3. On the Musculature and other Points in the Anatomy of the Engystomatid Frog, Breviceps verrucosus. By FRANK E. BEDDARD, M.A., F.R.S.

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(Text-figures 2–13.)

I have examined or dissected three examples of a species of Breviceps, which I refer to the species "verrucosus" on the following grounds. In the definition of the Frog by Boulenger* the body is stated to be "entirely covered with distinctly porous granular glands." This was the case with my specimens, which therefore appear to differ from *Breviceps gibbosus*. Inasmuch as our knowledge of this African and ant-eating Batrachian seems to be confined to its external and osteological characters, I have thought it worth while to bring before the Society a further contribution to the knowledge of its structure. The notes upon which the present communication is founded chiefly relate to those structures which are known to vary in their characters among the Anurous Amphibia. Other characters, however, are not altogether ignored.

§ Pelvis and Coccyx.

It is of course well known † that Breviceps is distinguished from (e.g.) Rana by the widely expanded transverse processes of the sacral vertebra and by the fusion of that vertebra with the ensuing coccyx. Since the latter point at any rate has been found, though rarely, to vary among the Anura, it is perhaps worth while to record here the fact that I found in two specimens a complete fusion between the sacrum and the coccyx. When the frog is extended with the dorsal surface uppermost, the ilia are not visible as they are in *Rana* to a great extent, and the ilio-coccygeal muscles descend on a plane which only forms a small angle with the plane of a sagittal section. The strongly expanded transverse processes of the sacral vertebra show no connection with the ilia when viewed from above. These bones are quite invisible if the dorsal surface of the transverse process has been cleaned and the underlying musculature left alone. The attachment of the ilia, in fact, is not to the edge of the broad transverse process as in some other Batrachians, but is completely ventral leaving the edge entirely free.

Another structure in connection with the pelvis of Breviceps remains to be described, which I have not noticed, or seen a description of, in other Frogs. On the dorsal surface of each sacral transverse process, lying, apparently, freely on that process, is a flat and somewhat oval plate of cartilage not so long as the transverse process is in an antero-posterior direction. This plate

* Cat. Batr. Sal. 1882, pp. 176, 177.
+ "Amphibia" in Bronn's Thierreich, pp. 608 & 640.

therefore lies completely on the expanded sacral transverse process. Anteriorly fibres of the—as I presume—ilio-lumbaris muscles are inserted upon the cartilaginous plate, and quite anteriorly it is connected, though feebly, round the edge of the transverse process, with the expanded end of the ilium. I imagine that this cartilage belongs to the ilium, and that it is in consequence related to it as the suprascapula is to the scapula. We have, in fact, in this frog an exaggeration of the grooving which the anterior end of the ilium of other forms shows at its line of articulation with the sacral vertebra. It is, moreover, interesting to observe that we find in this frog a kind of foreshadowing of the relations which the ilia bear to the sacrum in the higher Sauropsida—especially birds—where the ilia are not merely attached to, but cover, the sacral vertebra.

§ Hyoid.

This cartilaginous complex presents some peculiarities of form in *Breviceps*. Of these the most salient are shown in the accompanying figure (text-fig. 2) illustrating also some of the hyoid



Anterior cornua of hyoid and part of hyoidean musculature of Breviceps.

 h. Basihyal plate. h¹. Anterior cornu of hyoid. h¹¹. Lateral process of basihyal. H.abd. Hyoabdominal muscle. h.g. Hyoglossus. P.h. Petrohyoideus. Sh. Subhyoideus. Sm. Submaxillaris. St.h. Two divisions of sternohyoideus.

muscles. It will be there seen that the anterior cornua of the hyoid are particularly stout and strong which is correlated, 1908.]

perhaps, with the unusually strongly developed subhyoideus muscle. Again, correlated with these facts of structure is the mode of origin of the anterior cornua from the body of the hyoid. As the text-figure referred to shows, the anterior cornu on each side bifurcates near to its junction with the body of the hyoid, and shortly afterwards the two branches rejoin, thus forming an almost triangular foramen. Anteriorly there is no distinction between the cornu itself and the anterior process of the body of the hyoid, such as is so marked in *Rana*. In fact, the connection of the anterior cornua of the hyoid with the basihyal recalls the arrangement of the corresponding cartilages in the not nearly allied *Pelodytes*, but more so as there is a close approach in the middle line between the rounded-off ends of the conjoined anterior process and anterior cornu of either side; they do not, however, so nearly meet in Breviceps as is the case with Pelodytes.

The figures of the hyoid apparatus of other Frogs given by W. K. Parker * show no types which closely resemble *Breviceps* in these particulars. In many forms, however, there is no anterior process on either side of the basihyal, and in others there is an approximation between the anterior lateral process of the basihyal on each side and the corresponding cornu. The thyrohyals of *Breviceps* are also peculiar in certain respects. Each is ossified as usual and is of the customary hourglass-shape, being—that is to say—thinner in the middle than at its two ends. It is, moreover, rather bent in the middle outwardly. The end by which it articulates with the body of the hyoid is not affixed to that cartilage as in many (? most) Frogs. In the latter the bone is inserted on to the posterior edge of the basihyal cartilage. In *Breviceps* it is quite distinctly inserted on to the ventral surface of the cartilage in front of the posterior edge \dagger .

§ The Musculature of the Hyoid.

As might be expected from the habits of the Frog, the Hyoid muscles differ in many respects from those of *Rana*, &c. I shall describe under the heading of the abdominal muscles an important muscle which I term *hyoabdominal*, which is a part of the superficial abdominal sheath inserted on to the hyoid.

The sternohyoid is also a peculiar muscle. For it is composed of two perfectly distinct parts. The anteriorly attached part has the usual insertion on to the body of the hyoid ventrally between the (posteriorly) diverging halves of the geniohyoideus of its side. This part of the sternohyoideus arises almost entirely from the coracoid dorsally; the second half of the sternohyoideus is in contact at its origin with the last, and appears also to be continuous with such fibres of the very feeble rectus abdominis

* Phil. Trans. pt. i. 1881.

+ Parker's figure of *Engystoma carolinensis* suggests that this is also the case with that species, which is of the same family.

sternalis as reach the sternum. Its direction is from the very first different from that of the anterior portion of the muscle. It passes downwards at a greater angle with the plane of the coracoid and to the inside of the hyoabdominal, dorsally to which it then passes to be inserted opposite to the insertion of the outer part of the geniohyoid. The hyoabdominal thus passes between the two portions of the sternohyoid, and it is able to insinuate itself into the narrow space prepared for its reception, not by a diminution of its fibres or a lessening of its diameter by becoming converted into a tendon, but by bending over so that its broad and flat surface comes to be disposed perpendicularly instead of horizontally.

The geniohyoideus of Breviceps appears to offer no very great differences from the same muscle in Rana. But the two inner halves of the two muscles fuse together some way back over the subjacent hyoglossus more markedly than in Rana, and in this the muscle recalls the geniohyoid of the Pelobatide *.

I could find no trace whatever of an *omohyoid* muscle.

The *hyoglossus* completely envelops each thyrohyal. The fibres. run aggregated into coarse strands over the body of the hyoid. In the region of the thyrohyal the hyoglossus is overlain by a thin layer of muscle which appears to be perfectly continuous with the geniohyoid (see text-fig. 7, A, p. 28), that is of course with the inner division of that muscle. The fibres, however, are here transversely arranged to the longitudinal axis of the thyrohyal and are wrapped round the enormously thick hyoglossus. In view of their direction these fibres can hardly be referred to the geniohyoid and called by its name; but they appear to be clearly a differentiation of the same sheet of muscle. The function of this sheet of muscle appears to me to be possibly this: the enormously developed musculature-the hvoglossal-which enwraps each ceratohval tends to occlude, particularly during its contraction, the glottis, and thus to hinder free respiration. This would, however, be advantageous during swallowing. During relaxation of the hyoglossal the diameter of that muscle would, perhaps, be still further reduced by the contraction of the transverse sheet, and the orifice into the lungs in consequence enlarged.

The *petrohyoid* muscles are present in the normal number and are thick and fleshy leaving no gaps, and indeed overlapping each other. The posterior division of the muscle seems to be less attached to the thyrohyal than is usual among these Batrachians.

The *petrohyoideus posterior primus* has apparently some connection with the bony thyrohyal bar. When the latter is raised, the muscle is seen to underlie it (it is of course dorsal to the bone) and to be posteriorly attached to it. The muscle is, in fact, anteriorly inserted on to the edge of the body of the hyoid behind the posterior lateral process, this portion of the body of the hyoid being, as already explained, overlain by the thyrohyal

* See P. Z. S. 1907, p. 895.

which does not arise from its edge. When this first section of the petrohyoideus posterior is raised, it is seen to overlie the posterior portion of the petrohyoideus anterior, which latter therefore is a more extensive muscle than is usual among the Batrachia Salientia.

The *petrohyoideus posterior secundus* is attached in the present species as is the petrohyoideus posterior tertius of some other Frogs. It is inserted, in fact, on to the expanded lower extremity of the thyrohyal bone. Whether some fibres escape to be connected with the laryngeal apparatus I do not know.

The petrohyoideus posterior tertius is quite different in its relations from the corresponding muscle in other Frogs whose anatomy is known. In order to see the muscle the secundus has to be raised. When this is done, the muscle now under discussion is seen as a somewhat slender muscle running parallel with the other parts of the petrohyoideus posterior. But it has no relations whatever to the thyrohyal bone. This in itself is a point of likeness to the Pelobatidæ. But the resemblance ceases with this. For in *Breviceps* the muscle avoiding altogether the end of the thyrohyal ends in close juxtaposition to the æsophageal muscle on the walls of the commencement of the lung (see textfig. 7, B). Its action on contraction would appear from its position to be like that of the æsophageal muscle and would dilate the pulmonary cavity.

§ Superficial Muscles of the Ventral Surface.

The general appearance of these various muscles, after the skin has been removed, is very different from the corresponding view of the musculature of Rana. I shall proceed to describe these several muscles, commencing with the rectus abdominis and passing forward to the throat. All the muscles now in question are shown in the accompanying figure (text-fig. 3). As is well known, the thighs of this frog are included within the area of the body, the portion of the leg from the knee onwards alone projecting beyond the contour of the trunk. But when the skin was reflected and turned back, it was to be observed that the area lying between the anterior border of the thigh and the posterior border of the abdomen is not merely covered by skin. For closely adherent to the skin in this region, and indeed inserted upon it, is a layer of muscle (to be considered in greater detail later, p. 26) attached on the other side to the leg which bridges over the gap. The conditions are not, therefore, very widely different from those which characterise Xenopus * and Pipat, where muscles attached to the leg spread into the abdominal region and thus help to destroy the demarcation between thigh and abdomen.

The rectus abaominis muscle appears to me to have in pro-

^{*} Beddard, "On the Diaphragm &c. of Xenopus," P. Z. S. 1895, p. 844, fig. 3.

⁺ Id. "On . . . the Anatomy of Pipa," ibid. p. 838, fig. 4.

portion to the animal a very great thickness where it arises posteriorly by the usual two fleshy pillars, one for each half of the muscle. It is sharply crescentic in outline on each side, a state of affairs which appears to have been brought about by the inclusion of the thigh within the body and the consequent and mutual pressure. This is plainly shown in the figure (textfig. 3) and is to be contrasted with the relative form of the same muscle in *Rana*. The rectus abdominis of *Breviceps* also differs



Superficial ventral musculature of Breviceps.

D. Clavicular head of deltoid. P.abd. Pectoralis abdominalis. P.st.ant. Pectoralis sternalis anterior. P.st.post. Pectoralis sternalis posterior. R.abd. Rectus abdominis. Sk. Skin-muscle of thigh. S.m. Submaxillaris and subhyoideus hardly distinguishable for some way after their origin. S.ment. Submentalis. x, x¹. Muscles of jaw (not specially studied).

from that muscle in *Rana* by the fact that there is only one *inscriptio tendinea* instead of the four or five of *Rana* and of many other Frogs. This one tendinous inscription is placed a little way behind the origin of the abdominal portion of the pectoralis muscle which overlaps it nowhere. It is hidden anteriorly by the complete union across the middle line of some of the fibres of the abdominal pectoral

The pectoralis muscle comes next in order and consists of the usual three parts. The portio sternalis anterior is very much larger than the portio sternalis posterior, and is at its origin in the middle line nearly three times the diameter of the latter. It is incompletely divided into two portions. There is no gap between the two parts of the portio sternalis, nor between the posterior of these and the portio abdominalis; nevertheless the several muscles are not in any way confused at their origins: they are perfectly distinct. The portio abdominalis is large and important. It allows no trace to be seen of any scapular portion of the obliquus externus such as is figured in Ecker's work upon the Frog. It arises mainly from the surface of the rectus abdominis in front of the single tendinous inscription of the latter. There is also an origin not represented in Rana (or represented indeed by the posterior part of the portio sternalis of that Amphibian) from the expanded cartilaginous sternum. The fibres of the two sides of the body here meet in the middle line of the sternum. This region of the portio abdominalis is not, however, separated in any way from the rest of the muscle; its fibres lie side by side with those of the rest of the muscle and there is no gap anywhere. Indeed, on both sides of the body the sternal fibres of the portio abdominalis actually overlap the hinder edge of the portio sternalis posterior, that part of the latter muscle in fact which arises from the rhomboidal cartilaginous sternum: for the latter muscle arises more from the edge of the sternum. while the fibres of the portio abdominalis arise from the ventral surface of the same cartilage. There being no omosternum in Breviceps, there is no superficially visible equivalent of the sternoradialis of Rana. The only thoracic muscle visible in front of the pectoralis is the clavicular head of the *deltoid*, which is shown in the figure referred to (text-fig. 3, D).

The throat-muscles visible on the superficial view are again different from those seen in Rana without any further dissection than the removal of the skin. As in Rana, a large sheet of muscle occupies the throat which obviously consists, as in that Frog, of the submaxillaris and subhyoideus muscles. The two halves of each of these are separated along the median line by a very narrow tendinous raphe. But whereas in Rana by far the greater part of this sheet belongs to the submaxillaris, only a slender slip posteriorly being referable to the subhvoideus, the precise reverse is the case with Breviceps. In fact in the Frog which forms the subject of the present memoir, the diameter (antero-posterior) of the submaxillaris is 2.5 mm., and of the subhvoideus is 5.5 mm., the measurements being taken near to the middle line. This is accounted for of course by the reduced lower jaw of Breviceps; but not entirely so, since fibres of the muscle, which, did they continue in a straight course, would reach the ramus of the lower jaw, bend posteriorly to form part of the mass of the subhyoideus. It should be stated in explanation of the above, that medianly there is no differentiation of the two PROC. ZOOL. SOC.-1908, No. II.

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muscles: it is only when they diverge a little to the inside of the mandible that they can be distinguished. In front of this lies the submentalis which has quite normal relations. In addition to these three muscles of the throat which are quite as recognisable in Rana, Breviceps possesses another small muscle which is not visible in a corresponding dissection of Rana. This is seen on one side on the right (text-fig. 3, x), running along the inside of the jaw as a fairly broad slip of muscle passing out of sight just behind the submentalis. Between the subhyoideus and the wall of the skull and the articulation of the mandible, there is a considerable space left which is not occupied by muscle. It is filled with a loose tissue which I have not investigated farther. In it, however, lies a large circular flattened and somewhat muffin-shaped body which I take to be the thymus gland, on account of its general (though not minute) agreement in position with the thymus of Rana.

§ Muscles of Shoulder-girdle*.

The *latissimus dorsi* is not a large muscle, and it is entirely hidden for the whole of its course by the muscular origin of the *obliqui externus et internus*. And these latter muscles are too thick to allow of the latissimus dorsi being seen through them; they have to be dissected away to bring that muscle into view. Not only is the latissimus dorsi a small muscle relatively speaking, but it extends for a much shorter way backwards than in *Rana*, owing perhaps and partly to the very forward position and the small size of the suprascapula. The latissimus dorsi does not at all overlap the *infraspinatus*.

The *cucullaris* does not cover the occipital region of the longissimus dorsi as is the case with *Rana guppyi*; nor has it so straight a course from the occiput to the border of the suprascapula. Furthermore it skirts the curved dorsal border of the suprascapula to be inserted into the posterior angle of that cartilage.

The retrahens scapulæ belongs in this Anuran to the serratus (or transverso-scapularis) series, that is to say it arises from transverse process and not from spinous process. It is necessary to emphasise this point because I have shown that in *Rana* guppyi this muscle does so arise, and we may therefore fairly speak of it as a rhomboideus. I take this opportunity of confirming that fact on the results of the dissection of another individual. But whether *Breviceps* can be said to possess this muscle is a matter open to dispute. In *Rana* (guppyi as well as esculenta) there are three muscles which have been termed serrati, but which in Haslam's edition of Ecker (made use of by myself in the preparation of the present communication) are described as transverso-scapularis. Of these muscles two are broad and flat

* The *pectoralis* as well as the *omoabdominal* are described under the ventral musculature on p. 22.

and pass directly upwards, or very nearly so, from the region of the transverse process of the vertebra to the under surface of the suprascapula. They really arise from the transverse process. The third muscle (text-fig. 7, A, *t.sc.*, p. 28) is long and slender, arising from the tip of a transverse process and inserted lower down on the scapula. In *Breviceps* the slender third muscle (*transverso-scapulæ tertius*) is plain; but there are only two of the broad dorsally running portions, and one of these has been already referred to as the retrahens scapulæ. Moreover these muscles seem to me to arise from the surface of the *longissimus*, and not from transverse processes.

Coraco-humeralis.—When the posterior part of the portio sternalis and the portio abdominalis of the pectoralis are cut through and reflected, two muscles are brought into view without any further dissection and when the Frog is lying upon its back. These are of unequal size, the smaller of the two lying nearest to the coraco-humeral margin. I am disposed to regard this muscle as corresponding to that which I have termed "pectoralis minor" in Pipa and in Rana guppyi. It arises mainly from the coracoid, but some of its fibres appear to reach the sternum. It is inserted on the humerus to the posterior side of the insertion of the pectoralis abdominalis, i. e., below that muscle as seen in the position of dissection referred to. The larger muscle I term therefore coraco-humeralis, which arises from the same bone and cartilage as the last. Towards its insertion it is a much larger muscle than the last described, and its insertion is farther down the humerus, *i. e.*, nearer to the hand. Both muscles are fleshy throughout.

§ Muscles of the Dorsal Surface.

In Rana the muscles of the back are covered by, and also in some cases arise from, the fascia dorsalis which is attached in the middle line to the spinous processes of the vertebræ. In Rana *guppyi*, where on account of the size of the frog this fascia is specially thick, it has not obviously any more relations to the depressor mandibulæ than to the latissimus dorsi or the obliquus externus, all of which arise from it and are in perfect continuity with it. It cannot be spoken of as the tendon of origin of any one or indeed of all of these muscles. It is described by Ecker in his 'Monograph of the Frog' in a separate paragraph as something distinct from the ensuing muscles. It is to be assumed, however, that in common with many other tendinous structures this fascia dorsalis is to be referred to a previously existing sheet of muscle But there is nothing in *Rana* to connect it definitely with any of the muscles which arise from it, excepting perhaps the obliquus externus on account of its larger size. It must be remembered, however, that in Xenopus (Dactylethra) the latissimus dorsi is of very large size *, and in shrinking to the dimensions which it

* Maurer, "Die ventrale Rumpfmuskulatur der Anuren Amphibien," Morph. JB. 1895; and Beddard, P. Z. S. 1895, p. 846 (and footnote).

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shows in *Rana* may have, so to speak, left behind it a tract of tendon—the fascia dorsalis. The condition of the dorsal musculature in *Breviceps* suggests a different explanation. There is no fascia at all in the middle of the back; only anteriorly between and upon a portion of the suprascapulæ is a thin transparent sheet of ligament to be detached from the underlying structures.

Text-fig. 4.



Superficial dorsal musculature of Breviceps.

c. Cutaneous muscles at end of rectum. Cocc.Sac. Coccygeo-sacralis. H. Posterior lymph-heart of left side. On right the corresponding heart is represented as cut open. Inf. Infraspinatus. L.d. Longissimus dorsi. m. Extrinsic muscles of lymph-heart. Obl.ext. Obliquus externus. Obl.int. Obliquus internus. r. Muscles covering rectum. Sc. Suprascapula. Sk. Skin reflected, showing attachment of extrinsic muscles of lymph-heart.

Posteriorly this is continuous with a sheet of muscle on either side of the body the fibres of which pass obliquely backwards and ventralwards and which arise from the middle line of the back, *i. e.* from the spinous processes of the vertebræ. These fibres are continuous with some of those upon the ventral surface which I have shown reasons for believing to be the obliquus externus of Rana. Immediately beneath them, and equally plainly shown in the drawing (text-fig. 4), is a set of fibres, also arising from the spinous processes of the vertebræ, which run diagonally to the former and are in fact disposed at right angles to the longitudinal axis of the body. These are of course the fibres of the obliquus internus. I imagine that these two muscles together in their dorsal region represent the fascia dorsalis of Rana. In any case, apart from any question of homologies, it is remarkable to have to note the extreme muscularity of the back of this small burrowing toad when compared with Rana. This sheet of muscle completely covers the latissimus dorsi, but it only partly covers the infraspinatus, the anterior half of which appears, as is shown in the drawing (text-fig. 4), beyond its anterior margin. In this region, in fact, it passes into an aponeurosis. A striking feature of the dorsal musculature of this Frog as compared with Rana, is the absence of a depressor mandibulæ. Hence the suprascapula is visible directly the skin is raised. In view of the presumably feeble action of the jaws in this ant-eating toad, the absence of this muscle is not surprising. Posteriorly the obliquus internus ends abruptly at the commencement of the posterior lymphheart*. At that point the longissimus dorsi emerges from beneath its shelter, and is seen to arise from the coccyx to very far back, in fact within a millimetre of its posterior extremity. This is quite different to what occurs in Rana, where the greater part of the coccyx is free from the longissimus dorsi. It may perhaps be argued from this fact, coupled with the fact that the end of the coccyx is a long way from the anus, that Breviceps is as compared with Rana a short-tailed frog. It also follows that the insertion on to the coccyx of the *ilio-coccygeal* muscle is hidden by the longissimus dorsi.

Since only the extreme tip of the coccyx, represented in the figure to which reference has been made, is free from the attachment of the longissimus dorsi, it is plain that the coccygeo-sacralis must be either absent or have rather different relations. In view, however, of the very large transverse processes of the sacral vertebra in this Batrachian, the muscle would be hardly likely to be absent, and indeed I identify it as shown in the drawing (text-fig. 4, Cocc.Sac.). The muscles in question are attached on each side of the body to the strong transverse process of the sacral vertebra. Not, however, to the whole of that process. For the outer part bears the origin of the glutceus. The muscle (the coccygeo-sacralis) is pyramidal in form; it narrows from its wide origin to the region of the pyriformis, up to which muscle it passes, and is attached at the extremity of the coccy between the origins

* For the description of which see p. 33.

of the longissimus dorsi and the pyriformis. This is true of the superficial layer of the muscle. The deeper fibres are inserted upon the coccyx still farther forward, underlying the longissimus, but I have not drawn an exact boundary line between this and the ilio-coccygeal muscle.

When the region of the ilium is inspected from below, the *ilio*lumbaris muscle is very plainly seen. It arises quite from the tip of the ilium, where it overlaps not as might be expected the coccygeo-iliacus but the glutæus, or rather a portion of it. Owing to the abbreviation of the tail the origin of the coccygeo-iliacus is concealed on this aspect of the body. The ilio-lumbaris (text-fig. 7, A, Il. l., p. 28) is a strong muscle not broken up into segments as in Rana guppyi^{*}, but passing straight forwards to its termination on the transverse process of the third vertebra. It gives off from its concealed (*i. e.* dorsal) surface bundles of muscular fibres to the transverse processes of the intervening vertebra. This muscle, as it appears to me, is in some ways like that of the Pelobatide +. For instead of consisting only of detached slips as in Rana running from transverse process to transverse process, there is also a massive band of muscle running straight to the most anterior transverse process to which the muscle is attached. This muscle is not. however, separate as in the Pelobatidæ, arising from a lower (more posterior) part of the ilium; it is indistinguishable at its origin from the anterior end of the ilium from the rest of the muscle.

§ Abdominal Muscles.

The general aspect of the *rectus abdominis* as compared with that of Rana has been already described ‡, and need not be again here referred to. While in the Common Frog according to various authors the rectus abdominis does not extend far laterally, but is in those regions replaced by the *obliquus externus*, there is in Breviceps an absolute continuity between the fibres arising from the pubic symphysis in the two strong pillars already referred to and fibres running in a nearly dorso-ventral direction on the sides of the body (text-fig. 5). They form obviously one sheet which may be stripped off. These fibres extend a long way towards the dorsal median line. More towards the ventral median line, however, they become attached to the tendinous inscription, and with that break are continuous with anteriorly running fibres, some of which end on the sternum. Beyond the tendinous inscription arises, as has been already said, the portio abdominalis of the pectoralis. Beyond this again, *i. e.* nearer the shoulder-girdle, arises a sheet of muscle which is completely hidden by the pectoralis abdominalis. Nevertheless it lies above (ventral to) an underlying sheet of muscle, which latter lies on the same plane as the median region of the rectus abdominis, arising as it does from it or at least from the aponeurosis covering it. This muscle

> * Beddard, P. Z. S. 1907, p. 333, text-fig. 94. † *Id. ibid.* p. 877. ‡ *Suprà*, p. 15.

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arising from the surface of the deeper layer is very wide, and disappears anteriorly beneath the shoulder-girdle, being inserted dorsally upon the scapula. It would seem to correspond to the portio omo-abdominalis of the obliquus externus of *Rana*, but is clearly much more extensive. The direction of its fibres is on



Ventral abdominal musculature of *Breviceps* cut so as to display different layers.

hy.abd. Hyoabdominal. Obl.inf. Obliquus internus. Om.abd. Omoabdominal shown below at origin and above near to insertion, the intervening portion having been cut away. Pect.abd. Origin of pectoralis abdominalis. R.abd. Rectus abdominis.

the whole obliquely postero-anterior. It arises from near the edge of the underlying sheet of muscle also just referred to.

This latter is, as I take it, the *obliquus internus*. In the middle line it can be seen to be covered by the very thin sternal portion of the rectus abdominis. Here its fibres run obliquely forward from the median line, fairly parallel indeed in direction with the fibres of the adjacent and covering pectoralis abdominis. From the inscriptio tendinea the fibres of the obliquus internus run directly forward parallel to the long axis of the body; more laterally they run postero-anteriorly but obliquely towards the median ventral line of the abdomen. Passing round the abdomen the direction of the fibres is gradually changed, until anteriorly just behind the shoulder-girdle the fibres of the obliquus internus run exactly at right angles to the long axis of the animal's body. The obliquus internus, therefore, of *Breviceps* is very different from that of *Rana*, where the fibres run obliquely postero-anteriorly with a main dorso-ventral direction and with but a slight fanning out from the back towards the ventral surface. In Breviceps the fanning is much more marked and is in the opposite direction, *i. e.* the fibres converge towards a point upon the ventral surface on each side of the body. This point, or rather area, is formed by the origin of a very strongly marked muscle, flat and of considerable diameter, from the septum between itself and the obliquus internus and running forward parallel with the sternum to be attached to the hyoid. I term this muscle the hyo-abdominalis, and I regard it as being, like the omo-abdominalis, a portion of the obliquus externus. Against this view, however, is the fact that it is, in the greater part, covered by the omo-abdominalis. I would further remark that this muscle apparently has its homologue among the Pelobatidae*, where, however, it is not quite so important as in Breviceps and has a different insertion. I am disposed to regard this peculiar arrangement of the obliquus internus and its relation to a large hyo-abdominalis and the large size of the omo-abdominalis, as being connected with the ant-eating habits of Breviceps. The arrangement of the muscles in question is such as to produce a powerful pull upon the hyoid apparatus and tongue. The very slender sternal portion of the rectus is to be associated with the rudimentary and reduced state of the cartilaginous sternum. The large omo-abdominalis is possibly associated with the burrowing habits of the Frog. It would assist in producing a strong pull upon the shouldergirdle.

The abdominal musculature therefore of this Frog agrees with that of other Anura in the possession of only two layers of muscle. But the exact homology between the variously metamorphosed regions in this and other Anura is clearly difficult to settle. The obliquus internus, as I have termed the inner sheet of muscle, seems to be comparable not only with the obliquus internus of *Rana* but to that muscle *plus* certain parts of the rectus abdominis. For the anteriorly directed fibres of the muscle in

* Beddard, "On Megalophrys nasuta," P. Z. S. 1907, p. 340; id., "On Pelobatidæ," ibid. p. 894.

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Breviceps are obviously part of the same muscle, most of whose fibres have an oblique direction. But elsewhere the rectus abdominis is obviously external to the obliquus internus. It would seem, in fact, impossible to go further than to declare the two layers of the abdominal musculature homologous with the two layers in other Batrachians. An exact homology between individual muscles derived from these layers would seem to be impossible of assertion. It is quite remarkable to note what great differences in the disposition of the fibres in these two layers can exist between closely allied Batrachians, and how plastic these structures prove to be as contrasted with many others whose functions would also seem to be involved with the peculiar mode of life of this frog.

§ Muscles of the Thigh.

The muscles visible on the superficial aspect of the thigh are shown incidentally in the figure (text-fig. 3) representing a general view of the musculature of *Breviceps*, and in a more



Muscles of the inside of the thigh of Breviceps.

a. Skin-muscle referred to in text. Add.br. Adductor brevis (or magnus?). Add.L. Adductor longus. Add.m. Insertion on to knee of one of adductors, perhaps comparable to the adductor magnus of other Frogs. R.i.maj. Rectus internus major. R.i.min. Rectus internus minor. V.i. Vastus internus. x. A separate adductor slip.

elaborate way in the accompanying figure (text-fig. 6), which represents the thigh-muscles more highly magnified. I take as

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usual the corresponding set of muscles in Rana for comparison *, in order to set forth those of Breviceps. There is an important difference at the very beginning of this comparison. When the skin covering the thigh is removed or reflected, there is removed or reflected with it a thin sheet of muscle (text-fig. 6, a) which, in the middle of the thigh, lies superficial to all the other muscles of the thigh. Its insertion on to the knee is also the most superficial insertion. There seems to be no doubt that this muscle, which underlies the skin over a great part of the thigh, actually arises in part at least from the skin, and is therefore perhaps to be referred to the series of cutaneous muscles which have been described in Rana. But there would appear to be no corresponding muscle to this in Rana guppyi at any rate. Posteriorly the muscle is not to be distinguished for a great part of its course from the Rectus internus minor. Anteriorly it does not spread on to the abdomen. It seems to have nothing to do with the Rectus abdominis or adjacent muscles. It is purely a thigh-muscle in its position and extent. It is necessary to mention this in view of the peculiar relations of the abdominal muscles to the thigh in Pipa. Although, as already said, there is a close contiguity posteriorly with one part of the Rectus internus, its insertion onto the knee seems to be distinct from that of the said Rectus, which muscle will be dealt with presently. Apart from this muscle, which is something superadded, possibly in relation to the inclusion of the thigh within the contour of the body, the general plan of the femoral muscles appears to be not unlike that of Rana.

The sartorius courses obliquely over the thigh as in Rana; its insertion on to the knee is entirely fleshy. It is not a particularly large muscle, being markedly smaller than the neighbouring adductors. Nevertheless, its position and relations seem to fix its correspondence with the sartorius of Rana, &c. When cut across the muscle is seen to lie in the hollow between its much more massive neighbours. These I take to be the adductor longus and (possibly) the adductor magnus respectively. In the appearance of the former superficially upon the inside of the knee we have a character not found in Rana. This muscle, however, is also inserted on to the inner border of the femur for about the distal third of that bone, and must be, as I imagine, the equivalent of the adductor longus of Rana. In front of it lies, as should be the case if this homology be true, the vastus internus, which is a large muscle.

Between the insertions on to the knee of the two muscles last dealt with a portion of the insertion of another muscle is visible, as clearly shown in the accompanying figure (text-fig. 6, Add.m.). This also belongs to the adductor series, and may perhaps be regarded as the adductor magnus, the third adductor described above being in that case the adductor brevis. The importance of the adductor muscles in this frog is very striking. In a second specimen, the

* I have figured these muscles in Rana guppyi in P. Z. S. 1907, p. 887, text-fig. 234.

insertion of this adductor magnus (if I am right in so terming it) did not appear superficially. This variability, it will be observed, is precisely analogous to that exhibited by the constituents of the triceps femoris on the outside of the thigh, which will be presently described. Returning to the muscles visible on the inside of the thigh, the only ones visible without dissection, in addition to those already treated of, are the *recti interni major et minor*. The connection of the latter with a superficial muscle has already been dealt with. As in *Rana* the semitendinosus does not appear superficially.

On the outside of the thigh the most prevalent muscle is the equivalent of the triceps femoris of Rana, though its constitution in Breviceps differs somewhat. There are, however, three distinct portions which may be termed respectively rectus femoris, vastus externus, and vastus internus. They are, however, all of them inserted separately, instead of by one tendon as in Rana. Moreover, the most anterior of the three muscles, the rectus femoris anticus, instead of ending in an aponeurosis, is fleshy and thick The two specimens which I have dissected show a throughout. difference in the insertion of the middle of the three divisions of the triceps femoris. In one this goes as far as the knee; in the other individual the muscle is inserted on to the thigh up to about the middle of that bone only. It is therefore not only in the separateness of the three divisions of the triceps femoris, but also in their insertion and complete muscularity that Breviceps differs The biceps femoris in Breviceps is a particularly from Rana. slender muscle ending in a long tendon, not flattened, which pushes between the two heads of the gastrocnemius some way after their origins to be inserted a longish way down the fore The semimembranosus is of fair size. leg.

§ Esophageo-pulmonary muscle.

This muscle in *Breviceps* is a very stout muscle obscurely divided into three or four bundles which have hardly the value of separate muscles. It has no direct connection whatever with the muscles of the wall of the abdomen. It is not (that is to say, obviously) a detached sheet of the obliquus internus, as is the case with the corresponding muscle in all of the Pelobatidæ that have been hitherto examined*. It is in fact similar in many respects to its homologue in the Ranidæ and Bufonidæ. It arises in them from the transverse process of the fourth vertebra, and this is also the origin of the muscle in *Breviceps*. Its origin lies in front of, and contiguous with, the insertion of the ilio-lumbaris, and to the inside of the origin of the transverso-scapularis. The origin and course of the muscle is shown in the accompanying illustration (text-fig. 7). It nearly meets its fellow of the opposite side of the body in the middle line of the ventral surface of the œsophagus.

* Beddard, "On Anatomy of a Frog of the genus *Megalophrys*," P. Z. S. 1907, p. 324; and "On Anatomy of Pelobatidæ," *ibid.* p. 886.

A large number of its fibres end upon the œsophagus both laterally and ventrally. In fact the muscle is chiefly an œsophageal muscle, and has less relation with the respiratory apparatus. It is, however, connected with the root of the lung where the walls of this sac, as is shown in the figure referred to, are non-respiratory and thicker, and is undoubtedly attached along the dorsal median line of this region of the lung where it (the lung) forms one cavity with



Esophageal and neighbouring muscles of Breviceps.

A. These muscles *in situ* without disturbance of adjacent structures, which are, however, not all included in the figure.

B. A further dissection to show relation of asophageal muscle to root of lung.

Hg. Hyoglossus muscle. 11.cocc. Ilio-coccygeus. 11.1. Ilio-lumbaris. K. Kidney. L. Lung. as. Esophagus. as.m. (Esophageal muscle. P.h. Petrohyoideus posterior tertius. t.sc. Transverso-scapularis.

its fellow. So also of course is the muscle of the opposite side of the body, and the two muscles can be raised here from the surface of the œsophagus by pulling up the common cavity of the two lungs just where it opens into the larynx. The attachment continues on to the cricoid cartilage of the larynx ("annulus" of Wilder*) which forms in this Batrachian, as in so many others, a

* Zool. Jahrb., Abth. f. Anat. ix. 1896, pp. 290 &c.

1908.]

complete bar uninterrupted in the dorsal middle line. None of the fibres of the muscle appear to me to actually run on to the cricoid bar; but their action must result in moving this bar, seeing that it is intimately and strongly connected by their walls with the lungs. Any pull on the roots of the two lungs must tend to raise the cricoid cartilage dorsally.

§ Abdominal Viscera.

The Liver of this Frog (text-fig. 8) is of large size and has the unusual character among the Batrachia Salientia that the right lobe is considerably the larger of the two lobes into which it is divided. Furthermore, the left lobe can hardly be said to be divided into two lobes, as is again so frequently the case with Frogs, though an indentation on its border is an indication of such a subdivision. The liver is, as a whole, very square-shaped. Anteriorly its boundary line is almost straight and is on a level with the posterior border of the coracoid. The two lobes are nearly in contact in the middle line and hardly diverge posteriorly, so that the posterior border of the liver is almost straight. Anteriorly, however, in the middle line they diverge slightly and form a small triangular space; this discovers the heart, which is otherwise quite covered by the liver except for the narrow median ventral slit between the two liver-lobes, where it is apparent. The apex of the ventricle is situated a little way in front of the posterior border of the liver. The smaller left lobe is more triangular in shape than the right lobe. The gall-bladder is quite invisible on a superficial view; it lies beneath the inner corner of the right. lobe. As far as I can gather from Dr. Günther's account of the Bufonid Rhinophrynus dorsalis*, the liver of this toad bears. some likeness to that of Breviceps. For he remarks † that the heart of Rhinophrynus "is surrounded by the liver in a similar way as in higher animals, as in other Batrachians it is surrounded by the lungs." Furthermore, he observes of the liver that it is divided into a right half and a larger left half. This would seem to be the exact converse of what I note here in Breviceps. But elsewhere in the paper Dr. Günther speaks of the stomach being situated "quite on the right hand," which causes me to doubt whether right and left may not be used to express the positions as seen from above during a dissection. Furthermore the liver extends dorsally to the heart, which thus lies in cavities as it were excavated in the liver-substance, and it is almost completely surrounded and hidden by that viscus as in Reptiles and Birds. The likeness between Rhinophrynus and Breviceps in these features. of liver construction are remarkable as possibly related to the anteating habit which they have in common, since systematically they are placed in different families. Part of the stomach is concealed by the left lobe of the liver, and the small intestine passes

* "The Systematic Arrangement of the Tailless Batrachians, &c.," P. Z. S. 1858,
p. 339. *† Loc. cit.* p. 350.

directly anteriorly between the lobes of the liver; most of the coils of the intestine lay entirely above (i. e. quite concealed by)



Ventral surface of liver of two individuals of *Breviceps*. Ant.abd. Anterior abdominal vein. g.b. Gall-bladder. H. Heart. L., R. Left and right lobes of liver.

the large right lobe. The enormously distended large intestine was entirely uncovered by the liver. The peculiar nature of the liver and its relations to the heart have been brought about, or at any rate are accompanied, by an alteration in the normal (*i. e.* that found in *Rana*) disposition of the *anterior abdominal vein*. This vein in *Breviceps* gives off no branches to either lobe of the liver until it reaches and has passed some way beyond the apex of the heart.

Text-fig. 9.

	e e e e e e e e e e e e e e e e e e e
A.	<i>B</i> .

 A. Part of oviduct. B. Stomach of Breviceps (laid open).
 a. Demarcation between stomach and duodenum. as. Esophagus. f. Funnel of oviduct.

In a second specimen which I dissected, a male, and which was perhaps in consequence rather smaller than the first, measuring only 33 mm. in total length, the liver showed certain differences. The relative size of the two lobes was the same, but they were not by any means so closely approximated in the middle line as was the case with the larger example. This being so, much more of the heart was visible on a ventral inspection of the viscus, and the conditions more approached that to be seen in the Common Frog. Still, however, there was a considerable difference; for in *Rana* the heart is distinctly ventral of the liver and the lobes extend far beyond it in the direction of the cloaca. In *Breviceps*, even in this second example to which I am now referring, the liver only just extends beyond the heart and grasps it firmly, as it were, with a lobe on either side. And the pericardium comes into contact and is connected with the absolute ventral edge of the liver-lobe on either side. I could detect no furrowing of either lobe of the liver. The gall-bladder in this, the smaller specimen, instead of being completely hidden, was quite visible for the greater part of its extent between the ends of the two lobes of the liver and extending beyond them even towards the cloaca.

The Stomach of this Frog (text-fig. 9) seems to be peculiarly large, and its pyloric projection is sharply marked off from the ensuing duodenum, not only by a constriction but by the fact that the walls of the latter are much thinner than those of the pylorus. The pyloric region of the stomach in fact is quite distinct from the rest of that organ and forms a projection from it; there is no gradual passing of the one into the other as in Rana. The stomach itself was swollen and nearer to the spherical than to the ovoid in form. It was full of a mass of ants, among which I distinctly recognised "soldier ants" (with enormous heads) of a species which I have not attempted to identify. The muscularity of the stomach was very evident, and it thus contrasted with the gut. The esophagus, which suddenly expands into this large stomach, only just enters the abdominal cavity. On cutting open the stomach the smallness, relatively speaking, of the esophageal aperture into it can be realised.

The Lungs float very freely in the cœlom; it is only at the base that they are attached by ligaments. The texture is thin with large alveoli.



Intestinal canal of *Breviceps*. st. Stomach. L.i. Colon.

The *Intestine* (text-fig. 10) does not appear to differ greatly from that of *Rana* in its proportionate length. It differs, however, very considerably in certain features of its structure. The first portion

of the small intestine, that immediately following upon the pyloric constriction corresponding to the duodenal loop of Rana, is very short, about 5 mm. long (in the smaller male specimen), and directed rather forwards and parallel with the stomach as in Rana. It is of narrow calibre, about that of the pyloric process of the stomach. This passes into a middle section of the small intestine, the bore of which is quite twice that of the preceding part, and which forms therefore a very wide tube. This is no case of accidental dilatation, for the same structure was apparent in both examples, and the appearance of the swollen region of the intestine was quite different from the region in front of and behind it. Internally its mucous membrance is raised into transverse folds. which have not the watch-pocket shape of the corresponding folds in the intestine of Rana, but are thin wavy folds running right round the lumen. This wider portion of the small intestine passes into a narrow portion again, which is of greater length and of not greater calibre than the beginning of the duodenum. This opens suddenly by a slightly projecting os into the very wide but not very short large intestine.

The end of the colon, into the pear-shaped anterior section of which the ileum opens, bulges equally all round the ileum; that is to say, there is no unilateral cæcum. Shortly after the entrance into it of the small intestine the colon diminishes in its width and remains at about the same calibre to the anal apertures. That is to say, of course, the cloaca is no wider than the antecedent colon. The cloaca is of considerable length, and is shown in the figure on p. 20 (text-fig. 4). It occupies the whole of the space lying between the tip of the coccyx and the rather distant end of the body. Being, as it is, in this exposed situation and covered only by the skin, it would appear to be rather susceptible to injury from pressure upon the dorsal surface of the body. It is, however, protected from such injury, it may be supposed, by a thick covering of muscle upon the dorsal surface. This is obviously divided into two longitudinal bands by a furrow, and this arrangement becomes clearer still when the tube is cut across. This muscle arises, partly at least, from the tip of the urostyle and corresponds, I imagine, to the compressor cloace of Rana *. There are also two very tiny muscular slips attaching the end of the cloaca to the skin just above; they are also shown in the figure referred to.

§ Posterior Lymph-hearts.

These organs are so extraordinarily developed in *Breviceps* that they require a section to themselves for their adequate description. The general topography of their neighbourhood may be first described, as it differs greatly from that of *Rana* and is in relation to the large size of these sacs in *Breviceps*. As already mentioned, the thighs of this species are enclosed within the

* Ecker's 'Anatomy of the Frog,' Haslam's Translation, p. 348. PROC. ZOOL. Soc.—1908, No. III. 3 contour of the body which extends for a great distance behind In an example of *Breviceps* measuring 38 mm. the coccvx. from snout to anus the distance from the tip of the coccyx to the anus was quite 7 mm., i.e., more than one-fifth of the total body-Furthermore, the breadth of the thighs adds to the length. large space which intervenes between the posterior edge of the abdominal muscles where they reach the back and the posterior end of the trunk. It is in this large space (see text-fig. 4, p. 20), loosely covered by the skin which does not adhere to the leg until the knee, that the posterior lymph-hearts lie on either side. They do not, however, occupy the whole of this considerable tract. Each, however, is no less than 10 or 11 mm. long in the individual Breviceps whose total body-length has been mentioned above. The posterior lymph-heart of Breviceps is therefore between onequarter and one-third of its total body-length. With this may be contrasted the proportions found in Rana, where (in R. temporaria or R. esculenta—very much larger species) the length of the posterior lymph-heart is given in Haslam's Translation of Ecker's Frog' as "about two lines," i.e. 4 or 5 millimetres*. That is to say, the posterior lymph-hearts of a frog half or one-third of the size of Rana esculenta are twice or thrice the bulk of those of that Rana. This appears to me to be a very remarkable anatomical fact, and one which argues considerable physiological differences. The posterior end of each lymph-sac was about 4 or 5 mm. from the posterior end of the body. This space was occupied by a a lymph-sac corresponding, I presume, to the femoral lymph-sac It lies at any rate on the thigh-muscles. I found this of Rana. space on each side filled with a coagulated flocculent mass, probably lymph. This space bears a relation to its corresponding lymph-heart similar to that of an auricle to a ventricle. When the skin of the back is carefully reflected from the middle line, the lymph-heart is at once exposed. No muscles lie between it and the integument. It is, however, slightly attached to the skin here and there by fibres continuous with its own muscular These fibres arranged in slender bundles spread out in a walls. fan-shaped fashion over the skin. They form presumably a fixed point or points to render effective the contractions of the lymphheart. It may be also that the fibres thus attached belong really to the cutaneous muscular system and correspond in particular to the cutaneus dorsi of Rana; for other cutaneous muscles are associated with the septa of lymph-sacs. In a general way also these fibres suggest the "alæ cordis" of Arthropods. In any case the anatomical facts are as has been stated, and are shown in the accompanying figure (text-fig. 11). These fibres as well as the lymph-hearts lie dorsally to and unconnected with the dorsal muscles (which are described on another page †), although the anterior end of the lymph-heart overlaps the end of the dorsal

+ Suprà, p. 19.

^{*} In a large example of *Bufo vulgaris* measuring 115 mm., I found a lymphheart to be 5 mm.

muscles. It is mainly at least by the anterior half or threequarters of each lymph-heart that it is fixed to the integument by these muscular strands, which have to be cut through in order to free the organ. When it is thus freed it is seen to be of about the same shape as an acorn (without its cup) and divisible into two regions, an anterior and posterior, which are however not very sharply marked off from each other.



Left lymph-heart of Breviceps.

a, b. Extrinsic muscles of heart (H.). G. Tip of coccyx. Obl.int. Obliquus internus cut off short on both sides. o.d. Oviduct.

The anterior part of each lymph-heart (as is shown in text-fig. 12, p. 36), which represents one of these structures completely freed from its attachment to the integument, is of very dense muscular structure, and in consequence quite smooth. The posterior part (not half) of the heart, however, is of a basket-work conformation, strands—varying in breadth, but always broadish—of muscular fibres crossing each other at right angles. The bands of fibres which run in a longitudinal direction are ultimately lost in the regular even and muscular walls of the anterior part of the lymphheart. The cross-running bands are also seen in the figure to be also gradually differentiated from it. The interspaces between these bands are considerable, and possibly permit of the free entrance

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of the lymph into the heart from the lymph-sac already referred to which lies behind it. When a lymph-heart is cut open the structure presented is that which is represented in the lower figure, text-fig. 12. There is the same division into two regions, the walls of the anterior part being smooth and thick. In the posterior part the longitudinally-running bands of muscle stand out from the walls, projecting into the interior of the sac, as is shown in the figure.



Upper figure, lymph-heart of *Breviceps* isolated ; lower figure, view ot interior of same.

The attachment of each lymph-heart to the integument by strands of muscles would doubtless increase the efficiency of that organ as a pump by providing a fixed point for the contraction of its muscles to pull against. There is, however, another series of muscles attached to the opposite side of each heart, and acting in a direction parallel to and in the same plane as, but obviously opposite to, those integumental sheets. The resemblance of the extrinsic muscles of the heart to the "*alæ cordis*" of the Arthropod heart is thus increased, since there is (or at least may be) a pull on each side in opposite directions which would clearly dilate the cavity of the lymph-heart. The contraction of the heart is probably effected by the intrinsic musculature. This muscle, when the heart is viewed from the dorsal surface as in textfig. 11, is seen to reach the heart as two broad flat bands which fan out over its dorsal surface. They are seen to dip down ventrally between the heart and the ilium, and to unite to form one stout strap-shaped band of muscle. The position of this muscle is exactly on a level with the tip of the coccyx, and there is an exact symmetry between the two of opposite sides of the body. It is inserted on to the symphysis pubis.

In addition to the muscles just mentioned, which are indicated in text-fig. 4 (p. 20), and shown more in detail in a more enlarged representation of this region of the body (text-fig. 11), there is another muscle attached to each lymph-heart more ventrally than that which has just been described. This completes the mooring The of the lymph-hearts to the adjacent organs of the body. muscle now under consideration is single on each side of the body; that is to say, there is one of them to each lymph-heart. It is broad and flat and thin, and shows a metallic glitter on account of its structure; it arises in the neighbourhood of the edge of the expanded transverse process of the sacral vertebra, and thus partly covers over and conceals the coccygeo-sacralis muscle. The course is backwards, and it reaches the first described skeletal muscle of the lymph-heart at right angles to that muscle. It dips under it, and is therefore attached to the lymph-heart rather ventrally. The muscle is broader than that which runs from the pubis to the lymph-heart, but could be readily missed owing to its tenderness and the consequent ease with which it can be torn *.

§ Organs of Reproduction.

I have had the opportunity of examining both sexes of this frog, as has already been mentioned in relation to the alimentary system. In the male (text-fig. 13), the *testes* have the usual oval form and are not pigmented. From their considerable size, I gather that the individual was sexually mature. They lie very close together and actually indeed in contact, the mesocolon only just being able to push itself between them, as it were. Nor can they be separated by any manipulation short of forcibly tearing them away from the dorsal mesentery which attaches them and the colon to the middle dorsal line. The vasa efferentia seem to offer a new form of these ducts among the Anura. There is only a single

^{*} The appearance of the lymph-heart is by no means unlike that of the Tortoise as represented by Fritsch, "Zur Anatomie der Elephant-Schildkröte (*Testudo elephantopus*)," Prag 1870, from Abh. k. böhm. Ges. Wiss. 1871.

tube arising from each testis, and each of these meets its fellow of the opposite testis and forms with it a single duct; this occurs soon after each has emerged from the testis.

The two *ovaries* are, like the testes, closely apposed in the middle line, and as already mentioned each has a very large fatbody attached to it anteriorly. The eggs were of considerable size (some of them) and, as I should imagine, mature. But the ovaries were not extensive as they are in the mature females of other Batrachia. It may be therefore that the oviducts are not as complicated in their coiling as they would have been had the frog lived longer. In this specimen the oviducts were as is represented in text-fig. 9 (p. 32). Anteriorly the funnel is spoon-shaped with an elongated aperture on the lower surface.



Testes and kidneys of Breviceps.

f. Fat-body. p.c. Post-caval vein. t. Testes with single vas efferens arising from anterior end of each. u. Ureter.

The proximal section of the oviduct is narrow and straight in its course. The thick-walled glandular region of the oviduct only makes two loops, as is shown in the figure referred to. I am inclined to think that the oviduct is after all mature or very nearly so, for its walls are as thick as it seems likely they could become. The glandular part opens into the distal and thinwalled "uterus" which is flattened and strap-shaped. The two tubes approach each other in the same straight line behind the kidneys, and form one tube running of course at right angles to them towards its opening into the cloaca.

§ Fat-Bodies.

Although these organs are known to vary among the Anura, from individual to individual, from side to side of the body, and also shrink or become expanded at different times in the life of the individual *, I think it worth while to describe the appearances seen in the two specimens which I dissected. In both of them the fat-bodies were large and apparently fully developed. In the female they were much the larger; but then the female specimen was considerably larger than the male, a difference which I am disposed to put down as a sexual character. In the female the fat-bodies extended forwards a long way and appeared when the body was opened actually in front of the lungs. In the male they were much smaller and firmly adherent to the front margin of each testis †. Each fat-body was divided distally into five or six finger-like processes of the usual shape.

§ Renal Organs.

The kidneys of *Breviceps* are like those of *Rana* in that they are flat smooth bodies with no division into massive lobes such as occurs among the Pelobatidæ. They are represented in textfig. 13, which shows also the relations of the testes to them. The only peculiarity which they show (so far as I have ascertained) is the complete fusion in the middle line of the right and left viscus in the male. In the female they are very closely apposed but not fused. This fusion is, however, not complete; that is to say, the two organs in the male are not continuous with each other in the middle line throughout the whole of their length. It is only for about one-half of their extent that they are thus fused. Anteriorly the two kidneys are quite distinct until the emergence of the postcaval vein which bends downwards just in front of the point where the two kidneys become almost, if not quite, soldered together. Posteriorly a larger free region is left.

The common duct thus formed does not, as it does in the case of Discoglossus and Alytes, enter the ureter direct without passing through the kidney. In the present species the duct becomes lost in the substance of the kidney in a way which I did not follow out more minutely. In any case it did not bend round the anterior end of the kidney to join the ureter. The two kidneys are in very close contact below the testes. But the duct showed no signs of division into a branch of each kidney, but appeared to enter the middle line, and was at any rate concealed by kidneytissue before dividing. As the vasa efferentia referred to were exceedingly obvious on inspection with a lens, I imagine that

^{*} Boulenger, "The Tailless Batrachia of Europe," Ray Soc. Publication, 1897.
† I may observe that I found no "Bidder's Organ."

others have not been missed. At the same time I cannot of course positively assert that the individual was actually fully mature, though there was no reason against this view.

§ Resumé*.

As compared with *Rana*, *Breviceps* shows the following peculiarities of structure :---

- (1) The rectus abdominis has but one tendinous inscription and its fibres fan out laterally running dorsoventrally, thus replacing a portion of the obliquus externus.
- (2) Part of the obliquus externus is specialised into a strong muscle ending on the hyoid; on to the base of this is inserted the fan-shaped obliquus internus.
- (3) The sternoradialis is absent.
- (4) The subhyoideus muscle is twice the diameter of the submaxillaris.
- (5) A special muscle runs from the quadrate cartilage to the inner side of each ramus of the lower jaw.
- (6) The omohyoid is absent.
- (7) The sternohyoid is divided into two perfectly distinct muscles with widely separate insertions into the hyoid.
- (8) The obliquus externus is a purely fleshy muscle arising on either side in the middle line of the back by muscular fibres. There is thus no fascia dorsalis. The obliquus internus is similarly fleshy at its origin from the middle line of the back below the former.
- (9) There is no depressor mandibulæ muscle to be detected.
- (10) In the thigh the rectus internus minor is connected with a superficial cutaneous muscle, covering over a portion of the thigh, which is its chief head of origin. The biceps is very slender; the adductors very large.
- (11) The posterior lymph-hearts are of enormous size, measuring more than a quarter of the total length of the body. They are attached by muscles to the skin dorsally and by two separate and broad muscles to the transverse process of the sacral vertebra and the public respectively.
- (12) The liver is composed of two lobes only which largely cover the heart.
- (13) The testes emit each only one vas efferens; and the two tubes join before entering the substance of the kidneys (which are here fused) in the middle line.
- (14) The oviducts are very short owing to the fact that they are but little coiled.

* I do not include in the above *resumé* external and osteological characteristics already well known, nor all minutiæ of muscular structure.

- (15) The coccyx is abbreviated and does not extend to the end of the body. To compensate for this the end section of the cloaca which naturally extends beyond it is protected by a pair of strong muscles which are inserted on to the skin above the anus by short slips.
- (16) Upon each sacral transverse process is a detached plate of cartilage which is related to the adjacent musculature, and which perhaps corresponds to the supra-sacral portion of the ilium in Sauropsida.
- (17) The hyoid cartilage is marked by the double origin of the anterior cornua, a foramen therefore occupying the base of each cornu where it joins the body of the hyoid.

The above list contains a brief epitome of nearly all of the points in which I have found Breviceps to differ anatomically from Rana. In the present state of our knowledge of Batrachian anatomy, it is not possible to use them in order to criticise or confirm any view which has been held with regard to the systematic position of Breviceps, except of course to assert that it is in any case not a near ally of Rana, or of the family Pelobatidæ*. Some of its structural features would appear to be associated with its ant-eating proclivities; to this category I would refer the particularly strongly-developed hyoid muscles and the anterior cornua of the hyoid and the round, globular, somewhat gizzard-like stomach sharply marked off from both esophagus and duodenum. The burrowing habits of Breviceps are perhaps to be associated with some other muscular peculiarities; especially, as I should imagine, the extent and muscularity of the two obliqui and of their branches to the shoulder-girdle, and the very powerful muscles of the anterior part of the thigh, and the very thick gastrocnemius. Among the remaining characters of this Frog, those which are particularly noteworthy appear to me to be the following, viz. :--(1) The enormous size and muscularity of the posterior lymph-hearts with their special extrinsic muscles; (2) the presence of a plate of cartilage overlying the sacral transverse process and representing the supra-sacral portion of the ilium in higher types; (3) the nearly complete concealment of the heart ventrally by the liver-lobes; (4) the existence of only one vas efferens for both testes.

* Beddard, P. Z. S. 1907, p. 324, & p. 871.

1908.7



Beddard, Frank E. 1908. "On the Musculature and other Points in the Anatomy of the Engystomatid Frog, Breviceps verrucosus." *Proceedings of the Zoological Society of London* 1908, 11–41. https://doi.org/10.1111/j.1096-3642.1908.tb01831.x.

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