docks, canals, rivers and reservoirs, anchoring itself to any hard surface by its byssus; it can also live in water mains (**238**), though as it preserves the marine habit of a free-swimming larva its maintenance in running water must be rather precarious, and it is not clear that it would survive in fresh water in this country under natural conditions. It is fond of

[1] It would have been better if they had come from a less calcareous river.

fixing itself to *Anodonta* and *Unio*, and in their turn the fry may be incorporated in caddis cases (Swanton); the free locomotion of the young mussels has been described by Tate (**247**, p. 24) and Oldham (**248**). Kennard (**74**) records it as a fossil in London and Oxfordshire. It subsequently died out and in modern times was first found in 1824 in the London docks and within 20 years was known to be present in Scotland and in England from Lancs. and Yorks. to Devon; Kew (**73**, p. 210) gives a full account of its early history.

†*Sphaerium corneum* (Fig. 15) is widely spread throughout Britain in most kinds of waters, running and stagnant; other species are likely to be found with it, and it is a useful indicator of pretty good molluscan conditions: it can live in brackish water and occasionally in mountain lakes (e.g. L. Kinardochy, Perth, 1200 ft.), so that it has a wide range. It does not like dirty water nor does it live in drying ponds and streams.

†*Sphaerium lacustre* (Fig. 16) is rather less widespread and strangely rare in Ireland and tends to be found more in stagnant and less in running water and often by itself or with few companions in inferior loci including dew ponds and drying ponds (above, p. 131) in which *Sph. corneum* does not occur. In my analysis of the Aldenham ponds (**7**) *Sph. corneum* occurred in 18, *Sph. lacustre* in 13 and both in 5; *Sph. corneum* was concurrent with *Limnaea stagnalis* and perhaps *Planorbis complanatus*, *Sphaerium lacustre* with *Ancylus lacustris*, which to a collector perhaps expresses as well as anything else the difference in their tastes. Lukis says (in **246**, p. 12), and I have the same impression, that it is more active than *Sphaerium corneum*, especially when young, and crawls up into the plants more, which may aid its dispersal.

***Sphaerium rivicola* (Fig. 47) is a central English species as far north as Yorkshire: it fails in west Wales, south-west England and East Anglia. It lives in quiet rivers and canals, in deeper water than *Sph. corneum* (**176**).

Sphaerium* (*pallidum*) *ovale* (Fig. 48) was discovered as a new British species on May 17, 1856, by J. Rouse in the Grand Junction Canal at Kensal Green (75**), and has subsequently been found in Oxford, Gloucester, Northampton, Warwick, Worcester, Stafford, Shropshire, Montgomery, Cheshire, Lancs. and Yorks.: it lives in great profusion in some of the Manchester canals where it was first found in 1860 (**295**). All the trustworthy records (Roebuck MS.) are for canals except the Foss and Ouse at York which are canalised rivers and in which incidentally all four species of *Sphaerium* live together (**81**). It is unknown in Europe and is not the continental *Sphaerium ovale* (**77**) which has no relation to canals. It does not climb up the walls and plants as *Sph. corneum* and *Sph. lacustre* sometimes do.

Our knowledge of the 15 British species of *Pisidium* has been revolutionised in the last 20 years by the work of C. Oldham, R. A. Phillips and A. W. Stelfox, who have put the systematics of a difficult genus on a firm basis and by their intensive field work have given us as much knowledge of their distribution and habitats as we have for any other Mollusca. Unfortunately it has not been easy for others to join in what has proved to be an exceptionally interesting oecological enquiry because there is no printed account through which fresh workers might learn their species; most collectors therefore are unable to identify the more critical kinds and so neglect them. Some of them have very definite habitats, and I am indebted to Mr Oldham for the following summary.

As the species are as much (or more) affected by the nature of the bottom in which they live as by the character of the whole habitat, their preferences cannot always be described in ordinary terms and what is one locus as far as, for example, *Limnaea peregra* is concerned, may contain a number of *Pisidium* loci. The species may therefore be extremely localised in a habitat, and collecting them satisfactorily is something of a special art (**78**). 10 of the species occur throughout Britain, so that their habitats can be considered without any geographical confusion.

**P. amnicum* (Fig. 38): general in England, infrequent in Scotland (to Perth), west Wales and west Ireland: clean running water in rivers, streams, canals and lowland lakes.

†*P. cinereum* (*casertanum*) (Fig. 17): general: in all kinds of habitats, good and bad, the most catholic species.

†*P. conventus* (Fig. 18): mountain tarns, mostly high and cold, in north Wales, north Scotland and Kerry (**78**, p. 275): dredged from 400 ft. in L. Ness.

**P. henslowanum* (Fig. 39): distribution much the same as *amnicum* but extends to Shetland: running water, rivers, canals, lakes and running ponds, occasionally in marl pits.

†*P. hibernicum* (Fig. 19): general but less common in the south: mountain lakes, canals, rivers and streams; rarely in closed ponds.

†*P. lilljeborgii* (Fig. 20): north-western: in clean gritty sand or silt, not in mud, and characteristically in mountain lakes both at high altitudes and near sea-level; hence mostly in soft water: it lives, however, in hard water in Malham Tarn and Gormire in Yorks., L. Rea in Galway and in Anglesea (**142**), and the determining factor seems to be the nature of the bottom rather than of the water: analogous to *Unio margaritifer* (above, p. 133).

†*P. milium* (Fig. 21): general: ponds, rivers, canals, tarns, not in bad ditches or swampy places and not so ubiquitous as *cinereum*.

†*P. nitidum* (Fig. 22): general: much as *milium*, not in bad places.

†*P. obtusale* (Fig. 23): general: small ponds, stagnant water, peaty holes; not usual in rivers, streams and canals; often by itself.

†*P. personatum* (Fig. 24): general: stagnant water, puddles and temporary ponds, sometimes in wet places on land, prefers bad places (above, p. 130) and extends from the bottom of L. Windermere to 3000 ft. in Perth (**79**) and St Brendan's Well at 2700 ft. on Brandon Mt. in Kerry, which is "probably the highest possible habitat for a fresh-water shell in Ireland" (**80**).

†*P. pulchellum* (Fig. 25): general but not common: it likes mud with clean water as in running ditches and slow streams, sometimes in lakes and ponds.

†*P. subtruncatum* (Fig. 26): rivers, canals, lakes, draining ditches, also in ponds; very similar to *nitidum*.

***P. supinum* (Fig. 50): mud in rivers, mostly large ones (e.g. Thames, Severn, Wye, Trent, Teme, Ouse, Dee) and canals from Somerset and Surrey to Yorks.: not in Wales, Scotland or Ireland.

***P. tenuilineatum* (Fig. 51): rivers and canals in Thames basin, Northampton and Shropshire.

***P. torquatum* (*moitessierianum*) (Fig. 49): in mud in rivers and canals Cornwall, Wilts. and Surrey to Yorks., and in Ireland; very small and liable to be overlooked.

Mr Oldham has also with great generosity put at my disposal his careful records of his own collections of *Pisidium* from 466 loci scattered from Cornwall to Shetland with some in Ireland. These are the result of deliberate searching for *Pisidium*, not of casual collecting, and they are unrepresentative only in that the various habitats were not examined in proportion to their frequency, and a good deal of the work was directed to the discovery of rare or ill-known species such as *lilljeborgii* and *supinum*. Hence mountain lakes appear in excess and trivial lowland loci in defect of their actual relative abundance, and the figures in the last column of Table 1 do not give an accurate idea of the relative abundance of the different kinds. Otherwise Table 1 tells its own tale about the species found in the various kinds of habitats and Tables 2 and 3 give the concurrences[1] of the species with one another.

These records also show that *cinereum, hibernicum, lilljeborgii, milium, obtusale, personatum* and *conventus* can live at over 2000 ft., and that *nitidum* is not very rare at over 1000 ft., and exceptionally *subtruncatum*, which Stelfox (**80**) says does not live at that altitude in Ireland: from other sources (below, p. 157) we have a single occurrence of

[1] I have already explained why "association" conveys rather undesirable implications when the only thing which brings species together is a liking for the same type of habitat.

amnicum at 1250 ft., but *henslowanum*, *pulchellum*, *supinum*, *tenuilineatum* and *torquatum* are normally lowland species. By analysis or implication, *supinum*, *tenuilineatum*, *torquatum*, *henslowanum* and *amnicum* (i.e. the southern species) are addicted to hard water, whereas the other 10 can live in very soft water and, except *conventus*, equally in hard water: these are the species of general distribution.

Table 1. *Showing the occurrence of* Pisidium *in different kinds of habitats* (*Oldham*)

	Mountain lakes: Over 1000 ft.	Mountain lakes: Under 1000 ft.	Mountain lakes: Total	Lowland lakes and reservoirs	Rivers	Canals	Streams	Running drains, etc.	Ponds	Marshy places, ditches, trickles, etc.	Total
Number of loci	52	94	146	13	61	35	14	28	78	91	466
amnicum	0	0	0	3	39	23	1	1	0	0	67
cinereum	28	35	63	8	42	20	1	9	18	34	195
conventus	3	2	5	0	0	0	0	0	0	0	5
henslowanum	0	4	4	6	42	30	1	6	0	0	89
hibernicum	24	57	81	1	13	9	5	6	1	0	116
lilljeborgii	14	44	58	0	0	2	0	0	0	0	60
milium	10	27	37	7	17	9	3	15	23	10	121
nitidum	12	47	59	11	46	28	10	17	23	3	197
obtusale	7	11	18	2	0	0	0	3	26	25	74
personatum	2	7	9	3	4	3	1	1	7	50	78
pulchellum	0	7	7	2	8	5	2	13	1	0	38
subtruncatum	1	26	27	12	51	32	14	21	31	8	196
supinum	0	0	0	0	20	11	0	0	0	0	31
tenuilineatum	0	0	0	0	3	4	0	0	0	0	7
torquatum	0	0	0	0	9	14	0	0	0	0	23
Average number of species	1·9	2·8	2·5	4·2	4·8	5·4	2·7	3·3	1·7	1·4	2·8
Loci with only one species	26	28	54	0	0	0	2	6	41	60	163

Table 2. *Showing the concurrences of the species of* Pisidium *with one another* (*Oldham*)

	amnicum	*cinereum*	*conventus*	*henslowanum*	*hibernicum*	*lilljeborgii*	*milium*	*nitidum*	*obtusale*	*personatum*	*pulchellum*	*subtruncatum*	*supinum*	*tenuilineatum*	*torquatum*	Total
Alone	0	34	2	1	16	8	9	9	40	32	3	9	0	0	0	—
With other species	67	161	3	88	100	52	112	188	34	46	35	187	31	7	23	—
Total	67	195	5	89	116	60	121	197	74	78	38	196	31	7	23	—
amnicum	—	48	0	60	15	1	21	53	0	4	12	59	27	5	23	67
cinereum	48	—	1	59	40	26	46	93	16	38	9	95	29	6	21	195
conventus	0	1	—	0	1	3	0	1	1	0	0	0	0	0	0	5
henslowanum	60	59	0	—	20	5	25	72	0	5	17	76	29	6	23	89
hibernicum	15	40	1	20	—	36	46	66	16	8	15	52	3	1	2	116
lilljeborgii	1	26	3	5	36	—	15	31	7	1	5	17	0	0	0	60
milium	21	46	0	25	46	15	—	82	16	7	23	82	1	0	1	121
nitidum	53	93	1	72	66	31	82	—	10	13	29	146	23	6	20	197
obtusale	0	16	1	0	16	7	16	10	—	9	0	5	0	0	0	74
personatum	4	38	0	5	8	1	7	13	9	—	2	14	1	0	2	78
pulchellum	12	9	0	17	15	5	23	29	0	2	—	33	1	1	1	38
subtruncatum	59	95	0	76	52	17	82	146	5	14	33	—	25	7	23	196
supinum	27	29	0	29	3	0	1	23	0	1	1	25	—	6	18	31
tenuilineatum	5	6	0	6	1	0	0	6	0	0	1	7	6	—	6	7
torquatum	23	21	0	23	2	0	1	20	0	2	1	23	18	6	—	23
Average number of companions	4·7	2·7	1·4	4·5	2·7	2·4	3·0	3·3	1·1	1·3	3·9	3·2	5·3	6·3	6·1	

Table 3. *Showing the percentage concurrences of the species of* Pisidium *with one another, the total occurrences being taken as* 100 (*Oldham*)

	amnicum	*cinereum*	*henslowanum*	*hibernicum*	*lilljeborgii*	*milium*	*nitidum*	*obtusale*	*personatum*	*pulchellum*	*subtruncatum*	*supinum*	*torquatum*
Alone	0	17	1	14	13	7	5	54	41	8	5	0	0
With other species	100	83	99	86	87	93	95	46	59	92	95	100	100
Total	100	100	100	100	100	100	100	100	100	100	100	100	100
amnicum	—	25	67	13	2	17	27	0	5	32	30	87	100
cinereum	77	—	66	34	43	38	47	22	49	24	48	94	91
henslowanum	90	30	—	17	8	20	37	0	6	45	39	94	100
hibernicum	22	21	22	—	60	38	33	22	10	39	27	10	9
lilljeborgii	1	13	6	31	—	12	16	9	1	13	9	0	0
milium	31	24	28	40	25	—	42	22	9	61	42	3	4
nitidum	79	48	81	57	52	68	—	14	17	76	75	74	87
obtusale	0	8	0	14	12	13	5	—	12	0	3	0	0
personatum	6	20	6	7	2	6	7	11	—	5	7	3	9
pulchellum	18	5	19	13	8	19	15	0	3	—	17	3	4
subtruncatum	88	49	85	45	28	68	74	7	18	87	—	81	100
supinum	40	15	33	3	0	1	12	0	1	3	13	—	78
torquatum	34	11	26	2	0	1	10	0	3	3	12	58	—

Turning to the general character of the habitats, *amnicum, supinum, tenuilineatum* and *torquatum* are restricted to running water and so mostly are *henslowanum*, lowland *hibernicum* and *pulchellum*: *cinereum, milium, nitidum* and *subtruncatum* can live also in small closed ponds (as in the Aldenham ponds) and *obtusale* and *personatum* prefer such places, while *subtruncatum* and *nitidum* prefer running water: *conventus* and *lilljeborgii* have special habits. We may also construct a sort of hierarchy of gentility starting with *personatum*, which lives in the slums, through *obtusale, cinereum, milium, nitidum* and *subtruncatum, hibernicum* to *henslowanum* and *amnicum* which insist on the best places with 4 or 5 other species and *supinum, tenuilineatum* and *torquatum* which are even more particular. This is the same sort of series which I drew up for land snails without specialised habitats (**273**) and which may be made for most of our water snails though without such splendid data as Mr Oldham provides. The best indices of the position of any species are the frequency with which it occurs by itself and the number of other kinds which live with it, which is a measure of the general goodness of the locus: these are shown in Table 2. Thus *amnicum* "never" occurs by itself and is accompanied by *henslowanum, subtruncatum, nitidum* and *cinereum* in 90, 88, 79 and 77 % of its loci respectively. Contrariwise, *obtusale* is alone in 54 % of its loci and was never found with *amnicum, henslowanum, pulchellum, supinum, tenuilineatum* or *torquatum*. The curious thing is that *obtusale* and *personatum*, both common in bad places, are found together only in 11 or 12 % of their occurrences: *obtusale* occurs more often than *personatum* with *hibernicum* and *milium* and less often with *cinerum*, which suggests what is the fact, that it affects bad places with more water in them than those in which *personatum* is found. However, it would be tedious to set out at length the various conclusions and suggestions which anyone who cares to study the tables may make out for themselves.

Alkins' (**50**) intensive study of a small area in Staffs. shows *henslowanum, hibernicum, milium, nitidum* and *subtruncatum* in the remains of a canal and the ponds and streams connected with it (i.e. the good places) and *personatum* in the bad places (ditches and marshes): *cinereum* was found in good and bad alike except in the drying loci in which *personatum* occurred alone. Stelfox (**82**) notes a concurrence of *cinereum, obtusale* and *personatum* in peaty waters in Ireland, sometimes with *milium* but not *subtruncatum*.

In 163 of the 466 loci a species was found by itself, and it is of some interest to consider how these solitary occurrences are made up. All those of *personatum* (32 in number) are mean lowland loci: so are 39 of the 40 for *obtusale* (the other being a mountain tarn), but here "pond" is commoner than "ditch or swamp": of the 34 for *cinereum*, 18 are mountain tarns, the rest ponds, ditches, etc.; all the 16 for *hibernicum* are mountain lakes, and this is no doubt its primary habitat (it occurs in 60 % of *lilljeborgii* loci), and where it spreads to lowland loci it needs good places with several other species: montane places account for 2 each of the few solitary occurrences of *milium*, *nitidum* and *subtruncatum*. But in 65 % of Oldham's loci more than one species was present and in many 4, 5 or 6; the average is 2·8. The highest number actually recorded is 9: *amnicum*, *cinereum*, *henslowanum*, *hibernicum*, *milium*, *nitidum*, *subtruncatum*, *supinum* and *torquatum* in R. Ouse in Bedford, and there are only 2 others (*pulchellum*, *tenuilineatum*) which could reasonably be expected there: the same with *personatum* and *pulchellum vice supinum* and *torquatum* were found in R. Gade in Herts. But as appears to be the rule (above, p. 127) no one place has all the species it might, though the rivers and canals of the south of England come near it. Thus in Oldham's careful survey of 40 lochs in the far north (**78**) 11 species were found and 8 were fairly common: one place yielded 6 and four others 5, and the commonest species (*lilljeborgii*) was found only in 24.

Phillips and Stelfox (**83**) have published an account of *hibernicum* and its companions in 74 Irish loci: the following table gives the percentage occurrence of other species with it and shows as good correspondence with Oldham's data as can be expected:

	Phillips and Stelfox	Oldham
amnicum	5	13
cinereum	32	34
henslowanum	19	17
lilljeborgii	15	31
milium	54	40
nitidum	70	57
obtusale	18	14
pulchellum	7	13
subtruncatum	51	45

the average number of companions being the same in both series (2·7).

(*b*) *Operculates*

The 10 operculates live almost exclusively in running water; being gill breathers and unable to come to the surface and gulp in air as the pulmonates do, they presumably need water which is fairly well oxygenated and also free from particles which might choke their gills. .

Paludina *vivipara (Fig. 40) and **contecta (Fig. 41) both occur in England as far north as Yorks. in slow fair-sized (below, p. 163) rivers, canals and large draining ditches. Neither occurs naturally in stagnant water or closed ponds, though they will sometimes live, apparently permanently, in ponds into which they have been introduced (**84**), also in ornamental garden ponds (**23**), and they will breed in large aquaria (**15**). Roughly speaking their habits seem to be identical and the two are often found together, but there is presumably some difference in their requirements, for *vivipara* is decidedly more widespread (39 English and 3 Welsh counties) and commoner though in parts of East Anglia *contecta* (27 English counties) alone is found. In France, Germain (**77, 205**) says that *contecta* has less liking for running water than *vivipara* and frequents marshes and ponds rather than rivers and streams, and J. F. Musham (MS.) draws the same distinction in Lincolnshire.

Bithinia *tentaculata (Fig. 35) and **leachii (Fig. 42) form a similar pair. *B. leachii* lives in the south-east and midlands up to Yorks. with an outlier in Stirling (**101**) and in half a dozen Irish counties in slow rivers, backwaters, canals and ditches, "always" in good loci with many other species. Adams (**89**) was naturally surprised to find it in a pond in Essex with *Ancylus lacustris, Physa hypnorum* and *Sphaerium lacustre,* and I have seen it in a pond at Polegate (**177**) and in marl pits in Kent. *Bithinia tentaculata,* while still requiring good conditions, is less particular and much commoner and is found throughout England up to Edinburgh and throughout Ireland. It will be found in (nearly) every place where *leachii* occurs and also under less favourable conditions in lakes, reservoirs, quicker rivers and quite small streams. It never occurs naturally in small closed stagnant ponds, and attempts which I made to colonise it in 13 of the best of the Aldenham ponds all failed except that I found a few specimens in one of them (a running pond) 10 years later. But it does sometimes occur in the larger closed loci which marl pits provide in Cheshire (**85**) and Kent. Welch (**86**) points out that the distributions of *leachii* and *Planorbis corneus* are very similar both in England and Ireland.

***Valvata macrostoma* (Fig. 55) lives in draining ditches in Hampshire, the Sussex marshes and East Anglia—rich places with a good fauna of which Oldham (**87**) gives this example from Suffolk:

Ancylus lacustris	*Planorbis contortus*	*Bithinia leachii*
Limnaea peregra	*Pl. fontanus*	*Valvata piscinalis*
L. palustris	*Segmentina nitida*	*V. cristata*
L. truncatula	*Physa fontinalis*	*V. macrostoma*
Planorbis corneus	*Paludina contecta*	*Sphaerium corneum*
Pl. complanatus	*Bithinia tentaculata*	*Pisidium milium*
Pl. vortex		

†*Valvata piscinalis* (Fig. 11) is common throughout Britain and Ireland in all kinds of running water—rivers to quite small brooks, canals, ditches and lakes, including a few low-lying mountain lakes (e.g. L. Scarmclate, Caithness and L. Mhor East, Inverness); it is sometimes extremely abundant in running ditches, and trout may get a stomachful. Taylor (**88**) has recorded it in one pond used as a rubbish dump and Long (**220**) in an engine cistern, but such habitats are quite exceptional and it does not live in closed ponds. †*V. cristata* (Fig. 12) requires the peculiar combination of plenty of mud and running water which it generally gets among a dense growth of plants such as *Sparganium* in slow streams, backwaters, ditches, lakes, etc. It occurs throughout Britain and Ireland and is probably commoner than it seems to be, for it is easy to overlook and is frequently found on caddis cases (**43**).

†*Paludestrina jenkinsi* (Fig. 13) was first differentiated and described from specimens from brackish water in the Thames estuary in 1889 (**90**), and at that time there was nothing known in fresh water with which it could possibly have been confused. It was not, however, a new creation, for it has been identified in holocene deposits in England and Ireland and had been collected in Lough Neagh about 1837 and at Gravesend in 1859 (**94**). It was first found away from the coast in 1893 when Daniel (**91**) took it in a canal at Dudley; in 1897 Hann (**92**) found it in a stream at Middlesbrough, and in 1899 Taylor (**93**) in a canal at Droylesden. It has since become one of our common fresh-water species and has now been recorded in the Census of the Conchological Society for 56 of the 68 divisions of England and Wales, for 9 Scottish counties including Orkney, and for a number of places in the north and south of Ireland.

It is a most determined colonist and has been caught in passage with *Pisidium cinereum* and *P. subtruncatum* in mud on the bill of a scaup duck shot at Perth (**203**). Its passage from salt to fresh water is no doubt helped by its viviparous habit which gets round the difficulty that marine eggs do not contain enough salts for the development of the embryo (Needham, **167**). It is also parthenogenetic (**95**) which gives it an advantage over its unisexual allies (*P. stagnalis, P. ventrosa*) which lay eggs: it is also free from the parasitic castration by trematode larvae which is common in these other species. There is also something exceptional in its nitrogenous metabolism, for in a long list of terrestrial marine and fresh-water Mollusca examined by Needham (**96**) it is the only one which showed no uric acid. Experimentally fresh-water strains may easily be got to live and breed in sea water: Ellis (**97**) showed that the acclimatisation of *P. stagnalis* to fresh water was favoured by warmth.

Inland it lives in running waters, rivers, canals, brooks, ditches, *running* ponds, often in the meanest little trickles. In stagnant water and closed ponds it is very uncommon: the Hampstead bathing ponds (**98**) and a dew pond at 370 ft. on the downs near Eastbourne (Shrubsole, **177**) are the only certain instances I know, though suggestive cases are mentioned by others (**99**). In many of its loci it occurs in the greatest abundance, and the vegetation and mud may be black with it: Stelfox (**103**) and Welch in Ireland and Stubbs (**100**) in England remark on the destructive effect it has on the existing Mollusca when it invades a locality. Conversely it rather frequently disappears from a place in which it has been abundant. These extravagances are characteristic of a species which has not yet found its settled place in our fauna; what that eventually becomes will be interesting to see. According to Dean (**218**) carp have a passion for it while perch leave it alone.

Amnicola taylori (Fig. 60), which appears to be native and not as has been supposed an importation, was first found by F. Taylor in 1900 in the Manchester canals (**102**) where it still lives without having spread far, and recently in a timber dock at Grangemouth in Stirling by A. R. Waterston (**101**).

***Neritina fluviatilis* (Fig. 43) occurs in small and large rivers, especially in the rapid parts, river lakes and canals, sitting on stones, the masonry of bridges, etc., more rarely on the plants, throughout England from Somerset and Dorset to Westmorland and Yorks., and in the central parts of Ireland: it has not been found in Devon and Cornwall, Wales (except Glamorgan) or Scotland except for an outlying locus in Harray Loch in Orkney (which has hard water), where it has been known since the time of Edward Forbes. In Ireland Stelfox (**103**, p. 121) says "strictly calcicole", and Moquin-Tandon (**104**) the same for France (see below, p. 158).

(*c*) *Pulmonates*

Phylogenetically the pulmonates (*Ancylus, Limnaea, Planorbis, Physa*) are land Mollusca which have taken to an aquatic life. In consequence they can breathe air and all of them (except the limpets, *Ancylus*) do this more or less, especially in warm weather, when they are fond of coming to the top and crawling about on the surface film. Otherwise they separate air from the water into their pulmonary cavity for hydrostatic as well as respiratory purposes or absorb what oxygen they need from that dissolved in the water; this suffices in the winter and in deep cold water. Foul water encourages aerial respiration, and in a dirty deoxygenated pond, sealed with a thick mat of *Lemna*, frogbit, etc., they may be found crawling about on the surface of the vegetation. In *Planorbis* respiration is facilitated by the presence of haemoglobin which is present in considerable quantities (**249**) in the larger species (*corneus, complanatus, carinatus*) and less uniformly in the smallest (*nautileus*). Their ancestry is perhaps also reflected in their capacity to survive in dry air for surprisingly long times.

†*Ancylus fluviatilis* (Fig. 2), the fresh-water limpet, has been recorded for all the comital divisions of England, Wales and Scotland except there; in Ireland it is less universal but common enough. It normally lives on stones in quick-running water, hard or soft, not only in large and medium rivers but in small streams and tiny trickles and on wet rocks (**221, 247**), even at the edge of the sea (**227**), and in some mountain lakes to over 2000 ft. It needs a hard clean surface to sit on (which may be supplied by the shell of another snail or a mussel or the elytron of *Dytiscus*, on which it has been caught taking an aerial journey, occasionally by plants, as well as by stones) to which it fits snugly because the edge of the shell consists of periostracum only (**261**). In any one stream it is sharply restricted to those

places where the turbulence of the current is sufficient to keep the stones clean; hence it is generally found in a rippling place in a few inches of water, and none will be seen in quieter places close by where the flow allows silt and mud to coat the bottom. If a stone carrying it is moved from the ripples into a slow place of about equal depth perhaps a yard away, the limpets have all gone by the next day. Their oxygen requirements are, I believe, rather high, for they die easily in a corked tube on the way home, but though this probably helps to determine their absence from stagnant water it is not the factor which fixes their distribution in a small shallow stream where all the water is no doubt adequately aerated. Why they object so strongly to mud is not clear, but it presumably interferes with respiration. Sitting as they do, only a small part of their body is exposed to the water from which they have to get the oxygen they need, since they cannot come to the surface and take in air like the other pulmonates, and this part is the first to be covered with mud. If the necessary conditions of hard surfaces and absence of mud[1] are satisfied, quickly running water is not obligatory. Clean lakes will do, or, as Fysher (**184**) says, places in lakes where the wave wash keeps the stones clean: Moore (**105**) found it in a well and Heathcote (**106**) in a cement tank in the Isle of Man, and I have seen it in another in Hampshire. Oldham (**107**) and Schroeder (**196**) have shown that it can be bred in an aquarium without running water which I had failed to do. Its habit of living in very shallow water must be a protection from fishes.

Ancylus lacustris (Fig. 27), more a southern species, definitely prefers quiet and stagnant water, though it equally needs a firm surface to sit on which it commonly finds in the stiff leaves and stems of water plants such as water-lilies or *Sparganium* and on floating or submerged timber or the shells of other Mollusca. It is common in cattle ponds, lowland lakes, ditches and quiet rivers. Its typical habitat is quite different from that of *A. fluviatilis*. The same river may easily contain both, each in its respective niche, but they are occasionally found actually together in places such as slow rivers: I have twice so seen them on water-lily leaves in quietly flowing, moderately deep water, and collocations of the two species are mentioned by others (**108**). André (**261**) says that experimentally it lives well in badly oxygenated water which *fluviatilis* will not.

†*Limnaea peregra* (Fig. 3) occurs throughout Britain in all types of habitats in which Mollusca occur at all, in stagnant, still and running water, from brackish marshes to 2000 ft. and over. It is our commonest and most abundant fresh-water snail, and with the probable exception of *Pisidium cinereum* our commonest mollusc. It is, however, absent from many loci which contain other snails, and descriptions such as "in every stream and pond" which occur in some local lists are exaggerations: in 1915 there were in Aldenham 116 effectively separate watery loci which contained Mollusca of some sort and *peregra* was present in only 59. It lives well in many stony mountain lakes with no other Mollusca than *Pisidium* and occasionally *Ancylus fluviatilis*, and in the mountains of Ireland, Wales and Scotland it is by far the commonest water snail. In these situations it sometimes develops curious local races (*Limnaea* "*involuta*" in south-west Ireland and north-west Scotland (**260**), *L.* "*burnetti*" in L. Skene near Moffat) in which the spire is more or less sunk in the later whorls (**111**): some of these breed fairly true in artificial culture. All the British forms which I have examined have a sessile spermatheca and would be called *limosa* or *ovata* on the Continent (**51, 77**).

**Limnaea auricularia* (Fig. 28) is more southern and eastern and is normally restricted to roomy habitats—slow rivers, canals, lowland lakes, reservoirs and *large* ponds. It does not like quick-running water, and it is very uncommon in small ponds into which I have vainly tried to introduce it. Curiously enough it sometimes flourishes prodigiously in artificial garden ponds even in west Cornwall, outside its normal range, and fountains, and it

[1] Dr Pentelow tells me that in the upper Tees it lives on stones coated with the fine debris from stone crushing plants.

has been introduced into North America (**17**) which the much commoner and more catholic *peregra* has failed to reach. It is never found naturally without a good many other species. In Scotland, where it reaches as far as Elgin, frequently in Ireland and occasionally in England it does not achieve the full development of its shell but matures and breeds in a juvenile form known as var. *acuta* or *lagotis*. It breeds early and then dies off so that it may be impossible to get adult specimens after June. The anatomical distinction from *L. peregra* is now clear (**51, 77, 111**), and it appears (Taylor MS.) that our pioneer anatomist, C. Ashford, knew of the essential point—the long spermatheca duct—as long ago as 1885: it would have saved much trouble if he had published it.

Limnaea stagnalis* (Fig. 29) similarly has a preference for spacious habitats, though it is not so particular as *auricularia* and is not uncommon in cattle ponds and occurs sometimes in fairly swift rivers especially in the south-east of England. I have twice found it abundant in isolated dew ponds on the Wiltshire downs (as has Hurst (226**) and Shrubsole on the south downs), and thrice seen it appear in one of the Aldenham ponds, flourish for 2 or 3 years and then die out again without obvious cause. It may also breed long before it attains its full size, which as far as I know *peregra* and *auricularia* do not do in nature, though *palustris* does. Geographically it occurs throughout England except in the west, over most of Ireland and in a few places in the south of Scotland, where Forbes and Hanley (**254**) and Ritchie (**14**) say it has been introduced. Baillie's (**292**) attempt to colonise it in Sutherland apparently failed.

†*Limnaea palustris* (Fig. 4) has been recorded for all except 3 comital areas in Great Britain as far north as Perth and has been found up to Caithness: it is widely distributed in Ireland. It lives in quiet and stagnant water, on the one hand in rich loci with a number of other species and on the other in poor places such as marshes and drying ditches and plashy places with no companions (above, p. 132): in Ireland, Stelfox (**103**, p. 112) notes it in peaty places with *Pisidium cinereum* and *P. personatum* where other Mollusca cannot live. Considering its range of tolerance one would expect it to be commoner than it is.

Limnaea glabra (Fig. 56) has been already dealt with (above, p. 128).

Limnaea truncatula has obtained some economic notoriety and special study by being the ordinary host of the sheep fluke (*Fasciola hepatica*), a role sometimes taken by *L. peregra*. It lives mostly out of water, on the mud at the edge of rivers, streams and ditches: sometimes in damp grass in hollows in fields, and also in the slacks of sand dunes (e.g. at Braunton and Berrow), where it endures very hot dry conditions in the summer. In mountain districts it is generally common in small trickles of water, up to 3000 ft. in the Black Mountains, but it does not tolerate really acid peaty ground. It is only occasionally found living in permanent water, and in this paper I do not reckon it as a water species.

***Amphipeplea glutinosa* (Fig. 52) is one of our rarest species and some of the old records[1] are hardly reliable: the shell alone is hard to distinguish from some forms of *Limnaea peregra*. It was known to Montagu (**35**, p. 380 and Suppl. p. 139) from the ditches in the marshes at Deal where it still lives (**114**). It has also been found in the Thames valley near Reading and Oxford, in the Stroud Canal, Norfolk, north Lincoln and south-east Yorks.: in Ireland in the L. Neagh basin and in the central limestone plain from Dublin to the west. It lives chiefly in draining ditches and canals, also in slow rivers (**113**) and some shallow Irish lakes. It sits on stones and the mud rather than among the plants, though Ashford (**112**) found it on water-lily leaves as Montagu records. Its reputation for vagariously appearing and disappearing is probably due to the adults breeding early in the summer and then dying off so that only infants are present during the usual holiday season (**115**).

**Planorbis corneus* (Fig. 30) is essentially an English species, mainly south-eastern, extending to Northumberland and in the west to Exeter, Llangorse Lake in Brecon and the

[1] E.g. from Bala and Windermere in Jeffreys (**141**).

Shropshire Union Canal at Chirk: in Scotland it has been found in Lanark, and in Ireland it appears to be truly native in Dublin, Kildare and Queen's County. Outlying occurrences should be regarded with suspicion, for it is well known to aquarists and pisciculturists and is always liable to be introduced as it has been in Sligo, Northern Ireland and elsewhere (**116**): Standen doubts whether it is really indigenous in south Lancs., and Oldham has the same suspicion in Cheshire. Its natural transport is difficult (above, p. 125), and it is not found in closed cattle ponds though it lives in them well enough; in a wild state it affects slow rivers, good ditches, canals, lowland lakes and reservoirs. Webster (**237**) says it is very sensitive to injury and dies if its shell is cracked, but experiments which I have made indicate that it mends its shell as well as, for example, *Limnaea peregra* and *L. stagnalis*.

Planorbis complanatus* (Fig. 31) (*umbilicatus, marginatus, planorbis*) and **Pl. carinatus* Fig. 32) are a pair of closely allied species with almost identical geographical ranges over the whole of England, south Scotland and most of Ireland. Their habitats are similar to those of *Limnaea stagnalis*—slow rivers, canals, running ditches, lakes, also in small closed ponds and marshes. In Ireland (103, 193**) *complanatus* rather affects small ponds and ditches, while *carinatus* is found more in rivers and lakes, and roughly speaking the same distinction holds in England though with many exceptions. Müller (**43**) said of *carinatus* "in lacubus ac fossis" and of *complanatus* "in paludosis".

**Planorbis vortex* (Fig. 33) and †*Pl. spirorbis* (*leucostoma*) (Fig. 8) are another pair which it is not always easy to tell apart. They can occur together in large loci (rivers, lakes, canals), but typically *vortex* is found in running water with plenty of plants, while *spirorbis* affects stagnant and drying ponds and ditches (above, p. 129): *vortex* is occasionally present in closed ponds. ***Pl. vorticulus* (Fig. 53) occurs in draining ditches and a moat in Sussex and Norfolk.

†*Planorbis albus* (Fig. 5) is more catholic in its tastes than *complanatus, carinatus* and *vortex*, and has a wider geographical range through the whole of England, Wales and Ireland and up to Sutherland in Scotland. It lives freely enough in good loci with *Limnaea auricularia, Planorbis corneus*, etc., but it can put up with much meaner places—small ponds, small weedy streams, rather quick rivers, marshes, and it has been found by Oldham at 1450 ft. in the Welsh hills with *Pisidium lilljeborgii* and by Gyngell (**164**) under stones in a fast moorland stream in Yorks. It or *Planorbis contortus* is the most likely *Planorbis* to be found by itself in inferior loci with permanent water.

†*Planorbis contortus* (Fig. 9) is much the same, ranging to Shetland. In my own experience I should associate it particularly with running water in good loci, but it occurs fairly often in stagnant pools, ditches and marshes and sometimes in mountain lakes: in Ireland (**103**) it is frequent in peaty drains with no companions except *Pisidium*. White (**129**) says it is the most abundant *Planorbis* in Scotland.

**Planorbis fontanus* (Fig. 34) is also widely distributed, but it is rather more particular where it lives though one would never be surprised to find it in any water, running or stagnant, which contained other snails. It is particularly common (commoner than *albus* or *contortus*) in closed ponds in the south of England.

†*Planorbis nautileus* (*crista*) (Fig. 7) is widespread in stagnant and running water throughout Britain: it is small and rather easily overlooked, and its frequency would be better appreciated if it were searched for more carefully; it is often easiest found by taking home a bag of weed and rubbish and washing it out in hot water as was recommended by Unwin (**117**; **247**, p. 218). This is probably the explanation of its frequent absence from lists of Mollusca from rich loci which contain nobler and more impressive species. But, making allowance for this, it seems to have no great preference for "good" over "bad" places (above, p. 132), and it certainly occurs in many of the latter though I think I was wrong (**7**, p. 179) in suggesting that it is secluded into undesirable homes by competition. Shrubsole (**177**) has found it in a dew pond in Sussex.

Of *Planorbis glaber* (*laevis*) (Fig. 6) I know nothing by personal experience except that it is possible to breed it in an aquarium in quite hard water. Records of it, especially from odd or unlikely places, need critical scrutiny, for it is easy to confuse it with immature *albus* in which the longitudinal striation is badly developed: *Valvata cristata* has also been mistaken for it, even by the elect. Reliable records seem to show that it is a wild species mostly north-western and living characteristically in shallow low-lying "mountain" lakes, generally near the sea, either among the weeds or on bare stones (**78**). In such places it is common on the west coast of Ireland (**103**) and has been found in a good many places in Scotland and the north of England. Of many of the southern records I am more doubtful, but Cooper (**180**) has had it lately in a draining ditch at Aldeburgh in Suffolk.

***Planorbis acronicus* (*stroemii*) (Fig. 57) is confined to the Thames and its tributaries, where it lives in quiet parts of the rivers and backwaters.

Planorbis dilatatus is an American species, first found (**73**, p. 221) in 1869 by Thomas Rogers in two places in canals near Manchester. It has since turned up in a variety of similar habitats in the district (**118**) and in the R. Tame with which the canals communicate (**119**). But it has not spread further than Burnley (20 miles), where it was known in 1886 though almost the whole of England is open to it via the canals. It probably prefers places where the water is warmed by engine effluents, but it is not restricted to them.

***Segmentina nitida* is a rare southern and eastern species, going as far north as Yorks. and with outlying stations in the Severn valley in Montgomery (**120**) and Glamorgan. It flourishes chiefly in marsh draining ditches as round Deal, in Sussex, Norfolk, Cambridge and Lincoln, and an example of its companions has been already given (above, p. 140). But it has also been found scattered about here and there in ponds, not apparently always very attractive ones, as in the lower Thames valley (**35**, **121**) and at Welshpool, Blackpool, Stourport and Highclere. In Yorkshire it lives in Askern Bog, Dringhouses (and Askham) Bog and Hornsea Mere and the neighbouring ponds (**122**): these places are relics of larger marshes, and it seems likely that its natural habitat is in marshes which used to be much more widespread than they are now (**123**) and occupied the valleys of the untamed rivers. If it occurs at all in rivers, streams and canals it is very uncommon.

†*Physa fontinalis* (Fig. 10) occurs all over England, Wales and Scotland, as far as Aberdeen, and generally in Ireland. It is characteristic of clean, bright, running water with plenty of plants in rivers, streams, running ditches and sometimes lakes (e.g. Windermere and L. Skene in Aberdeen, where Macgillivray (**124**) found it 92 years ago and A. R. Waterston last year). It is not particular about volume and so lives in quite small loci, as in a closed pond on blown sand in Co. Mayo (Oldham). It is "never" (see below, p. 166) found in closed ponds or stagnant water, but it will breed in a good-sized aquarium (Oldham).

Physa hypnorum (Fig. 59) has been considered above (p. 131).

Physa acuta (Fig. 58) is a polymorphous species scattered over Europe and the Near East which reaches its northern limit in this country where it occurs either in greenhouses (e.g. at Kew, Newcastle, Glasgow) or in engine tanks which may be always warm, e.g. at Aberdeen (**126**), or only sometimes, e.g. at Kettering, or in the open air as in the R. Brent at Golder's Green or the R. Tame at Ashton-under-Lyne (**119**) or the Manchester canals or the canal at Aylesbury (**125**). A few attempts which I made to colonise it from the Brent to cattle ponds met with no success. The idea that some of these occurrences represent the American *P. heterostropha* is not clearly justified.

4. THE RELEVANT QUALITIES OF HABITATS

As with land Mollusca, it is unsatisfying to make lists of the inhabitants of loci distinguished and described by their general nature and appearance without trying to determine the particular qualities of them which are important to the Mollusca. We need, if possible, to look at the world from the molluscs' point of view, and it is unlikely that their categories correspond with our own. "Woods", for example, do not form a significant category for land Mollusca, for we find that what they contain depends on their age and the soil they grow on rather than on their botanical constitution, and that "woodland" species occur in a number of places which are not woods at all in the ordinary sense of the term. In the same way water Mollusca do not look on "rivers" or "ponds" as one of the primary kinds of places which are available for them to live in: what matters to them is rate of flow, nature of bottom, quality of water, etc., and the Mollusca of one river may differ more from those of another river than from those of a lake or pond. In this section, therefore, I try to make out what it is in different habitats which snails really care about. As one would expect, the various factors are almost inextricably mixed with one another, and the final result is often the product of conflicting elements:

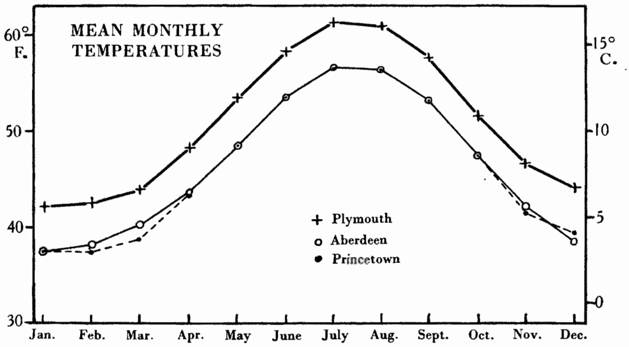


Fig. 1.

thus rate of flow may compensate for absence of sunshine, sunshine for indifferent water, lime for stagnation, and so on. With land Mollusca, the main factors are lime and shelter (which means dampness), and I think the following discussion may be summed up by saying that *the chief considerations for water Mollusca are lime and water which is clean in the sense of being transparent and not overcharged with the products of animal and vegetable decay:* it should at any rate be read with this conclusion in mind.

(*a*) *Altitude*

Browsing in the *Book of Normals* issued by the Meteorological Office (1919) I was surprised to find that the mean monthly temperatures at Princetown on Dartmoor were almost identical with those at Aberdeen (Fig. 1), the mean annual figures being 46·2 and 46·3° F. respectively. Princetown is 1243 ft. above Plymouth, 14 miles distant, where the annual mean is 51·0° F. These figures correspond well enough with the usual allowance (**274**) of 1° F. of mean temperature for each 300 ft. altitude and each 100 miles latitude. I know of nothing but casual temperature records for high British mountain lakes and streams, and the data for air temperatures cannot be transferred to them without qualification. On the whole high lakes are probably colder than would correspond to the calculated air temperatures even when all the winter snow is gone, because water temperatures depend a great deal on direct sunshine which in mountains is defective owing to cloud and fog, and corrie lakes facing north lose much of what sunshine there is. Certainly such lakes as L. Coire an Lochain in the Cairngorms at 3267 ft. (the highest named loch in Britain[1] and free from Mollusca) can be uncomfortably cold to paddle in in August. Shallow lakes open to the sun may, however, warm up fairly well: West (**284**) notes up to 67° F. at 2200 ft. and (**282**, vol. I, p. 165) mentions 70° F. in "small hill lochs" in Scotland, perhaps because such temperatures struck him as exceptional. Without having any of the desirable details therefore it seems that a lake at 2000 ft. in North Wales or at 1000 ft. in Perthshire is, *quâ* temperature, somewhere north of Britain altogether.

Since practically all the ground over 1500 ft. is on the older, siliceous rocks, the water in high loci also differs from that in lower places by being soft and often very soft with the single exception of Malham Tarn at 1250 ft. in north-west Yorkshire, which is the only calcareous mountain lake in Britain and as will be seen (below, p. 157) an illuminating place. Bwch Llyn (p. 155) at 970 ft. in Radnor is also calcareous though not exactly a mountain lake.

The following list contains what I have been able to collect about the occurrence of our Mollusca at altitudes of 1000 ft. or thereby and over, the 7 species marked * occurring at these heights only in calcareous water:

Ancylus fluviatilis: 2300 ft. Brandon Mt., Kerry (**80**); 2000 ft. L. Cwm Clyd, north Wales; 1700 ft. L. Skene, Dumfries (**111**), etc.

**A. lacustris*: 970 ft. Bwch Llyn, Radnor (J. W. Vaughan).

Limnaea peregra: "2400 ft." Lochan a' Chait on Ben Lawers (**283**, 1895, p. 246); 2000 ft. Farragon, Perth (J. Leslie in **45**); 1750 ft. L. Glas in Cwm Clogwyn, north Wales (Oldham); 1600 ft. L. Einich, Inverness: *L.* "*burnetti*", 1700 ft. L. Skene; *L.* "*involuta*", 1600 ft. L. Toberavanaha, Cork (**111**), etc.

**L. stagnalis*: 1250 ft. Malham Tarn, Yorks.; 970 ft. Bwch Llyn.

L. glabra: 1100 ft. Stafford (**46**).

Planorbis albus: 1450 ft. L. y Garn, Merioneth (Oldham); 1100 ft. L. Hilyn, Radnor; 950 ft. L. Ordie, Perth (A. R. Waterston); up to 1000 ft. in Scotland (**129**).

**Pl. nautileus*: 1250 ft. Malham Tarn.

Pl. spirorbis: 1250 ft. marsh by Malham Tarn (Roebuck MS.); 1000 ft. Breidden Hill, Montgomery (J. B. Morgan).

Pl. contortus: 1600 ft. L. Skiach, Perth (A. R. Waterston); 1250 ft. Malham Tarn; 1046 ft. L. Morlich, Inverness (J. E. Somerville); 984 ft. L. Ogwen, N. Wales (Oldham).

**Pl. fontanus*: 970 ft. Bwch Llyn.

Physa fontinalis: 950 ft. L. Ordie (**130** and A. R. Waterston).

**Bithinia tentaculata*: 1250 ft. Malham Tarn; 970 ft. Bwch Llyn.

Valvata piscinalis: 1250 ft. Malham Tarn; 970 ft. Bwch Llyn; 950 ft. L. Ordie.

[1] So say the Geological Survey (**131**). But C. Plumb (*Walking in the Grampians*, 1935, p. 91) seems rightly to give the record to Lochan Buidhe at 3650 ft. 2½ miles to the east.

Sphaerium corneum: 1600 ft. Little L. Skiach, Perth (A. R. Waterston); 1250 ft. Malham Tarn; 1200 ft. L. Kinardochy, Perth.

Sph. lacustre: 1050 ft. Stafford (**225**).

**Pisidium amnicum*: 1250 ft. Malham Tarn.

And for the smaller *Pisidium*, the unlocalised lakes being in Snowdonia and the records mostly by Oldham, from whose register the number of additional loci over 1000 ft. are taken:

Pisidium cinereum: 2400 ft. Ffynnon Felen in Cwm Glas; 2300 ft. Cam Chreag, Perth (Waterston); 2250 ft. L. Glas in Cwm Glas; 2000 ft. Kelly's Loch, on Lug Naquillia, Wicklow, and 28 more over 1000 ft.

P. conventus: 2400 ft. Ffynnon Felen; 2300 Brandon Mt., Kerry (Stelfox, **80**); and 3 more.

P. hibernicum: 2300 ft. Brandon Mt.; 2000 ft. Kelly's Lough; and 24 more.

P. lilljeborgii: 2300 ft. Cam Chreag; 2250 ft. Lochan a' Chait, Perth (F. F. Laidlaw[1]); 2000 ft. Kelly's Lough; 2000 Llyn Lync y Caws; 2000 ft. Llyn Cwm Clyd; and 14 more.

P. milium: 2300 ft. Cam Chreag; 2250 ft. Ffynnon Loer; and 10 more.

P. nitidum: 1600 ft. L. Toberavanaha, Cork; 1450 ft. L. y Garn, Merioneth; and 10 more.

P. obtusale: 2300 ft. Cam Chreag; 2250 ft. Kelly's Lough; 1740 ft. Llyn Dulyn, Merioneth; and 6 more.

P. personatum: 3000 ft. Perth (W. Evans, **145**); 2700 ft. Brandon Mt., 2250 ft. Llyn Glas in Cwm Glas; and 2 more.

**P. pulchellum*: 970 ft. Bwch Llyn.

P. subtruncatum: 1560 ft. Angle Tarn, Patterdale; 1100 ft. Llyn Hilyn, Radnor.

(*b*) *Lime*

There can I think be no doubt that as with land Mollusca lime is favourable and that hard water is better than soft, but in the absence of more ample analytical data than we have it is rather difficult to demonstrate and assess its importance. The great trouble is to disentangle the quality of the water from (*a*) geographical distribution, with which indeed it is obviously connected, for in a general way our calcareous strata lie in the south-east and the soft-water districts in the west and north, and (*b*) the physical characters of the habitats, since in the calcareous areas the rivers are mostly slow and ponds abundant, while elsewhere we have rapid rivers and numerous springs and streams. Hence it is not easy to find habitats close together which differ in nothing else than the hardness or softness of the water, and I suspect that such convenient contrasts can hardly be expected, for hard water generally contains much more plant growth than soft water (see **229**, **284**), which inevitably produces a difference in shelter, humus, etc., which is significant for snails and other animals. We have, too, to bear in mind that the final effect of oecological factors is their sum and that, again as with land Mollusca, the beneficent influence of calcium may be overridden by other unfavourable circumstances, and more Mollusca may be found in a quiet soft-water lake than in a rough calcareous stream.

[1] This is the taking from which *P. lilljeborgii* was first recognised in this country by B. B. Woodward (**146**): picture of the lake by G. West on plate iv of vol. 1 of the *Bathymetrical Survey of Scottish Fresh-water Lochs* (1910).

To appreciate the influence of lime, we must realise that the snails' scale of "hardness" is not the same as our own. Domestically, water will not be called "hard" with less than about 50 mg. calcium per litre (=about 12 "degrees of hardness"), and will not be complained about with less than about 80 (=20 degrees). Correspondingly, water with 20 will be called "soft". In experience, 30 is perceptible in washing one's hands, and water in a hotel (which proved on analysis to have 33) once led me to finding some entirely unsuspected hard water in the neighbourhood. Similarly, while water at 20 is undoubtedly "soft" in the ordinary sense it is definitely inferior for shaving and bathing to water at 2. From the admittedly very imperfect data available it appears that there are a number of Mollusca which do not live in water with less than about 20 mg. calcium per litre, and water of this grade is "hard" to their way of thinking, while water of 40 or more seems "very hard". So, too, on the snail scale water is "soft" only if it has about 10 or less, and between 10 and 20 it might be called "rather soft", but any very detailed classification must obviously wait on further data. Other organisms calibrate the scale in a different way: thus Butcher (**229**), discussing the macrophytic vegetation of rivers, calls water with less than 8 "non-calcareous", with 8–40 "slightly calcareous", with 40–80 "moderately calcareous", and with over 80 "highly calcareous", and sanitarians (**148**) may call up to 60 "slightly hard". A completely graded series can be divided into sections only with reference to the application in hand, and some day we may be able to specify the range of hardness within which each species commonly lives.

In a large way the hardness of waters may be guessed a good deal more accurately from the geological map than the calcareousness of the surface soil (**132**, p. 9), since the water represents the deeper substance of the land rather than the superficial layers. But one meets with unexpected lime just as one does on land. Thus the old red sandstone of Herefordshire is calcareous on the surface only in small patches where cornstones crop out or there is calcareous glacial drift. But the few analyses of springs and streams which I have made myself all show hard water (78–134), and Richardson's ample data (**285**) indicate that all the underground waters of the area are hard. The same seems to be true of the old red sandstone in Caithness and Orkney, though the formation is not generally thought of as biologically calcareous. Similarly, I was shocked to find a roadside spring on the Devonian slates near Croyde in north Devon with 79. I have met with no instance of unexpected soft water. In a calcareous area, water which comes from underground seems to be harder than water collecting on the surface, and water standing in contact with highly calcareous ground may not dissolve very much: thus spring ponds on the very limy sand at Braunton Burrows gave 23 and 56, and a pond at Aldenham about half floored with lumps of chalk only 50. The nature of the calcareous strata also makes a difference: chalk is most soluble and gives water round 80–120 (above, p. 134), oolite is hardly less effective as seen in the upper parts of the Thames or in Dorset; but mountain limestone gives rise to less calcareous streams, e.g. R. Tees is 32, R. Lune and its components 29–55 (**133**), R. Tyne 35, the stream which comes out of the Mendips in Cheddar Gorge 55. Rivers which are geologically dubious are generally hard, though the Whitby Esk is only 6 while the geological map shows much oolite in its basin. Ponds in cultivated areas will generally be more or less calcareous owing to the lime which agriculture and human occupation bring with them, although their water is for the most part rain water: 83 of the Aldenham closed ponds, which are in clay with flints or London clay overlying deep chalk, ranged from 16 to 85 with an average of 48, 3 were under 20 and 35 over 50. So, too, 14 closed cattle ponds in the red clay of Herefordshire were 28–101, average 61. For 13 dew ponds, some cemented, on the Sussex downs Martin (**134**) gives 11–121, average 43. Marl pits are always calcareous, since they were dug to get out calcareous boulder clay or some other form of lime. Even domestic rain water may collect a good deal of lime from asbestos tiles (**148**) or oolite slates. It is possible that the calcium content of surface ponds is raised by the rooted plants collecting salts from the soil and adding them to the water where they decay.

My figures are mostly from those which I have collected myself and from some kindly given me by Dr W. H. Pearsall: there are not nearly enough of them. The only substantial series of analyses that I know of are those of domestic supplies, actual or potential, made by E. Frankland and J. C. Morton, 60 years ago, for the River Pollution Commission (**135**), and the hardness figures in the official *Return as to water undertakings in England and Wales* (1915). Putting together all the data it seems that all the rivers—and by inference the rest of the waters too—of England are hard or rather hard (i.e. over 30) except in Cornwall, parts of Devon, most of Wales, the Lake District and the head waters of the streams which arise in the Pennines; in Scotland soft water is found in the south-west and in the northern half. The map of the distribution of *Limnaea stagnalis* (Fig. 29) represents pretty well the area in which hard water may be presumed. Really soft water comes mostly from uncultivated areas which is as it should be, since an adequate amount of lime is a prime necessity for any but the meanest agriculture. The soil in these areas, siliceous to begin with, remains undisturbed, the rainfall is generally high, and so the surface is thoroughly leached and the emergent water may be somewhere near distilled water. As follows from Pearsall's work on the evolution of lakes (**136**) the water tends to take more salts into solution and become harder as it goes further, so that the composition may vary a good deal at different points. Thus the R. Exe at Thorverton, 6 miles above Exeter, is 10 and no doubt above this softer still, but it soon afterwards receives the R. Creedy 29 and the R. Culm 51, so that the Exeter Ship Canal is 21–34: the Severn, in odd samples I have picked up, gave 5 at Llanidloes, 15 at Welshpool, 28 at Shrewsbury and 46 at Worcester.

There is no fresh-water species which is certainly calcifuge as *Zonitoides excavatus* is on land: *Limnaea glabra* may be (above, p. 129), and none of the few known loci for *Pisidium conventus* is calcareous. But all the other kinds have been found habitually frequently or occasionally in hard water, and it is easier to examine the matter by considering what species are known to occur fairly frequently in quite soft water (i.e. with calcium less than 5 or at any rate under 10). Most of our evidence comes from lakes which fortunately are more comparable among themselves than most other types of habitat. Of the snails, *Limnaea peregra* is by far the commonest: from south-west Ireland we have 8 instances in water of calcium 1 or less (**111**), from north Wales in less than 1, 1, 2, 5 and 8, from Scotland 20 instances under 5, the lowest being under 1. *Ancylus fluviatilis* is the next most common: from Kerry we have it in water of 1 and 2, from Wales in 2, 3 and 4, from Scotland in 2, 3, 4 and 4: both these species have also been found frequently in lakes and streams which are presumably soft but for which we have no analyses. Of the bivalves, *Unio margaritifer* is common (above, p. 133), and in *Pisidium*, *cinereum*, *hibernicum*, *lilljeborgii* and *nitidum*, which are known from a number of soft waters, the lowest calcium being 3, less than 1, 1 and 1 respectively: *milium* and *subtruncatum* are less frequent but have been found in water as soft as 1 and 3. The other species are not common: *Planorbis contortus* is in L. Ogwen in north Wales and in L. Morlich, Inverness, both with calcium under 1; *Pl. albus* in L. Gareg-wen in Carnarvon with 7; *Ancylus fluviatilis*, *Limnaea peregra*, *Planorbis contortus*, *Pl. albus* and *Valvata piscinalis* in L. Lubnaig, Perth (**283**, 1895) with calcium 3; *V. piscinalis* in L. Assynt in 6; *Sphaerium corneum* in L. Padarn, north Wales, at 2 and in L. Kinardochy, Perth, at 8; *Pisidium conventus* from Cwm Glas, Snowdon, at 2 and *P. obtusale* from Cork at under 1. And for a number of occurrences in montane lakes we have no analytical evidence.

Under more generally favourable conditions, about 10 more may be added to this list of 15 species. Windermere (calcium 6–8, Pearsall; Butcher (**229**) gives $3\frac{1}{2}$), which is an exceptionally good soft-water lake, 128 ft. above sea-level, $5\frac{1}{2}$ square miles, mature, sheltered with plenty of plants, silt and mud and varied subhabitats in different parts, has 17 species (**137**, **164**):

Ancylus fluviatilis	*Planorbis contortus*	*Sphaerium lacustre*
A. lacustris	*Pl. spirorbis*	*Pisidium hibernicum*
Limnaea peregra	*Physa fontinalis*	*P. lilljeborgii*
L. palustris	*Valvata piscinalis*	*P. personatum*
Planorbis albus	*V. cristata*	*P. pulchellum*
Pl. nautileus	*Sphaerium corneum*	

In the same neighbourhood Farrer (**138**) records *Ancylus lacustris* from Bassenthwaite (calcium 7) and *Planorbis spirorbis* and *Valvata cristata* from Derwentwater (calcium 6) and Cockerell (**275**) *Limnaea peregra*, *Physa fontinalis* and *Valvata piscinalis* from Conistone Lake (calcium 5). Most soft-water lakes are at high altitudes or latitudes and deficient in plants and humus, but another particularly productive one is L. Leane at Killarney at 66 ft., 9 square miles, with calcium 7–11 in different samples where we found (**111**, **139**) 17 species, 13 of which are in Windermere:

Ancylus fluviatilis	*Planorbis contortus*	*Sphaerium corneum*
Limnaea peregra	*Physa fontinalis*	*Pisidium cinereum*
L. palustris	*Valvata piscinalis*	*P. hibernicum*
Planorbis albus	*V. cristata*	*P. lilljeborgii*
Pl. nautileus	*Paludestrina jenkinsi*	*P. nitidum*
Pl. spirorbis	*Unio margaritifer*	

This list of 26 species—those in the Windermere and Leane lists *plus* *Limnaea glabra*, *Pisidium conventus*, *P. milium*, *P. obtusale* and *P. subtruncatum*—includes all those which we can find in soft water without surprise and one—*Ancylus lacustris*—which I think ought not to be in the list. *Limnaea glabra* and *Pisidium conventus* have not been found in hard water and *Unio margaritifer* and *Pisidium lilljeborgii* are much more frequent in soft, but apart from these four they all live in, for example, R. Thames with calcium 80 or more and prefer hard water to soft. *Unio margaritifer* (above, p. 134) and *Pisidium lilljeborgii* (above, p. 136) have been taken in hard water often enough to show that it is not wholly repugnant to them. The various races of


2 *Ancylus fluviatilis*


3 *Limnaea peregra*


4 *Limnaea palustris*


5 *Planorbis albus*


6 *Planorbis glaber*


7 *Planorbis nautileus*


8 *Planorbis spirorbis*


9 *Planorbis contortus*


10 *Physa fontinalis*


11 *Valvata piscinalis*


12 *Valvata cristata*


13 *Paludestrina jenkinsi*


14 *Unio margaritifer*


15 *Sphaerium corneum*


16 *Sphaerium lacustre*


17 *Pisidium cinereum*


18 *Pisidium conventus*


19 *Pisidium hibernicum*


20 *Pisidium lilljeborgii*


21 *Pisidium milium*


22 *Pisidium nitidum*


23 *Pisidium obtusale*


24 *Pisidium personatum*


25 *Pisidium pulchellum*


26 *Pisidium subtruncatum*

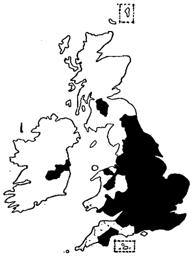
SOFT-WATER SPECIES

Figs. 2—26.

27 *Ancylus lacustris*

28 *Limnaea auricularia*

29 *Limnaea stagnalis*



30 *Planorbis corneus*

31 *Planorbis complanatus*

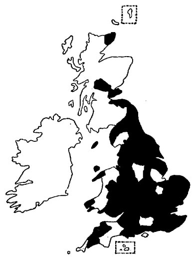
32 *Planorbis carinatus*

33 *Planorbis vortex*

34 *Planorbis fontanus*

35 *Bithinia tentaculata*

36 *Anodonta cygnea*



37 *Anodonta anatina*

38 *Pisidium amnicum*

39 *Pisidium henslowanum*

40 *Paludina vivipara*

41 *Paludina contecta*

42 *Bithinia leachii*

43 *Neritina fluviatilis*

44 *Dreissena polymorpha*

45 *Unio pictorum*

46 *Unio tumidus*

47 *Sphaerium rivicola*

48 *Sphaerium pallidum*

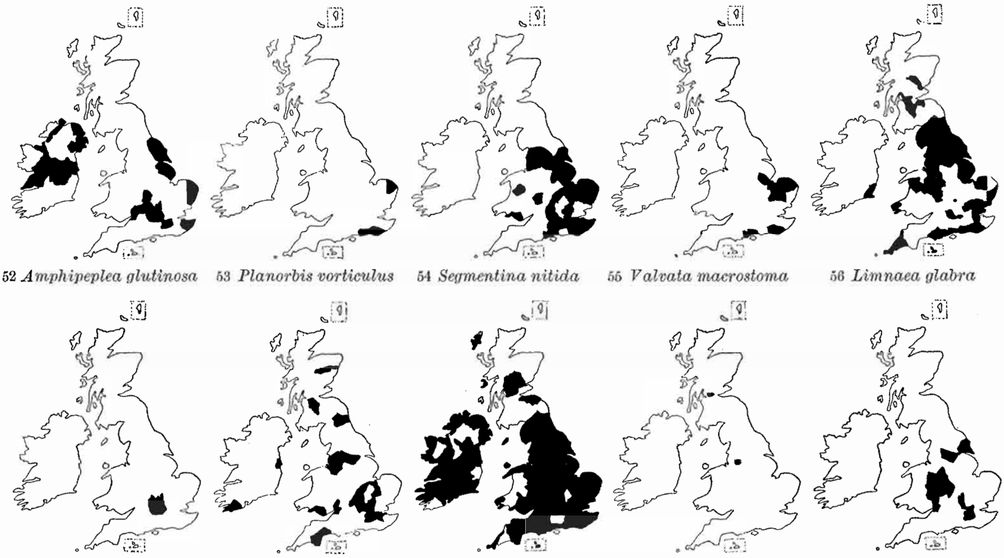
49 *Pisidium torquatum*

50 *Pisidium supinum*

51 *Pisidium tenuilineatum*

CALCIPHILE and CALCICOLE

Figs. 27—51.



52 *Amphipeplea glutinosa* 53 *Planorbis vorticulus* 54 *Segmentina nitida* 55 *Valvata macrostoma* 56 *Limnaea glabra*

57 *Planorbis acronicus* 58 *Physa acuta* 59 *Physa hypnorum* 60 *Amnicola taylori* 61 *Pseudanodonta sp.*

Figs. 52—61.

Limnaea peregra from very soft water bear transplantation to water of 60 or 80 with complete equanimity.

Like the corresponding land snails which can do with very little lime (**132**, p. 34), these soft-water species are mostly small and widely spread in Britain (Figs. 2–26); many extend to northern Europe and some are holarctic: 21 of them have been found at 1000 ft. or over (above, p. 147).

Of the remaining species, for 6 (*Planorbis glaber*, *Pl. dilatatus*, *Physa acuta*, *Ph. hypnorum*, *Amnicola taylori* and *Dreissena polymorpha*) I have no adequate data on which to base any conclusion about their relation to lime: they can all live in hard water and none has been proved to occur in soft. *The other* 30 *are all calciphile or calcicole in the sense that they are habitually found in hard water*, and there is evidence that ordinarily they need water with at least 20 mg. calcium per litre and some of them more:

Ancylus lacustris
Limnaea auricularia
L. stagnalis
Amphipeplea glutinosa
Planorbis corneus
Pl. complanatus
Pl. carinatus
Pl. acronicus
Pl. vortex
Pl. vorticulus
Planorbis fontanus
Segmentina nitida
Bithinia tentaculata
B. leachii
Valvata macrostoma
Paludina contecta
P. vivipara
Neritina fluviatilis
Anodonta cygnea
A. anatina
Unio pictorum
U. tumidus
Pseudanodonta sp.
Sphaerium rivicola
S. ovale
Pisidium amnicum
P. henslowanum
P. supinum
P. tenuilineatum
P. torquatum

These are all more or less southern or south-eastern in range (Figs. 27–51) and are unknown or rare in Devon and Cornwall, Wales, the Lake District and most of Scotland. A number of them have large and heavy shells. Their distributions either roughly correspond to, or are included within, the area in which practically all the water is hard and the coincidence is certainly suggestive. The best evidence that it is not fortuitous comes from a study of the periphery of the occupied areas towards the north and west, where soft water begins to be common; of the north I have no details and can give some data only about Wales and the south-west, where the outlying loci of various species prove to be calcareous.

Llyn Maelog, in Anglesea, is an outlying locality for *Limnaea auricularia*, *L. stagnalis* and *Anodonta*. It is a good-sized (about 800 × 400 yd.) shallow lake in the old sand-hills at Rhos Neigr with rocks at one end, a stony or sandy bed and sparse vegetation, including *Lobelia dortmanna* and *Subularia* as well as *Elodea*[1] and a reed bed on the western side. I am much indebted to Dr N. Woodhead of Bangor for much information about the persistent alkalinity of the water (pH 7·3–8·6): three samples gave calcium 17, 21 and 23, due no doubt to the calcareous sea sand, for the geology of that part of the island makes no suggestion of hard water. The conspicuous Mollusca have been known for 50 years (**140**, **142**), and the whole list is now:

Ancylus fluviatilis	*Planorbis contortus*	*Pisidium hibernicum*
Limnaea peregra	*Physa fontinalis*	*P. lilljeborgii*
**L. auricularia acuta*	*Paludestrina jenkinsi*	*P. milium*
**L. stagnalis*	*Valvata piscinalis*	*P. nitidum*
L. palustris	**Anodonta anatina*	*P. pulchellum*
Planorbis albus	*Sphaerium corneum*	*P. subtruncatum*
Pl. nautileus	*Pisidium cinereum*	

* Calciphile.

L. Coron, 4 miles to the east, is practically a replica with calcium 23: it contains the same species *minus Limnaea palustris*, *Planorbis nautileus*, *Pl. contortus*, *Ancylus fluviatilis* and *Pisidium hibernicum* and *plus Ancylus lacustris*, **Anodonta cygnea* and **Pisidium henslowanum*.

There is no good local control for these lakes. The low-lying lakes round Snowdon are of a different type, stony river lakes with soft water[2] and no snails beyond *Limnaea peregra*, *Ancylus fluviatilis*, *Spherium corneum* and various *Pisidium*. But near Portmadoc, 25 miles away, there is the small L. Gȧreg-wen which, like Maelog, is embedded in the old sand hills against the rock. It has a sandy floor and abundant reeds, water-lilies, *Potamogeton perfoliatus*, *Myriophyllum*, *Littorella*, etc., and I have often wondered why it contained only *Limnaeȧ peregra*, *Planorbis albus*, *Pisidium milium*, *P. nitidum* and *P. subtruncatum* until I examined the water and found the calcium only 7.

Bwch Llyn (sometimes called Llynbychllyn Pool) in Radnor, 6 miles south-east of Builth, is another significant locus discovered conchologically by J. W. Vaughan in 1905 (Roebuck MS.). About 700 × 250 yd., it lies in enclosed grassland at about 970 ft. on Silurian rocks which are not obviously calcareous:

[1] *Elodea* is very uncommon in soft water: on the other hand *Lobelia* is characteristic of soft water (**284**).

[2] L. Padarn calcium 2, L. Gwynant 4, L. y Ddinas 3, L. Quellyn 3.

there is a large reed bed, in parts a carpet of *Littorella* and much *Menyanthes*, water-lilies and *Potamogeton* "*lucens*": three samples of water each gave calcium 21. The Mollusca are:

Ancylus lacustris	*Pl. contortus*	*Sphaerium corneum*
Limnaea peregra	**Planorbis fontanus*	*Pisidium nitidum*
**Limnaea stagnalis* (up to 52 mm. long)	*Physa fontinalis*	*P. personatum*
Planorbis albus	**Bithinia tentaculata*	*P. pulchellum*
	Valvata piscinalis	*P. subtruncatum*

L. Gwyn[1], 14 miles away near Rhayader, is very similarly situated in a hollow of the hills at about 700 ft. on older Silurian strata. There is hardly any vegetation except *Littorella*, no snails and the calcium was 2: the contrast with Bwch Llyn is impressive.

Llangorse Lake (Llyn Safaddan), over which I had much help from Dr Betenson, on the old red sandstone near Brecon is another place which few would suspect of having hard water unless they saw it or the list of Mollusca (**143**) found in it: altitude 502 ft., about $1\frac{1}{4} \times \frac{1}{2}$ miles = 353 acres; abundant reed beds and aquatic vegetation with muddy or sandy floor, in parts with *Littorella* carpet. Two samples gave calcium 36 and 37, the effluent R. Llynfi 33 and its inflow 58 (in drought): the lime must come from neighbouring cornstones. The Mollusca are:

Ancylus lacustris	*Planorbis spirorbis*	**Unio pictorum*
Limnaea peregra	*Pl. contortus*	*Sphaerium corneum*
**L. auricularia*	*Pl. fontanus*	**Pisidium amnicum*
**L. stagnalis*	*Physa fontinalis*	**P. henslowanum*
L. palustris	**Bithinia tentaculata*	*P. milium*
**Planorbis corneus*	*Valvata piscinalis*	*P. nitidum*
**Pl. complanatus*	*V. cristata*	*P. pulchellum*
Pl. "*glaber*"	**Anodonta cygnea*	*P. subtruncatum*
Pl. nautileus		

The profusion of Mollusca is extraordinary, and fishing from the landing stage among the *Potamogeton natans*, *Elodea* and *Lemna trisulca* reminds one of a first-rate calcareous locus in the south-east of England. In the effluent, *Limnaea stagnalis* and *Planorbis corneus* (which appeared in the lake between 1904 and 1928) were in such numbers as I do not think I have ever seen, and many *corneus* were as much as 33 mm. in diameter: *Bithinia tentaculata* reached 15 mm.

L. Maelog and L. Coron are the most westerly[2] loci for *Limnaea stagnalis*, and they are about 60 miles to the north and west of its nearest known habitat. Outside Glamorgan and Pembroke, in which there is a good deal of limestone, Wales is in general a soft-water area, and in this the species is known only from the four loci I have detailed with calcium 20, 23, 21 and 36, from a pond near Wrexham (Shrubsole, **65**) with calcium 28 and from one near Welshpool of which I know nothing further. In Herefordshire, next to the east and well to the west of the calcareous area of south-east England, it occurred in three

[1] The picture in the *Cambridge County Geography* of Radnor, p. 33, is not L. Gwyn, as it is labelled, or Bwch Llyn.

[2] Except for a rather dubious record from near Tenby based on a single young specimen.

places for which I have analyses—R. Lug with 58 and two running ponds with 70 and 88. L. Maelog and Bwch Llyn are softer than most of its homes, and now that it is known that these outlying Welsh lakes are calcareous most places where it is found can, I think, be presumed to have hard water. The position in England and Wales seems to be much the same as in Ireland where, Stelfox (**103**, p. 111) says, it is "widely distributed but seldom abundant outside the limestone areas of the central and eastern counties and absent from such peat-covered districts as west Cork, Kerry, north-west Mayo and north-west Donegal....It reaches the west coast in the sand dune" [and presumably calcareous] "lakes of west Mayo but does not live on any of the western islands". Shrubsole's (**65**) specimens from Wrexham were badly eroded, as he thought from the water being too soft, and Crowther (**276**) records the pertinent observation that he brought some into an aquarium at Leeds (where the tap water about 1929 had calcium 12), where they gnawed off the tops of one another's shells. Adult and young specimens from R. Colne (calcium 100) died in 2 days in R. Teign water (calcium 4).

Another place which brings out the favourable effect of lime on *Limnaea stagnalis* and others is Malham Tarn (plate 4) near Settle in Yorks., 153 acres at 1250 ft., up to 14 ft. deep, a wild stony lake with no marginal and little submerged vegetation (which, however, includes *Potamogeton lucens*, *praelongus* and *perfoliatus* (**258**)), many crayfish: Frankland (**135**) in 1869 gives the calcium as 54, Burrell (**149**) in 1899 found 32, and in 1935 we got 31, the lake lying on Silurian rocks at their junction with mountain limestone. The Wests (**286**) found plenty of desmids and nothing special in the phytoplankton, and do not seem to have known that the water was calcareous. The place has been frequently examined by members of the Yorkshire Naturalists' Union (**150**), and the Mollusca are:

Ancylus fluviatilis	*Planorbis contortus*	**Pisidium amnicum*
**Limnaea stagnalis*	*Physa fontinalis*	*P. cinereum*
L. peregra	**Bithinia tentaculata*	*P. hibernicum*
L. palustris	*Valvata piscinalis*	*P. lilljeborgii*
Planorbis albus	*Sphaerium corneum*	*P. nitidum*
Pl. nautileus		

Limnaea stagnalis, *Planorbis nautileus*, *Bithinia tentaculata* and *Pisidium amnicum* are unknown elsewhere at more than 1000 ft., and the fauna of Bwch Llyn (p. 155) at 970 ft. gives similar evidence of the encouraging influence of lime on *Ancylus lacustris* and *Planorbis fontanus*. No other loci for *Limnaea stagnalis* approach these altitudes and I know of no other place at 1000 ft. or over with anything like their faunas: most of the high lakes in north Wales and many of those in Ireland and Scotland have been examined conchologically.

The argument for the other species of this group is much the same and it need not be set out in detail. Towards the south-west, just where the soft-water area begins, *Limnaea auricularia*, *Planorbis corneus*, *Paludina vivipara* and *Sphaerium rivicola*, all species of characteristic calcicole distribution and habit, have their last home in the Exeter Ship Canal and canalised river which, in a sample kindly obtained for me by Dr R. J. Lythgoe, showed calcium 34 and in a later specimen 21. Another western locus for *Paludina vivipara* in the Brecon and Newport Canal at Talybont gave calcium 27; the species, dreadfully eroded, lives here in profusion with *Bithinia tentaculata*, *Anadonta cygnea*, *A. anatina*, *Pisidium amnicum* and *P. henslowanum*, as it has been known to do for 62 years. For the Wye in Herefordshire I have a number of analyses varying from 15 to 33, and from the data given by Duncan and Ellis in Richardson (**285**) it appears that in times of drought the calcium may be a good deal higher: it contains *Bithinia tentaculata*, *Anodonta anatina*, *Unio pictorum*, *Pisidium amnicum*, *P. henslowanum*, *Neritina fluviatilis*, *Unio tumidus*, *Pisidium supinum* and *P. torquatum*, and going west from Hereford the conchologist will see little of any of them and nothing of the last four before he reaches the Irish Sea. The only Herefordshire habitat for *Planorbis corneus* was a running ditch with calcium 85, though it lived there for some years in a garden tank with about 20, as it did in Laver's water butt (above, p. 125). Shrubsole (**65**) put specimens from the Trent Canal (calcium 58) into Chester water (calcium 21) and found that they did badly and became deeply eroded.

The few calcareous loci known among the overwhelming majority of soft-water lakes and rivers in the northern half of Scotland also provide significant evidence, for it is in this hard water that the few calciphile southern species which spread so far north have been found. There are three highly calcareous lakes in the isle of Lismore, one of which is known to have water of calcium 60, (**282**) visited by Scott (**283**) and Standen and Hardy (**287**); five more on the Durness limestone in Sutherland investigated by Oldham with water from 20 to 32; about 8 on the old red sandstone in the north-east of Caithness where, Dr George Dick tells me, all the wells yield hard water, where Crampton (**288**) describes the flora of limy lakes and L. Watten has calcium 104 (Dr J. F. Tocher) and Yarehouse Loch 31; and perhaps half a dozen more in Orkney, where there is much lime in the old red sandstone and in the blown calcareous sand (**289**), all the deep and surface spring waters are very hard (Dr W. B. Bannerman) and Harray Loch[1] has calcium 78. In all, therefore, we know of about 20 calcareous lochs in the north, and they have been looked at conchologically (by Baillie, Scott, Oldham and others) more thoroughly than might have been expected. Four of the five southern calciphiles which have been found in the far north have occurred in these calcareous loci and are unknown or rare in the rest of Scotland; *Neritina fluviatilis* in Harray Loch in Orkney and *Planorbis vortex* in L. Hempriggs; *Anodonta anatina* in the River of Wick and *Pisidium henslowanum* in L. of Mey in Caithness. Of L. Achnacloich in Ross East where Scott (**283**) found *Planorbis fontanus* I know nothing relevant, nor of Hellier's Loch in Shetland where also Oldham got

[1] From Mr Robert Rendall.

Pisidium henslowanum: but it is not very rash to predict that when their waters are examined they will be found to be hard. But the molluscan fauna as a whole is poor, and apart from the five species mentioned the whole of Ross, Sutherland, Caithness, Orkney and Shetland[1] have only:

Ancylus fluviatilis	*Physa hypnorum*	*Pisidium hibernicum*
Limnaea peregra	*Paludestrina jenkinsi*	*P. lilljeborgii*
L. palustris	*Valvata piscinalis*	*P. milium*
Planorbis albus	*V. cristata*	*P. nitidum*
Pl. glaber	*Unio margaritifer*	*P. obtusale*
Pl. nautileus	*Sphaerium corneum*	*P. personatum*
Pl. spirorbis	*Sph. lacustre*	*P. pulchellum*
Pl. contortus	*Pisidium cinereum*	*P. subtruncatum*

and the Lismore lakes have 7 from this list.

It is quite clear that the absence of conspicuous southern calciphiles such as *Limnaea stagnalis*, *L. auricularia*, *Planorbis corneus*, *Pl. complanatus*, *Ancylus lacustris* and *Bithinia tentaculata* is not due to the absence of hard water. The calcareous lakes too are richer than the others; in a direct comparison in Sutherland Oldham got an average of 6·8 species per lake for the former against 2·7 for the latter, and it seems that, as with some of the land snails, some of the soft-water species become calciphile in the north.

Such is, as I believe, the general truth about the relationships of the various species to hard and soft water and geographical distribution, and it will commonly hold good, at any rate in England, Wales and the south of Scotland. Also apparently in Ireland where the calcareous area is central and north-eastern. As Stelfox (**103**, **152**) describes it, such species as *Ancylus lacustris*, *Limnaea stagnalis*, *Amphipeplea glutinosa*, *Planorbis complanatus*, *Pl. carinatus*, *Pl. vortex*, *Neritina fluviatilis*, *Anodonta cygnea* and *Pisidium amnicum* are central; *Planorbis albus*, *Pl. fontanus*, *Bithinia tentaculata* and *Sphaerium corneum* are mainly central, and though they occur in the generally non-calcareous districts of the south-west and north they are rare; while *Ancylus fluviatilis*, *Limnaea peregra*, *L. palustris*, *Planorbis nautileus*, *Pl. spirorbis*, *Pl. contortus*, etc., are ubiquitous. He attributes the absence of what I should call the calcicole species from the periphery to the difficulty they have had in crossing mountain ranges from the central plain. So, too, any critic who did not much believe in the importance of lime might take the maps on pp. 152–4 as illustrations of the varying capacity of the different species to spread through Britain from the south-east as the glacial period faded away.

And just as indifferent species may find a good supply of lime necessary or pleasant in the extreme north, so, under exceptionally good general conditions, calcicole species may live in quite soft water. The north-western branches of the Shropshire Union Canal are filled with water above Llangollen from the R. Dee, a typical turbulent mountain river with calcium 4 or 5. At

[1] Scott (**283**) examined 55 lochs in Shetland and found *Limnaea peregra* in 13, *Planorbis albus* 1, *Pl. glaber* 1, *Pl. nautileus* 9, *Pl. contortus* 1, and *Pisidium* 10.

the Chain Bridge such water as is necessary passes into a quiet, gently flowing stream in the canal, free from floods and any great fluctuations of level, moderately supplied with plants, including *Elodea* and frogbit, and now practically undisturbed by traffic: various samples taken in 1934 and 1935 showed calcium figures of 5–8 over the first 10 miles. In 1935 Oldham and I found the following 12 calcicoles:

Limnaea auricularia	*Planorbis vortex*	*Pisidium amnicum*
L. stagnalis	*Pl. fontanus*	*P. henslowanum*
Planorbis corneus	*Bithinia tentaculata*	*P. tenuilineatum*
Pl. carinatus	*Sphaerium pallidum*	*P. torquatum*

most of which Oldham had taken in 1922 when he found also *Bithinia leachii* which is in the ordinary way addicted to highly calcareous water. There were in addition 15 indifferent species. Further south near Welshpool, where the water has taken up more lime and has calcium 11–13, we found also

Paludina vivipara	*Unio pictorum*	*Sphaerium rivicola*
Anodonta anatina		

and here *Unio termidus* was found by Morgan (**290**) years ago. This locus is of course artificial, and to it snails have access through continuous water from the whole of the Midlands as well as very acceptable conditions when they get there. It is of particular interest because it flatly breaks the rules for about 15 species, none of which are known elsewhere from water with less than calcium 20 at least; it does not show that the rules are not sound but that one oecological factor must be balanced against another. The canal is perhaps analogous to an aquarium, and what happens when one tries to breed calcicole species in soft water no one seems to know.

The decided preference which most Mollusca have for hard water is due to several causes. (*a*) They need lime for their shells, and the calcicole species have on the whole larger and heavier shells than those which are content with soft water. This is not, however, a universal difference: on the one hand *Amphipeplea glutinosa* confined to quite hard water has a thin shell, while *Unio margaritifer* grows very heavy shells in quite soft water, though some which Oldham got from the Burn of Setter in Shetland had so little substance that the contraction of the periostracum on drying cracked the shells across, while specimens from the Hereford Wye, which has more calcium than most of its habitats, are small and rather thin (**257**). Bloomer (**178**) notes that the thickness of *Anodonta* is not always related to the hardness and softness of the water. *Limnaea peregra* from very soft water nearly always have thin shells (weighing 2 or 3 mg.) which may be so little calcified as to be flexible when they are fresh as in *L.* "*praetenuis*", though *L.* "*burnetti*" is an exceptionally large heavy form (135 mg.) and comes from water with calcium only 4. The thin-shelled races which I have bred in hard water have invariably responded by thickening the shell, so that cleaning out the body ceases to be the hazardous procedure it is with the soft water original (**111**). (*b*) The second great function which lime plays for snails is to agglutinate

Photo. Harmer, Settle

Phot. 2. Malham Tarn, north-west Yorkshire. The only calcareous lake in Britain over 1000 ft., calcium 39 mg. per litre; 1250 ft. above sea level; open and exposed, the highest ground near being only 1800 ft. Mollusca: 16 species (see p. 157).

Photo. Frith, Reigate

Phot. 3. Cwm Glas on Snowdon, Carnarvonshire. Illustrating about the extreme austerity which mollusca tolerate in Britain. In the larger lake behind (Ffynnon Frech; 2250 ft.; calcium 2) are *Ancylus fluviatilis* and *Pisidium personatum*: the smaller one in front (Ffynnon Felen; 2400 ft.; calcium 2) contains *Pisidium conventus* and, at a trickle entering it, *P. cinereum*. The distant lakes are L. Cwm y Ffynnon (1254 ft.) above Penygwrhyd and L. Mymbyr (588 ft.) at Capel Curig.

and precipitate particles of clay and so produce clear, bright water which will let in the sunlight: permanently and densely muddy waters contain hardly any plants and no Mollusca except sometimes *Anodonta*. The bad effect can be readily demonstrated by making an aquarium persistently muddy with clay, when after a few weeks the plants and snails wilt away. Particles, too, must be objectionable to the gill-breathing operculates. Quite soft natural water is generally clear enough, for it is found in places where there is little or no clay, and it may remain clear even in heavy floods: very hard chalk streams are also brilliantly clear because the clay is precipitated. Cloudiness is generally seen in moderately hard water and where the particular clay is resistant to agglutination. Different clays vary widely in this respect (**7**) and I have analysed a permanently very muddy pond at calcium 55. (*c*) A good supply of soluble salts, of which calcium itself may not be the most important, is desirable for the growth of most water plants, and the vegetation of hard water is always richer than of a corresponding habitat with soft water (**195**, **229**). West (in **282**) says that "peaty" water inhibits the natural decay of vegetable debris and that in it the plants are remarkably free from epiphytic organisms. (*d*) Calcium in river water also helps estuarine animals to bear the alternations between fresh and salt water (**206**).

(*c*) *Reaction*

It would be unconventional beyond the bounds of propriety to make no mention of hydrogen-ion concentration. Broadly speaking, for the natural waters of this country the reactions run parallel with the quantities of calcium, and *p*H determinations have the advantage over calcium measurements that they can easily be done at once on the spot, whereas calcium estimations need laboratory facilities or an amiable collaborator. A bottle of the "universal indicator" of British Drug Houses is indeed as useful in the field as one of acid for soil testing, but though it is a good servant it is, I think, a bad master, and I have been dissatisfied and rather bewildered by the results I have obtained. Frankly acid peaty water of *p*H 6 or less contains no snails as Carpenter (**153**) points out, and *Limnaea peregra* soon dies in water of 5·6; I have not come across any such water except in peat, and it should be noted that water stained brown from peat is not necessarily acid; it may have a *p*H of 7–7·5 (**229**), hence "peaty water" can be ambiguous. Ordinary soft mountain water is commonly about 6·5–7 and contains some Mollusca, though the calcium may be less than 1, and as the alkalinity increases we find more and more snails till we reach the highest figure of about 8·5 found in this country in which the calcium will normally be of the order of 60 or more and Mollusca abundant. It is the difficulty of being precise between 6·5 and 8·5 which is disappointing: this is due to the preponderating influence of the CO_2. Is one to take the *p*H of the water as it stands or after bringing it into equilibrium with air as Atkins (**233**) and others have done? Many acid waters become alkaline when they are so treated, and the change is much more in some waters than in others. Thus a hard-water spring with calcium 134 may at its source be colorimetrically identical with a softish river (calcium 17) into which it falls, and Saunders (**202**) found that spring water of *p*H 7·2 soon rose to 8·2–8·5 as it flowed along and might reach 9 with much vegetation and sunshine. The effect of green plants and illumination is indeed disconcerting if one wants to attach a particular figure to a particular water. The late F. M. Turner showed me that a jar with *Elodea* may start at 6·5 in the morning and be alkaline to phenolphthalein before the end of a sunny day—a hundredfold decrease in hydrogen ions: corresponding changes occur in tanks and ponds (**200**), and different parts of the same pond may give different results: the diurnal change is perceptible even in rapid rivers (**154**) where the proportion of plants to water is quite small. Atkins and Harris (**169**) record variations from 7·6 to 9·3 and 6·0 to 8·0 in the same habitat at different seasons, and Welch (**278**) gives other examples in his interesting book on the conditions of life in fresh waters which has appeared too recently for me to refer to it as fully as it deserves. It is then hard to see how the *p*H of any water is to be specified, and it is impossible to make a scale relating it to the calcium content which seems to be the more important factor. If a definitive stable constant is wanted for any water the only thing to do seems to be to take its *p*H in equilibrium with air which may fail to express the actual existing conditions. The method therefore has considerable limitations, though no one would of course dispute its usefulness in quickly distinguishing acid and alkaline water in the field.

The oscillations in reaction which have been mentioned should theoretically be accompanied by changes in the calcium content in the sense that as the water becomes more alkaline from loss of CO_2 calcium carbonate should be precipitated. I do not know whether this has actually been quantitatively verified in nature, but the decalcifying effect of vegetation and sunlight would in effect make little difference to the snails for whom the calcium would still be available on the floor or, more conveniently, on the leaves of the plants mixed with the epiphytic Algae of which they are so fond.

The hardness in its turn does not remain constant, but the variations are proportionately much less than those of the *p*H. Thus in weekly trials over a year the Thames at Pangbourne varied from calcium 88 to 113, the Kennet from 82 to 108 and the Enborne, a much smaller stream, from 45 (in a flood) to 95 (**252**), and 134 samples in 12 months from the same point in the Thames varied from 68 to 140 (**148**). Butcher (**235**) found the R. Wharfe between 32 and 48 at monthly examinations over 2 years, and I have had figures from 15 to 33 for the R. Wye at Hereford, depending on what proportion of the water is coming from the Welsh moors.

Gammarus pulex is a familiar indicator of loci which are good for snails: Atkins (**212**) says that it dies in water less alkaline than 7·4, and though it often occurs in soft water it is much more abundant in hard.

(*d*) *Size and volume*

The larger units of water are liable to contain the more Mollusca if only because the chances of importation have been greater and they contain a greater variety of subhabitats—a consideration which applies particularly to *Pisidium*. There are, too, a number of species, mostly big ones, which show a great preference for and are almost restricted to what may be called large loci, i.e. good-sized rivers, canals, large draining ditches, lakes and large ponds (by which I mean ponds of about ¼ acre area and upwards, the depth being perhaps as important as the area). Among these are:

Limnaea auricularia	*Unio pictorum*	*Anodonta anatina*
Bithinia leachii	*U. tumidus*	*Pseudanodonta* sp.
Paludina contecta	*U. margaritifer*	*Sphaerium rivicola*
P. vivipara	*Anodonta cygnea*	*Pisidium supinum*
Neritina fluviatilis		

For the large mussels the explanation may be that the fish on which they are dependent need roomy places; for *Paludina* that they want deep water into which they may retire for the winter (**22**). Other species:

Limnaea stagnalis	*Planorbis complanatus*	*Bithinia tentaculata*
Planorbis corneus	*Pl. carinatus*	

show the same habit but less markedly, and all of them are found from time to time in small (e.g. surface 200 sq. yd.) ponds or (*Bithinia*) in small streams.

The failure of a number of these species to reach the upper, smaller parts of the rivers in which they live may be due to this size question or to the generally more rapid currents, but whatever the explanation the rich fauna of a river such as the Thames fades away progressively as one goes up its branches without there being any very conspicuous change in the obvious physical characters. Montagu (**35**, p. 387) notices the phenomenon for *Paludina* in the Kennet, Kendall, Dean and Rankin (**155**, p. 359) for *Neritina* in Lonsdale, French (**156**) for the same and "other species" in Essex. It is true for *Paludina* and *Neritina* in the Hertfordshire Colne, in the Lea and the upper branches of the Thames; for *Bithinia tentaculata* in the Herefordshire Wye. No species, except perhaps *Limnaea glabra* and *Pisidium personatum*, show any disinclination to live in large habitats as such, and we have none in this country which are particularly attached to springs and small streams as, for example, *Bythinella* is in Europe.

In lakes and large rivers of normal contours and in large deep ponds such as clay pits, the area occupied by molluscs is only a small part of the whole, and the proportion of animals and plants to water is much less than in a shallow pond. In the depths there may be some *Pisidium* though we know little of the Mollusca which live in water more than 6 or 8 ft. deep: *Anodonta* and *Unio* commonly live in shallower water, and when the emptying of a pool or lake allows a comprehensive view they are limited to a defined depth zone of 2–4 ft. (**28**, p. 96; **157**), though in a reservoir with steep sides they may have to live in 15–20 ft. *Sphaerium*, most *Pisidium* and the gastropods all live their active lives in quite shallow water—an inch to 2 ft. or thereabouts—and so occupy only a narrow zone[1] round the edge of a large locus where most of the plants also grow. If there are plants such as *Potamogeton lucens* or water-lilies which root in deeper water, some of the pulmonates may be found among them, but beyond the greatest plant depth (which is largely determined by the transparency of the water (**136**, **158**)) there will be none. The effective occupied volume is therefore in contact with a larger, often much larger, volume of what may be called "free" water, and this is of some importance in promoting cleanness and diluting the products of activity and decay. Large loci of good depth are in this way equivalent to running water to which all the 13 species in the list on p. 163 are addicted: *Gammarus* has analogous habits, occurring as it does in lakes, *large* ponds and running water and not in the small ponds where *Asellus* flourishes.

Lists for several large lakes have been already given (pp. 151, 156) and the best follows (p. 172). The largest I know for closed ponds are both from Cheshire. Milne and Oldham (**84**) record

Limnaea peregra	*Planorbis albus*	*Anodonta anatina*
L. auricularia	*Pl. vortex*	*Sphaerium corneum*
L. stagnalis	*Paludina contecta*	*Sph. lacustre*
Planorbis corneus	*Bithinia tentaculata*	*Pisidium* spp.
Pl. complanatus	*Anodonta cygnea*	

the *L. stagnalis* and *P. contecta* having been introduced. Britten and Williams (**85**) found in about a third of an acre:

Limnaea peregra	*Planorbis vortex*	*Anodonta cygnea*
L. palustris	*Physa fontinalis*	*Sphaerium corneum*
Planorbis albus	*Bithinia tentaculata*	*Pisidium* spp.
Pl. nautileus	*Valvata cristata*	

These closed ponds are large enough to carry some species (*Limnaea auricularia*, *Planorbis vortex*, *Physa fontinalis*, *Bithinia tentaculata*, *Anodonta*) commonly associated with running water, and in comparison I give the list, for which I am indebted to Dr J. W. Jackson, of a larger habitat of a peculiar local type in the same neighbourhood with a stream running through it—Rostherne Mere, 118 acres, calcium 27 (**279**):

Ancylus fluviatilis	*Paludestrina jenkinsi*	*Pisidium henslowanum*
A. lacustris	*Bithinia tentaculata*	*P. hibernicum*
Limnaea peregra	*Valvata piscinalis*	*P. milium*
L. auricularia	*V. cristata*	*P. nitidum*
Planorbis carinatus	*Anodonta cygnea*	*P. obtusale*
Pl. albus	*Sphaerium corneum*	*P. personatum*
Pl. vortex	*Sph. lacustre*	*P. pulchellum*
Pl. contortus	*Pisidium cinereum*	*P. subtruncatum*
Pl. fontanus		

[1] The importance of this marginal zone is predominant. Ponds with vertical sides make poor habitats as do many reservoirs. In streams and reservoirs in which the water level fluctuates violently this zone is disturbed and disorganised and snails thoroughly dislike such places. Fresh rain water also seems to be disagreeable and few Mollusca can be found in loci flooded up with it, perhaps because it contains too little trihydrol (**210**); if so, water from melting snow or ice ought to be favourable.

At the other end of the scale, we know that quite small loci may contain many snails though their average content is small (above, p. 127). Among the Aldenham closed cattle ponds we have one which at its fullest (seldom reached) measures 17 × 9 yd. with about 3 ft. of water at the deepest which contains

Ancylus lacustris	*Planorbis fontanus*	*Pisidium milium*
Limnaea peregra	*Sphaerium corneum*	*P. personatum*
Planorbis nautileus	*Sph. lacustre*	

and another 9 yd. across with about 18 in. of water with

Limnaea stagnalis	*Planorbis nautileus*	*Sphaerium lacustre*
Planorbis complanatus	*Pl. fontanus*	*Pisidium milium*

To both of these *Planorbis corneus* was added without any deterioration of the existing faunas which have remained constant for about 18 years. Other species which can be comfortable in these restricted loci are

Limnaea palustris	*Planorbis contortus*	*Pisidium obtusale*
Planorbis albus	*Pisidium cinereum*	*P. subtruncatum*
Pl. vortex	*P. nitidum*	

making some 18 species for which such places are adequate. Loci of standing water which are smaller than this are commonly not permanent and dry up in the summer: here we have (above, p. 128):

Limnaea peregra	*Planorbis spirorbis*	*Pisidium cinereum*
L. palustris	*Pl. nautileus*	*P. obtusale*
L. glabra	*Physa hypnorum*	*P. personatum*

The tiniest loci are necessarily running water and are provided by springs and trickles with miniature rapids and pools and with perhaps nowhere more than a couple of inches of water. *Pisidium cinereum* and *P. personatum* are the commonest inhabitants and in some places frequent: *Limnaea peregra*, *L. palustris* and *Paludestrina jenkinsi* can also survive, and also *Ancylus fluviatilis*.

(e) *Still and running water*

About two-thirds of our species evidently prefer and are generally found in water which is more or less running, but, as far as I can see, none is inseparably attached to running water *per se*. The most familiar species which one associates with quick streams and rivers are *Unio margaritifer* and the limpet *Ancylus fluviatilis*, and the latter is plainly adapted to live in currents. But the pressure of running water is unnecessary, for both of them flourish in clean river lakes in which the current is hardly perceptible. What they both need is clean water free from silt and mud, and this is usually attained by a rapid flow; if, however, it is achieved otherwise, a flow can be dispensed with. The same principle lies behind the general superiority of gently running over quite stagnant water: slow rivers, canals and marsh drains are among our richest habitats, and a cattle pond with a trickle of water through it shows more species than a similar closed pond—in the Aldenham series an average of 9 against one of 3·7, the best (21 × 15 yd.) giving 13:

Ancylus lacustris	*Planorbis vortex*	*Pisidium milium*
Limneae peregra	*Pl. contortus*	*P. obtusale*
L. palustris	*Pl. fontanus*	*P. personatum*
Planorbis albus	*Paludestrina jenkinsi*	*P. subtruncatum*
Pl. nautileus		

Movement mixes up the water and secures better oxygenation, it washes away the debris of plants and the products of their decomposition and prevents the excessive overgrowth of slimy algae (which snails do not like). Some closed ponds form satisfactory self-contained units which go on indefinitely like a balanced aquarium: others are choked with decaying vegetation and the decay may be putrefactive, the water is foul and there are no snails.[1] Long's (**220**) extraordinary record for an engine cistern at Burnley—*Limnaea peregra, Planorbis corneus, Pl. albus, Pl. dilatatus, Pl. fontanus, Bithinia tentaculata, Valvata piscinalis, Sphaerium corneum* and *Sph. lacustre*—must in part at least be due to the constant renewal of the water.

Water which runs too fast is relatively sterile. There is no mud and, it may be, not even sand for plants to root in, and what there is is constantly being disturbed. No Mollusca except the larger bivalves, adult *Dreissena* and *Ancylus* can avoid being swept away by the current and in floods even these will be killed by the moving stones. Hence violent streams generally contain no molluscs and indeed little life of any kind unless there are quiet corners of retreat. All rivers and streams are in fact largely dominated by their current as regards the vegetation (**229**) in which the pulmonates mostly live, and when it dies down in the winter (as much of it does) they lose its protection though in its summer heyday it helps them by keeping the water quieter. Hence pulmonates and especially *Planorbis* are more affected than the operculates and bivalves which live on the bottom, though *Sphaerium* and *Pisidium* are related to the plants as agents for gathering mud and silt. Fox and Simmonds (**293**) show that *Asellus* from running water uses more oxygen than from quiet water, which may have something to do with the poverty of fast streams.

Considering the species individually, there are a certain number which any collector would associate with water which is running fast enough to ripple in shallow places and to stream out the plants:

Ancylus fluviatilis	*Paludestrina jenkinsi*	*Unio margaritifer*
Limnaea peregra	*Neritina fluviatilis*	*Pisidium amnicum*
Physa fontinalis		

[1] The flow through closed ponds has no gross cleaning effect. Rain water comes in, and passes out largely by percolation through the sides and floor. Since the average annual rainfall in south England exceeds the loss by evaporation by about 10 in. and the ponds keep somewhere about the same level, the amount passing through is not inconsiderable, but it carries nothing particulate away with it though it tends to prevent the concentration of dissolved substances becoming excessive.

But the list is indeterminate because "running water" is a vague term, and it will be more precise to catalogue those which frequently live in stagnant water such as is found in closed ponds:

Ancylus lacustris	*Planorbis complanatus*	*Pisidium cinereum*
Limnaea peregra	*Pl. spirorbis*	*P. milium*
L. palustris	*Pl. contortus*	*P. nitidum*
L. stagnalis	*Pl. fontanus*	*P. obtusale*
L. glabra	*Physa hypnorum*	*P. personatum*
Planorbis albus	*Sphaerium corneum*	*P. subtruncatum*
Pl. nautileus	*Sph. lacustre*	

and to realise that all the other species prefer and are mostly restricted to water which is in some degree moving. As has been suggested, a slow flow may be imitated by increasing the proportion of unoccupied or "free" water, hence large, deep, stagnant loci may contain running water species. Some deep marl pits near Sissinghurst in Kent used to contain (**242**) *Bithinia tentaculata, B. leachii, Anodonta cygnea* and *Unio pictorum,* and *Bithinia tentaculata* lives in similar pits near Manchester (**84**, **85**). *Limnaea auricularia, Planorbis corneus* and *Paludina vivipara* live well in garden fountains which are flushed and kept clean.

Of the 20 in the stagnant list, all (except possibly *Limnaea glabra, Physa hypnorum, Pisidium personatum* and *P. obtusale* (above, p. 128)) are equally content with gently running water and several of them prefer it. Hence "running" water (which I should interpret as clean oxygenated water) is more favourable than stagnant water so long as it does not run too violently: which corresponds with common experience.

(*f*) *Sunlight and pollution*

In clean running water some Mollusca can live in the dark and have been found in water mains (e.g. **238**), though whether they breed in such situations is less certain. But as Huggins (**159**) and Crowther (**168**) have noted, snails enjoy sunshine and are more active in it both in aquaria and in the field, and their response is so immediate that it must be to the light rather than the warmth. Carnally more important, however, is the indirect effect through the plants, great and small. Adequate light means green plants to oxygenate the water and coating Algae for the snails to eat. Through the oxygenation it also ensures that the decomposition of plant and animal remains, which is a necessary part of the water cycle, shall take a bland course without gross foulness or putrefaction which uses up the oxygen in the water and produces poisonous substances. I do not pretend to understand the detailed differences between aerobic and anaerobic (putrefactive) decomposition, but I know that foul water is generally snailless, that when an aquarium jar "goes wrong" and smells the snails will die although they can get plenty of oxygen at the surface and that ponds with stinking black mud do not generally yield any bivalves though the water above may be clean and fruitful.

In thick muddy water into which sunlight cannot penetrate there is little animal or vegetable life and in consequence little decomposition; it fails as a molluscan habitat in a negative way. The positive harmfulness of poisonous substances is added in densely shaded ponds and streams which have few or no plants and are littered with a trash of twigs and leaves. Leaves are bad, especially perhaps oak leaves, though I have found *Planorbis nautileus* and *Sphaerium lacustre* in ponds floored with them. Woody tissue seems to be worse; I have never found anything in ponds in woods,[1] and field ponds sufficiently shaded with trees or bushes to depress the vegetation are usually poor places. The same result is seen when the water is shaded with a thick growth of reeds (*Typha*, *Phragmites*, *Phalaris* etc.) or, towards the end of the summer only, with a mat of *Lemna*. Sunlight, in short, prevents what may be called natural pollution.

Artificial pollution acts in the same way. Effluents from sewage works, beet factories, metalliferous mines and various industrial processes contain either putrescible material or poisonous substances which kill the plants or animals or both. The devastating effects are familiar to conchologists in the north of England (**160**) and have lately been described in detail for a beet factory (**53**) and for lead and zinc mines in Wales by Carpenter (**161**). The pollution may be only temporary, and sterilised streams are repopulated from uncontaminated branches. A small amount of organic (sewage) contamination may actually increase the Mollusca by encouraging plants and improving the humus, and water snails are strikingly immune to the effects of smoke which is so injurious to land Mollusca (**187**, **223**) as the rich fauna of the Manchester canals shows (below, p. 175).

(*g*) *Temperature*

Generally speaking, our Mollusca are active, grow and breed only in the summer, and within the range of our climate the hotter it is the better. We have no cold rivers fed from permanent snow fields, and the cool upland head streams which have interesting relations with some planarians (**162**, **163**) would have no more Mollusca if they were warm. Nor are we much concerned with large deep lakes such as L. Ness or L. Morar or L. Tay, in which the surface temperature does not rise above 60° F. in the summer or fall below about 42° F. in the winter (Wedderburn in **282**); James Murray and Scott (**283**) remark that they are very poor in Mollusca. The loci in which most of our snails live are so small that their temperatures quickly follow the air temperatures and sunshine and so mean that few data have been collected. Wesenberg-Lund (**282**) emphasises the importance of shallow water and sunshine, and Pearsall (**291**) gives useful data and points out that the water is over 50° F. (10° C.) and over 59° F. (15° C.) for 5 and 2 months respectively in the large Cumberland lakes and for 7 and 5 months in neighbouring ponds.

[1] Mr Oldham tells me that *Pisidium obtusale* sometimes occurs in such places.

The papers of Guppy (**170**) are an illuminating example of what a sensible naturalist can do with a thermometer. He points out, for instance, that what matters to snails and many other small fresh-water animals and to the plants is the temperature in the very shallow weedy water at the edge of the pond or river; most of them live in this zone, and the water readily heats up in sunshine till it is a good deal hotter than the air, and being entangled in vegetation it is not much cooled by mixture. Ponds round Kingston are at the surface 6–12° F. (3–7° C.) warmer than the neighbouring Thames, and the shallow marginal water may reach 80 or 85° F. (27 or 29° C.) on a hot summer afternoon; it has, too, a daily range of as much as 20° F. (11° C.) and the Thames only 1 or 2° F. My own observations, as far as they go, fully bear this out, and a hot sunny day often raises the temperature of the snails' immediate surroundings to 30° C. or thereabouts. In a pond crowded with vegetation there is little mixing and there may be marked stratification, e.g. 65° F.

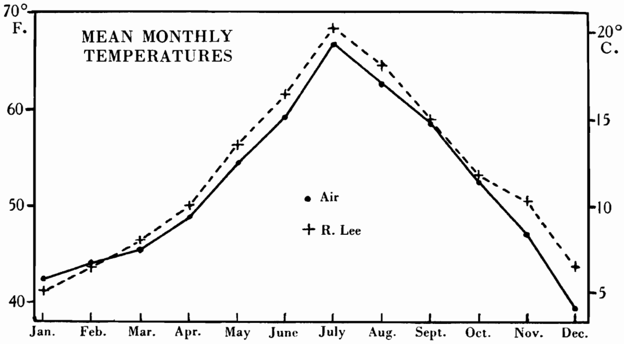


Fig. 62.

(18° C.) at bottom 4 ft. deep, 75° F. (24° C.) at surface and 85° F. (29° C.) at edge. With open water, with wind action and still more with running water the whole is at much the same temperature which tends to be higher the smaller the volume. On the whole the temperatures of lowland waters are rather higher than the corresponding air temperatures, especially during the night.

A continuous temperature of 30° C. is probably more than our species could tolerate: warm greenhouses are certainly bad places for breeding aquaria which do much better out of doors than inside a house: there is indeed experimental evidence (**171**) that brief spells of daily cooling promote the breeding of *Limnaea stagnalis*. In aquarium jars a temperature of 104 or 113° F. (40 or 45° C.) for several hours or repeated on successive days is needed to kill *L. peregra* or *Planorbis nautileus*, the eggs being rather more delicate. Such figures are occasionally reached in hot sunny weather, but the natural habitats never approach this fatal heat.

Correspondingly, cold such as we experience does no perceptible harm[1] except perhaps by killing the susceptible *Elodea*, and like other fresh-water animals snails can be frozen into ice for a good time without being killed (**172**). There is no resting phase: the animals mostly pass the winter about half-grown, never as eggs. They hibernate in the mud or deeper water and are difficult to find, though a hardy species such as *Limnaea peregra* or *Planorbis corneus* may sometimes be seen crawling about under ice and I have noticed *Pl. spirorbis* quite active in water at 1° C. In mild spells in the winter *Limnaea peregra* can make considerable growth

It is natural to suppose that the cooler climate is responsible for the failure of so many southern species to live in the northern two-thirds of Scotland, but it is difficult to be sure about it. The soft-water districts in Cornwall, west Wales and the Lake District are not much richer in species for all their blander climates, and some of the southern species (e.g. *Limnaea stagnalis, Planorbis corneus, Bithinia tentaculata*) in Scandinavia and Siberia live through far more severe winters than we have anywhere, though a hot summer is perhaps more important than a relatively warm winter. From their altitudes, Malham Tarn (p. 157) and Bwch Llyn (p. 155) should be climatically equivalent to Orkney and Fort William. Hence one might not unreasonably suppose that a suitably calcareous lake in the north of Scotland would have a rich fauna just as the maritime calcicoles on land (e.g. *Helix itala, H. barbara*) spread right up the west coast to Cape Wrath. We now know, however, that this is not so (above, p. 159), and rejecting the chemical and suspecting the climatic explanation we may contemplate the possibility that the southern species have, with few exceptions, not yet had time and opportunity to get so far. The nearness of suitable habitats to one another is an important factor in the dispersal of water snails, and for a species needing calcareous water the journey through Scotland is difficult, for such places are few and far between.

(*h*) *Vegetation*

Most of the germane points about plants have been incidentally mentioned already. We may note also these:

(1) While a good supply of submerged vegetation is in every way favourable, too thick a growth is harmful. This is best seen with *Elodea*, and a pond overfull, or, as one says, "choked" with it, will not produce many snails, or if it has several species none of them will be abundant. The same is true of aquaria which may easily have too much weed. The injurious effect of the filamentous Algae known as "blanket" or "flannel" weed (**209**) may be analogous. Both impede free movement, and the Algae often attach themselves to the apex of the shells with the result that the snails are "absalomed".

(2) A free growth of plants is an important factor in providing the humus

[1] The altogether exceptional winter of 1933–4 in which the ponds were frozen when they were more or less empty seems to have had a devastating effect on the plants and snails.

which helps so much to make the bottom of a field pond watertight and the locus permanent and offers a safe refuge for the Mollusca if the place goes dry in an exceptional summer: drying does no damage so long as the bottom is soft and pulpy even if it is not perceptibly damp (**9**); ponds which dry every year have no chance to grow plants and accumulate humus, they dry hard and the results are disastrous to any but the few species which can tolerate the conditions (above, p. 128). On the other hand emergent marginal plants (*Alisma*, *Sparganium*, etc.) collect earth and mud at their roots and largely help in converting water into dry land, first at the edge and then by their progressive invasion over the whole, so that in the end the locus is destroyed.

(3) These emergent plants are also effective in drying up small loci, and their transpiration puts the finishing touch to the effects of a hot dry summer. Ponds without these hold water longer under severe conditions, and in the summer of 1934 a cement tank in my garden with three good clumps of *Alisma plantago* lost 19 in. of water, while a precisely similar tank 6 ft. away with *Potamogeton crispus* and *Lemna* lost only 5 in. The roots of plants are also said to perforate the puddle of dew ponds and make them leak (Shrubsole).

5. THE MOLLUSCA OF DIFFERENT HABITATS

Apart from a few rare species of quite limited distribution (*Planorbis vorticulus*, *Pl. acronicus*, *Valvata macrostoma*, *Amnicola taylori*, *Pisidium conventus*, etc.) we have a certain number with specialised habitats (*Planorbis glaber*, *Limnaea glabra*, *Physa hypnorum*, *Unio margaritifer*, *Sphaerium pallidum*, *Pisidium lilljeborgii*, *P. personatum*), and besides some 40 species of which it might be said with rather vague monotony that they live in "rivers, canals, streams or ponds" or some such combination—at any rate by anyone whose standard of experience was based on collecting in the southern half of England.

Ancylus fluviatilis	A	B	C	D	*Valvata piscinalis*	A	B	C	D
A. lacustris	A	.	C	D	*V. cristata*	A	.	C	D
Limnaea peregra	A	B	C	D	*Paludestrina jenkinsi*	.	B	.	.
L. auricularia	(A)	B	C	D	*Neritina fluviatilis*	A	B	.	D
L. stagnalis	A	B	C	D	*Anodonta cygnea*	.	B	C	D
L. palustris	A	B	C	D	*A. anatina*	.	B	.	.
Planorbis corneus	.	B	C	D	*Unio pictorum*	.	B	.	D
Pl. complanatus	A	B	C	D	*U. tumidus*	.	B	.	D
Pl. carinatus	A	.	.	.	*Sphaerium corneum*	A	B	C	D
Pl. albus	A	B	C	D	*S. lacustre*	.	B	.	.
Pl. nautileus	A	.	.	.	*S. rivicola*	.	B	.	.
Pl. vortex	A	.	C	D	*Pisidium amnicum*	A	B	C	D
Pl. spirorbis	A	.	.	D	*P. cinereum*	A	B	.	D
Pl. contortus	A	.	C	D	*P. henslowanum*	.	B	C	D
Pl. fontanus	A	.	C	D	*P. hibernicum*	A	.	C	.
Physa fontinalis	A	B	C	.	*P. milium*	A	.	C	D
Paludina contecta	.	.	.	D	*P. nitidum*	A	B	C	D
P. vivipara	.	B	.	.	*P. obtusale*	A	.	.	.
Bithinia tentaculata	A	B	C	D	*P. pulchellum*	A	.	C	D
B. leachii	.	B	C	D	*P. subtruncatum*	A	B	C	D

A, Lough Rea; B, Grand Junction Canal; C, R. Colne backwater; D, R. Nene.

As with the land Mollusca, these sorts with generalised habitats may be arranged in a scale, at one end of which are tolerant species which may not infrequently be found by themselves or with few companions and tend to have a wide geographical range, while at the other are exacting species which commonly have a number of others living with them which are equally or less particular and have a more restricted distribution. *Limnaea peregra, Planorbis albus, Pl. contortus, Sphaerium lacustre, Pisidium cinereum* are tolerant species; *Limnaea auricularia, Planorbis corneus, Paludina contecta, Bithinia leachii, Pisidium amnicum* are exacting species; *Limnaea stagnalis, Planorbis complanatus, Bithinia tentaculata, Pisidium subtruncatum* are intermediate. Since the tolerant species have no objection to living in the loci required by the exacting, the goodness or badness of a habitat may be pragmatically measured either by the number of species living there or by their quality: any place with more than 20 kinds or with one or more exacting species may be accepted as being "good".

If the foregoing discussion of the relevant qualities of habitats in any way represents the facts, we should expect to find most sorts and more of the "choosey" species in a good-sized locus, in parts too deep for the growth of plants, but with adequate vegetation at the gently shelving edges, well exposed to sunlight, in the south-east of England and charged with slowly flowing, clear, calcareous water. Such a habitat, and many of its subvarieties, is provided by the R. Thames, and no doubt in the main river and its various branches and diverticula at, for example, Oxford all the 40 species in the list on p. 171 can be found, and in addition *Planorbis acronicus, Pseudanodonta, Pisidium torquatum, P. personatum, P. supinum* and *P. tenuilineatum*—in all about 45. Another very rich locus is the calcareous L. Rea in the Galway limestone described by R. A. Phillips (**193**) who has been good enough to give me the detailed list of 30 species: 27 of them are marked A on p. 171, and there are in addition *Planorbis glaber, Pisidium lilljeborgii* and *P. personatum*; *Limnaea auricularia* occurs in a small communicating lake and *Physa hypnorum* in drains entering the lake. Considering that *Paludina, Unio pictorum, U. tumidus* and *Sphaerium rivicola* do not occur in Ireland, this is a remarkable list and only *Paludestrina jenkinsi, Anodonta cygnea* and *Pisidium henslowanum* are absent of those which might reasonably be looked for. It should be compared with the list of 17 species for L. Leane (above, p. 151), 85 miles away, which is equally favourable in its position and configuration, but contains soft water instead of hard. Oldham's list for the Grand Junction (now the Grand Union) Canal at Berkhamsted includes 27 sorts marked B on p. 171, and also *Dreissena, Pisidium torquatum* and *P. supinum*, while *Pseudanodonta, Sphaerium pallidum, Pisidium hibernicum, P. milium* and *P. tenuilineatum* live in the canal not far off, i.e. about 34 species. As a fourth example of a rich habitat we may take a quiet backwater of the R. Colne with 26 species marked C. Llangorse Lake (p. 156) and Rostherne Mere (p. 164) also contain as many as 25 kinds.

As a habitat fails to have the combination of good qualities which results in such prolific yields, so its content in snails diminishes. If the water is quite soft, we expect at the best less than 20 species (above, p. 151) and the exacting ones disappear. If the water is stagnant, 10 is a good number; if it is shaded 5 or less, and so on until we come down to the poorest places with nothing but *Pisidium cinereum* or some other tolerant species. Examples of these have been already given.

(*a*) *Rivers*

Rivers such as the Thames which are calcareous, naturally quiet and have in many instances been canalised and tamed, are fruitful enough, and most slow south-eastern rivers will yield pretty well: Kendall (**230**) gives a list of 32 kinds for the R. Nene in Northampton marked D on p. 171, with the addition of *Dreissena* and *Pisidium supinum*. But as a class they are not very good habitats: a calcareous river such as the R. Tees in the neighbourhood of Barnard Castle (calcium 32) may be too swift for anything nobler than *Limnaea peregra* and *Ancylus fluviatilis*, and many soft-water rivers in the north and west contain even less. The chief difficulties seem to be that the current is too fast, the quiet places too deep, and the shallow places too rapid, the banks go straight down without shelving and the whole is liable to be periodically scoured out with floods. These are the defects of the Herefordshire Wye which, with water just on the "hard" limit (calcium 23), contains only some 19 species with a striking deficiency in pulmonates:

Ancylus fluviatilis	*Unio pictorum*	*Pisidium henslowanum*
Limnaea peregra	*U. tumidus*	*P. nitidum*
Bithinia tentaculata	*U. margaritifer*	*P. pulchellum*
Valvata piscinalis	*Sphaerium corneum*	*P. subtruncatum*
Paludestrina jenkinsi	*Pisidium amnicum*	*P. supinum*
Neritina fluviatilis	*P. cinereum*	*P. torquatum*
Anodonta anatina		

Streams and brooks are also poor places unless they flow through ponds or have quiet bays in which plants can grow and Mollusca do something else than hang on in the current. In the absence of plants, *Planorbis* sometimes gets protection under stones as *Bithinia tentaculata* may do.

(*b*) *Canals*

Canals luckily reproduce the qualities of the best rivers, and are of such interest that they deserve fuller notice. Apart from a few ancient waterways such as the Foss Dyke in Lincolnshire, which was made by the Romans, and the Exeter ship canal, which is Elizabethan, the first modern canal was built by Francis Egerton, third duke of Bridgwater (1736–1803), who is commemorated by the monument erected in 1832 to "the father of inland navigation", which looks out from the chalk escarpment at Ashridge over the reservoirs of the Grand Junction Canal which joins the Thames to the central plain of England. Disappointed in a matrimonial enterprise in London, he retired to his estates in Lancashire, and with the aid of Brindley the canal from Worsley to Manchester to carry coal from his pits was opened in 1761.

The Manchester to Liverpool canal followed and gave such a demonstration of the commercial possibilities of this new form of transport that canals were projected and executed with great enthusiasm all over the country, ultimately, with the canalised rivers, reaching a length of about 3800 miles (about 18 times the length of the Thames). Most of them were made before 1800 after which progress became slower and finally the boom died out as good roads and railways developed: practically nothing fresh has been done since about 1830. Much information and some excellent maps will be found in the reports of the Canal Commission of 1909. The "lodes", "levels" and draining ditches of the fens in Cambridge, Norfolk and Lincoln and the Somerset "rhines" were made for another purpose and date from various periods, chiefly the seventeenth century: conchologically they are equivalent to canals detached from the main system.

Canals are important to us because they have joined up all the river basins of central England and have provided a particularly favourable type of habitat. They communicate in one way or another with most of the rivers with which they come in contact, and about the middle of last century a snail could start in the Thames at London and travel in uninterrupted water to Norfolk or Leeds or Kendal or Newtown in Montgomery or Hereford or Trowbridge, or by slipping into the upper waters of the Avon in the vale of Pusey even to Christchurch or Southampton: the area open to it, which may conveniently be called the "canal basin", is roughly shown in Fig. 63, where it is if anything too small. These facilities have since to some extent deteriorated: the Gloucester and Hereford canal was drained and abandoned just when I began to collect shells, and I have a vivid recollection of its wealth, for it was by far the richest locus in the county; the Tenbury and Leominster canal was then only a grassy groove; the Wilts and Berks canal has long been derelict and a more important link, the Thames and Severn canal, has now been abandoned in its upper parts though the two rivers are still in communication via Oxford and the midlands. But the main system still survives in continuity and will presumably continue even if out of use so long as it needs no trouble to keep it full of water. In Scotland canals have done little to upset the natural arrangements, but in Ireland the Grand and Royal canals have united the main river basins and joined Belfast and L. Neagh with the R. Erne, the R. Shannon, Dublin and the R. Barrow in the south.

The Canal Basin

Fig. 63.

As habitats canals are better than they often look. If they are in active use the water is probably turbid, water weeds are abundant only in quiet recesses, there may be oil and scum on the surface and the bottom may be stony or even largely composed of cinders. But they are always worth examination, and it is surprising how abundant Mollusca may be in places which have a thoroughly dirty and unprepossessing appearance. This is due to their having a good volume of water with a steady slow and never violent flow; the water-level remains almost constant and there are no floods. The rate of flow varies with the differences of level, the number of locks and the frequency with which they are used: the Grand Junction Canal falls 420 ft. in 40 miles from Tring to Brentford and about half as much in the opposite direction, whereas the R. Thames falls 315 ft. in 158 miles from Ewen to London and the R. Severn 180 ft. in 90 miles from Shrewsbury to Gloucester. Locks, leaking or working, do a good deal to aerate the water: those at Tring, which are fairly busy, use about 3 million gallons a day or about 1/400 of the flow of the Thames and 1/6 of that of the R. Lark. Jackson (**186**) points out that the Polyzoa, *Plumatella* and *Fredericella*, and the sponge, *Ephydatia fluviatilis*, which are sensitive indicators of adequate oxygenation, are abundant in the foul-looking Manchester canals. The rush of water and the recesses by locks also provide good patches of mud and silt for bivalves. The southern and midland canals all contain hard water: it may be soft in some places in the north. Hot engine water is sometimes discharged into them which the Mollusca seem to like, but we have no species for which it is necessary.

Hence canals as a class are the richest habitats we have. Lists of more than 30 species from the Grand Junction and Shropshire Union canals have been already given (above, pp. 171, 160), and conditions evidently favour bivalves, operculates and pulmonates alike. The difference is, however, chiefly seen in the larger bivalves and operculates for which many districts provide few suitable natural habitats. Thus Davies (**187**) in a thorough survey of the smoke-begrimed built-up district round Eccles to the west of Manchester found 27 species in the two canals, 22 of them in the historic Bridgewater canal:

Limnaea peregra	*Physa fontinalis*	*Sphaerium corneum*
**L. auricularia*	**Ph. acuta*	*Sph. lacustre*
L. stagnalis	**Bithinia tentaculata*	**Sph. pallidum*
L. palustris	**Valvata piscinalis*	**Pisidium amnicum*
Planorbis carinatus	*Paludestrina jenkinsi*	*P. cinereum*
Pl. albus	**Anodonta cygnea*	*P. henslowanum*
**Pl. dilatatus*	**Unio tumidus*	*P. milium*
Pl. vortex	**Dreissena polymorpha*	*P. nitidum*
Pl. fontanus	**Sphaerium rivicola*	*P. subtruncatum*

The 11 species marked * occurred only in the canals and in none of the numerous ("upwards of a hundred") ponds and ditches in the neighbourhood which in their turn showed 9 species (*Limnaea glabra*, *Planorbis corneus*, *Pl. complanatus*, *Pl. nautileus*, *Pl. spirorbis*, *Pl. contortus*, *Physa hypnorum*, *Pisidium obtusale* and *P. personatum*) which were not found in the canals.[1]

[1] These data also illustrate the relative immunity of water snails to smoke: the same district had only 20 sorts of land Mollusca with nothing more fastidious than *Helix hispida*.

Similarly, Alkins (**50**) says that 8 of the 30 species found in his district in north Staffs. occur only in the canal (*Ancylus lacustris, Limnaea auricularia, Planorbis corneus, Physa fontinalis, Paludina vivipara, Valvata piscinalis, Sphaerium rivicola* and *Pisidium amnicum*). Ellis (**280**) lists 25 species *plus Pisidium* from Leicestershire, and Hargreaves and Firth (**189**) give another typical collection from the Wakefield canal:

Limnaea peregra	*Physa fontinalis*	*Pseudanodonta* sp.
L. stagnalis	*Bithinia tentaculata*	*Unio pictorum*
L. palustris	*Valvata piscinalis*	*U. tumidus*
Planorbis corneus	*Neritina fluviatilis*	*Sphaerium corneum*
Pl. complanatus	*Anodonta cygnea*	*Sph. rivicola*
Pl. vortex	*A. anatina*	*Pisidium amnicum*

Taking the whole British list there are, I think, only 6 species which have not been recorded for canals (*Limnaea glabra, Pisidium conventus, Planorbis glaber, Pl. vorticulus, Segmentina nitida* and *Valvata macrostoma*), and it is about equally true that these have not been found in rivers either while the last 4 occur in, and the last 3 are characteristic of, large draining ditches which are equivalent in nature and origin to canals. Even *Unio margaritifer* is recorded by Jeffreys (**141**, p. 38) from the Swansea canal, and *Pisidium lilljeborgii* by Oldham and Stelfox in the Shropshire Union canal near Llangollen.

That one of the essential virtues of canals is the flow of water is shown by the poor fauna of the stagnant remains of abandoned undertakings which may be so choked with vegetation and the products of its decomposition that they are less productive than good ponds: Bowell (**211**) noted the same in the Grand Western Canal in Devon.

How far the continuity of this canal-river system has enabled Mollusca to spread through England is impossible to say, for the canals anticipated any accurate knowledge of distribution: da Costa (**190**) in 1778 naturally makes no mention of them, and his field work is poor and many of his localities dubious; Montagu (**35**) in 1803 mentions "the canal intended to make a junction of the Kennet and Avon" only as the place where he found "*Helix fragilis*", though his path from Lackham House to the wood where he first found *Ena montana* crossed the route of the Wilts and Berks canal as well as the R. Avon in which he found many species: both canals were put in hand about 1795, and in 1799 Montagu had gone to Kingsbridge. Turton (**191**) in 1831 mentions them several times, but in no significant connection. But it seems very likely that they have helped *Sphaerium pallidum* and *Dreissena* to spread from the metropolitan area, as the operculate *Lithoglyphus naticoides* has passed from the Danube via Ludwig's canal to Holland and France (**77**, p. 656). The distribution of a number of species (Figs. 40–42, 44–48) which are fond of canals is also curiously similar to the canal basin (Fig. 63):

Bithinia leachii	*Unio pictorum*	*Sphaerium rivicola*
Paludina vivipara	*U. tumidus*	*Sph. pallidum*
P. contecta	*Dreissena polymorpha*	

In Ireland *Bithinia leachii* is almost restricted to the Grand and Royal Canals and the communicating R. Barrow (**62**, **192**, **193**).

It is, too, evident that on a smaller scale continuity and suitability have extended several species beyond their natural range, and it seems certain that it is along the Shropshire Union Canal that *Limnaea auricularia*, *Planorbis corneus* and *Bithinia leachii* have reached Denbigh and *Planorbis corneus*, *Paludina vivipara*, *Unio pictorum*, *U. tumidus*, *Dreissena* and *Sphaerium pallidum* have spread to Montgomery, which in its natural state contains no appropriate habitats. Similarly the old canal was responsible for *Limnaea auricularia*, *Paludina vivipara*, *Dreissena* and possibly *Limnaea stagnalis* in Herefordshire.

Detached canals which communicate only with local rivers and the sea give various results, but they also illustrate the importance of a good habitat. The Tiverton Canal is overgrown and stagnant and it contains nothing of note except *Limnaea auricularia* (F. F. Laidlaw). The remnants of the Bude canal yielded *Anodonta anatina* and *Pisidium torquatum* as well as ordinary species. The Newport and Brecon Canal has *Paludina vivipara*, which might, I suppose, have somehow survived a sea passage on a barge from Gloucester, and so have the Cardiff and Exeter (**144**) Canals, so that the five most westerly occurrences of that species are in canals with which Tate (**247**, p. 55) thinks it is particularly associated. The Exeter Canal and the canalised R. Exe have also *Limnaea auricularia*, *Planorbis corneus*, *Dreissena* and *Sphaerium rivicola*, and how these characteristic canal species got so far west of their nearest habitats is unknown; the canal is accessible only to ocean-going shipping, and the projected conjunction of the Exe with the Somerset rivers *via* the Grand Western Canal was never completed: somehow or other the appropriate Mollusca seem in the end to reach suitable habitats, and in this instance they have had 350 years to do it in. The eastern end of the Forth and Clyde Canal has provided the only Scotch loci for *Bithinia leachii* and *Amnicola taylori* (**101**). *Limnaea stagnalis* was first found in Glamorgan in the Cardiff Canal in 1915, since when it has spread freely in the neighbourhood (J. D. Dean).

(*c*) *Lakes*

Most natural *lakes* are relatively unproductive because they belong to the type which has come to be called "mountain" (or "highland"): their essential quality is not, however, that they lie at high altitudes, for they are found in barren soils at sea-level, but that, as Tansley (**195**) points out in discussing the vegetation, they contain soft water. Altitude increases their austerity because, apart from climate, the lakes nearer the summits have the softer water which is indeed in some instances not far from distilled water. In extreme cases there is no phanerogamic vegetation and no macroscopic life: with rather more dissolved salts a sparse vegetation appears with characteristic plants such as *Lobelia dortmanna*, *Isoetes* and *Subularia*, and as conditions improve we find perhaps *Littorella*, *Potamogeton natans*, *Myriophyllum* and the small water-lilies. But the total quantity of plants remains very small and the floor is mostly made up of rocks and stones with a few patches of silt and humus in which *Pisidium* live. In such places, with a calcium content of about 5 mg. per litre or less, *Pisidium cinereum*, *P. hibernicum*, *P. lilljeborgii* and *P. nitidum* are fairly common, *P. milium*, *P. obtusale* and *P. subtruncatum* rather less frequent, *Limnaea peregra* and *Ancylus fluviatilis* are not rare on the stones and *Planorbis albus*, *Pl. contortus* and *Sphaerium corneum* occur occasionally. With equal amounts of lime, the fauna is likely to be richer at low altitudes than up in the mountains. As Pearsall (**136**) shows, a complete gradation can be traced from the primitive barren lakes to such places as Windermere or L. Leane (above, p. 151), where with calcium about 10 or rather less there is much more vegetation and humus and a good many Mollusca (*Valvata piscinalis*, *Physa fontinalis*, etc.).

If the water is calcareous, the lake may, as at Malham Tarn, continue to have a bare "highland" appearance with a richer snail fauna, or the whole character of the place may change, as at Bwch Llyn which, while climatically perhaps "highland", is floristically and conchologically a "lowland" lake, and through such habitats as Llangorse Lake (above, p. 156) grades into the lakes and reservoirs which occur in lowland cultivated country, have calcareous water and are mostly good places for Mollusca, though they do not figure much in the literature or our experience because of their scarcity, and because they are so often spoiled by being denatured in various ways such as stocking with ornamental birds or killing the "weeds" with copper sulphate (which is excessively poisonous (**201**) to snails) or by mechanical disturbance (e.g. by boating) which water snails dislike as much as land Mollusca. What such habitats can produce under favourable conditions is shown by L. Rea (above, p. 171), and as an example of a mediocre fauna I give the list for the Elstree Reservoir (59 acres) in Herts which was made about 130 years ago:

Limnaea peregra	*Planorbis nautileus*	*Sphaerium lacustre*
L. auricularia	*Pl. vortex*	*Pisidium cinereum*
L. stagnalis	*Pl. spirorbis*	*P. nitidum*
Planorbis corneus	*Anodonta cygnea*	*P. obtusale*
Pl. complanatus	*Unio pictorum*	*P. subtruncatum*
Pl. albus	*Sphaerium corneum*	

The nomenclature is obviously unsatisfactory because it attempts to describe oecological categories in lay terms: "mountain" and "lowland" might well be replaced by "non-calcareous" (calcium under 10) and "calcareous" (calcium over 20), and the nature of the water can probably in most cases be deduced from the snails and plants (**284**) present.

6. Summary and conclusions

Water Mollusca are not dependent on other animals except that *Anodonta* and *Unio* have an obligatory parasitic phase on fish. Nor have they any specific foods. There are indications that the habitats of a few species are partly determined by competition with other Mollusca, but in general this is unimportant and most of the species which occur in the worst places are found also in the best. Hence each species can live in any place where its characteristic needs are met by the physical and chemical conditions. The more important features of favourable habitats are (1) cleanliness of water, (2) absence of disturbance, and (3) presence of lime: other factors such as rate of flow, volume of locus, vegetation, etc., are of moment because of their influence on the first two. Bivalves, operculates and pulmonates can each be divided into a group which can live in soft as well as hard water and one which ordinarily needs a fair amount of lime: also into those which can tolerate stagnant water (which include no operculates) and those which need clean and usually running water. With a few exceptions, the needs of the species are so similar that habitats can be classed as good or bad for Mollusca as a whole: the richest places are calcareous rivers, lakes and canals, the poorest rapid streams, mean ponds and mountain lakes.

This paper has, I hope, asked more questions than it has answered. The descriptive phase of the study of the habitats of Mollusca is far from complete, but it has reached the point where it suggests explanations and general principles which are open to analysis, and, though there is still room for collecting at large, field work is likely to be more fruitful if it is planned to throw light on definite problems and guided by some theory. It may centre round the study of particular habitats or of particular species, and since the Mollusca have so little direct relation to one another or to other animals it will mostly be concerned with the investigation of the environment, and ideas which arise in the field may in many instances be tested by experiments in aquaria and by well-considered transplantations.

My information about geographical distribution and localities is largely derived from the accumulation of data made with such devotion by W. D. Roebuck for J. W. Taylor's *Monograph* and for his own *Census of Distribution*, maintained since his death by the Conchological Society. The maps are based on the *Census* records with the addition of a few reported occurrences which seemed sufficiently credible, although no actual specimens have been verified by the Society's referees.

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ADDENDA

p. 120. M. J. Longstaff (*J. Conch.* 13: 108) records 17 young in *Sphaerium lacustre*, and N. H. Odhner (*ibid.* 16: 219) 20 in *Pisidium hibernicum* and 16 in *P. obtusale.*

p. 122. An enemy which destroyed most of the snails in a locus each year without discriminating between different kinds might well delay or prevent the establishment of a new species which arrived in small numbers.

p. 128. W. E. Hoyle (*J. Conch.* 9: 109) notes *Limnaea glabra* with *L. stagnalis* and *L. peregra.*

p. 137. It may not be clear that "number of loci" in Table 1 means "number of loci containing *Pisidium* of some kind".

p. 147. *Limnaea peregra* and *Ancylus fluviatilis* occur in Ffynnon Lloer, N. Wales, at 2250 ft. (C. Oldham, *J. Conch.* 13: 353 add 15: 54) and *A. fluviatilis* in Ffynnon Frech at 2250 ft. (plate 4). W. D. Roebuck (*J. Conch.* 7. 367) records *Limnaea auricularia acuta* found by L. W. Hinxman at "1400 to 1600 ft." at Inchrory in Glenavon, Banff, but the locality seems very unlikely and elsewhere the species is essentially lowland.

p. 151. *Sphaerium corneum* occurs in L. Gwernan on Cader Idris (C. Oldham, *J. Conch.* 16: 287) which has calcium 5.

p. 160. S. G. Rich (*Science* 42: 579) describes *Unio complanatus* with a soft flexible shell from waters on granitic gneiss in New England.

p. 176. Without impugning Montagu's accuracy, it must be confessed that his canal "between Chippenham and Laycock" is, in nineteenth century terminology, the Wilts and Berks canal which makes a junction with the Thames at Abingdon.