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(128 a) * *Glyphodes bocchorialis*, sp. n.

♂. Ochreous white; palpi with the second joint above and at extremity black; vertex of head and thorax mixed with black; fore tibiae banded with black; abdomen with obscure blackish bands. Fore wing with almost basal, sub-basal, and antemedial fulvous yellow bands with sinuous black edges; a large fulvous yellow discoidal ocellus with black centre and black edges extending to costa; a black-edged fulvous yellow band, slightly excurved from vein 6 to below 2, then retracted to discoidal ocellus and bent outwards again to inner margin, connected with the antemedial band at vein 1 and with its own sinus, a white line on its outer edge from costa to vein 6 and some white spots between vein 5 and inner margin; the terminal area black; a subterminal series of irregular white spots conjoined towards apex; cilia black, yellow above and below middle. Hind wing with black-edged fulvous yellow discoidal spot connected by a black line with the inner margin towards which it forks; the terminal area black with irregular inner edge, a yellow spot on it between veins 3 and 5 and a subterminal series of irregular white marks, double towards apex; cilia yellow with a black line near base, black at apex, middle, and tornus.

Hab. STRAITS SETTLEMENTS, Padang Rengas. *Exp.* 16 mm. Type in Coll. Rothschild.

[To be continued.]

LXVII.—On some Reptilian Lower Jaws.

By D. M. S. WATSON, M.Sc.

THE object of this paper is to describe the lower jaws of some fossil reptiles and amphibians of Permian and Triassic age from South Africa, and to discuss briefly the bearing of their structure on some morphological questions.

Deinocephalia.

The structure of the Deinocephalian lower jaw has been briefly described by Seeley (1896) and Broom (1910, 1911), but is not completely known. No known specimen shows the splenial or coronoid.

The outer aspect is very like that of *Dimetrodon*, and the
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whole structure is very similar in the two types. The surangular and angular are flat bones overlapped by the dentary in front and covering the outer side of the small articular and the long prearticular. The articular has two cotyli for the double condyle of the quadrate, and has a small post-articular process which is directed backwards and slightly downwards.

Pelycosauria.

The lower jaw of *Dimetrodon* is now well known from the work of E. C. Case; its structure is shown in fig. 1, which is diagrammatized from his published figures and photographs, checked by specimens at Munich and Tübingen.

Fig. 1.

A. Left ramus of the lower jaw of *Dimetrodon*, inner aspect. B. Right ramus of the same jaw, outer aspect. Teeth omitted. $\times \frac{1}{4}$.

ANG., angular; ART., articular; CR., coronoid; DEN., dentary; PR.ART., prearticular, Williston, = dermartialar, Kingsley, = goniale, Gaupp; SP., splenial; SUR.ANG., surangular.

The large dentary meets its fellow in a loose symphysis, and at the back overlaps the surangular and angular. These latter are thin flat bones covering the outer faces of the articular and prearticular. The angular is remarkable for possessing a notch on the lower border towards the back; it will be shown in this paper that this notch more or less

modified occurs in all known types of Therapsids, and it occurs in no other reptiles whatever.

The splenial is a long narrow strip of bone lying on the inner side of the dentary, but not entering the symphysis. The coronoid has never been figured, but is said to be a narrow slip of bone, presumably lying inside the dentary over the splenial.

Anomodontia.

The structure of the lower jaw of *Dicynodon* has been described by Owen and Broom. Seeley has described the lower jaw of *Endothiodon*, which has an essentially identical structure. None of these descriptions is complete or altogether accurate.

The present description is founded on a beautifully preserved lower jaw of a new species of *Dicynodon* (*Oudenodon* = female *Dicynodon*) from the *Cisticephalus* zone of Kuils Poort, Beaufort West District, collected by the author. Several other jaws in the British Museum have been used for comparison, the sutures between the bones of the back of the jaw being best shown in a fragmentary jaw of *Kannemeyeria** collected by the author at Winnaarsbaaken, Burghersdorp District.

The dentary is a very powerful bone, uniting with its fellow in a median symphysis which completely closes even in quite young individuals. The posterior part of the bone is produced into two processes, the upper of which is split vertically into an inner and an outer plate, leaving between them a deep groove which receives the anterior ends of the surangular and angular.

The lower process, which is separated from the upper by a deep notch, forms only the outer surface of the same groove, the inner side being provided by the splenial.

The splenial is a short bone, meeting its fellow in a very strong fused symphysis. Behind the region of the symphysis the bone is a thin plate, separated from the dentary by the groove already referred to, which in this region receives the angular and prearticular.

The coronoid is a thin slip of bone lying on the inner face of the dentary, separated from it and the splenial by very

* *Kannemeyeria* is a genus founded by H. G. Seeley in 1908 on an imperfect skull of *Dicynodon simocephalus*, Weithofer. The genus is easily distinguished from *Dicynodon*, and I know three species belonging to it. The lower jaw does not differ from that of *Dicynodon*.

distinct sutures in several specimens, and apparently just entering the symphysis.

Fig. 2.

A. Left ramus of lower jaw of *Dicynodon*, inner aspect. B. Right ramus of the same jaw, outer aspect. C. Left articular region viewed from above and behind. $\times \frac{1}{2}$.

For key to reference-letters see fig. 1.

The surangular is a thin plate of bone whose upper edge is thickened so as to form a ridge on the outer surface, nearly

the whole of which is covered by the angular. Posteriorly it unites by a suture, which is very seldom visible, with the articular. A good deal of its inner surface is covered by the prearticular.

The angular is a very large bone, consisting essentially of a more or less flat plate tightly applied to the outer sides of the surangular and prearticular and separated above and behind by a suture from the surangular. Its anterior end is bevelled off to a point and received in the groove between the dentary and splenial. This plate is, however, modified by a great development of the notch mentioned above in *Dimetrodon*, protected and covered by a strong reflected lamina from the outer face of the bone, which forms a pocket open backwards. The body of the bone and the reflected lamina combine to form a deep descending flange on the lower border of the jaw.

The articular is perhaps the most characteristic bone of the whole skeleton of *Dicynodon*. Its articular face is directed upwards and backwards; it is throughout divided by a median keel which fits into a groove in the pulley-shaped quadrate. The anterior part of the articular face is shallowly concave and narrow from side to side; the concave region passes quite smoothly into a very convex (antero-posteriorly) surface, the sides of which are bounded by upstanding parapets, which render the bone much wider in this region; the outer of these is much the higher and clasps the side of the quadrate. Posteriorly the articulating face is bounded by a continuation of the edges of these parapets. The whole arrangement permits a great backward and forward motion of the jaw, together with an alteration of the angle which the upper surface of the dentary makes with the palate even when the mouth is closed.

The whole structure is quite unique, but very characteristic of Anomodonts, occurring as it does in a less pronounced form in *Endothiodon*.

The hinder end of the articular is continued into a post-articular process which is directed downwards and lies entirely in front of the hinder end of the articulating surface. It is still fairly large, and its flat posterior surface would afford good attachment to the digastric muscle. This process is continued forward by a ridge which forms a very narrow keel on the under surface of the body of the bone and is connected with the prearticular.

The prearticular is a long narrow bone, united by a suture, which is seldom visible, with the inner side of the keel on the under surface of the articular, and stretching forward on

the inner side of the surangular and angular until it passes inside the splenial nearly to its symphysis. The enormous development of this bone occurs in all Anomodonts, and is no doubt correlated with the great massiveness of the whole jaw.

Terocephalia.

Scymnosuchus whaitsi, Broom, is taken as the type of the Terocephalia, of which it is a fairly primitive member. The material on which the description is founded consists of the two rami of the same lower jaw, the right of which has the bones naturally arranged and exposed from the outer side, whilst the left has the bones somewhat displaced, the back of the jaw being separated from the front; this jaw is free from matrix on all sides.

Fig. 3.

A. Left ramus of lower jaw of *Scymnosuchus whaitsi*, inner aspect.
B. Right ramus of the same jaw, outer aspect. Teeth omitted.
 $\times \frac{1}{2}$.

The dentary is long and narrow, thick at the symphysis, where it is loosely articulated with its fellow, and thinning off posteriorly to an oblique feather-edge, which overlaps the surangular and angular. There is a large coronoid process which projects freely above the surangular.

The splenial is a thin strip of bone lying on the inner side of the dentary, and meeting the corresponding bone of the

opposite side in a relatively large symphysis. Its position in the figure may be slightly misplaced, being that which it now occupies in the somewhat disturbed jaw. The posterior narrow part of the bone is separated by a wide crack, and may conceivably be a somewhat misplaced part of the pre-articular.

The coronoid is a very thin bone whose shape is shown in the drawing lying on the inner aide of the dentary in the position shown.

The surangular is a very thin sheet of bone whose outer surface is almost entirely overlapped by the angular. Posteriorly it thickens and is united with the articular by a visible suture, its hinder edge overhanging the outer part of the articular facette.

The angular is a large thin bone overlapping the surangular and itself overlapped in front by the dentary. It is strengthened by a narrow rib which crosses its outer surface diagonally, and its lower border has a deep notch which is overhung by a reflected lamina exactly as in *Dicynodon*.

The articular is a small bone, triangular in shape when viewed from above, whose outer face is covered by the surangular. The base of the triangle is formed by the articular facette, which is directed backwards and very slightly upwards. The inner and lower faces of the bone are covered anteriorly by the prearticular. The lower side of the bone bears a very small and reduced postarticular process.

The prearticular is a long bone, flat anteriorly, but bearing a prominent ridge behind where it covers the articular, from which it is very obviously distinct in the specimen.

Cynodontia.

The lower jaw of *Cynognathus* has been described by Seeley, whose description is, as usual, quite accurate, although hard to follow in the absence of intelligible figures. Most of his determinations of individual bones, although offered with great reserve, are also accurate. Broom has also described the type, but his reading of its structure is not quite correct.

The following account is founded on the perfectly preserved and prepared lower jaw of the type specimen of *Cynognathus crateronotus*, but I have compared it with all the other known specimens of higher Cynodonts.

The dentary is a very large bone fused with its neighbour at the powerful symphysis, produced backward into an enormous coronoid process and overlapping all the other bones of the jaw.

The splenial is a narrow strip of bone lying on the inner side of the dentary and having a relatively large symphysis.

The coronoid is a large thin flim of bone tightly pressed onto the inner side of the dentary and overlapping the surangular and prearticular at the back. It is remarkably similar to the corresponding bone in *Scymnosuchus*.

The surangular is a narrow sheet of bone whose outer surface is largely covered by the angular and dentary; its

Fig. 4.

A. Left ramus of lower jaw of *Cynognathus crateronotus*, inner aspect.
 B. Right ramus of the same jaw, outer aspect. Teeth omitted.
 $\times \frac{1}{4}$.

inner face must be applied to the articular, but in no specimen is the suture between the two bones visible.

The angular is a plate of bone thickened below and covering a large part of the outer face of the surangular; its lower border has the usual notch placed very far forward and provided with a vestigial reflected lamina, not completely preserved in *Cynognathus*, but very well shown in *Diademodon*.

The articular is a small bone almost completely surrounded

by the others; the articular face points backwards and slightly upwards, and the downwardly directed postarticular process is a scarcely visible knob.

The prearticular is a long, thin, straight bone covering the inner side of the articular, from which it is separated by a scarcely visible suture. It lies inside the angular, and its forward end is covered by the coronoid.

It is a remarkable fact that in Cynodonts increasing size of the dentary, and of the masticatory muscles which in *Cynognathus* must be inserted on it, is correlated with a reduction and weakening of the back part of the jaw, which alone articulates with the skull; not only are the actual bones small, but their attachment to the dentary is weak, they merely rest in a groove in that bone and are often displaced in the fossil skulls. Examination of any higher Cynodont skull with the mandible in place will show that the very powerful masseter had its attachment on the dentary, and can scarcely have had any connection with the angular, and the temporal muscles were obviously inserted in mammalian fashion on the coronoid process of the dentary. The action of these powerful muscles must have set up such great stresses in the hinder part of the jaw that it is doubtful if it could have supported them. Directly correlated with increase in size of the dentary and reduction in size of the angular &c. is an increase of the descending process of the pterygoid. It is noteworthy that this takes place not only between the higher and lower Cynodonts, but also in the Therocephalian "*Lycosaurus*" *curvimola*, which pretty certainly comes from the *Cisticephalus*-zone of Upper Permian age. These processes give rise to the anterior part of the pterygoidal muscles, and their increase in size no doubt implies a corresponding increase in the muscles, which in reptiles are normally attached to the angular. As it is impossible that a muscle should increase whilst its point of attachment is degenerating, it appears probable that the pterygoidal muscles were mainly inserted onto the postero-inferior angle of the dentary, which is thickened. Thus inserted these muscles, whilst tending to close the mouth, will produce stresses in the hinder part of the jaw in the opposite direction to those induced by the masseter and temporal muscles, in this way permitting the reduction of the hinder part of the jaw which we actually see. The fact that in higher Cynodonts all the masticatory muscles have their attachments on the dentary renders the freeing of the articular and quadrate demanded by the quadrate=incus

theory of the mammalian ossicula auditus much more understandable.

The most marked characteristic of the Therapsid mandible is that it is no longer hollow and box-like, as in the Stegocephalia and the majority of the other reptiles, but that the bones of the inside of each ramus are tightly pressed against the outer bones, making it very narrow and solid. This feature (which is not very easy to describe) is eminently characteristic of the group and seems to occur in no other reptiles.

Pariasaurus.

The lower jaw of *Pariasaurus* has been somewhat incompletely described by Seeley, but three jaws in the British Museum enable one to get a clear idea of the principal lines of its structure, although in one or two cases the sutures, shown dotted in the figures, are doubtful. The jaw is hollow, all the bones except the articular simply surrounding a cavity.

The dentaries meet in symphysis and pass backwards on the outer side of the jaw to overlap the angular and surangular; it is doubtful if the dentary ever reaches the lower border of the jaw—if it does so, it is only for a very small space just in advance of the angular. The wide tooth-bearing area of the dentary forms the roof of the cavity of the jaw.

The splenial is a bone having a large symphysis with its fellow of the opposite side; it certainly forms a good deal of the lower border of the jaw and apparently a good deal of its outer surface, but here the suture is not certain. On the inner aspect on each side the splenial is separated from the dentary by a narrow slit-like vacuity, which is bounded outwardly by the upper margin of the splenial rising rapidly to near the top of the jaw. Posteriorly the upper edge of the bone is separated from the dentary by the anterior part of coronoid, which is wedged in between the two bones. The hinder end of the splenial overlaps the prearticular and angular, forming also a small part of the border of the interior mandibular vacuity.

The coronoid is a small bone forming the front border of the supra-Meckelian vacuity, and prolonged forward by a thin strip which is wedged in between the splenial and dentary.

The surangular and angular are not separated by a satisfactory suture, but are overlapped anteriorly by the dentary and splenial, and form the outer and lower walls of the jaw;

the well-known process on the underside of the jaw is formed entirely by the angular, as Seeley thought.

The articular is a rather large bone fitting as a plug into the cavity of the back of the jaw, and extending rather far forward; its outer face is largely covered by the surangular

Fig. 5.

A. Left ramus of lower jaw of *Pariasaurus*, inner aspect. B. Right ramus of the same jaw, outer aspect. Teeth omitted. $\times \frac{1}{4}$.

and angular, and its inner side by the prearticular. The articular face has two cotyli for the condyles of the quadrate.

The prearticular is a large bone covering the inner face of the articular, overlapping the angular, and being itself covered by the splenial and coronoid in front.

There can be no doubt that the bones which in the preceding descriptions I have called by the same name are

homologous. It remains to show that they correspond with the bones which bear those names in *Crocodylus*, the standard animal for reptilian nomenclature. No doubt arises as to any of the bones except the splenial and coronoid. In all these types except *Dimetrodon* the splenial enters the symphysis and in some cases has a very large articulation with its fellow. In *Crocodylus* the splenial does not enter the symphysis, but in all Mesozoic crocodiles, in which there can be no doubt of its identity, it has a symphysis, sometimes a very large one. There is, in fact, no doubt that in all primitive reptiles the splenial takes a large part in the symphysis; it does so, for example, in *Cotylosauria* (*Pariasaurus*, *Limnoscelis*, *Diadectis*, *Labidosaurus*, *Captorhinus*, *Procolophon*), *Therocephalia* (all types examined), *Cynodontia* (all types examined), *Anomodontia* (all types), *Sauropterygia* (*Nothosaurus*, *Peloneustes*, *Pliosaurus*), *Ichthyosauria* (*Ichthyosaurus*, *Ophthalmosaurus*), "*Rhynchocephalia*" (*Rhynchosaurus*, *Hyperodapedon*?, *Champosaurus*), *Thecodontia* (*Belodon*, *Mystrisuchus*), *Crocodylia* (*Mystrisaurus*, *Steniosaurus*, *Metriorhynchus*)—a list which might be extended indefinitely.

The identity of the coronoid is not quite so obvious, owing to the fact that it frequently extends far forward, in *Dicynodon* probably reaching the symphysis. In the living crocodiles it is a very small bone forming the front of the supra-Meckelian vacuity. In *Metriorhynchus*, however, as has been described by Deslongchamps and as Dr. Andrews has demonstrated it to me, it is a long bone stretching far forward between the splenial and dentary, much as in *Pariasaurus*. In *Peloneustes* Dr. Andrews has shown that the coronoid, which has exactly the same relations as in *Metriorhynchus*, may extend forward to the symphysis, and does extend far forward in all Plesiosaurs.

These facts seem to me to justify the terminology of this paper; it is, however, interesting to examine a Stegocephalian jaw in the light of them. The Stegocephalian mandible is best known from the work of Branson on *Anaschisma* and *Eryops*, checked and accepted for *Eryops* by Case, and supported by Seeley's description of the hinder part of the lower jaw of "*Labyrinthodon*" *lavisii* and Smith Woodward's of the mandible of "*Labyrinthodon*" *leptognathus*.

These descriptions, when compared with the less well-known mandibles of other types, go far to show that the plan of structure is the same in all *Temnospondylus* and *Stereospondylus* Stegocephalia.

Bothriceps is a small *Temnospondylus* Stegocephalian of

Upper Permian age from the Orange Free State, South Africa; the excellent series of specimens in the British Museum show all points of the structure of the mandible with great clearness, except the upper edge, which in all cases is obscured by the skull.

The dentary is a long shallow bone meeting its fellow in a loose suture and extending backwards on the outside of the jaw until it meets the angular and surangular: it never reaches the lower border of the mandible.

A. Left ramus of lower jaw of *Bothriceps*, inner aspect. B. Right ramus of the same jaw, outer aspect. Teeth omitted. $\times 1$.

The splenial is the bone figured by Branson in *Anaschisma* and *Eryops* without determination and with some doubt. It was clearly figured by Smith Woodward in *Labyrinthodon leptognathus*, and called infra-dentary by analogy with the bones of that name in the Crossopterygian jaw; the homology implied by this nomenclature is no doubt correct.

In *Bothriceps* it is a small element with a large symphysis, forming the lower border of the anterior part of the jaw; posteriorly it meets and overlaps the angular.

Dr. A. S. Woodward, in his account of the *Labyrinthodon* jaw, described a little slit on the inside of the jaw lying on each side of the symphysis, bounded by the "infra-dentary" below and the dentary above. These little vacuities also occur in the type specimens of *Rhinesuchus oweni* (Lydd.) and *Rhytidosteus africanus*, Owen, and no doubt generally in the group. They correspond exactly with the similarly placed openings in *Pariasaurus* described above, and are clearly shown in Williston's figure of *Casea* and Williston and Case on *Diadectes lentus*.

The coronoid is the bone usually described as splenial in the Stegocephalian mandible; it is a long strip of bone lying on the inside of the jaw and overlapped by the splenial and angular; behind, it forms a good deal of the lower border of the supra-Meckelian vacuity, overlaps the prearticular, and forms the anterior border of the small interior mandibular vacuity. It cannot be seen in *Bothriceps* whether it enters the symphysis, but as it does not in any other known amphibian, including *Trimerorachis* (which is nearly identical with *Bothriceps*), it probably does not in *Bothriceps*.

In *Eryops*, *Anaschisma*, and *Labyrinthodon* this bone forms a parapet on the inner side of the tooth-bearing area of the dentary.

I have pointed out above that in all early reptiles the splenial is a bone of the mandibular symphysis, and that in its appearance and relations it is identical with the "infra-dentary" of Stegocephalia. The so-called "splenial" of Stegocephals is equally similar to the coronoid of such forms as *Pariasaurus*, *Peloneustes*, and *Metriorhynchus*, in which it is a long narrow splint bordering the tooth-bearing area of the hinder part of the dentary, and overlapped below by the splenial; in *Peloneustes* and probably *Dicynodon* the coronoid actually reaches the symphysis, so that the great forward extension of the "splenial" of Stegocephalia cannot be advanced against this correlation.

The only sound piece of evidence against this interpretation is the occurrence, recorded by Branson, of a small coronoid-like bone lying between the "splenial" and the dentary in front of the supra-Meckelian opening in *Anaschisma* and *Eryops*. It seems to me easier to regard this bone, for which I propose the name epicoronoid, as having disappeared in the reptilian jaw, than to imagine that it should secondarily acquire a forward extension, that the "splenial" should extend forward and gain a symphysis, and downwards by the disappearance of the "infra-dentary" to form the lower border of the jaw, completely mimicking in the appearance of its anterior part the "infra-dentary" which it displaced.

As Smith Woodward has pointed out, the bone here regarded as splenial in the Stegocephalia is apparently homologous with the first or one of the infra-dentaries of the Crossopterygian mandible. The true coronoid will be homologous with the "splenial" of the fish, and Branson's "coronoid" in *Anaschisma* may correspond to the last of the little bones which in *Holoptychius* and all allied fish lie between the dentary and the "splenial."

I wish to express my thanks to the Trustees of the Percy Sladen Fund, who assisted me to visit South Africa; to Messrs. J. Strydom and M. de Jager, on whose farms I found some of the specimens described above; to the Rev. J. H. Whaits, to whom the British Museum owes the *Scymnosuchus*; and to Drs. A. Smith Woodward and C. W. Andrews, for their constant kindness at the Museum.

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