

Danach ist also die Grenzlinie, die die Lücke im Vorkommen von *Daudebardia rufa* in Südwestdeutschland umschreibt, im weiteren Verlauf von Dinkelscherben aus nach Süden zu mindestens westlich von Irsee (7 km von Kaufbeuren) zu ziehen.

Daudebardia rufa, eine südöstliche Art, deren Nordgrenze durch die Krim, durch Siebenbürgen, Galizien, Schlesien, Sachsen, Thüringen, Hessen bis zum Rhein sich erstreckt, erreicht um Elberfeld im Bergischen Lande ihre Nordwestgrenze 7.). Von da zieht sich ihre Westgrenze über Bonn, wo sie an zahlreichen Stellen bekannt geworden ist, zum Hunsrück. Dort wurde sie bei Neupfalz in der Nähe von Stromberg östlich des Soonwaldes und bei Simmern westlich des Soonwaldes festgestellt. Des weiteren zieht sich ihre Westgrenze herab vom Hunsrück zum Nahetal, wo sie am Rheingrafenstein bei Münster a. St. gefunden wurde. Damit reicht die Schnecke dicht an die Pforten der Rheinpfalz. Schließlich findet sie sich im Elsaß wieder. 8). — In der Rheinpfalz ist die Schnecke bisher noch nicht nachgewiesen. Dort wird in der nächsten Zeit mein Augenmerk auf sie gerichtet sein.

P. S. Inzwischen habe ich die Schnecke tatsächlich bereits für die Pfalz feststellen können, und zwar auf Lemberg.

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Air Breathing Mollusca.

A Sketch of their Development.*)

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According to our present knowledge Water must be taken as the original home of Life. There the supply of moisture necessary for

*) Read before the Malacological Society of London, December 14, 1923, and primarily intended for publication in the Proceedings of that Society, this paper was written in English and has been left in its original form.

the maintenance of protoplasmatic activity, was guaranteed. As regards the quality of water where life first began, it may be supposed that it was of equal osmotic tension with the interior of the organism. If the internal and external liquids were not isotonic, the organism will either lose its salt dissolved in the protoplasm by osmosis, or attain too high a concentration of salt. With the time of course organisms learnt to prevent this osmosis by physico-chemical, or by mechanical means. Anyhow these processes are acquisitions and the state of equal osmotic tension of cell and medium must have been the primitive condition. The water which best answers to such conditions, is sea water.

It may be taken as certain that animal life arose in the sea and that the great phyla of the Animal World originated there. All of them are represented in the sea, but only some of them have developed forms adapted to fresh water or terrestrial life, and moreover there is no single phylum peculiar to fresh water or dry land. At present the hypothesis of the marine origin of animals has been almost generally accepted and needs no further discussion here nor an enumeration of the different dissenting opinions. Also the fact that not all parts of the Ocean were equally favourable to rising life, but that living organisms were probably first formed in quiet and shallow bays with tropical temperature, must not be discussed here as it does not come within the scope of the present study. It would appear to me that as regards the *Metazoa* this view of their marine origin is strongly supported by the investigations of L. Fredericq¹⁾ and others who found that the body liquids in marine Invertebrates and of the Selachians among Vertebrates are isotonic with the sea water, while they present a higher molecular concentration than the surrounding medium in fresh water animals. This possession of a saline body liquid must be necessary for all animals, and in fresh water creatures be explained as an inheritance of their marine ancestors. Where direct osmotic exchange of body fluids with the surrounding medium occurs, the possibilities of habitat expansion are rather limited although not quite invincible as e. g. in the Mediterranean where the blood of the invertebrates shows a somewhat higher concentration of salt than in the Atlantic or the North Sea. But better chances for animal excursion into water with a different concentration of salt and also into fresh water are secured by physico-chemical or mechanical protection against the osmotic tensions. An instance for adaptation of this kind has been described by A. Rogenhofer²⁾ who found larger excretory organs in fresh water animals than in allied marine groups (Isopods,

¹⁾ L. Fredericq: Sur la concentration moléculaire du sang et des tissus chez les animaux aquatiques. Archives de Biologie. Tome XX. Liège et Paris 1904. pag. 709—730.

²⁾ A. Rogenhofer: Ueber das relative Größenverhältnis der Nierenorgane bei Meeres- und Süßwassertieren. Verhandlungen der Kaiserlich-Königlichen zoologisch-botanischen Gesellschaft in Wien. Band LV. Wien 1905. pag. 11.

Amphipods, Decapods). This enlargement of the Kidneys in fresh water animals may be taken as an expression of increased functional activity, since the detrimental dilution of the body fluids caused by steady influx of a hypotonic solution from the medium outside must be paralyzed by constant excretion of the superfluous water. In Selachians osmotic equilibrium of blood and surrounding medium is maintained by a considerable amount of urea dissolved in the body fluids but not diffusible through the semipermeable body membranes. In Teleostean fishes which have a lower molecular concentration of their blood than sea water a protection against osmotic streams, in addition to a mechanical protection has been attained by the characteristic arrangement in layers of the epidermis for Vertebrata in general except the *Acrania* (*Branchiostoma*), but absent in all Invertebrata. By these walls separating blood and water, the uppermost cell layers of which may become horny, Teleosteans have become independent from the surrounding medium in the composition of their body fluids. It is these, therefore, that have taken part in a prominent degree in the colonization of regions of the sea with deviating salt concentration and of fresh water.

But where did marine animals enter other media? They came into contact with fresh water at the mouths of the great rivers. The movement of the water, especially the tides, undoubtedly carried many forms into water with a different concentration of salt. There too may have been active migration of the more resistant species into new regions, where they met with less competition. From sea water through brackish lagunes animals have reached veritable fresh water. This way can be studied even now in a considerable number of cases.

Marine animals have reached dry land in the tidal zone. Low tide left behind it a lot of living organisms; the first step towards adaptation would be to come unharmed through the critical hours between one high tide and another. At first this was effected by the animals remaining motionless, successful as long as it was more or less protected against drying up. Soon the animal itself attempted to improve its position; but only those succeeded which could adapt their body to the different mechanical condition of the lighter air (viz. there are no *Coelenterata*, *Echinodermata* or *Tunicata* on dry land). The work performed involved a consumption of oxygen. Some animals retained a supply of water containing oxygen; but those being able to procure all the oxygen they wanted directly from the air had a clear advantage; they were more independent. The faculty of assimilating oxygen from the air either by specially developed organs or through the skin once gained was more and more improved by the animal, for oxygen was nowhere better obtainable than in atmospheric air.

The transition from a life in water to a residence in air was most easy in a moist atmosphere, where the slightest changes were required and were developed in the most natural manner. Such typical conditions are found in many existing tropical countries, e. g. especially in the

Malay Archipelago. In the damp coastal districts of those countries we still find forms from the most different phyla which still exhibit the type of marine animals nearly unchanged. Such instances are the Climbing Perch, *Anabas* (*Vertebrata*), the Land Crabs of the family *Gecarcinidae*, and *Birgus latro* Herbst (*Crustacea*), the Land Leeches (*Annelida*), and the Land Planarians (*Platyhelminthes*), etc. Most probably the development of land animals from marine ancestors has been affected on such tropical coasts.

The most simple way of transition from the sea to another medium was the direct one, i. e. from the sea through the tidal zone on the dry land, or from the sea through brackish lagunes into fresh water. Another way of changing the medium is also possible, i. e. from the dry land into fresh water, or from fresh water to land. As these animals originally also came from the sea, we then have three stages: sea water — land — fresh water, or sea water — fresh water — land. Further combinations could of course result by reimmigration to the sea. As a matter of fact all of these ways have been used by different groups, and frequently their organization still shows traces of their phylogeny.

As regards the *Mollusca* their marine origin can be taken as fairly certain. From the sea marine members of this tribe have succeeded in colonizing both fresh water and dry land. In this paper I shall only speak of those groups whose adaptation has enabled them to use oxygen from the atmosphere for breathing. It is not members of all classes of the molluscan tribe that have succeeded in this direction; only those of some groups, mostly united as *Gastropoda*, that include air breathing animals. If marine *Mollusca* of other classes happen to be thrown ashore, some of them only have adapted the possibility of protecting themselves against being dried up until the tidal wave returns.

Before entering into a definite description of air-breathing Mollusca I shall have to make a few remarks upon the general system of the classes in question; I must touch the problem of diphyletic origin of Mollusca, a view recently taken up again by H. von Jhering³⁾ but denied by most specialists on this group. But I shall not discuss here this much vexed question further than it is necessary for a grouping of air-breathing Mollusca. As regards the diphyletic origin of von Jhering's *Arthomalakia* and *Platymalakia* I am not of his opinion; yet I think he has convincingly shown the great difference of the animals usually grouped together as *Gastropoda* Cuvier. Undoubtedly his *Cochlides* and *Ichnopoda*, which, on the whole, correspond to J. W. Spengel's *Streptoneura* and *Euthyneura* are molluscan phyla which must have been differentiated from one another long ago and should best be given the full rank of classes like the *Scaphopoda*, *Acephala*, and *Cephalopoda* among the higher organized Mollusca. The *Heteropoda* and *Pteropoda*, according to von Jhering, Boas,

³⁾ H. v. Jhering: Phylogenie und System der Mollusken. Abhandlungen des Archivs für Molluskenkunde. Band I, Heft 1. Frankfurt a. M. 1922.

Pelseneer, Spengel, and others, must be included with other groups as members which have adopted pelagic life and organisation, viz. the *Heteropoda* with the *Cochlides* and the *Pteropoda* with the *Ichnopoda*. As to the question of nomenclature I prefer to retain the well known name of *Prosobranchia* Milne Edw. 1848 instead of *Cochlides* v. Jhering, because it is a well defined group, to which only the *Heteropoda* have been joined later. The other class is better named *Ichnopoda* v. Jhering (*Opisthobranchia* Milne Edw. 1848 † *Pulmonata* Cuv. 1817 † *Pteropoda* Cuv. 1804); *Euthyneura* Spengel is a synonym. According to opinion the division of the *Gastropoda* Cuvier may be varied, so long as the *Prosobranchia* and *Ichnopoda* are either regarded as classes or as subdivisions of one class; but it is certain, that two groups, separated since early times, must to be distinguished. These two groups, I take them as classes, are the only *Mollusca* which have developed air breathers.

Prosobranchia.

Both orders of the *Prosobranchia*, the *Diotocardia* and the *Monotocardia*, have developed various air breathing forms which most live on land. Among the *Prosobranchia* we are acquainted with a number of forms which prove our hypothesis that in the damp air of tropical countries there are terrestrial forms which have only slightly deviated from the type of subaqueous species. In the East Indies and the adjacent Pacific Islands the genus *Neritodryas*, that lives on trees, has its nearest relations living in brackish or fresh water. In addition to that it is reported that some Polynesian species of typical *Nerita* behave in the same way. It is on the sea shore, that marine shells come in touch with air and that representatives of various families have probably begun to adapt themselves, as an early attempt to terrestrial life, to the tidal zone and its characteristic features. Thus certain forms of *Patellidae* are able to store and to consume air in their mantle cavity which serves as a lung. In the genus *Cerithidea* belonging to the family *Cerithidae*, which lives on the sea shore and almost exclusively out of water, the gill is rudimentary, but salient vascular arborizations are present. Similar adaptations will be more widely spread than is usually supposed, especially in the tropics. The majority of species in the Monotocardian family *Littorinidae* also furnish a direct example of adaptation in the tidal zone; regardless of their gills, organs for respiration in water, they are always found in localities with damp and humid air; apparently many species of *Littorinidae* are able to admit both water and air into their breathing cavity. Undoubtedly these forms of the tidal zone which occur in different families of *Prosobranchia* are the point of departure for the terrestrial forms proper, most of which have lost their gills, and can only consume air in their breathing cavity.

Among the *Diotocardia*, three families, *Hydrocaenidae*, *Helicinidae* and *Despoenidae* have lost their gills, and can only con-

sume air in their breathing cavity. All of them are probably derived from forms at least nearly allied to the *Neritidae*, but should have developed independently from one another. They also differ in the degree of adaptation to terrestrial life. The *Hydrocaenidae* are generally found in the tidal zone, thus indicating their origin; but the genus *Georissa* has left its place of origin for the interior of the country, and has been found in the Khasi Hills, Assam, even at an altitude of 4.000 ft. The *Helicinidae* which are chiefly found in tropical countries, are perfectly adapted to terrestrial life; they occur together with other land shells of different origin. The *Despoenidae* have deviated more from the primitive type than most *Diotocardia*, and they have been most perfectly adapted to terrestrial life. They have even lost their operculum and instead furnished the interior of their shell with lamellae, a feature not found in an other terrestrial Prosobranch. There should be a connection in the development of these organs, but it is not clear which of them has taken precedence. Theoretically it might well be that the operculum which prevented the animal from adhering to the subsoil when it withdrew into the shell, was first reduced, and later on the aperture of the shell was narrowed to protect the animal from drying up, or against the ravages of enemies. In these lamellae they would have an advantage in enabling the animal to regulate the moving of the shell from all sides; but just this may have been the primary requirement, and, once developed, it may have secondarily made superfluous the operculum which was at once a protective organ and an obstacle to adhesion.

Here a few notes on the operculum may be added which relate to all terrestrial *Prosobranchia*. In changing from water to land all of the species kept it, except the *Despoenidae* just mentioned. It not only protects animals of the damp atmosphere mechanically, but also materially prevents their being dried up. How important this is can be seen from the fact that organs which prevent desiccation have been developed by *Prosobranchia* of extremely different types of adaptation. The most striking example is the Monotocardian species *Palaina mirabilis* v. Moell., and some forms related to it, in which the ribs on the last whorls of the shells have become widely spread, enlarged and vesicular, being thus virtually turned into water reservoirs. In such *Prosobranchia* in which the aperture is entirely closed by the operculum, but to whom on the other hand air is necessary for breathing, special adaptations have been developed, either by the shell becoming penetrable for air to a certain degree (e. g. *Pomatias elegans* Müll. and others), by the forming of holes in the peristome (e. g. *Pupina* and others), or the development of a remarkable sutural tube on the exterior of the last whorl, near the aperture (as for instance *Spiraculum*, *Pterocyclus*, *Opisthoporus*, also, but less pronounced, in *Alycaeus*). The operculum becomes a distinct disadvantage in climbing animals, where on the animal returning into its shell it prevents any adhesion to the point of attachment and would cause the

animal to drop. As a consequence many, probably most terrestrial *Prosobranchia* have remained ground living animals, e. g. *Pomatias elegans* Müll. But by special adaptations a number of species have surmounted even this difficulty and become tree living animals. Thus in *Cochlostoma* Jan (= *Pomatias* auct.) that part of the sole of the foot which, when the animal withdraws, fills the aperture of the shell, is furnished with two mucous glands, secreting two broad mucous bands which are pressed out from between shell and operculum and harden in the air; with this substance *Cochlostoma* sticks to rocks and trees, and is thus able to exist away from the ground.

All the land shells last mentioned are already *Monotocardia*, this order including the bulk of operculate land shells. The family *Truncatellidae* which have retained well-developed gills in their breathing cavity, are essentially shore forms and never venture far inland; their origin is not quite clear yet, but they are possibly allied to the *Rissoidae* or some related group. From the *Truncatellidae* the *Geomelaniidae* must have been directly derived; they are not restricted to the coastal zone, but have ascended the Antillean mountains. It is not known to me whether they still have gills, but their reduction is quite possible. The *Acmeidae* which are already in possession of a pleural cavity without gills, have possibly a similar origin as the *Truncatellidae*. They are minute shells belonging to the European fauna, living a hidden life under decaying wood in a humid atmosphere. Of course they cannot compete with other land shells in the colonization of places with dry air, and are no better adaptations to a terrestrial life than the *Truncatellidae*. Only their mode of life in decaying material enable them to go far inland; therefore they are always minor forms, as contrasted with the *Truncatellidae*.

From the *Hydrobiidae* are probably derived the *Assimineidae*, a family furnished with a pleural cavity without gills and therefore exclusively air breathers. The species of the genus *Assiminea* are purely inhabitants of the sea shore and never go far inland; they still unmistakably exhibit their origin. The genus *Acmella*, however, leaves the coast for the interior and has even gone up into mountainous districts. There the species of this genus live under moss and decaying material.

There are three terrestrial families of *Monotocardia* which in all probability must be derived from the *Littorinidae* where the formation of land forms was still indicated; at least a common origin for all of them may be supposed. These families are the *Realidae*, *Pomatiasidae* and *Annulariidae*, all of them pure air breathers, without gills and probably nearly related to one another. The *Realidae* appear to me the most primitive; but no final decision can be arrived at without a close comparative study of the anatomy of the families in question.

The same must be said of the *Cyclophoridae*, *Aperostomatidae*, *Alycaeidae*, *Pupinidae*, *Craspedopomatidae*, *Cochlostomidae* and *Diplommatinidae*. According to current view these families are nearly

related to each other, and are often united as subfamilies of a great family *Cyclophoridae*. Their origin cannot be stated with certainty, but it would appear to have been also somewhere near the *Littorinidae*. With regard to the formation of families with small forms such as the *Diplommatinidae* a derivation from some forms related to the *Rissoidae* or *Hydrobiidae* is not at all improbable. I do not however, believe in their descent from fresh water *Prosobranchia* of the *Viviparidae* group, as has been supposed by some authors. The families of air breathing *Prosobranchia* mentioned are all distinctly terrestrial animals which have lost their gills in their breathing cavity; they have moreover developed the most different adaptations to the difficulties of terrestrial life.

Among air breathing *Prosobranchia* there is also one family of fresh water shells, the *Ampullariidae*, which inhabit the tropics. Their respiratory cavity is divided; they possess a true branchial cavity with well developed gill, which however, by an opening in its roof is connected with another cavity which is a protrusion of this roof and is furnished with a vascular capillary system thus serving as a pulmonary sac. In this way the species of *Ampullariidae* are able to breath atmospheric air and to live in such water ponds where, in consequence of their poor supply of oxygen, other animals breathing by gills alone cannot exist. This curious development of a double mode of respiration may have been developed by the invasion of such water. The breathing of atmospheric air is an acquisition which these shells have in common with a number of animals with analogous ecological derivation, viz. many fishes. The origin of this family has not yet been traced with certainty; it seems most probable to me that they are a branch from a stock related to the *Naticidae*, that had emigrated from the sea into fresh water; those in expanses of water poor in oxygen may finally have acquired double respiration.

Ichnopoda.

In the Ichnopoda two well defined orders have become air breathers, viz. the molluscs commonly united as the *Pulmonata*. With our present knowledge however this group can no longer be a phylogenetic unit but merely a biological one. It embraces two different orders of *Ichnopoda*, whose separate origin has been repeatedly maintained, a view pronounced most clearly and definitely by von Jhering in his papers on the phylogeny of molluscs. The new names *Branchiopneusta* and *Nephropneusta*, however, are absolutely identical with the old terms *Basommatophora* and *Stylommatophora* which should be adopted, although originally proposed for subdivisions of *Pulmonata*, at present no longer a systematical unit.

Basommatophora.

In all probability the *Basommatophora* are closely connected with the marine Ichnopod order *Tectibranchia* (= *Steganobranchia*

v. Jher.). By inversion their mantle forms a mantle cavity which corresponds to the pleurome of the *Tectibranchia*; originally this mantle cavity was a branchial sac; in some genera it even now contains one or more gill blades. By adaptation to air breathing this branchial sac was transformed into lungs by the rich vascularization of its walls. The primitive *Basommatophora* are animals of shore and tidal zones; of the known forms the *Siphonariidae* may have best preserved the original type; the *Siphonariidae* and *Gadiniidae* have, therefore, even been placed as an aberrant branch among the *Tectibranchia*. The respiratory sac of the *Siphonariidae* still contains a gill, but is, however, with its well vascularized walls, also used for air breathing. It is to be supposed that the *Gadiniidae* are closely related to the *Siphonariidae*; they have already lost their gills. The *Siphonariidae* are mostly found in the zone of high water mark, the *Gadiniidae* on the other hand occur between tide marks; the latter are probably primitive as regards their habitat in spite of their more developed respiratory organs. Although, as an unique instance of an operculate Ichnopod, the *Amphibolidae* possess an operculum in the adult stage, a feature often found only in larval forms of this class (e. g. *Siphonaria*), they must be placed near the two families just mentioned. The representatives of this family live in brackish water in the estuaries of rivers which they have probably reached from the tidal zone, where in touch with atmospheric air they may be transformed into air breathing animals. Their respiratory sac is already devoid of gills.

A great variety of shore forms is displayed by two further Basommatophorine families, the *Ellobiidae* and the nearly allied *Otinidae*; so far as I know, their respiratory sacs show no trace of gills. They have certainly been transformed into air breathers in the shore zone. The majority of genera of this group, *Melampus*, *Plectotrema*, *Phytia*, *Pedipes*, *Otina*, and others still live there. But some *Ellobiidae* have successfully tried to extend their habitat; the species of the genus *Scarabus* for instance are typical land shells living under dead leaves in woods near of water. On the other hand there are *Ellobiidae* which have reverted to shallow brackish or sea water, such as most species of *Cassidula* and *Ellobia*; this aquatic mode of life should be a secondary phenomenon, else the acquisition of air breathing could be hardly explicable, and their allies of the tidal zone make this process still more probable.

The family *Carychiidae* which holds about the same biological and probably systematic position to the *Ellobiidae* as the *Acmeidae* do to the *Truncatellidae* among terrestrial *Prosobranchia*, left the sea coast and have become mere land forms. Like the *Acmeidae* the *Carychiidae* are diminutive forms which live in humid air, and are found hidden under moss and decaying wood and leaves. One of their genera, *Zospeum*, has colonized the subterranean caves of Central Europe, and become blind.

But the *Basommatophora* have not developed such pronounced land shells as have the *Prosobranchia*; their attempts have been cut short at the *Carychiidae*. They have, however, developed a series of other air breathers, the different forms of fresh water lung-mollusca. It has been much disputed whether they are descended from aquatic or terrestrial ancestors. The fact that, with the exception of some imperfect forms, mostly enumerated above, there are no representatives of the *Basommatophora* on dry land, was in favour of a derivation from aquatic forms, but their respiration of air was against it, for which the development of conditions similar to the ones which led to the formation of air breathers as *Ampullariidae* can hardly be supposed. My own view is that all the ancestors of fresh-water lung-shells have adopted air breathing in the tidal zone. Later on they may have lived, as many *Ellobiidae*, in the overflowed parts of the tidal zone and have there become adapted to brackish water; thence they have gone up into river estuaries and at last reached pure fresh water. Certain members of the families in question still go into brackish water now. Even in temperated zones, as in Europe, *Lymnaea* for example ventures into the brackish districts of the Eastern parts of the open Baltic. I suppose that phylogenetically fresh water lung-mollusca are nearly related to the shore forms among the *Basommatophora*. Quite recently this view has been emphasized again by C. Hedley, who supposes an Ellobiid ancestry for *Lymnaea* ⁴). The families in question are the *Chiliniidae*, *Physidae*, *Latiidae*, *Planorbidae*, *Ancylidae* and *Lymnaeidae*. It remains doubtful whether all of them have directly descended from the *Ellobiidae*. The *Otiniidae* and perhaps some more forms no longer existing, may have had their share in the formation of fresh water lung-mollusca, as for instance that of certain *Latiidae*. Phylogenetically the most distant group may be the *Chiliniidae*. The remaining families are nearly allied to one another, and I think they are not yet clearly separated from each another. Thus the anatomy of the genus *Isidora* shows closer relationship to some *Planorbidae* than to the *Physidae*. The *Ancylidae* and *Latiidae* must be representatives of different families, which exhibit a simple patelliform shell. But only close anatomical studies will give final results here. Most of the forms of these families breathe atmospheric air at the surface of the water. They have developed a true pulmonary cavity, which, however, still contains gills in certain genera (e. g. *Isidora*, *Miratesta*, *Protancylus*). All of these molluscs whose ancestors in the tidal zone have once acquired the faculty of breathing air, preserve this adaptation as much as possible, and only abandon it in emergencies. Thus in the depths of Alpine lakes the *Lymnaeidae* have reacquired aquatic breathing, apparently because procuring air at the surface of the water was too difficult or even

⁴) C. Hedley: Has *Lymnaea* an Auricoloid Ancestry? Proceedings of the Malacological Society of London. Vol. XII. London 1917. pag. 125-126.

impossible, when the waves were going high. Their respiratory sac is filled with water and its vascularized walls take the oxygen suspended in water as in their ancestral forms did from atmospheric air; there are no gills and no secondary ones in these *Lymnaeidae*. In countries with winter climate where air breathing lung-mollusca are hidden in mud during winter times and not in touch with atmospheric air, they probably take up from the water the oxygen necessary for their diminished functions of life through the skin.

The independence from water as a breathing medium caused by the development of aerial respiration has also enabled certain air-breathing fresh water lung-mollusca to quit the water and to live a terrestrial life in humid places. This has been reported of the water-frequenting mollusc *Galba (Galba) truncatula* Müll. *Brondelia gibbosa* Bourg., belonging to the *Ancylidae*, is an inhabitant of moist rocks in the Algerian forests. On tropical islands with a moist atmosphere a departure from the water is still more easily possible, as mentioned above. Thus *Lantzia* lives in moss in the mountains of the island of Réunion.

Stylommatophora.

The phylogeny of the *Stylommatophora*, the second air breathing order of the *Ichnopoda*, is still a much debated problem; it need only be discussed here, however, so far as is necessary for the present researches. Attempts have been made to derive them from the various groups of marine *Ichnopoda*; personally I am inclined to trace their descent from the *Phanerobranchia* as the most likely, especially on account of the structure of the liver which, as von Jhering has pointed out, is composed of a larger posterior portion and two minor interior ones, with a corresponding number of bile-ducts. This same arrangement as in the Phanerobranch family *Aeolidiidae* is found in primitive *Stylommatophora*, such as the *Onchidiidae* and the *Veronicellidae*. Between the *Stylommatophora* and the *Basommatophora* there is no direct connection. Also as regards the ability to breathe atmospheric air, the respective organ in *Stylommatophora* has probably an origin different from the one in *Basommatophora*. In no single instance have traces of gills been found in the respiratory organ of the *Stylommatophora*. Without entering into a detailed discussion of the various respective theories I should mention here that, according to our present knowledge of the organisation of these animals, derivation of the respiratory organ of the *Stylommatophora* from the lower end of the ureter in connection with an adaptive change of function, a view maintained by von Jhering, appears at last possible, if not probable, although further investigations seem to be necessary for its confirmation. The biological conditions which have led to the development of terrestrial *Stylommatophora* may well be harmonized with von Jhering's explanations.

Again archaic *Stylommatophora* are found in the tidal zone, where they have developed air breathing. In these primitive forms the ancestral organisation is clearly enough recognised and well agreeing with von Jhering's theory; in higher *Stylommatophora* this is much less so. Primitive families are the *Onchidiidae*, *Rathouisiidae* and *Veronicellidae*, usually united as *Soleolifera*. Among other things some of them have not yet developed retractile ommatophores, which is a special adaptation to life on dry land. Most of the *Onchidiidae* are amphibious inhabitants of the tidal zone, a number of species having already become more independent of water; on the contrary other forms have returned to a more aquatic life than their ancestors which first developed air breathing. *Rathouisiidae* and *Veronicellidae* are decidedly terrestrial forms; they have gone far inland, but as a whole prefer humid places. In spite of this both families which are distinctly differentiated from each other, have preserved more primitive conditions than have the *Onchidiidae*, in the last named family the pulmonary cavity and the kidney being secondarily separated and the kidney opening into the posterior gut. Apparently these families are not the ancestors of higher *Stylommatophora*, but side branches of the main stem. Recently again G. Colosi has tried to separate these families entirely from the *Stylommatophora* as a result of comparative anatomical studies of their respiratory organs which had led him to suppose for them an independent descent.⁵⁾ If this assumption should be confirmed, the *Ichnopoda* would of course have given rise to terrestrial forms in three instead of two separate groups. The general considerations of this paper would remain unchanged.

The *Athoracophoridae* are terrestrial *Stylommatophora* living inland, but mainly in damp localities; they are distinguished by a number of special adaptations of which only the breathing apparatus will be discussed here. The vascular system of their lungs has developed a dense network which has so much enlarged at the expense of the respiratory sac itself, that Plate has made a special group of this family, the „*Tracheopulmonata*“ in contrast to all of the remaining forms or „*Vasopulmonata*“. Although this is probably an exaggeration, I must regard the *Athoracophoridae* as an aberrant Stylommatophorine group.

As to their respiratory organs the higher *Stylommatophora* form a rather uniform group. All of them are merely terrestrial shells, widely distributed in all continents. According to their varied habitat, they have developed all kinds of adaptations, even more so than have terrestrial *Prosobranchia*. In many groups there is a tendency for the secondary development of slug forms, which possess a more easy and rapid mode of locomotion. Carnivorous forms in different stages

⁵⁾ G. Colosi: Sul Sistema dei Gastropodi. Bollettino dei Musei di Zoologia ed Anatomia comparata della R. Università di Torino. Vol. XXXVI. Nr. 737 Torino 1921. pag. 1-7. 1. Tav.

of this adaptation that were formerly erroneously united systematically, have cropped up in various families. As regards classification, the higher *Stylommatophora* are grouped most naturally according to their renal anatomy as H. A. Pilsbry has pointed out. There are three groups *Orthurethra*, *Heterurethra* and *Sigmurethra*.

The *Orthurethra* are the most primitive. The oldest forms of this group are usually of small size and often live a hidden life in moist places under moss or decaying leaves and wood (*Pupillidae*, *Valloniidae*, *Cochlicopidae*, *Tornatellinidae*). In the damp climate of the Pacific islands larger forms were developed (*Partulidae*, *Amastriidae*, *Achatinellidae*). The larger forms from dry climates are probably the most recent branches of this group (*Enidae*, probably derived from *Pupillidae*).

It may be supposed that both, *Heterurethra* and *Sigmurethra* have sprung from an Orthurethrid ancestry. Most forms of the Heterurethrid family *Succineidae*, as a special adaptation, have colonized the moist banks of inland waters. A few of them, probably archaic forms (e. g. *Succinea (Lucena) oblonga* Drap. in Europe) were even able to live at a distance from water.

The *Sigmurethra* embrace the great bulk of terrestrial *Ichnopoda* and the most striking types. They have adapted themselves to all kinds of adverse conditions of terrestrial life better than any other molluscan group. Hence at present they have a very wide distribution on dry land. It will not be necessary to enumerate their various families here as the structure of their respiratory organs is uniform; therefore in this paper they can all be treated together.

After having discussed the different forms of air-breathing *Mollusca*, we find in recapitulating the facts presented in this paper that quite different conditions obtain within these two branches, the *Prosobranchia* and the *Ichnopoda*. In the *Prosobranchia* families of most heterogeneous origin have developed air-breathing forms, in some of them the attempts have been cut short in the beginning, whereas others have made such progress as to enable them to develop highly organized land forms which have colonized wide tracts of dry land. In the *Ichnopoda*, on the contrary, only two orders have tried to adopt a terrestrial mode of life. The *Basommatophora* acquired air breathing in the tidal zone, but have not succeeded in the formation of highly specialized land forms, only species inhabiting moist places being known; they have, however, colonized fresh-water and competed there with gill-breathers, but have retained the faculty once adopted of breathing atmospheric air. The *Stylommatophora* have made rapid progresses in the production of terrestrial forms and have adapted themselves to the most different conditions. As regards age terrestrial *Prosobranchia* would appear to be older than terrestrial *Ichnopoda*; I should think that quite a number of fossil forms, especially the older ones, hitherto classed with the *Ichnopoda*, will, on renewed examination, be proved to belong to the *Prosobranchia*.

In concluding this paper the great advantage must be noted again which terrestrial animals enjoy as compared with those living in water on account of the oxygen at their disposal being in a more abundant and concentrated form. In one liter of water 7 ccm of oxygen are dissolved, but the same amount of air contains 207 ccm. This circumstance allows land animals either to do with a smaller breathing surface or to materially increase the intensity of their metabolism, which in turn produces a greater activity, in many groups which have become terrestrial. Thus, where animals, from any reason, have adopted air-breathing, they usually firmly stick to it, and even if they should return to the water (secondary aquatic animals), they only give it up in cases of emergency, as for instance the *Lymnaeidae* from the depths of Alpine lakes as mentioned above; on the contrary they occasionally, and in addition to their faculty of breathing atmospheric air, have acquired a fresh mode of aquatic respiration as in certain sea-serpents and marine Chelonians which have developed a superficial network of capillaries on the jaws and in the mouth. In terrestrial *Mollusca* there is no increase in metabolism nor vivacity, but they manage with a much smaller respiratory surface than do their gill-breathing relatives. As respiratory organs for breathing air they either use the mantle cavity, which is only slightly enlarged, or, as in the *Stylommatophora* of the *Ichnopoda*, a similar respiratory organ probably developed from the end piece of the ureter by change of function. The breathing surface is thus distinctly reduced by the atrophy of the gills with their greater total surface; in addition to this the transport of breathing air in changing it into the breathing cavity is rather badly organized. Where, as in different terrestrial *Ichnopoda*, and especially in some slugs, an increased activity is observable, these animals either have a reduced shell or no shell at all and are therefore more mobile, since they do not carry so much dead weight.

Mikrolepidopterenfauna des Gouvernements von Stavropol (Russland, Ciscaucasien).

Von

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(Mit 1 Tafel.)

Im Sommer 1920 und 1921 hatte mein Bruder, J. Filipjev, ehemaliger Professor der Zoologie am Stavropolschen landwirtschaftlichen Institut, sich sehr eifrig dem Sammeln von Schmetterlingen ge-

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Zeitschrift/Journal: [Archiv für Naturgeschichte](#)

Jahr/Year: 1925

Band/Volume: [91A_1](#)

Autor(en)/Author(s): Boettger Cäsar Rudolf

Artikel/Article: [Air Breathing Mollusca 81-94](#)