

it, to say the least, no support, but rather are deemed by one competent to judge to be decidedly adverse to what is here claimed.

The palæontological contradiction shown in the plants and animals of the Fairplay beds is not unknown to American geology, as every one is aware; but I do not know that it has been pointed out in this country at this horizon or in this direction—the discordance appearing later in time and the plants indicating a younger and not an earlier age than the animals. An exactly parallel case appears to be shown in Eastern Russia, for in discussing the poorer strata of Kargalinsk, which he refers to the Permian, Twelvetrees says, "As regards the flora [eleven species] the list has a Palæozoic aspect, but a Secondary one as respects the reptilian remains" [four species cited]*.

Exploration of the locality will continue, and it is hoped that future material may throw more light upon the question. It may, however, be added that the few other insects found appear to have no Palæozoic relations whatever.

XXXII.—On the Affinities of the Onchidia.

By Dr. R. BERGH†.

THE remarkable group of marine or amphibious Ichnopod Mollusca which has long been known under the name of *Onchidium* has often given rise to scientific controversies, which of late years have also had relation to the affinities of these animals, and consequently to their position in the system.

In their external characters these animals strongly resemble the Doridæ; like these they are also marine or amphibious, and they belong, like the Doridæ, chiefly to the Indo-Pacific marine regions. When closely examined as to *their internal structure*, however, the *Onchidia*, notwithstanding the "opisthobranchiate" position of the heart, prove to be very different from the Doridæ, and rather agree with the Pulmonata, even to the extent of being furnished with lungs. For this reason, although Blainville placed the *Onchidia* (*Peroniæ*) near the Doridæ in the group Nudibranchiata, most investigators and systematists since Cuvier and Férussac have referred them to the Pulmonata.

Very recently, as already mentioned, a very interesting

* Quart. Journ. Geol. Soc. Lond. xxxviii. p. 495.

† Translated from the 'Morphologisches Jahrbuch,' Band x. pp. 172-181.

controversy as to the systematic position of these animals has broken out. H. von Ihering, as is well known, has adopted a former notion of Milne-Edwards (1857), and has endeavoured to demonstrate that the so-called lung of the *Onchidia* in its principal mass morphologically represents the dilated terminal section of the kidney of other marine Ichnopoda, or a cloaca. According to Ihering, therefore, the *Onchidia* would be the lowest forms, the stem-forms, of his so-called "Nephropneusta" (stylommatoporous Pulmonata), and should perhaps be incorporated with the order Pulmonata; but they come near to the marine naked Mollusca*, and from these (especially perhaps the Phanerobranchia) the *Onchidia* should be derived.

There is, however, much to be urged against this theory of Ihering's, as has, indeed, already partly been done by Semper†. Semper's objections are directed principally against Ihering's derivation of the lung of the "Nephropneusta" from a terminal section of the kidney of the Phanerobranchia, and he demonstrates that the walls of the pulmonary cavity of the *Onchidia* contain no urinary concretions, and consequently cannot belong to the kidney, which, on the contrary, is enclosed by the lung. This kidney also consists of the two typical sections, the true kidney with the urine-chamber and the urinary duct; close by there is a pulmonary cavity, which, consequently, cannot represent the terminal section of the kidney. The lung, according to Semper, has not originated from the kidney of the Phanerobranchia, but is (as in the other Stylommatophora) a branchial cavity adapted for aerial respiration, which has been developed from the branchial lung of the Basommatophora. In the characters of the generative organs of the *Onchidia*, moreover, he finds a confirmation of his conception of the affinities of these animals, which he regards as Pulmonata.

To the derivation of naked Pulmonata (such as the *Onchidia*) from shell-bearing forms there is, on the whole, nothing to be objected, especially within this group. So many transitional forms occur here, from animals with a large external shell which can contain the whole animal, to those with a rudimentary shell which cannot conceal the animal (*Testacella*), and, further, to those with the shell

* H. von Ihering, 'Ueber die systematische Stellung von *Peronia*,' 1877, p. 30. See also 'Anatomie des Nervensystems und Phylogenie der Mollusken,' 1877, p. 223:—"We might perhaps with equal justice refer them to the Phanerobranchia as to the Nephropneusta."

† Semper, "Einige Bemerkungen über die Nephropneusten, v. Ihering," in Arb. zoolog. zoot. Institut in Würzburg, iii. 1877, pp. 480-488.

small and half-concealed (*Parmacella*) or quite internal (*Limax*). Even within the different groups of the Stylomatophora naked and shelled forms occur side by side, as *Limax* and *Vitrina*, *Arion* and *Helix* *. And now, since a shell has been demonstrated in the larva of *Onchidium*, that difficulty no longer exists.

Thus, in a monographic memoir by Joyeux-Laffuie †, the developmental history has recently been described, not indeed of a typical *Onchidium*, but of *Onchidium celticum*. From the author's description it appears clearly that the animal, as a larva, possesses a shell, which is afterwards cast off. As regards the other anatomical characters of the animal, Joyeux-Laffuie especially points out that *Onchidium* "possesses no organ representing the pulmonary or branchial cavity;" the so-called lung is only the cavity of the true kidney, the vascular system of which is also inserted into the venous circulation in the manner characteristic of the Mollusca generally; but nevertheless the organ does function as a lung ‡. At the same time, however, he represents as the most essential the respiration by means of the papillæ of the skin (which are branched in many *Onchidia* [*Peronia*]), and has also demonstrated in them a strong vascular development § (as already asserted by Ihering in opposition to Semper); and, moreover, he has experimentally proved the predominant importance of this cutaneous or branchial respiration ||. Joyeux-Laffuie further indicates the agreement of the *Onchidia* and the Pulmonata in the structure of the nervous system and of the digestive organs, and on the whole regards the *Onchidia* as "marine branchiferous Mollusca with a tendency towards pulmonary respiration and a terrestrial existence." It is therefore essentially rather upon physiological than morphological grounds that the author nevertheless places the animals with the Pulmonata, at the same time referring to Forel's well-known observations upon the *Lymnææ* of the Lake of Geneva (*L. abyssicola*).

Of Joyeux-Laffuie's monograph Brock ¶ has given a detailed report, to which he has appended a critical examination, through which, however, he comes to quite other conclusions than those of the French author. According to him

* H. von Ihering, *loc. cit.* p. 33.

† Joyeux-Laffuie, "Organisation et développement de l'Oncidie," Thesis in Paris, 1882, pp. 1-159, and Arch. de Zool. expér. et génér. x. (1882) pp. 225-383, pls. xiv.-xxii.

‡ *Loc. cit.* p. 148 (372).

§ *Loc. cit.* p. 53 (277), pl. xv. fig. 4.

|| *Loc. cit.* p. 56 (280).

¶ J. Brock, in Biol. Centralbl. iii. 12, 1883, pp. 370-374.

the resemblance in the structure of the nervous system and reproductive organs which the *Onchidia* present especially to the basommatophorous Pulmonata is of quite a superficial nature; while he also ascribes no importance to various other anatomical characters of the *Onchidia* which also occur in the Pulmonata, either because they (such as the position of the seminal duct) occur "only" in atypical Pulmonata (*Vaginalus*), or because they (such as the position of the typical eyes) have originated in another way than in the Pulmonata*. With regard to the kidney, Brock is of opinion that "wherever we may begin with the phylogeny of the Pulmonata, the kidney of the *Onchidia* is a true kidney, and only in its adaptation to aerial respiration engaged in a change of function, which, even if we regard the organ as in course of becoming a lung, certainly has nothing to do with the analogous adaptive phenomenon in the Pulmonata." With regard to the affinities of these animals, however, the developmental processes as displayed by Joyeux-Laffuie seem to him to be quite decisive. Unfortunately this ontogeny, which is so interesting on its own account, has for the moment the less interest, because the *tertium comparationis*, or complete developmental history, embracing the first stages, of one of the so-called Nudibranchiata, is, so to speak, completely wanting. Here, however, the strong development of the velum in the larvæ of *Onchidium* must on no account lead us to hasty conclusions; Semper† has already stated that the larvæ of "different species of the genera *Auricula* and *Scarabus*, which belong to the Pulmonata, bear opercula;" and in the (still unpublished) sketches of the larvæ which Semper has sent to me the larva bears a large velum, exactly like the *Onchidium*-larva, to which ‡ Semper's figures present a great resemblance§. The Pulmonate nature of *Scarabus* can, however, hardly be doubted||. Ihering is certainly, at least for the present, partially justified in expressing himself¶ against the over-estimation of ontogeny in the interpretation of phylogenetic relations and in classification, and, in opposition to both Hæckel and Semper, placing comparative anatomy in the foreground in the discussion of such questions. From his whole revision of the above-mentioned work Brock concludes that *Onchidium* is "a Nudibranchiate,

* Brock, *loc. cit.* p. 372.

† Semper, 'Die natürlichen Existenzbedingungen der Thiere,' 1880, ii. p. 101. English edition, p. 282.

‡ See Joyeux-Laffuie, *l. c.* pl. xx. figs. 8, 9, pl. xxi. figs. 1-3.

§ See also Ihering, *Vergl. Anat. d. Nervensyst.* 1877, pp. 203, 221.

|| Semper, *loc. cit.* i. 1880, p. 238.

¶ Ihering, 'Ueber die syst. Stellung von *Peronia*,' 1877, pp. 37, 38.

perhaps aberrant in certain points," and in process of becoming an air-breather*.

Against this conception of *Onchidium* as a Nudibranchiate, comparative anatomy must, I think, enter an absolute protest. From the outwardly superficially similar Doridæ these animals are very widely separated; and, indeed, there is no single group of that order, rich as it is in forms, to which the *Onchidia* closely approach, or from which they could naturally be derived, not even the Ascoglossa, with their varying nervous systems. An alliance with, or derivation from, the Steganobranchiata (Tectibranchiata) would certainly be much more possible. *Comparative anatomy, however, must quite decidedly claim the Onchidia as Pulmonata.* The examination of a large new *Onchidium* (*O. melanopneumon*, Bgh.) from the Pacific (Fiji Islands), brought home by the 'Challenger' expedition, as well as that of other *Onchidia* (*O. tonganum*, Q. & G., *O. verruculatum*, Cuv.), has taught me nothing else †.

The central nervous system of the *Onchidia* agrees with none of the types occurring in the Nudibranchiata, at any rate there is only a superficial resemblance to the Ascoglossa, which are otherwise so distant (and derived from the Steganobranchiata). It is almost unintelligible how Ihering could see here "exactly the same type of the nervous system that is displayed by the Æolidiæ and Doridæ." On the contrary, *the nervous system of the Peroniæ does not differ essentially from that of the Pulmonata.* In the latter, as is well known, it consists of two superior cerebral ganglia, two inferior pedal ganglia, and several (up to 5 or 6) ganglia placed more or less unsymmetrically below the latter, and belonging chiefly to the visceral nervous system. The nervous system of the *Onchidia* is also of this kind, only with the lowermost part more condensed and reduced.

The central nervous system‡ of *Onchidium tonganum* appears, when still enclosed in its sheath, as a broad ring, of which the upper and lower arches are strongly flattened;

* Brock, *loc. cit.* p. 372.

† R. Bergh, "Report on the Nudibranchiata," in Reports on the Scientific Results of the Exploring Expedition of H.M.S. 'Challenger,' &c., vol. ix. 1884, pp. 126-150, pl. iv. figs. 25-27, pl. v. figs. 1-27, pl. vi. figs. 5-21, pl. vii. figs. 1-12, and pl. viii. fig. 14.

‡ From want of material I was unable accurately to define the central nervous system of the *Onchidia* formerly investigated by me (*loc. cit.* pp. 130, 141, 147), and the preceding investigations (see Ihering, *l. c.* p. 230, Taf. iv. fig. 16) are scarcely of any use. I have therefore resumed this investigation upon two large specimens of *O. tonganum*, Q. & G., from the Nicobars. The relations of the ganglia were perfectly in accordance in both individuals.

where these arches meet together there occurs a strong thickening (cerebral ganglion), and the inferior arch, which is the further back, is thicker than the upper one, and penetrated by a strong extramedian (right) artery. It is very difficult to prepare the nervous system, which appears in all parts yellow or brownish yellow, out of the whitish firmly adherent sheath, which is continued to a considerable distance around the thicker nerves. The ganglia are all coarsely nodular, the nodules projecting strongly at the surface, sometimes pedunculate. *Cerebral ganglia* of rounded triangular form, somewhat flattened. The intercerebral commissure thin, sometimes scarcely occupying one sixth of the breadth of the superior ring, longer than the transverse diameter of the ganglion. The left cerebro-pedal connection is very short, the right one much longer. The left *pedal ganglion* is larger than the right one, which is submedian in position; both flattened, of oval form, giving off three or four strong *nervi pediaci*; the pedal commissure short*. Behind and beneath the preceding ganglia lie the three *visceral ganglia* quite unsymmetrically. The largest and rather thick right one is united almost directly by a very short cerebro-visceral connective with the cerebral ganglion, and by a viscero-pedal connective, which unites with the cerebro-pedal connective, with the right pedal ganglion. The *right* visceral ganglion is united by a short commissure with the *median* (genital) ganglion, which is also situated to the right, and it is also connected with the left ganglion by a long and powerful commissure; behind the last-mentioned commissure lies the much thinner subcerebral commissure, which may be traced into the cerebral ganglia. The *left* visceral ganglion is more depressed than the others, and is connected with the cerebral ganglion by a tolerably long connective, and with the pedal ganglia by a somewhat shorter one. As in the Pulmonata, so also here the *gastro-æsoophageal ganglia* which always occur in the Dorididæ (perhaps with the exception of many *Polycerata*†) are *deficient*.

The *ophthalmophores* of the *Onchidia* are like those of the stylommatophorous Pulmonata, and such as occur elsewhere in no Gasteropoda. If it should really be the case, as Joyeux-Laffuie states (*l. c.* p. 141 [365]), that the *eye* here is first of all formed on the head, and only ascends afterwards with the ophthalmophore, while in the Stylommatophora it is deve-

* A doubling of this commissure, such as is described by Joyeux-Laffuie in *O. celticum* (*l. c.* p. 79 (303), pl. xvii. fig. 4 a, b), does not occur in this case.

† See R. Bergh, "Beiträge zur Kenntniss der Polyceraden III.," in Verhndl. k.-k. zool.-bot. Ges. in Wien, Bd. xxxiii. (1883), p. 157.

loped later by invagination upon the already-formed ophthalmophore (Eisig, Fol), it is certainly not of the importance which Brock would attach to this circumstance.

The relations of the *pedal gland* in the *Onchidia* are very much as in the Stylommatophora. While in some species (*O. tumidum*, Semper) this gland remains entirely, or for the most part, enclosed in the foot, as in *Philomycus**, in most it projects with its posterior part more or less into the body-cavity†. The gland is much more strongly developed and freer in position in *Limax marginatus*, Drap.‡, in *Janella*§, and *Limax pectinatus*||, but especially in *Triboniophorus*¶.

The *digestive system* of the *Onchidia* (including the liver) shows hardly any important difference from that of the Stylommatophora.

The *Onchidia* are certainly "Opisthobranchiate," but so also are the *Veronicellæ*, nay even *Arion* and *Limax***, all of which, however, are undoubted Pulmonata. This *position of the heart* is consequently here of no systematic significance, especially as there are Opisthobranchiata which are proso-branchiate (*Acera*, *Gasteropteron*).

The *kidney* of the *Onchidia* is parenchymatous, which is never the case in the Nudibranchs; it is for the most part enclosed by the substance of the lung, or at least reaches the wall of the pulmonary cavity only at a few points. Its character again is essentially as in the Pulmonata, only the neighbouring *pulmonary cavity* is much smaller because the respiration is to a great extent cutaneous. Joyeux-Laffaie denies to *O. celticum* any real lung-substance, and represents the organ in question as consisting exclusively of renal tissue; but this assertion is scarcely correct, and will hardly be confirmed by later investigations. The organ of communication between the pericardium and the renal cavity ("Nieren-spritze" of Bergh), which always occurs in the Nudibranchiata, has been of late years recognized by Semper†† and

* R. Bergh, "Untersuchungen des *Triboniophorus Schüttei*, K.," Verhandl. k.-k. zool.-bot. Ges. in Wien, Bd. xx. (1870), pp. 860, 865.

† Keferstein, "Zur Anatomie von *Philomycus carolinensis*," Zeitschr. f. wiss. Zool. Bd. xvi. (1866), p. 187, pl. ix. fig. 2, *gp.*; R. Bergh, 'Challenger' Expedition, *l. c.* pl. vii. fig. 1.

‡ Zeitschr. f. wiss. Zool. Bd. viii. (1857), p. 351 (Semper).

§ Keferstein, "Ueber die Anatomie der *Janella bitentaculata*," Zeitschr. f. wiss. Zool. Bd. xv. (1865), p. 449, pl. xxxiv. fig. 3, *gp.*

|| Malakolog. Blätter, 1865, p. 107, pl. ii. fig. 3, *gp.*

¶ Keferstein, "Ueber die zweitentakeligen Landschnecken," Zeitschr. f. wiss. Zool. Bd. xv. (1864), p. 84, pl. vi. fig. 4, *gp.*; Bergh, *l. c.* (1870), p. 850.

** See Ihering, 'Nervensystem,' &c. 1877, p. 226.

†† Semper, *l. c.* (1877), p. 485, note 1.

Nüsslin* in various Pulmonata. The absence of this organ in *Onchidium*, asserted by Joyeux-Laffuie and Brock, is also incorrect, seeing that I have ascertained its existence in *O. tumidum*, Semp.†. The very fine aperture in the pericardium occurs beneath the bottom of the auricle, a little to the left side. At the hindmost part of the upper wall of the pulmonary cavity there is the fine *renal pore*; it leads into a *urine-chamber*, at first narrow and afterwards wider, which extends, rather superficially, through the whole length of the kidney, bending with that organ. *The lung is therefore not a dilated terminal section of the kidney*, and this the more because the structure of the kidney and that of the wall of the lung are quite different.

The relationship of the *Onchidia* to the Pulmonata appears with special distinctness in the structure of the *generative system*. What strikes one here above all is the *position of the seminal duct* in the lateral wall of the body. A similar condition occurs in no Nudibranch, and has indeed only been demonstrated in the Pulmonata. In the *Veronicellæ* (*Vaginulæ*) the position of the seminal duct is the same, only the portion of the duct enclosed in the musculature of the body is shorter, because here the vulva is removed more forwards to the middle of the length of the body. In the Auriculaceæ and Lymnææ the same anatomical relation again makes its appearance, but the enclosed portion of the duct has become still shorter. Ihering's attempt‡ to homologize the ciliated groove of the *Onchidia* with that of the Steganobranchiata, and to interpret the seminal duct of the former as only a vessel constricted off from the bottom of the ciliated groove, is hardly a very happy one.

Consequently, then, *the Onchidia agree with the Pulmonata* in the structure of the *nervous system*, in the existence of a *lung* and of a *parenchymatous kidney*, in the presence of the peculiar *pedal gland*, and in various peculiarities of the *generative system*. From a tolerably extensive knowledge of the so-called Nudibranchs I cannot but regard the *Onchidia* as pretty widely separated from them. On the contrary they branch off from the Pulmonata; *they are Pulmonata which have adapted themselves to an amphibiotic or marine mode of life*.

* O. Nüsslin, "Beiträge zur Anatomie und Physiologie der Pulmonaten," 1879, pp. 14, 15, fig. 3.

† R. Bergh, 'Challenger' Expedition, *l. c.* p. 137, note 2.

‡ H. von Ihering, 'Ueber die systematische Stellung von *Peronia*,' 1877, p. 29.



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