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[From the American Journal of Science, Vol. XX, November, 1880.]

REVISION OF THE LAND SNAILS OF THE PALEOZOIC ERA, WITH DESCRIPTIONS OF NEW SPECIES.

By J. W. Dawson.
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The Gasteropods as a class occur as early as the Upper Cambrian, but all the earlier known types are marine. That portion of the group distinguished by the possession of air sacs instead of gills (Pulmonifera) has not hitherto been found in any formation older than the Carboniferous, and only four Carboniferous species have been described. In the present paper
I propose to state some additional facts respecting the species already known, to discuss their affinities, and to describe two additional species, making six in all from the Paleozoic rocks, including one from the Erian or Devonian. For reasons to be mentioned in the sequel, I do not admit the genus *Pulmonaria* founded, by some German naturalists, on fossils which I believe to be tubes of Annulids.

It may be useful to premise that of the two leading subdivisions of the group of Pulmonifera, the Operculate and Inoperculate, the first has been traced no farther back than the Eocene. The second, or Inoperculate division, includes some genera that are aquatic and some that are terrestrial. Of the aquatic genera no representatives are known in formations older than the Wealden and Purbeck, and these only in Europe. The terrestrial group or the family of the Helicidae, which, singularly enough, is that which diverges farthest from the ordinary gill-bearing Gasteropods, is the one which has been traced farthest back, and includes the Paleozoic species. It is further remarkable that a very great gap exists in the geological history of this family. No species are known between the Carboniferous and the early Tertiary, though in the intervening formations there are many fresh-water and estuarine deposits in which such remains might be expected to occur. There is perhaps no reason to doubt the continuance of the Helicidae through this long portion of geological time, though it is probable that during the interval the family did not increase much in the number of its species, more especially as it seems certain that it has its culmination in the modern period, when it is represented by very many and large species, which are dispersed over nearly all parts of our continents.

The mode of occurrence of the Paleozoic Pulmonifera in the few localities where they have been found is characteristic. The earliest known species, *Pupa vetusta*, was found by Sir Charles Lyell and the writer, in the material filling the once hollow stem of a Sigillaria at the South Joggins in Nova Scotia, and many additional specimens have subsequently been obtained from similar repositories in the same locality, where they are associated with bones of Batrachians and remains of Millipedes. Other specimens, and also the species *Zonites priscus*, have been found in a thin, shaly layer, containing debris of plants and crusts of Cyprids, and which was probably deposited at the outlet of a small stream flowing through the coal-formation forest. The two species found in Illinois occur, according to Bradley, in an underclay or fossil soil which may have been the bed of a pond or estuary, and subsequently became a forest sub-soil. The Erian species occurs in shales charged with remains of land plants, and which must consequently have
The species describe two Peristome, describe two Peristomata rocks, which species to be the genus *Paleorbis* which I believe received abundant drainage from neighboring land. It is only in such deposits that remains of true land-snails can be expected to occur; though, had fresh-water or brackish water Pulmonates abounded in the Carboniferous age, their remains should have occurred in those bituminous and calcareo-bituminous shales which contain such vast quantities of debris of Cypris, Lamellibranchs and fishes of the period, mixed with fossil plants.

With reference to their affinities, the Paleozoic land snails present no very remarkable peculiarity except their close resemblance to some modern forms. Of the known species, four belong to the genus *Pupa* in its wider sense, and are very near to sub-generic types still represented on the American continent and its islands. One is a small helicoid shell not separable from the modern genus *Zonites*, and the remaining one, though it has been placed in a new genus, is very near to some small American snails of the present day (*Stenotrema*, etc.) All the species are of small size, though not smaller than some modern shells of the same type.

I shall now proceed to give the characters and descriptions of the several species, adding to the account of those previously known, such new facts as have occurred in my more recent explorations and examinations. I should state here that many of the new facts detailed have been obtained in the course of excavations for the extraction of erect trees holding land animals, undertaken with the aid of a grant from the Government fund for aiding original researches, at the disposal of the Royal Society of London, and carried on within the past three years.

1. *Pupa vetusta* Dawson. (Figs. 1 to 4, and 14, a, b.)


**Description.**—Shell cylindrical, somewhat abruptly conical at the apex, in some specimens tending to diminish in diameter in the later turns or whorls of the shell. Whorls nine in adult shells, slightly convex, in width equal to half the diameter of the shell. Suture impressed. Aperture evenly rounded, not continuous above, rather longer than broad, destitute of teeth; peristome slightly reflexed and smooth. Surface shining, marked with longitudinal smooth ridges, separated by spaces a little wider than the ridges; spaces about ¾ inch in width. Shell calcareous, thin, prismatic in structure. Young specimens abruptly conical and helicoid in form. Young round, smooth, the first turn below the nucleus marked with
rows of little pits which gradually pass into the continuous striae. The last whorl of the adult presents irregular lines of growth, instead of the regular microscopic ribs of the middle turns. Mature ovum membranous, or so slightly calcareous that it can be compressed without breaking; the embryo shell sometimes visible within. Length of adult shell rather less than 1 centimeter, breadth in middle 4 millimeters.

Variety tenuestriata.—Along with the ordinary form there are others of similar size and general structure, but with the apex less obtuse and a somewhat greater tendency to diminish in diameter in the later whorls. They have also the microscopic ridges in the shell about half as far apart as those of the ordinary form. This form I was at first disposed to regard as specifically distinct, but there seems to be a gradual transition from one to the other, and the two forms seem to accompany each other throughout the entire range of the species.

State of preservation.—The shells are usually entire, but often somewhat flattened, and cracked or distorted in the process. Many fragments of shells, however, occur with the entire specimens, and some of these have a whitened or bleached appearance like that of modern land shells after having been exposed to the weather. In one layer I found impressions of several flattened shells, the substance of the shell having been altogether removed. Ordinarily the shell remains in such a state as to show its structure, and the more perfect specimens found in the erect trees have a grayish brown color, like that of some modern Pupas.

The habitat of this species was in forests of the Coal-formation period, composed of Sigillaria, Calamites, Lepidophloios and Ferns. The only known locality is the South Joggins, Nova Scotia. At this place the shells have been obtained in considerable numbers, though perfect specimens which can be disengaged from the matrix, are comparatively few. They have been found in erect Sigillaria and also in a bed of shale. The lowest and highest beds in which they occur are separated by 2,000 feet of vertical thickness of strata including no less than thirty-five beds of coal and many underclays supporting erect trees, so that the species must have inhabited this locality for a very long time and must have survived many physical vicissitudes.

The first specimen, which was also the first known Paleozoic land shell, was found by Sir Charles Lyell and the writer in 1851, in breaking up the contents of an erect tree holding reptilian bones. The specimens obtained from this tree having been taken by Sir Charles to Cambridge and submitted to the late Prof. Jeffries Wyman, the shell in question was recognized by him and the late Dr. Gould, of Boston, as a land shell. It
the continuous regular lines of the middle calcareous embryo shell are rather less perfect.

By form there is, but with the tendency to diminish the microscopic those of the to regard as gradual transition to accompany species.

entire, but have be in the pro with the entire or bleached having been impressions of having been forms in such a direct specimens like that of Coal-formation Callophloios and luggins, Nova having been determined in can be dis. They have shale. The separated by no less than eruating erect locality for geological vicissis-

Fig. 1, Pupa retusta, magnified 8 times lineally; 2, same, showing the aperture, \( \times 8 \); 3, same, nuclear whorl, \( \times 25 \); 4, same, mature egg and embryo shell, \( \times 25 \). 5, 6, Pupa Bigsbii, \( \times 8 \); 7, Pupa Vermilionensis, \( \times 8 \); 8, same, showing aperture \( \times 8 \), the small tooth on the columella somewhat exaggerated; 9, same, section of aperture, showing tooth \( \times 16 \). 10, Zonites priscus, \( \times 8 \); 11, same, crushed specimen, showing aperture \( \times 20 \).
was subsequently examined by M. Deshayes and Mr. Gwynn in Jeffries, who concurred in this determination; and its micaceous scopic structure was described by the late Prof. Quekett, which London, as similar to that of modern land shells. The singhickne specimen obtained on this occasion was somewhat crushed and he should not have shown the aperture. Hence the hesitation as to its Log natural, and the delay in naming it, though it was figured in and described in the paper above cited in 1852. Better specimens of men showing the aperture were afterward obtained by the writer, and it was named and described by him in his "Aima alred breathers of the Coal Period," in 1863. Prof. Owen, in his essay on "Palaeontology," subsequently proposed the generic name Denzonites dropupa. This I have hesitated to accept, as expressing a few generic distinctness not warranted by the facts; but should such the shell be considered to require a generic or sub-generic distinctness, Owen's name should be adopted for it. There seems a fragmentary, however, nothing to prevent it from being placed in one of the many modern sub-genera of simple-lipped Pupae. With regard to the stream form of its aperture, I may explain that some currency has occurred to be given to an incorrect representation of it, through an only fortunate accident. In the case of delicate shells like this, though imbedded in a hard matrix, it is of course difficult to work out would the aperture perfectly; and in my published figure in the "Air In be breathers," I had to restore somewhat the broken specimens sandy in my possession. This restoration, specimens subsequently or in a found have shown to be very exact. Nevertheless it was criticised by some English conchologists, and when Sir Charles Lyell was about to publish his Student's Manual, he asked me to give him one of my best specimens to be figured. This I sent with micro-photographs of others. It seems, however, that the artist or engraver mistook the form of the aperture and gave it an entirely unnatural appearance in the Student's Manual. That now given is taken from a photograph of the most perfect and least compressed specimen in my possession.

As already stated, this shell seems closely allied to some modern Pupae. Perhaps the modern species which approaches most nearly to it in form, markings and size, is Macrocheilus Gossei from the West Indies, specimens of which were sent to me some years ago by Mr. Bland, of New York, with the remark that they must be very near to my Carboniferous species. Such edentulous species as Pupa (Leucochila) fallax of Eastern America very closely resemble it; and it was regarded by the late Dr. Carpenter as probably a near ally of those species which are placed by some European conchologists in the genus Pupilla.

The lowest bed in which Pupa vetusta occurs belongs to group VIII of Division 4 of my section of the South Joggins,
and Mr. Gwyned is between Coal 37 and Coal 38 of Logan's section, being 27 feet below Coal 37. The next horizon, and that in which Prof. Quekett, which the shell was first discovered, is 1217 feet of vertical strata above this horizon. The next higher, in group XY of Formation 4 of Logan's section, is 1217 feet of vertical strata above this horizon, and the next higher, in group XV of Division 4 of my section, is 1217 feet of vertical strata above this horizon.

It will be seen that the shells occur here in an erect Sigillaria, standing on Coal 15 horizon. The third horizon is in group XXVI of Division 4, and it was figured in Logan's section, about 800 feet higher than the last. Here also the shells occur in an erect Sigillaria.

Better specimens of these shells occurred in the lowest of these three horizons, the shells are found, as already stated, in a thin bed of concretionary clay of dark grey color, though associated with reddish beds. It contains a micaceous substance, and the name Dezontites priscus as well, though this is very rare, and there are fragments expressing a few valves of Cythere and shells of Nautilides as well as carbonaceous matter; but the conspicuous fragments, fronds of ferns, Trigonocarpus, etc. The Pupeae ub-genera are mostly adult, but many very young shells also occur, as well as a small part in one bed about an inch in thickness. This bed is one of the rarest shells in the area of the Student's possession.

In the erect Sigillariae of group XV, the shells occur either in a sandy matrix, more or less darkened with vegetable matter, or in a carbonaceous mass composed mainly of vegetable debris. The shells are usually thick, and flattened, the shells in these repositories are usually filled with brownish calcite. From this I infer that most of them were alive when imbedded, or at least that they contained the bodies of the animals; and it is not improbable that they sheltered themselves in the hollow trees, as is the habit of many similar animals in modern forests. Their residence in these trees as well as the characters of their embryology are illustrated by the occurrence of their mature ova.

They may also have formed part of the food of the reptilian animals whose remains occur with them. In illustration of this I have elsewhere stated that I have found as many as eleven unbroken shells of Physa heterostropha in the stomach of a modern Menobranchus. I think it certain, however, that both the shells and the reptiles occurring in these trees must have been strictly terrestrial in their habits, as they could not have found admission to the erect trees unless the ground had been sufficiently dry to allow several feet of the imbedded hollow trunks to be free from water. In the highest of the three horizons the shells occurred in an erect tree, but without any other fossils, and they had apparently been washed in along with a grayish mud.**

** The discovery of the shells in this tree was made by Albert I. Hill, C.E.
2. *Pupa Bigsbii* s. n. (Figs. 5 and 6.)

*Description.*—Shell half the size of *Pupa vetusta*, or between three and four millimeters in length and one and five-tenths millimeters in breadth. Form, long conical. Body whorl about one-third of the entire length, giving the shell a somewhat bulimoid form. Whorls five in the largest specimens found, tumid, suture much impressed. Surface smooth. Aperture apparently oval in form, but not perfectly known, as the body whorl is crushed in all the specimens.

A few specimens, none of them quite perfect, were found on the crest trees of group XV at the Joggins, along with *Pupa vetusta*. They differ from that species in smaller size, different form and absence of sculpture. The specimens do not show whether the aperture was toothed or simple, but it was probably the latter, as the lip is evidently very thin and delicate. From its form it is probable that it belongs to a different subgenus from *Pupa vetusta*. It is very much more rare than the species in the crest trees, and has not been found elsewhere.

I dedicate it to my venerable and dear friend Dr. Biggsby F.R.S., of London, a pioneer in American geology, and still an indefatigable worker in the science.

3. *Pupa Vermilionensis* Bradley. (Figs. 8 and 9, and 14c.)


*Description.*—Shell spindle-shaped, tapering to an obtuse apex, covered with microscopic ridges (25 to 30 in a millimeter) parallel to the lines of growth. Aperture oblique, oval. Outer lip thin, slightly reflexed. Columella lip reflexed, thickened; furnished with a single central curved tooth, projecting nearly half way across the aperture. Junction of columella and outer lip somewhat angular and dentiform. In old individuals the columella tooth is often continuous through an entire turn or farther. It is not seen on shells having less than three turns. The last turn forms nearly half the length of the shell. Whorls rounded. Suture impressed. Surface glossy. Color black or gray. Length three and six-tenths millimeters. Width two millimeters. Some individuals are smooth or destitute of the fine microscopic ridges, but whether this is a natural peculiarity or a result of injury to the outer surface, is not certain.

As compared with *Pupa vetusta* this shell is less than half the size, of a less cylindrical form, its whorls more rounded, and its body whorl much larger in proportion. Its sculpture is much finer. The conspicuous tooth in the aperture is of

* Slightly modified from Bradley.
course also a strong mark of distinction. The shell is thin, and from its black color and failure to show structure under the microscope, I infer that it must have been of a horny or corneous texture, with little calcareous matter. The matrix is a somewhat whitish colored and concretionary, and somewhat hard and calcareous. 

As compared with modern American species, P. Vermilionensis is very near to several of the smaller forms with teeth in the aperture. In its form and aperture it approaches closely the immature shell of P. (Leucochita) corticaria of Say, or to the immature shell of P. rupicola. It has also some resemblance to the western species P. hordacea Gabbr, from Arizona.

This shell was discovered by the late Mr. F. H. Bradley in 1869, in concretionary limestone accompanying the underclay of Coal No. 6, Wabash Valley Section, at Polly's Fort, Vermilion River, Illinois. In the first notice, which appeared in the Report of the Geological Survey of Illinois, it was referred to elsewhere. *Pupa vetusta*, but was subsequently described by Mr. Bradley and Dr. Bigsby in the American Journal of Science, under the name above cited.

I am indebted for specimens of this shell to Mr. John Collett, of the Geological Survey of Indiana, and also to Mr. W. Gurley, of Danville, Illinois.

4. *Zonites* (Conulus) priscus Carpenter. (Figs. 10 and 11, and 14d.)


**Description.**—Shell small, helicoid. Length two and five-tenths millimeters, width two and eight-tenths millimeters. Spire little elevated. Nucleus small. Whorls four, somewhat flattened, with the suture little impressed. Base somewhat excavated with large umbilicus. Aperture oblique, suboval, somewhat regularly rounded. Lip simple. Surface marked with uneven stria and somewhat more conspicuous ridges of growth. Angle of divergence about 130°. Shell thin and probably horny.

This little shell was discovered in 1866, in the bed already referred to as the lowest of those at the South Joggins in which *Pupa vetusta* has been found. Shortly after I had discovered this bed, being impressed with the probability that it might hold other remains of land animals beside the *Pupa*, I had some excavations made in it, and a considerable quantity of material taken out. I found, however, that the thin layer containing the land shells was not continuous but in limited patches, and was rewarded only by the discovery of a few

* Slightly modified from Carpenter.
specimens of *Zonites priscus* and a small and not determined fragment of bone, in addition to specimens of *Pupa vetusta*, though

The specimens found at this time were submitted to the geologist Dr. P. P. Carpenter, by whom the species was named and described. One or two crushed specimens have been subsequently found in the erect trees holding *Pupa vetusta* in group XV, but the species is extremely rare in comparison. This may be due to some difference in habitat or mode of life, rendering it less likely to be imbedded in the deposit in process of formation. It is also to be observed that the shell is much more delicate than that of *Pupa vetusta*, and therefore less likely to be preserved.

With regard to its affinities, it was compared by Dr. Carpenter with the African species *Paryphanta* *Caffra* Fer., "on an extremely small scale." Dr. Carpenter also compared it with *Stenotrema* *Hygromia*, and stated that it might well be ranked under *Paryphanta*.
not determined; *mollusca* of Morse, with the living species *minuscula* and *exigua*. *Pupa vetusta,* thought it best, however, to place it in the subgenus *Conulus* ascribed to the genus *Zonites,* as defined by Messrs. Adams. With *Pupa vetusta,* was named to the subgeneric name, Dr. Carpenter explained that have been subgenus *Conulus* of Fitz, 1883, appears to be synonymous *vetaustina* in *Trockiscus* Held, 1837 (non Sby.); also with *Petaia* Beck, Pis. *Zonites* is named. This is not to be entered into these subgeneric distinctions, observed that may designate the species as a *Zonites,* or even, speaking loosely, *Pupa vetusta,* as *Helix.* The shell seems to be separate more than specifically, from the smaller helicoid snails with thin shells and simple aperture.

5. *Dawsonella* Meek Bradley. (Figs. 12 and 13.)


**Description.**—Shell broad, depressed, helicoid. Spire oblique, consisting of three to three and one-half turns. Length three and two-tenths millimeters, width four millimeters. Surface smooth, but with fine microscopic lines of growth, about fifteen in a millimeter. Aperture oblique, oval, greatly contracted by a broad lamellar expansion of the columella, extending more than half way across, even in small individuals. Outer lip thickened, slightly reflected. Suture little impressed, imperforate, but last turn slightly excavated in the umbilical region. The shell is usually black in color, and under the microscope shows no distinct structure, from which it may be inferred that it was conocephalous in texture. It is thicker than the shell of *Zonites priscus.*

This species is found along with *Pupa Vermilionensis,* and was discovered by Bradley, who was, however, at first disposed to refer it to *Anomphalus* of Meek; but subsequently, and with good reason, regarded it as distinct and as a land shell. In size and general form it resembles *Zonites priscus,* though expanding less rapidly and with rounder whorls; but it is at once distinguished by its want of the somewhat coarse sculpture of that species, and by the plate which partially covers its aperture. Its nearest modern allies in eastern America would seem to be such shells as *Helix* (*Triodopsis* palliata), and *H. (Stenotrema) monodon.*

For specimens of this shell I am indebted to the persons above named as having furnished specimens of *Pupa Vermilionensis.*

6. *Strophites grandava,* s. n. (Fig. 15.)

by Dr. Carpenter.

**Description.**—Shell cylindrical, with obtuse apex. Whorls four or more. Surface covered with sharp vertical ridges,

* Modified from Bradley.
separated by spaces three times as wide. The body whorl about 4 millimeters in diameter, with about thirteen vertical ridges visible on one side. Length of a specimen probably not quite perfect, about 8 millimeters. The shell, which has disappeared, must have been very thin, and the surface remaining is smooth and shining. In general form, so far as can be ascertained from a very imperfect specimen, this shell must have closely resembled the modern Pupæ of the genus *Strophia* of Albers.

The only specimen known is from the Erian (Devonian) plant-beds of St. John, New Brunswick, which, besides affording great numbers of remains of land plants, have produced the only Erian insects as yet known. It was sent to me by Mr. G. F. Matthew, of St. John, along with specimens of fossil plants, several years ago, but I hesitated to describe it, waiting in hope of additional specimens. As these have not occurred, and I have now carefully examined the whole of the material from these beds to which I have been able to obtain access, I venture to name it as probably the oldest known land shell, the beds in which it is found being either middle or upper Erian.

If a land snail, it is larger in size and probably of higher type than any of those known from the Coal-formation. This would not be wonderful, when we consider the greater variety of surface and the high character of the vegetation, which, as I have elsewhere endeavored to show, distinguished the later Erian age in Northeastern America.

Concluding Remarks.

It may be proper to mention here the alleged Pulmonifera of the genus *Pulmonifera* described by some German naturalists. These I believe to be worm-tubes of the genus *Spirorhis*, and in fact to be nothing else than the common *S. carbonarius* or *S. pusillus* of the Coal-formation. The history of this error may be stated thus. The eminent paleobotanists Gæpbert and Geinitz have referred the *Spirorhis*, so common in the Coal-measures to the fungi, under the name *Gyromyces*, and in this they have been followed by other naturalists, though as long ago as 1868 I had shown that this little organism is not only a calcareous shell, attached by one side to vegetable matters and shells of mollusks, but that it has the microscopic structure characteristic of modern shells of this type.* More recently Van Beneden, Cenius and Goldenberg, perceiving that the fossil is really a calcareous shell, but apparently unaware of the observations made in this country by myself and Mr. Lesquereux, have held the *Spirorhis* to be a pulmonate mollusk allied to *Planorbis*, and have supposed that its presence on fossil

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* Acadian Geology, 3d edition, p. 205.
plants is confirmatory of this view, though the shells are attached by a flattened side to these plants, and are also found attached to shells of bivalves of the genus Naiadites. Mr. R. Etheridge, Jr., of the Geological Survey of Great Britain, has recently summed up the evidence as to the true nature of these shells, and has revised and added to the species, in a series of articles in the Geological Magazine of London, vol. viii.

If we exclude the alleged Palaeorbis above referred to, all the Paleozoic Pulmonifera hitherto found are American. Since, however, in the Carboniferous age, Batrachians, Arachnids, Insects and Millipedes occur on both continents, it is not unlikely that ere long European species of land snails will be announced. The species hitherto found in Eastern America, are in every way strangely isolated. In the plant-beds of St. John, about 9,000 feet in thickness, and in the Coal-formation of the South Joggins, more than 7,000 feet in thickness, no other Gasteropods occur, nor, I believe, do any occur in the beds holding land snails in Illinois. Nor, as already stated, are any of the aquatic Pulmonifera known in the Paleozoic. Thus, in so far as at present known, these Paleozoic snails are separated not only from any predecessors, if there were any, or successors, but from any contemporary animals allied to them.

It is probable that the land snails of the Erian and Carboniferous were neither numerous nor important members of the fauna of those periods. Had other species existed in any considerable numbers, there is no reason why they should not have been found in the erect trees, or in those shales which contain land plants. More especially would the discovery of any larger species, had they existed, been likely to have occurred. Further, what we know of the vegetation of the Paleozoic Period would lead us to infer that it did not abound in those succulent and nutritious leaves and fruits which are most congenial to land snails. It is to be observed, however, that we know little as yet of the upland life of the Erian or Carboniferous. The animal life of the drier parts of the low country is indeed as yet very little known; and but for the revelations in this respect of the erect trees in one bed in the Coal-formation of Nova Scotia, our knowledge of the land snails and Millipedes, and also of an eminently terrestrial group of reptiles, the Microsaurs, would have been much more imperfect than it is. We may hope for still further revelations of this kind, and in the meantime, it would be premature to speculate as to the affinities of our little group of land snails with animals either their contemporaries or belonging to earlier or later formations, except to note the fact of the little change of form or structure in this type of life in that vast interval of time which separates the Erian Period from the present day.