CHAPTER V.

RESPIRATION IN LAND CRABS.

Among the numerous facts in the natural history of the Crustacea upon which a new and clear light is thrown by Darwin's theory, besides the two forms of the males in our Tanais and in Orchestia Darwinii, there is one which appears to me of particular importance, namely, the character of the branchial cavity in the air-breathing Crabs, of which, unfortunately, I have been unable to investigate some of the most remarkable (Geocarcinus, Ranina). As this character, namely, the existence of an entrance behind the branchiae, has hitherto been noticed, even as a fact, only in Ranina, I will go into it in some detail. I have already mentioned that, as indeed is required by Darwin's theory, this entrant orifice is produced in different manners in the different families.

In the Frog-crab (Ranina) of the Indian Ocean, which, according to Rumphius, loves to climb up on the roofs of the houses, the ordinary anterior entrant orifice is entirely wanting according to Milne-Edwards, and the entrance of a canal opening into the hindmost parts of the branchial cavity is situated beneath the commencement of the abdomen.
The case is most simple in some of the Grapsoidae, as in *Aratus Pisonii*, a charming, lively Crab which ascends the mangrove bushes (*Rhizophora*) and gnaws their leaves. By means of its short but remarkably acute claws, which prick like pins when it runs over the hand, this Crab climbs with the greatest agility upon the thinnest twigs. Once, when I had one of these animals sitting upon my hand, I noticed that it elevated the hinder part of its carapace, and that by this means a wide fissure was opened upon each side above the last pair of feet, through which I could look far into the branchial cavity. I have since been unable to procure this remarkable animal again, but on the other hand, I have frequently repeated the same observation upon another animal of the same family (apparently a true *Grapsus*), which lives abundantly upon the rocks of our coast. Whilst the hinder part of the carapace rises and the above-mentioned fissure is formed, the anterior part seems to sink, and to narrow or entirely close the anterior entrant orifice. Under water the elevation of the carapace never takes place. The animal therefore opens its branchial cavity in front or behind, according as it has to breathe water or air. How the elevation of the carapace is effected I do not know, but I believe that a membranous sac, which extends from the body cavity far into the branchial cavity beneath the hinder part of the carapace, is inflated by the impulse of the fluids of the body, and the carapace is thereby raised.
I have also observed the same elevation of the carapace in some species of the allied genera *Sesarma* and *Cyclograpsus*, which dig deep holes in marshy ground, and often run about upon the wet mud, or sit, as if keeping watch, before their burrows. One must, however, wait for a long time with these animals, when taken out of the water, before they open their branchial cavity to the air, for they possess a wonderful arrangement, by means of which they can continue to breathe water for some time when out of the water. The orifices for the egress of the water which has served for respiration, are situated in these, as in most Crabs, in the anterior angles of the buccal frame ("cadre buccal," M.-Edw.), whilst the entrant fissures of the branchial cavity extend from its hinder angles above the first pair of feet. Now that portion of the carapace which extends at the sides of the mouth between the two orifices ("régions ptérygostomiennes"), appears in our animals to be divided into small square compartments. Milne-Edwards has already pointed this out as a particularly remarkable peculiarity. This appearance is caused partly by small wart-like elevations, and partly and especially by curious geniculated hairs, which to a certain extent constitute a fine net or hair-sieve extended immediately over the surface of the carapace. Thus when a wave of water escapes from the branchial cavity, it immediately becomes diffused in this network of hairs and then again conveyed back to the branchial cavity by vigorous movements of the appendage of the
outer maxilliped which works in the entrant fissure. Whilst the water glides in this way over the carapace in the form of a thin film, it will again saturate itself with oxygen, and may then serve afresh for the purposes of respiration. In order to complete this arrangement the outer maxillipeds, as indeed has long been known, bear a projecting ridge furnished with a dense fringe of hairs, which commences in front near their median line and passes backwards and outwards to the hinder angle of the buccal frame. Thus the two ridges of the right and left sides form together a triangle with the apex turned forwards,—a breakwater by which the water flowing from the branchial cavity is kept away from the mouth and reconduted to the branchial cavity. In very moist air the store of water contained in the branchial cavity may hold out for hours, and it is only when this is used up that the animal elevates its carapace in order to allow the air to have access to its branchies from behind.

In *Eriphia gonagra* the entrant orifices of the respiratory cavity serving for aerial respiration are situated, not, as in the Grapsoidæ, above, but behind the last pair of feet at the sides of the abdomen.

The swift-footed Sand-Crabs (*Ocypode*) are exclusively terrestrial animals, and can scarcely live for a single day in water; in a much shorter period a state of complete relaxation occurs and all voluntary movements cease. In these a peculiar arrangement

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1 As this was not observed in the sea, but in glass vessels containing sea-water, it might be supposed that the animals become exhausted.
on the feet of the third and fourth pairs (fig. 12) has long been known, although its connexion with the branchial cavity has not been suspected. These two pairs of feet are more closely approximated than the rest; the opposed surfaces of their basal joints (therefore the hinder surface on the third, and the anterior surface on the fourth feet) are smooth and polished, and their margins bear a dense border of long, silky, and peculiarly formed hairs (fig. 13). Milne-Edwards who rightly compares these surfaces, as to their appearance, with articular surfaces, thinks that they serve to diminish the friction between the two feet. In considering this interpretation, the question could not

and die, not because they are under water but because they have consumed all the oxygen which it contained. I therefore put into the same water from which I had just taken an unconscious Ocypoda, with its legs hanging loosely down, a specimen of Lepocephalinae which had been reduced to the same state by being kept in the air, and this recovered in the water just as the Ocypoda did in the air.

2 Fig. 12. Posterior entrance to the branchial cavity of Ocypoda rhombea, Fab., nat. size. The carapace and the fourth foot of the right side are removed.

3 Fig. 13. Points of some of the hairs of the basal joints of the foot, magn. 45 diam.
but arise why such an arrangement for the diminution of friction should be necessary in these particular Crabs and between these two feet, leaving out of consideration the fact that the remarkable brushes of hair, which on the other hand must increase friction, also remain unexplained. But as I was bending the feet of a large Sand-Crab to and fro in various directions, in order to see in what movements of the animal friction occurred at the place indicated, and whether these might, perhaps, be movements of particular importance to it and such as would frequently recur, I noticed, when I had stretched the feet widely apart, in the hollow between them a round orifice of considerable size, through which air could easily be blown into the branchial cavity, and a fine rod might even be introduced into it. The orifice opens into the branchial cavity behind a conical lobe, which stands above the third foot in place of a branchia which is wanting in Ocypoda. It is bounded laterally by ridges, which rise above the articulation of the foot, and to which the lower margin of the carapace is applied. Exteriorly, also, it is overarched by these ridges with the exception of a narrow fissure. This fissure is overlaid by the carapace, which exactly at this part projects further downwards than elsewhere, and in this way a complete tube is formed. Whilst in Grapsus the water is allowed to reach the branchiae only from the front, I saw it in Ocypoda flow in also through the orifice just described.

In the position of posterior entrant orifice and the accompanying peculiarities of the third and fourth
pairs of feet, two other non-aquatic species of the same family, which I have had the opportunity of examining, agree with *Ocyypoda*. One of these, perhaps *Gelasimus vocans*, which lives in the mangrove swamps, and likes to furnish the mouth of its burrow with a thick, cylindrical chimney of several inches in height, has the brushes on the basal joints of the feet in question composed of ordinary hairs. The other, a smaller *Gelasimus*, not described in Milne-Edwards' 'Natural History of Crustacea,' which prefers drier places and is not afraid to run about on the burning sand under the vertical rays of the noonday sun in December, but can also endure being in water at least for several weeks, resembles *Ocyypoda* in having these brushes composed of non-setiform, delicate hairs, indeed even more delicate and more regularly constructed than in *Ocyypoda*.

What may be the significance of these peculiar hairs,—whether they only keep foreign bodies from the branchial cavity,—whether they furnish moisture to the air flowing past them,—or whether, as their aspect, especially in the small *Gelasimus*, reminds one of the olfactory filaments of the Crabs, they may also perform similar functions,—are questions the due discussion of which would lead us too far from our subject. Nevertheless it may be remarked that in both species, especially in *Ocyypoda*, the olfactory filaments in their

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4 This smaller *Gelasimus* is also remarkable because the chameleon-like change of colour exhibited by many Crabs occurs very strikingly in it. The carapace of a male which I have now before me shone with a dazzling white in its hinder parts five minutes since when I captured it, at present it shows a dull gray tint at the same place.
ordinary situation are very much reduced, and when they are in the water their flagella never perform the peculiar beating movements which may be observed in other Crabs, and even in the larger *Gelasimus*; moreover, the organ of smell must probably be sought in these air-breathing Crabs, as in the air-breathing Vertebrata, at the entrance to the respiratory cavity.

So much for the facts with regard to the aerial respiration of the Crabs. It has already been indicated why Darwin's theory requires that when any peculiar arrangements exist for aerial respiration, these will be differently constructed in different families. That experience is in perfect accordance with this requirement is the more in favour of Darwin, because the schoolmen far from being able to foresee or explain such profound differences, must rather regard them as extremely surprising. If, in the nearly allied families of the Ocypodidae and Grapsoidae, the closest agreement prevails in all the essential conditions of their structure; if the same plan of structure is slavishly followed in every thing else, in the organs of sense, in the articulation of the limbs, in every trabecula and tuft of hairs in the complicated framework of the stomach, and in all the arrangements subserving aquatic respiration, even to the hairs of the flagella employed in cleaning the branchiae,—why have we suddenly this exception, this complete difference, in connexion with aerial respiration?

The schoolmen will scarcely have an answer for this question, except by placing themselves on the theo-
logico-teleological stand-point which has justly fallen into disfavour amongst us, and from which the mode of production of an arrangement is supposed to be explained, if its "adaptation" to the animal can be demonstrated. From this point of view we might certainly say that a widely gaping fissure which had nothing prejudicial in it to *Aratus Pisonii* among the foliage of the mangrove bushes, was not suitable to the *Ocypoda* living in sand; that in the latter, in order to prevent the penetration of the sand, the orifice of the branchial cavity must be placed at its lowest part, directed downwards, and concealed between broad surfaces fringed with protective brushes of hair. It is far from the intention of these pages to enter upon a general refutation of this theory of adaptation. Indeed there is scarcely anything essential to be added to the many admirable remarks that have been made upon this subject since the time of Spinoza. But this may be remarked, that I regard it as one of the most important services of the Darwinian theory that it has deprived those considerations of usefulness which are still undeniable in the domain of life, of their mystical supremacy. In the case before us it is sufficient to refer to the *Gelasimus* of the mangrove swamps, which shares the same conditions of life with various Grapsoïdæ and yet does not agree with them, but with the arenicolous *Ocypoda*. 