

PRESIDENTIAL ADDRESS.

THE HOLOCENE NON-MARINE MOLLUSCA OF ENGLAND.

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Delivered 9th February, 1923.

MALACOLOGY, like other sciences, contains within its borders many branches of research. There is the literary side, partly the result of the laws of nomenclature, necessitating a knowledge of books and all that pertains thereto. This, though sometimes derided by superficial critics, does enable one to become acquainted with the literature of the subject, an extremely important factor in all scientific work. Judging by some recent work there is, alas, too often a tendency to consider that all previous work can be safely ignored, a misconception attended by disastrous results. Anatomy, Ecology, Embryology, Genetics, Palæontology, and Systematics all form part of that science which we are banded together to promote, whilst the importance of the mollusca as food, the value of their "gouty" products as gems, and the fact that some species are the intermediate hosts of deadly internal parasites, of Man and domesticated animals, enable us to add Economics as well. For myself the borderland between palæontology and zoology has always been a very attractive sphere, and to-night I would crave the indulgence of the Members and endeavour to place before them the results of recent work on the Holocene Non-marine Mollusca of England. For various reasons into which there is no need to enter, this branch of study is a comparatively recent one, and even the use of the word Holocene with us only dates from 1897 (*Essex Naturalist*, x, July, 1897, p. 92 and table; and *Quart. Journ. Geol. Soc.*, vol. liii, p. 434).¹

With regard to the history of the subject, the earliest reference I can trace is the account of a deposit and its contained mollusca at Mears Ashby in Northamptonshire by the Rev. J. Morton (*Phil.*

¹ Mr. C. Davies Sherborn, however, in January, 1916, drew the attention of Mr. B. B. Woodward and myself to the following quotation, the existence of which had been quite unknown to us: "À ce point de vue, les êtres organisés qui ont remplacé ceux du pliocène et les terrains dans lesquels nous en recueillons les dépouilles, ont été plus justement nommés *Pleistocènes*, ceux aux quels ils ont succédé portant les noms de Pliocènes, Miocènes et Éocènes. On pourrait aussi appeler *Holocènes*, ceux de l'époque historique, ou dont le dépôt n'est pas antérieur à la présence de l'homme; mais, ainsi que nous l'avons dit, il ne paraît pas que l'on doive les séparer des terrains diluviens eux-mêmes ou des premiers dépôts pleistocènes, puisque ceux-ci renferment certaines espèces de Mammifères qui ont évidemment continué à vivre jusqu'ici. Sous ce rapport, les terrains pleistocènes méritent également le nom de terrains holocènes." (Paul Gervais, "Sur la répartition des Mammifères fossiles entre les différents étages tertiaires," etc.: *Mém. Acad. Sci. Montpellier, Sect. des Sci.*, Tom. i [pt. iv, 1850], p. 413.)

Trans., vol. xxv, No. 305, 1706, pp. 2210-14). The investigation was carried out in the true scientific manner by means of a special excavation; the identifications of the shells can be easily checked by the references to Lister, whilst the postulating of a deluge as an explanation of the observed facts is not unknown even to-day.

Later workers have not always maintained the high standard which was thus set, and the illuminating phrase, "a number of snail shells occurred at this level," has been considered quite sufficient to satisfy all the reasonable demands of the student.

A very long period of quiescence then ensued, and it was not until early Victorian times that any additions to our knowledge were made, principally by John Brown, of Stanway, Lyell, Mantell, and S. P. Woodward. Their work, however, was of a sporadic nature, and no real systematic work was accomplished until 1890, when the foundations were laid by B. B. Woodward by the publication of a paper dealing partly with the Holocene mollusca of the London district (*Proc. Geol. Assoc.*, vol. xi, pp. 331-88). The great feature in this paper is the careful checking of previous records, a procedure entailing great labour, but the results amply justified the work, the drudgery of which can only be estimated by those who have worked on similar lines. It is far easier, and more imposing to the uninitiated, to publish long lists of undigested records, many of them dating from the early days of science, the names of the species and the deposits occurring again and again under their various synonyms, but the real value is *nil*.

Inspired by Mr. B. B. Woodward's work, a number of papers have been published by many writers dealing with numerous deposits in many parts of England, whilst archæologists and geologists have begun to realize the importance of these formerly despised objects in helping to solve their problems. Though much still remains to be done, yet sufficient facts have been accumulated to enable us to see that there is a coherent story, though, alas, too often the details are blurred and obscure.

In a civilized area like England human activities have had an enormous effect on the state of the country, and those of us who, like myself, have no personal acquaintance with a virgin country necessarily find it difficult to visualize an England untouched by the hand of man, yet such it was within, geologically speaking, recent times. These human activities have had great influence on the fauna, especially that branch with which we are more interested, an influence sometimes beneficial and sometimes inimical.

The uniting of drainage areas by the canalization of rivers and the construction of canals has enabled the freshwater species to pass barriers which were formerly insurmountable, and has greatly increased the number of suitable habitats for the deeper water forms such as *Dreissensia polymorpha* (Pall.). The making of innumerable ponds and of lakes and reservoirs has also been favourable to many

species, whilst the abnormal conditions often prevailing in these habitats has been reflected in their molluscan inhabitants, and consequently in the list of varietal names. Marshes and fens have been drained, thus reducing the areas suitable for the damp-loving species, whilst the conversion of woodland into pasture and tilth has been of great advantage to some forms and injurious, if not destructive, to others.

Charlton Wood, the original habitat of *Clausilia rolphii*, Gray, was thus destroyed, and as a consequence Dr. Leach noted "no specimens have been taken for several years" (*Synopsis Moll. Gt. Britain*, 1852, p. 86). The construction of numerous stone walls in many parts of the country has provided welcome oases for such species as *Pyramidula rupestris* (Drap.) and *Lauria cylindracea* (Da Cost.). Horticulture, too, has played a considerable part in the dissemination of many of the slugs, as well as such forms as *Helicella draparnaldi* (Beck) and *Opeas pumilum* (Pfr.). The growth of motor traffic and the consequent tarring of the roads has had a very adverse effect on the molluscan fauna of the bordering hedges, ditches, and ponds. The molluscan inhabitants of many ponds in West Kent have thus been quite exterminated. Though hedges are often of modern origin, and thus not a "natural" habitat in the botanical sense, yet in many parts of England, especially in the east and south-east, they are often strips of old woodland left when the land was originally cleared, and have been havens of refuge for the fauna. Building operations, too, have destroyed many recorded localities, and it is useless now to look for *Clausilia biplicata* (Mont.) in Hyde Park, Chelsea meadows, or Fulham meadows; *Fruticicola* (*Zenobiella*) *subrufescens* (Mill.)¹ at Blackheath; *Succinea oblonga*, Drap., and *Pisidium supinum*, A. Schm., in Battersea meadows; whilst H. C. Huggins informs me that the original habitat of *Jacosta* (*Xeroclivia*) *elegans* (Gmel.)¹ at Lydden is now buried by the tip from a neighbouring colliery.

It is thus obvious that it is quite impossible by the most careful collecting to ascertain the true molluscan fauna of any given district, or to say whether a species is a casual, a colonist, a denizen, or a native. To solve these problems one must turn to the Holocene deposits, always remembering the imperfections of the geological record, and the relatively small attention that has been paid to these beds. Some species, too, such as *Zonitoides excavatus* (Ald.) and *Margaritifera margaritifera* (Linn.), from their pronounced calcifuge habits, are not likely to be preserved in a fossil state, whilst the constitution of the shell of *Fruticicola* (*Zenobiella*) *subrufescens* (Mill.) will account for its absence from all deposits.

¹ In view of the fact that the species constituting these two genera are now frequently referred to under the subgeneric or sectional names direct, the latter have been introduced throughout this address.

It is difficult to classify Holocene deposits, but they may be divided into seven groups, viz. :—

1. River deposits.
2. Lacustrine deposits.
3. Swamp deposits.
4. Buried land surfaces.
5. Rain-washes.
6. Cavern deposits.
7. Ancient graves.

Of these, all but the two last may be considered as sealed deposits, though the possibility of disturbance by burrowing animals must always be remembered. River deposits need special consideration for two reasons. They often represent the sweepings of a large area, and the shells may have travelled a considerable distance, whilst there is also the probability that they may contain shells derived from earlier beds. The alluvial beds of the Thames and Lea, the results of the slow intermittent sinking of the land, often contain not only true river deposits but also old land surfaces and swamp deposits, as was plainly seen in the New Albert Docks.

Lacustrine and swamp deposits need no elaboration, the contained mollusca having lived practically where they were entombed. Swamp deposits are frequent in Essex and the Midlands, Copford being perhaps the best known. In this group, too, may be classed the various tufaceous deposits, such as Blaskenwell, in Dorsetshire, and Totland Bay, Isle of Wight.

Old land surfaces are principally found in sand dunes, but many archæological sites such as Grimes Graves, Norfolk, and Cissbury, Sussex, may well be included. In these also the possible margin of error is extremely small, and the evidence derived from their fossils may be relied upon. Rain-washes are very common on the slopes of the chalk-hills, and probably owe their formation to the destruction of the woodland on the ground above them, thus exposing the soil and the already disintegrated subsoil to the action of rain. Their accumulation was thus very rapid, and practically ceased as soon as the vegetation covered the slopes again. Where there is evidence that the slopes have not been disturbed, these rain-washes are absent. Though not relevant to our subject, it may be mentioned that the rain-wash at Otford is situate below the so-called Pilgrims Way, which has been claimed to be a pre-Roman road. Now, when the deposit was accumulated, there must have been an unbroken slope of bare chalk soil, and the road cannot have existed. Since the rain-wash can be definitely dated on archæological evidence as of Roman age, it follows that this part of the road is not as old as enthusiasts would wish us to believe. As a rule, mollusca are common in these deposits, and they furnish interesting evidence as to former conditions.

Cavern deposits are particularly liable to disturbance by

burrowing animals, and great care must be used in dealing with the contained mollusca. Caves, too, are often frequented by birds of prey, and the crops of their victims, killed perhaps miles away, would contain undigested shells and thus add to the confusion. This is the only explanation of the presence of *Sabinea ulvæ* (Penn.) in Chudleigh Cave, and of the same species and *Zonitoides excavatus* (Ald.) at Nanna's Cave, Caldey.

Ancient graves are of great importance as furnishing archæological evidence as to age, but in many instances the smaller burrowing mammals have provided easy means of ingress for hibernating mollusca, whilst the systematic rifling of grave mounds from Roman times to the present has too often completely destroyed all reliable evidence.

Having thus briefly described the characteristics of the varying deposits from which the Holocene mollusca have been obtained, we will now examine the evidence which has been accumulated.

On comparing this with the admirable census recently published as a memorial to the late W. D. Roebuck (*Journ. of Conch.*, vol. xvi, 1921, pp. 165–211), many differences will be noted. A few species are unknown in a fossil state, three fossil forms have not been detected living, some species have greatly extended their range, whilst the area of distribution of others has apparently diminished. In endeavouring to arrive at proper conclusions it is better to ignore the slugs, for the determination of species from their scanty remains, so easily overlooked except by the trained observer, is always very difficult, and in the case of the Arionidæ quite impossible, whilst obvious accidental introductions must be similarly treated.

Excluding these, there are only twenty-eight living species which are unknown from the Pleistocene, and of these nine have never been found fossil at all. These are:—

- Jacosta (Xerophila) neglecta* (Drap.).
- „ *(Xeroclivia) elegans* (Gmel.).
- Fruticicola (Zenobiella) subrufescens* (Mill.).
- „ *(Capillifera) odeca* (Loc.).
- Euparypha pisana* (Müll.).
- Margaritifera margaritifera* (Linn.).
- Pseudanodonta rothomagensis*, Loc.
- Pisidium tenuistriatum*, Stelf.
- „ *steenbuchii* (Möll.).

As already noted, the shell of *Fruticicola (Zenobiella) subrufescens* (Mill.) contains so little lime that it is extremely unlikely to be preserved after death, and this species is the only widely distributed form unknown in a fossil state. From its habits it is improbable also that *Margaritifera margaritifera* (Linn.) would occur in a fossil state, but the periostracum of this species has been detected in the Holocene beds of the Clyde, the shell having completely

vanished (*Trans. Geol. Soc. Glasgow*, 1866, vol. ii, p. 109, and vol. xvi, 1915, p. 108). In Wales, too, an imperfect valve of this species was found in the Perthi Chwaren Cave, near Llandegla, Denbighshire, a sepulchral cave of Neolithic age, and its presence there is clearly due to Neolithic man (J. W. Jackson, *Lanc. Nat.*, 1913, p. 321). This specimen had originally been recorded as *Mya truncata*, Linn. (*Journ. Ethnol. Soc. Lond.*, 1871, p. 443). The remaining seven species are all extremely local forms. Whether they are really native species with a formerly wider distribution, or recent introductions, it is impossible to say, for we are dealing with negative evidence, which is too often a broken reed. In this group, I think, *Eulota fruticum* (Müll.) should also be included, for though it is found in the Pleistocene, yet its restricted modern distribution and its absence from all Holocene beds leads one to infer that it may be only a modern re-introduction. The following species are known from the Holocene, but not from earlier beds:—

- Helicella draparnaldi* (Beck).
- Jacosta (Candidula) gigaxii* (Pfr.).
- Theba cantiana* (Mont.).
- „ *cartusiana* (Müll.).
- Helix pomatia*, Linn.
- Clausilia biplicata* (Mont.).
- „ *dubia*, Drap.
- „ *rolphii*, Gray.
- Limnæa auricularia* (Linn.) (typical form).
- Planorbis stroemii*, West.
- Paludestrina jenkinsi* (Smith).
- Vivipara vivipara* (Linn.).
- Assiminia grayana*, Leach.
- Theodoxus fluviatilis* (Linn.).
- Dreissensia polymorpha* (Pall.).
- Pseudanodonta elongata* (Holl.).
- Pisidium hibernicum*, Westld.

Helicella rogersi (B. B. Woodw.) probably belongs to this assemblage, for the two Pleistocene records, Ightham Fissure, Kent, and Langwith Cave, Derbyshire, are both cavern deposits, and in each case there had been disturbance. It is, of course, possible that it may yet be found in a sealed bed, but the course I have suggested appears to be the correct one. Thus the vast majority of our living species have been resident here for a much longer period than was formerly considered to be the case, and it may be noted that nearly all the presumed post-Pleistocene immigrants are confined in the British Isles to England.

Three species have apparently become extinct during the Holocene period.

Goniodiscus ruderatus (Stud.) is known from the Holocene of Copford, Essex, and Wheatley, Nottinghamshire. It is also known

from the Forest Bed (Cromerian) of West Runton, Norfolk, as well as from a number of Pleistocene deposits, being fairly common at Woodston, Northamptonshire, and Clacton, Essex. It is possible that it may yet be found living, but I think that the story of its occurrence at Grange-over-Sands, Lancashire, probably arises from an error in locality.

Fruticicola (Ponentina) montivaga (Westld.) was found in the deposits at Harlyn Bay, Cornwall, by the Rev. R. Ashington Bullen, the only record for the species in England, and it had apparently been able to maintain itself there for some considerable time. But the possibility that it may be only an extreme form of *Fruticicola (Ponentina) subvirescens* (Bellamy) must be remembered.

Unio auricularius (Spengl.) has been dredged in some quantity from the gravels of the Thames at Barn Elms and Mortlake. The gravels from which these shells have been obtained have recently been claimed to be of Pleistocene age.

G. F. Lawrence, through whose hands passed all the specimens that have been obtained, informed me that polished stone axes also occur in these gravels, but no metal objects, thus proving conclusively that the associated shells are early Holocene and not Pleistocene, a conclusion strongly supported by the other mollusca found with the *Unios* (*Proc. Malac. Soc. Lond.*, Vol. X, 1913, p. 332).

There are eight species of which it can be definitely said that their area of distribution at the present day is much greater than was formerly the case. They are:—

Helicella draparnaldi (Beck).

Jacosta (Cernuella) virgata (Da Cost.).

„ *(Candidula) caperata* (Mont.).

„ „ *gigaxii* (Pfr.).

Theba cantiana (Mont.).

Fruticicola (Capillifera) striolata (C. Pfr.).

Helix aspersa Müll.

Paludestrina jenkinsi (Smith).

Known only from the Holocene of Newquay, Cornwall, and Anstice Cove, near Torquay, Devonshire, *Helicella draparnaldi* (Beck) has now a very wide range, but an examination of the records reveals the fact that many of these are based on occurrences in gardens or even greenhouses, scarcely natural habitats. It is only in the west of England that it occurs away from human habitations, and there alone can it be considered a true native. As already suggested, horticulture has probably been the chief agent in the modern distribution of this form, and it is not improbable that examples of this species were introduced into many parts of England by this means during mediaeval times from the Continent. It is often associated with monastic ruins. This dual origin may account for the slight differences that have been noted in both the animal and the test between the eastern and western forms of this species.

The case of *Jacosta (Cernuella) virgata* (Da Cost.) is an extremely interesting one. At the present day it is very common throughout the whole of England, and one would naturally infer that it is a true native, but the geological evidence tells a very different story. Common in the early Holocene beds of Cornwall and Devon, elsewhere it is practically absent from all Holocene deposits, the exceptions being Cleeve Hill, Gloucestershire, of Late Celtic age, and St. Catherine's Down, Isle of Wight, a deposit that sadly wants re-investigation. The Chalk districts of Kent and Surrey are particularly favourable to this species, yet it is absent from every rain-wash, whether pre-Roman, Roman, or later. It is true that the growth of tilth has been beneficial to the species, but there must have been very large areas of cornland in Roman times, yet this species is always absent from Roman deposits. The only conclusion is that over the greater part of England *Jacosta (Cernuella) virgata* (Da Cost.) must be considered a very modern immigrant, certainly within the last three or four hundred years.

Jacosta (Candidula) caperata (Mont.) has an exactly similar geological history, occurring as a fossil only in Cornwall and Devonshire. Elsewhere it is absent, except a doubtful record from St. Catherine's Down. One can only conclude that the duration of residence of this species also is a very limited one. I am quite at a loss to account for the rapid dissemination of these two species, and we know too little of their life histories to speculate with any degree of certainty.

Jacosta (Candidula) gigaxii (Pfr.), unlike the preceding forms, is not a western species. It has occurred in several deposits in Kent, Surrey, and Sussex, and one of these, Northfleet, is certainly pre-Roman. It is, however, decidedly rare as a fossil, and it is only since Roman times that it has been able to extend its range to any great degree. It may possibly be an introduction into England by human agency in late Celtic times, for it is quite absent from all early Holocene deposits.

Theba cantiana (Mont.), though so abundant at the present day, owing to its absence from all pre-Roman and Roman beds, must be considered a modern introduction, and one is tempted to suggest that it arrived here in Norman times. It occurred in the Ightham fissure in close proximity to the bones and bell of a ferret, a good example of the doubtful value of unsupported cavern evidence.

Helix aspersa, Müll., is extremely common in all Roman deposits, and examples were found in London in the crevices of the Roman Wall. Its size prevents its being overlooked by the archæologist, and hence its recorded occurrences with Roman objects are numerous, whilst this association has on more than one occasion been the cause of its being labelled "Roman snail", with the added information for the benefit of the public that the scientific name was "*Helix pomatia*"! It occurs in the early Holocene of Cornwall and Devon,

and in a Bronze age tumulus in Somerset, but being unknown from any pre-Roman deposit over the greater part of England, it has proved a useful zone fossil. Since this species does not burrow to hibernate, human habitations and their surroundings furnish excellent hibernacula, and the large population and high civilization which existed in England in Roman times will account for its wide distribution during that period, while the recent extension of its range may well be attributed to the same causes.

Fruticicola (Capillifera) striolata (C. Pfr.) is known from several early Holocene deposits in the South of England, so that it is undoubtedly a true native, but its modern distribution differs greatly from the fossil records, and its area of distribution was probably greatly increased during Roman and more modern times. A. W. Stelfox has suggested that it is quite a modern introduction into Ireland (*Proc. Malac. Soc. Lond.*, vol. x, 1913, pp. 290-1), a view strongly supported by the geological evidence (*Proc. Geol. Assoc.*, vol. xxviii, 1917, p. 167). It has a marked partiality for the neighbourhood of human habitations, especially gardens.

Paludestrina jenkinsi (Smith) is a puzzling form. It is known fossil from Barking (Essex), Blythburgh (Suffolk), and Clevedon (Somerset). The two former deposits are mediaeval, and there is no evidence as to the age of Clevedon, but it is clear that the theory that it was introduced into this country during the last century must be discarded. One thing, however, is certain, and that is that it has enormously increased its range during the last fifty years. Now that this species is known from Denmark and Germany, it will be interesting to see if it will be able to extend its range in those countries in so rapid a manner. There are a number of species which are apparently more abundant at the present day than formerly. These include *Helicella rogersi* (B. B. W.), *H. alliaria* (Müll.), *Pyramidula rupestris* (Drap.), *Helix hortensis*, Müll., *Ena obscura* (Müll.), *Lauria cylindracea* (Da Cost.), *Abida secale* (Drap.), *Balea perversa* (Linn.), *Limnæa glabra* (Müll.), *Dreissensia polymorpha* (Pall.), and *Sphærium lacustre* (Drap.). All these forms are decidedly rare as fossils, though the records show that there has been no great, if any, extension of range. *Helicella rogersi* (B. B. W.) is absent from all the Kentish rain-washes, yet at the present day it is very common on the chalk hills. Its occurrence in an early Holocene bed at Walton Heath, Surrey, as well as other records, show that it is a native.

Helicella alliaria (Müll.) is decidedly rare as a fossil, though the records prove that it was widely spread. It has a curious partiality for pigsties, scarcely a natural habitat.

Why *Helix hortensis*, Müll., should be so rare as a fossil is a problem I cannot answer and in only one Holocene deposit was it common, the early Neolithic flint mines of Grimes Graves, Weeting, Norfolk. It does not occur in many of the Kentish rain-washes, though living

abundantly in the neighbourhood. *Ena obscura*, Müll., too, is another form far more abundant than formerly.

Lauria cylindracea (Da Cost.) has a marked partiality for old stone walls covered with ivy, and I have never yet seen an old churchyard wall of this description that did not yield this species.

The fragility of the shell of *Balea perversa* (Linn.) may account in some degree for its rarity as a fossil, and the lack of suitable habitats may be the cause of the former scarcity of *Sphærium lacustre* (Drap.). Though known from the Pleistocene, this last species is absent in the Holocene from all pre-Roman beds.

Dreissensia polymorpha (Pall.) has been claimed as an introduction during the early part of last century, but its occurrence as a fossil in a Roman deposit at Whitefriars, London (*Proc. Geol. Assoc.*, vol. xi, 1890, p. 342), as well as at Clifton Hampden, Oxfordshire, completely negatives this view, and it must be considered a true native, a view which was always advocated by Gwyn Jeffreys. To nearly all these species human agencies have been beneficial by increasing their suitable habitats.

Those species whose area of distribution has apparently diminished are :—

Theba cartusiana (Müll.).

Ena montana (Drap.).

Acanthinula lamellata (Jeff.).

Lauria anglica (Fér.).

Vertigo substriata (Jeff.).

„ *moulinsiana* (Dup.).

„ *alpestris*, Ald.

„ *pusilla*, Müll.

„ *angustior*, Jeff.

“ *Truncatellina minutissima* (Hart).”

Planorbis stroemii, Westld.

Acicula lineata (Drap.).

Theba cartusiana (Müll.) in Kent is unknown living west of Canterbury, yet it occurs in all the pre-Roman and Roman rain-washes at the foot of the chalk hills from Otford to Snodland, as well as at Northfleet and Greenhithe, clearly proving that this species was formerly a widely spread and common form in West Kent, whilst linking up this area with its present distribution, it has been found fossil at Hollingbourne. Though unknown living in Essex, it occurs fossil at Harwich and Felstead, whilst it has also occurred in a deposit at Butley, Suffolk, thus proving that the isolated colonies in Norfolk and Suffolk are not accidental introductions, but are the last survivors of a formerly common species.

Acanthinula lamellata, Jeff., is quite a common form in some of the Essex deposits as well as at Wheatley, Nottinghamshire, and from neither of these counties is it known living.

Similarly *Ena montana* (Drap.), known fossil from Reigate, Surrey,

and Blashenwell, Dorset, has not yet been detected living in either county.

Lauria anglica (Fér.) is now known fossil from Totland Bay (Isle of Wight), Copford, Shalford, and Felstead (Essex), Harlton (Cambridgeshire), Ledbury (Herefordshire), and Askern (Yorkshire), and of these comital divisions it is to-day apparently absent from the first three.

Vertigo substriata (Jeff.), too, has been found in deposits at Ledbury (Herefordshire), Wilstone (Hertfordshire), Mottisfont (Hampshire), and Totland Bay (Isle of Wight), and is unrecorded living from any of these counties.

Vertigo moulinsiana (Dupuy) is as yet unknown in a recent state from Gloucestershire, South Essex, and Kent, though occurring fossil at Westbury on Severn, Walthamstow, Chingford, and Deal, whilst the two fossil records for *Vertigo alpestris*, Ald., Wheatley (Nottinghamshire), and Chignal St. James (Essex), clearly show that this species was once far more widely spread than at present.

Vertigo pusilla, Müll., has now been detected fossil at Totland Bay (Isle of Wight), Blashenwell (Dorset), Ightham and Crossness (Kent), Tilbury (Essex), Reigate (Surrey), and Southampton and Mottisfont (Hampshire), six divisions which still remain blank in the recent census.

The former abundance of *Vertigo angustior*, Jeff., has often been commented upon, for to-day it is one of our rarest shells. It is an abundant species in the early Holocene beds of Copford, Felstead, and Chignal St. James, Essex, and has occurred in a bed of similar age at Harlton, Cambridgeshire, and in neither county has it yet been found living.

“*Truncatellina minutissima* (Hart.),” and I use this name for the aggregate species since the value of the suggested segregates has yet to be tested, is only known fossil from Northfleet, Greenhithe, and Cuxton (Kent), near Staines (Berkshire), Westbury (Gloucestershire), and Grimes Graves (Norfolk), and the recent census has no record from any of these counties.

Planorbis stroemii, Westld., is only known living from one locality in Oxfordshire, yet in the Holocene beds of the Lea and the Thames it is a common species, being known from Berkshire, Buckinghamshire, Essex, Middlesex, Oxfordshire, and Surrey. So far it has not been found in the extensive Holocene beds of the Kennett. This shell was found living in a bed of *Chara*, and there is nearly always abundant *Chara* débris in the beds in which it is found. Possibly the cause of the almost total extinction of this species has been the destruction of its natural habitats by the canalization of the rivers and better drainage of the surface waters.

Acicula lineata (Drap.) is another species common in the early Holocene beds of Essex, and it must have been an abundant species there in former times, a condition of things very different from that

experienced by recent collectors. Its occurrence in rain-washes at Cuxton and Greenhithe, Kent, and in the Neolithic flint mines at Grimes Graves, Weeting, Norfolk, clearly show that this species was able to live at one time on what is now dry chalkland.

Besides these species there are several other forms whose area of distribution has slightly diminished. *Helicodonta obvoluta* (Müll.), from its occurrence in the Neolithic flint mines at Cissbury (*Archæologia*, vol. xlv, 1880, p. 339), had formerly a more easterly distribution in Sussex.

Helix pomatia, Linn., occurred at Northfleet, Kent, in association with Roman remains, and in a pre-Roman rain-wash. It is quite absent from the district at the present time, but probably intensive cultivation will account for this. So far nothing has been found enabling us to link up the two areas of distribution in Kent.

The only Holocene record for *Succinea oblonga*, Drap., is at Harlton, Cambridgeshire, a county in which it has not yet been detected living, whilst *Clausilia rolfhii*, Gray, though unknown living in North Essex, occurs fossil at Copford and Felstead.

It will be noted that nearly all the species whose area of distribution has diminished are damp-loving forms, and it may be urged that this is the result of human agencies in draining the swamps and marshes, and thus decreasing the natural habitats. The deposits yielding these species, however, are not confined to the low-lying grounds, but occur on the slopes of the chalk hills well above the springs, and where the influence of man cannot be traced. Thus at Cuxton, Kent, *Helicella radiatula* (Ald.), *Arianta arbustorum* (Linn.), *Lauria cylindracea* (Da Cost.), *Vertigo substriata*, Jeff., and *Acicula lineata* (Drap.) occur in a Neolithic deposit, but do not occur on these same dry slopes at the present time. Moreover in the same deposit the form of *Fruticicola* (*Capillifera*) *hispida* (Linn.), differs markedly from the chalk-hill form, the var. *nana*, Jeff., which is now living there. At Totland Bay (Isle of Wight), Blashenwell (Dorset), at Caerwys (Flintshire), and Leckwith (Glamorganshire) this damp-loving fauna is found in tufa which has long ceased to form, and in the case of Blashenwell the tufa is certainly Neolithic (C. Reid, *Proc. Dorset Nat. Hist. and Antiq. Field Club*, vol. xvii, 1896, pp. 67-75). Wherever it is possible to date these deposits by archæological evidence the result is always the same, that they are early Holocene, when human activities were negligible, and the conclusion is inevitable that at one period, at least, formerly the rainfall of England must have been much greater than it is to-day.

Besides the presence or absence of certain species, there is another important series of facts the full significance of which cannot yet be ascertained, and that is the varying development of the individual. It is easy enough to conceal our ignorance by using such phrases as "suitable conditions" or "congenial environment", but the fact remains that we know next to nothing of the multiple

factors which combine to produce these conditions, and for my purpose it is essential to ascertain what these factors are and their relative importance. The methods and times of reproduction of the mollusca, the history of their early stages, their powers of resistance to extremes of temperature and aridity, their food under natural conditions and not in a state of captivity, their enemies whether external or parasitic, how little do we really know about all these things. One welcomes, therefore, all such contributions as that by Dr. A. E. Boycott recently published in our proceedings (*Proc. Malac. Soc.*, Vol. XIV, 1921, pp. 163-72) and the numerous observations compiled by J. W. Taylor in his "Monograph".

I had hoped that some careful observer with more leisure than falls to my lot would have published ere this his observations on the results amongst the mollusca of the semi-arid conditions prevailing in England in 1921.

So far as my limited experience goes with the land mollusca, it was only the slugs that suffered. There was a very welcome decrease in their numbers, especially in the case of *Agriolimax agrestis* (Linn.), arising, I think, from the destruction of the young. Xerophiles were as abundant as ever, and other forms showed no diminution when the autumn rains allowed them to resume activity. Very different was it with the plants and insects, which suffered greatly, and a well-known entomologist informed me that he was afraid that many isolated colonies of the rarer insects had been extirpated.

With the freshwater mollusca, however, the dessication of the ponds and ditches only slightly reduced their numbers. The small volume of water in the Thames enabled the brackish tidal water to flow far above the usual limit, a fact which was realized too late at Kew Gardens. But for the locks and the strict limitation of the flow, the tidal waters would have reached still higher, and the destruction of the flora and fauna, extensive as it was, would have been much greater. But for human interference the Upper Thames would have been reduced to a series of pools connected by small streams, with the inevitable effects on the unfortunate mollusca. But this would have been only an episode, normal conditions would soon have returned, and there would probably have been no trace in the geological record. The deposits we are considering are certainly not the products of such episodes, but represent stable conditions over a considerable period of time.

Ecologists, too, may be asked to give more details in their interesting papers. The relative abundance of species in an artificial habitat is interesting as showing the presence or absence of enemies such as ducks and fowls, but the development of the individuals is usually ignored. This is of paramount importance. It must be remembered that Ecology was founded by botanists, and in plants there is a keen competition between the species. This is not so with the mollusca, and facts that are important to the botanist are trivial to the malacologist.

Yet in spite of this lack of knowledge I shall venture to put forward tentative views based on the mean development of the individual.

Here I must pay a tribute to the work of J. R. Bourguignat, who was the pioneer in this line of research. Opinions may differ as to the wisdom of the "New School" in departing from the original conception of a species, yet the idea of the founder was by so doing to furnish the nomenclatorial details to enable us to ascertain what were the circumstances and climate when such deposits as I am now discussing were accumulated. For this purpose he considered that the varying forms arising from environment should be ranked as species and described and figured as such. Whether the conclusions arrived at in his "Mollusques terrestres et fluviatiles des environs de Paris à l'époque quaternaire", "Histoire des monuments mégalithique de Roknia", and "Histoire de la colline de Sansan" are absolutely correct or not time alone can tell, but there can be no doubt that many will stand the test. I trust I may be permitted to lay a wreath of appreciation on his grave, more especially as in his case "the crown of the innovator was a crown of thorns". In studying his work and the adverse criticisms passed on it, one is impressed by the fact that there are two viewpoints in nomenclature, that of the systematist and that of the palæontologist, and each of these is based on their needs. The former has no interest in the variation of forms, and has grudgingly admitted even the existence of sub-species. He has no need to name syntonic forms, and the more comprehensive the species the easier the work of placing it in its correct relative position. But the palæontologist has other aims. He wishes to reconstruct the past, and how can he do this if a specific name, say *Fruticicola* (*Capillifera*) *hispida* (Linn.), indicates an allied group of forms living from Southern Europe to the Arctic Circle that flourishes in damp situations, and is equally common on a dry hillside and in intermediate situations, each distinct habitat possessing its own form. In such a case the systematist only needs and uses one name, but to the palæontologist this name conveys little or nothing.

Bourguignat was at heart a palæontologist; he realized their needs, and he endeavoured to the best of his ability, and it was certainly of no mean order, to provide a scheme of nomenclature that would satisfy their requirements. It failed principally through the excesses of his followers, who possessed neither his knowledge nor his "flaire". The older system is based on the immutability of species, a view which received its deathblow many years ago from the "Origin of Species". I think that had Bourguignat thrown over the fetish of binominalism and adopted the trinominal system he would have had a much larger following, and this course will eventually be found to be the means of reconciling the two divergent views.

In considering the question of the development of the mollusca

it is essential to have large series of specimens, for giants and dwarfs are not uncommon, and the contrasted series must be from the same geological formation. It would be misleading to compare fossil shells that had lived on the Chalk and recent shells collected on the Gault. Exigencies of space prevent me from giving the numerous measurements, and after all the results are the important matter, and these show that in many deposits, some of which can be dated archæologically, the average size of the mollusca is decidedly larger than the mean of those now living in the immediate neighbourhood. The cause of this is in my opinion changed meteorological conditions.

If we compare the non-marine mollusca of South Devonshire and Kent, differences in the size will be noted. The former possesses what is known as an insular type of climate, but little frost and absence of extreme heat in summer, whereas Kent approaches to the continental type with hotter summers and colder winters.

Xerophiles such as *Jacosta* (*Cerneuella*) *virgata* (Da Cost.), *J.* (*Xerophila*) *itala* (Linn.), and *J.* (*Candidula*) *caperata* (Mont.) are far more abundant and larger in Kent than in South Devon, whilst *Helix aspersa*, Müll., attains a larger size in the former county.

Devon examples of *Helix nemoralis*, Linn., are perhaps brighter coloured, a character of no value to the palæontologist, but are certainly smaller than Kentish specimens. The chief difference, however, is the comparative abundance of heavy shells in South Devon compared with their extreme rarity in Kent. This no doubt arises from the mild winters being favourable to longevity, a fact which has long been known to Harley Street specialists. Kentish examples of *Arianta arbustorum* (Linn.) and *Fruticicola* (*Capillifera*) *striolata* (C. Pfr.) are decidedly larger than those from Devon, and this remark applies to many of the land and freshwater forms. When we compare English examples with foreign similar differences are noted. With *Helix aspersa*, Müll., the largest examples are from Algiers and Greece, whilst shells from Beyrout, Italy, Spain, and Majorca are not far behind. Shells from Crete, Tasmania, Melbourne, and Mauritius are about an English average, whilst those from Cape Town and the Canaries are slightly smaller. These are larger than examples from Portugal and Costa Rica, whilst the smallest are from St. Helena, the Seychelles, and Lord Howes Island. From these facts one may infer that a "continental" climate is more favourable to this species than an "insular".

The largest examples of *Helix nemoralis*, Linn., are found in Lombardy, the Pyrenees, Portugal, Switzerland, and in Ireland in Co. Clare and the Aran Islands, West Galway; whilst French and German examples are certainly larger than English.

Now these facts do not agree with the data for *Helix aspersa*, Linn., for the Irish examples of *H. nemoralis* are an apparent exception, but the Irish localities are exceptionally arid, being

practically dry stretches of limestone with innumerable crevices into which the animals retreat during hot weather, and here again we can come to the same conclusion as with *Helix aspersa*, Müll. The largest examples of *Arianta arbustorum* (Linn.) are from Central Europe, whilst the large size attained by *Succinea putris* (Linn.), *Limnæa stagnalis* (Linn.), *L. palustris* (Müll.), and *Planorbis corneus* (Linn.) in Austria has often been noticed. The examples of *Cochlicella acuta* (Müll.) from Sussex are much larger than those from the West of England, whilst German examples of *Helix pomatia*, Linn., are decidedly larger than English.

It would thus appear that the "continental" type of climate is far more beneficial to the development of the mollusca than the "insular", and it is not presuming too much to conclude that the evidence derived from the Holocene mollusca points distinctly to at least one period of this character.

We have seen that the Molluscan fauna of England has varied greatly in Holocene times, and I have endeavoured to show that this variation has arisen from changes of climate. From archæological and stratigraphical evidence a sequence in these changes can be deduced, and it is now necessary to compare this with the results obtained from other lines of research.

Perhaps the clearest exposition of the Holocene period is that given by Professor F. J. Lewis, based on the results of his work on the great masses of Scotland, an investigation undertaken to ascertain what changes of climate had occurred (*Trans. Roy. Soc. Edinburgh*, vol. xli, 1905, p. 679; vol. xlv, 1906, p. 335; vol. xlvi, 1907, p. 33; and vol. xlvii, 1911, p. 793).

According to this author the present conditions may be considered as dry, and the sequence in descending order is:—

1. Sphagnum: humid.
2. Upper Forest Growth.
3. Sphagnum: humid.
4. Subarctic plants (colder).
5. Sphagnum: humid.
6. Lower Forest Growth.
7. Subarctic plants.
8. Arctic plants.
9. Moraine.

This differs markedly from the succession recently suggested by C. E. P. Brooks (*The Evolution of Climate*, London, 1922, pp. 126–58). This author only recognizes three principal periods:—

1. The "Classical" Rainfall, maximum, 1800 B.C.–A.D. 500.
2. The Forest period (dry), 3000 B.C.–1800 B.C.
3. The post-glacial optimum, a warm period.

There are a number of minor changes postulated, principally from literary evidence, which in these matters is always doubtful.

Our facts, however, strongly support the views of Professor Lewis, whilst the occurrence of two forest growths separated by

a long interval is a common feature in many alluvial deposits, especially in the lower Thames valley, so for my purpose I shall only consider the first sequence. It is open to question whether stages 7, 8, and 9 should be included in the Holocene. In these matters it is always difficult to draw the division line. Stage 9 is certainly Pleistocene, and since the two succeeding stages are really part of the preceding glacial period, I prefer to classify them with it.

Stage 6. The lowest forest growth is well known and has been recognized in many places in Northern Europe and in Ireland (*Proc. Geol. Assoc.*, vol. xxviii, 1917, pp. 144, 157). The well-known deposit at Dogs Bay, West Galway, yielding the large and heavy examples of *Helix nemoralis*, Linn., is of this age. This form has been named var. *pura* by Westertund (*Verhandl. Zool.-Bot. Gesell. Wien*, vol. xlii, 1892, p. 34). The derivative examples of this species found in the Neolithic flint mines at Grimes Graves, Norfolk, also belong to this stage (*Report of the Excavations at Grimes Graves*, 1915, pp. 220-3). To this period I would also assign the lacustrine deposit at Perranzabuloe, Cornwall (*Proc. Malac. Soc. Lond.*, vol. viii, 1909, pp. 247-50) and the remarkable chara deposit at Haweswater, Silverdale, Lancashire (*Journ. of Conch.*, vol. xi, 1905, pp. 147-51; and *Lanc. and Chesh. Nat.*, 1914, pp. 135-40 and 197-201), as well as many of the chara marls of the Fen Country (*Fenland Past and Present*, p. 572). It may be noted that in this country it was the late Dr. R. Munro, the able archæologist, who first pointed out the true age of the marl deposits from the molluscan evidence, for he said, "The suggestion that the period of maximum development of the freshwater testacea which produced the shell marl deposits of Scotland correspond chronologically with that of the forest growths is not therefore unreasonable" (*Prehistoric Scotland*, 1899, p. 26). As already noted, lack of knowledge prevents me from deducing accurately all the climatic conditions, but I can assume that the summers were much warmer than the average of to-day, probably resembling that of 1921, but with a greater rainfall in the remaining seasons than in that year.

Stage 5. The succeeding humid period is well represented in England, and it may be called "the maximum development of the damp-loving species". Copford, Felstead, Chignal St. James, and Shalford (Essex), Blashenwell (Dorset), Totland Bay (Isle of Wight), Allen's Farm, Ightham, and the Neolithic grave at Cuxton (Kent), the Cornish Towan deposits, Harlton (Cambridgeshire), Wilstone (Hertfordshire), Grimes Graves (Norfolk), Wheatley (Nottinghamshire), and many other Midland deposits may all be assigned to this stage. There is no evidence so far as we are concerned of the supposed colder phase No. 4, and it is probable that it may represent the maximum of humidity (see *Proc. Geol. Assoc. Lond.*, vol. xxxiii, 1922, p. 142), and thus the stages 3, 4, and 5 would represent one phase in climatic change.

C. E. P. Brooks has suggested that this stage practically coincides

with the introduction of Bronze into England, but the evidence is against this. Grimes Graves (Norfolk), Blashenwell (Dorset), as already noted, and the Neolithic grave at Cuxton, Kent (*Proc. Malac. Soc. Lond.*, vol. viii, 1909, pp. 375-6) are all Neolithic, and certainly not late Neolithic. The mollusca (as yet undescribed) obtained from the recent extension of the new Albert Docks are of this age, for they occurred between the two forest growths, and here again the only archæological objects noted were flint flakes and implements. As to the climate one can only say with safety that it was much damper than the present.

Stage 2. The Upper Forest Growth. This is a return to a "continental type" of climate, but not so pronounced as in Stage 6. On archæological evidence this can be shown to be of Bronze Age about 1500 B.C., and the recent exploration of a Bronze Age tumulus at Micheldever, Hampshire, has yielded strong confirmatory evidence from the mollusca, for they are all well developed.

Of the succeeding damp stage No. 1 we have no evidence. It was certainly not so extreme as the preceding damp stage, and it may be that it was confined to Scotland. There is, however, slight evidence that during the Roman occupation of this country the climate was slightly warmer than at present, for in Roman deposits the mollusca are nearly always slightly larger than those now living near the sites.

We thus see that there is a marked agreement between the conclusions derived from the mollusca and those deduced from the peat mosses, and we can, I think, conclude that the scheme of Professor Lewis is in the main correct.

It is interesting to note that there are but few abnormalities in the Holocene mollusca, although an enormous amount of material has passed through my hands. Only one sinistral shell has been found, an example of *Arianta arbustorum* (Linn.), at Uxbridge, Middlesex, whilst a few scalariform *Limnææ* and *Planorbis* have occurred in the Lea Valley deposits. The *Limnææ* at Perranzabuloe, Cornwall, were, however, nearly all abnormal, and this was certainly the result of the conditions in which they lived. I would suggest that in this case the lake was subject to slight incursions of the sea.

I have endeavoured to show that the formerly ignored or despised and maltreated Holocene mollusca are of great importance in several lines of research, and that they can be used as evidence in solving many problems, and I would take this opportunity of thanking those numerous friends by whose kind assistance this has been possible. In pioneer work of this character, based, as I have already noted, on imperfect knowledge, temporary mistakes are bound to occur, to be rectified as our learning increases. I have had to make bricks with but little straw. Whether they will be lasting or not the future will tell, but this is certain—that the work has not only given me interest and pleasure, but has produced friendships which will last to the end of the chapter.

THE HOLOCENE SEQUENCE.

<i>Professor F. J. Lewis</i> (1911).	<i>C. E. P. Brooks</i> (1922).	<i>Divisions based on Molluscan evidence.</i>	<i>Localities.</i>	<i>Human Industries.</i>
Present day (dry).		Present day (dry).	Watford, Wall, Darenth, Borstal.	
Sphagnum (humid).	Classical rainfall maximum, 1800 B.C.-A.D. 500.	Slight Continental climate.	Otford, London Wall, Ightham, Bermondsey, Bath, Northfleet, Ruckland.	Roman period.
Upper Forest Growth.		Continental climate.	Cleeve Hill, Northfleet.	Late Celtic.
Sphagnum (humid).			Micheldever, Wick.	Bronze Age.
Sub-Arctic plants (colder).	Forest Growth, 3000 B.C.-1800 B.C.	Insular climate, heavy rainfall.	Copford, Felstead, Shalford, Chignal St. James, Roxwell, Blashenwell, Totland Bay, Allens Farm, Ightham, Cuxton, Cornish Towans (part), Harlton, Willstone, Grimes Graves, Cissbury, Wheatley, New Albert Docks, Ipswich, Westbury, Clapham, Ledbury.	Neolithic.
Sphagnum (humid). Lower Forest Growth.	Post-glacial optimum.	Continental climate.	Perranzabuloe, Haweswater, Chara marls, Newquay (Nemoralis zone), Barn Elms.	Early Neolithic.

NOTES ON THE GENUS *STENOCHITON* AND THE DISCOVERY
AND RECOGNITION OF THE TYPE OF BLAINVILLE'S
CHITON LONGICYMBA IN *STENOCHITON JULOIDES*, ADAMS
AND ANGAS.

By EDWIN ASHBY, F.L.S.

Read 9th March, 1923.

THIS remarkable genus of Polyplacophora, while evidently rightly placed under the Ischnochitonidæ, in habits and characters its members are evidently widely removed from any other known form.

Instead of harbouring or living on stones, shells, or blocks of timber, the members of this genus have as their host and probably their food supply, various species of that order of marine flowering plants known as Sea Grasses.

The genus *Stenochiton* was formed by Adams and Angas in 1864, for the reception of the South Australian shell described by them under the name *S. juloides* (Proc. Zool. Soc., 1864, p. 193). As shown later, the same shell had been described by De Blainville in 1825, under the name of *Chiton longicymba*, from a specimen collected by Péron and Lesueur, at King Island in 1803.

The next species, *S. pilsbryanus*, was described by Bednall in 1897 (Proc. Malac. Soc., vol. ii, pt. 4) as having been found "on sea-weed? *Zostera*". This being the first intimation of the possibility of its habitat being other than rocks, etc. In 1900 the writer described a third species under the name of *S. pallens*, Ashby. In May, 1918, he read a paper before the Royal Society of S. Australia showing that Bednall's description did not apply to any particular species, but that the figures and description were a sort of conglomerate made up from parts of two or more species. In the same paper he described two more forms under the names of *posidonialis*, Ashby, and *cymodocealis*, Ashby, and finally in a paper read before the same Society in July, 1919, he described a further species as *pilsbryanus*, Bednall.

It will be seen that we have five known species all described from South Australia.

Habitat.—The writer in his paper (Trans. Roy. Soc. of S. Austr., vol. xlii, 1918) was able to show that all the members of this genus live, not as had been previously supposed on "*Pinna* shells, old boots, glass bottles", or on rocks, but on the growing stems and leaves of flowering plants known as "Sea Grasses", being found during the day time hidden away in the brown sheaths of old *Posidonia* leaves, usually buried several inches deep in coarse shell grit and sand. They probably come out at night time and feed on the leaves of growing *Posidonia*, only returning as day approaches to the protection of the sheaths near the roots of the plant. One needs a digging tool to get the plant up by the roots, and then in sheltered localities the *Stenochiton* is found to be quite common.



Kennard, A. S. 1923. "PRESIDENTIAL ADDRESS: THE HOLOCENE NON-MARINE MOLLUSCA OF ENGLAND." *Proceedings of the Malacological Society of London* 15, 241–260. <https://doi.org/10.1093/oxfordjournals.mollus.a063812>.

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DOI: <https://doi.org/10.1093/oxfordjournals.mollus.a063812>

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