# NEW DESCRIPTION OF THE PERMIAN STEGOCEPHALIAN *DASYCEPS BUCKLANDI* (LLOYD) FROM KENILWORTH*

For more than 60 years there lay in the museum at Warwick, Central England, a very complete large stegocephalian skull from the Permian sandstone of Kenilworth, a few miles north of Warwick. It was made known by LLOYD in 1849 in a very short report at the meeting of the British Association (Rep. Brit. Assoc. 1849 (1850), Sect. p. 56). It is mentioned under this name by J. MORRIS (Cat. Brit. Foss., p. 350). In 1859 HUXLEY found the generic difference from *Labyrinthodon* and gave the new name *Dasyceps* in a footnote in Quart. Jour. Geo1. Soc. XV, 647; directly afterwards followed his description with two figures (appendix to HOWELL, Mem. Warwick Coalfield (Mem. Geol. Surv. 1859, 52-56). Later it was mentioned incidentally, based on HUXLEY's description, by MIALL in 1874 (Rep. Brit. Assoc. 159) and by PHILLIPS in 1871 (Geology of Oxford etc., 96)).

When I saw the skull for the first time in autumn 1907 I was struck by its completeness and I decided to study it more closely at the next opportunity. This opportunity presented itself in September 1909. I am indebted to Rev. M. J. MELLO of Warwick for the kindness with which he made the specimen in the museum there available to me, and he gave me every assistance in drawing and photographing it.

The skull lies in two slabs of coarse red sandstone with clay balls, split apart. The Permian age of this sandstone is indeed recognised (see, e.g. LAPWORTH and WATTS: Sketch of the geology of the Birmingham district, 1898 and Proc. Geol. Assoc. XV, 10, 1899), but an exact horizon within it has not been determined. From the same quarry come[1] a pelycosaur jaw, *Oxyodon britannicus* v. HUENE and a 2-headed rib fragment (see v. HUENE: Neue und unverkannte Pelycosaurierreste. Centralbl. f. Min. etc., 1908, 432ff). The rock is a coarse, soft, rather clayey sandstone, yellowish-red to dark red with very small red clay pieces in it. In the piece of stone in which the maxilla of *Oxyodon* lies there are large red marl pieces. One slab (Pl. I (XLIV)) shows the inner view of the skull roof in its entire extent, partly also the impression of the outside; the other slab (Pl. II (XLV)) shows the posterior half of the skull roof with the snout tip missing and a part from the anterior part of the palate in dorsal view. HUXLEY (loc. cit.) gives a representation of some bone sutures. Some of them are very difficult to see. I have spent two whole days in tracing them and I believe I have achieved this as far as possible. In several points this representation differs from that of HUXLEY. The skull is traversed by many cracks, grooves and fractures, which must not be confused with sutures. Thus the difficulty in the determination of the bone sutures arises.

## Description

The skull has an elongate triangular outline with moderately pointed snout. Measured in the midline, it is 25 cm long and the posterior skull angles reach a further 5 cm backwards. At the broadest place behind it is 28.5 cm wide. The posterior skull angles are long and drawn out sharply backwards; beside each of these is a deep otic notch and medially from them lie the long so-called epiotic spines. Further, two sharply projecting processes are present between them (Fig. 1 and Pl. I (XLIV)).

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[1] Preserved in the museum of the Geological Survey of England, Jermyn Street, London.

The orbits lie at the beginning of the last third of the skull length rather far from each other and they are small. At the end of the first third of the skull length are found the very small nasal openings, very far apart, and between and in front of them lies a large median apple-pip-shaped perforation, 8 cm long and 4 cm broad. The parietal fossa lying rather behind the eyes is comparatively large (10 x 8 mm).

The premaxillae are unusually large; they occupy a full third of the skull length, but they form the jaw edge in only ½ their length; thus they accompany the medial edge of the maxillae a long distance backwards. At the snout point and at the "facial pit" the premaxillary suture is visible in the midline and in the middle it seems to divide so that perhaps a small separate bone nucleus exists there (see Fig. 1). On the left beside and in front of the "facial pit" one can see a mucus canal. The "facial pit" is surrounded by sharp, smooth bone edges and can be no accidental structure. The posterior suture runs in a finely serrated S-shaped curve from the "facial pit" diagonally to the nasal opening and laterally from it touches a small process back-wards.

The maxilla forms a jaw edge 17 cm long. Several teeth are still visible; on both slabs together there are still 23 preserved (LLOYD saw 20 and HUXLEY only 11). I can add nothing to HUXLEY's description of the teeth so I repeat it here: "These teeth are pointed, much curved, and about a quarter of an inch (8 mm) long, their bases having a diameter of three fortieth of an inch (c. 2 mm). They are directed outwards, their curved sides being downwards and inwards (in the natural position). They are ancylosed to the margins of the jaw, which exhibits no alveolar groove. Their bases are longitudinally striated, and they present apparently a wide pulp cavity." The maxilla is bordered by the premaxilla, nasal, lachrymal and jugal; the posterior point occurs very near the anterior one of the quadratojugal. The maxilla occupies only a narrow space on the upper side of the skull; it is broadest beside the middle of the lachrymal.

The nasals after the premaxillae occupy the broadest and largest space on the upper side of the skull. They form the posterior edge of the "facial pit" and border the nasal openings. Laterally they meet the maxillae for a very short distance and are accompanied for a long stretch by the lachrymals; behind, they border on prefrontal and frontal.

The frontals are smaller than the nasals; they are long, border laterally on the prefrontals and postfrontals, behind on the parietals. The anterior suture, like the posterior, forms large bulges.

The prefrontals lie long and rather narrow between frontal and lachrymal and border medially behind with an oblique suture on the postfrontal and form a part of the edge of the orbit laterally behind.

The lachrymal projects with a long point, wedge-shaped, between nasal and maxilla and borders rather broadly on the anterior end of the jugal; it reaches the anterior edge of the orbit with a narrow branch.

The parietals are strikingly short but comparatively broad. In their middle they surround the parietal foramen. The serrated middle suture runs remarkably obliquely in front of the hole.

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The postfrontals border medially on parietal and frontal, in front on the prefrontal, laterally on the orbit and the postorbital and behind on the supratemporal with rather angularly running suture.

The postorbital surrounds the orbit from behind and laterally; medially it is bordered by the postorbital and behind it forms a point which is formed medially in a serrated suture from the supratemporal and laterally in close-packed, fine windings from the squamosal. Laterally and in front the jugal borders the postorbital for a short distance.

The jugal is a long, rather broad bone, blunt in front and pointed behind. It is bordered laterally by the maxilla and in long close serrations by the quadratojuga1; medially by lachrymal, orbit, postorbital, squamosal and quadratojugal; and in front by the lachrymal and with a small edge by the maxilla.

The very large quadratojugal forms the posterior skull angle and the long backwards directed point.

The squamosal inserts between postorbital and jugal with a point, meets the quadratojugal laterally and the supratemporal and the so-called epiotic medially; behind, it forms a part of the otic notch edge.

The supratemporal is a small bone plate which encroaches upon the parietal with its anterior medial angle; further it borders in front on the postfrontal and the postorbital; laterally it meets the squamosal; behind, it forms a curve towards the so-called epiotic in a strongly toothed suture; medially it borders the supraoccipital plate behind the parietal.

The supraoccipital plates (= dermal supraoccipitals) lie right behind the parietals and are of about the same size. Each sends out a sharp process backwards. Since these processes are quite indistinct, HUXLEY did not see them, but LLOYD probably did (loc. cit.). They are like those of *Cochleosaurus bohemicus* FRITSCH (see Fig. 4). LLOYD had held them for condyles. But the condyles are not visible.

Long spine-like processes backwards form the so-called epiotic plates. They meet the supraoccipital plates, supratemporal and squamosal.

Several traces of the mucous canals are to be seen (Fig. 2). One can see most clearly the lyra of the snout point reaching to the medial edge of the orbits, then the eyes are surrounded in a close curve medially and behind and the canal runs from the lower edge of the orbit downwards. Something of the jaw canal is also to be seen on both sides.

Palate (Fig. 3 and Pl. II (XLV)): The second slab shows a few interesting parts of the palate beside parts of the skull roof; therefore it is rather difficult to decipher this slab.

In the middle in front one sees the inner opening of the "facial pit" which thus also perforates the palate. Only the posterior part of its outline[2] is rounded and not pointed as in the skull roof. The most posterior place is found 1 cm further in front than there and in the palate it is bordered entirely by the premaxilla. It is only just touched by the vomer right behind.

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[2] But a part of this outline is fracture edge, see Fig. 3.

Further, the inner nasal openings are visible. The right one is 4 cm long and 2.5 cm broad. They are found rather behind the outer nasal openings. They are bordered in front and the largest part of the medial extent by the vomer, a small part medially by the pterygoid and laterally probably entirely by the palatine and behind possibly by the transversal, at least a suture seems to me to be present between the surfaces which I have ascribed to the pterygoid on the one side and the transversal on the other, as a deep twisting groove.

In three places, in which the palatal bones themselves are missing and only their impressions are preserved, one sees traces of palatal teeth. On the left palatine and transversal large cavities are to be seen, close to each other and at similar distances apart, which must correspond to rather large palatal teeth. Also on both premaxillae, where the bone is chipped off, there are very small sharp cavities that also arise from palatal teeth.

Comparison

In the distribution of the covering bones and the position of the skull openings as well as the outline, *Cochleosaurus*, *Chelydosaurus*, *Melosaurus*, *Osteophorus* and *Nyrania* have the greatest similarity with *Dasyceps*. The named genera are representative of the Palaeozoic family Melosauridae. Certainly none of the named forms possesses a “facial pit”. This will be ignored at first in the comparison.

*Cochleosaurus* (see BROILI, Palaeontographica 52, 1907, 5): The skull outline is sharper in front in *Dasyceps*. The posterior skull angles are perhaps rather longer in *C*, but in *D* show first an expansion towards the side and then the sharp process behind (Fig. 4). The “epiotic spines” are much larger in *D*. Whether the so-called supraoccipital processes possessed similar ones or not is not certain because of their indistinct preservation in *D*. The entire middle posterior part of the skull roof projects more strongly than in *D*. The orbits are larger and placed rather further in front than in *D*. I have not been able to establish an intertemporal for certain, but I am not completely sure whether the posterior half of the left surface, named postorbital, is not separated by an indistinct suture or whether it is only a question of a crack; certainly I can uncover nothing on the right of a corresponding suture; otherwise the bones have strikingly similar distribution and form.

*Chelydosaurus* (see FRITSCH, Fauna der Gaskohle etc., II, 1, 1885, p 21): *Ch* has no “supraoccipital process” and the “epiotic angles” are not larger then in *Cochleosaurus*. Also the posterior skull angles are similar to the latter. The orbits lie further forwards and are larger in *D*. The frontals are very much larger, lachrymals seem to be missing and the prefrontals are very small and of very different structure; the postorbitals surround the entire lower edge of the orbits and separate them completely from the jugal (Fig. 5).

*Melosaurus* (see H. v. MEYER, Palaeontographica 7, 1860, Pl. 10): In the outline of the skull roof *M* and *Chelydosaurus* are similar, only the otic notches in *M* are deeper. The snout is longer in *M*. *M* has a small postorbital; the jugal approaches the orbit. A lachrymal seems to be absent; the prefrontal is large (Fig. 6).

*Osteophorus* (see H. v. MEYER, Palaeontographica 7, 1860, Pl. 11): The skull is shorter and broader than the foregoing. The “epiotic plates” seem to form long processes. The postorbitals are very small, as in *Melosaurus* and the jugals form the entire lower edge of the orbit (Fig. 7). The prefrontals are large and like *Melosaurus*, but elongated lachrymals are also present which do not quite reach either the nasal openings or the orbits with their points. A characteristic of *O* is a long, median bone piece between the frontals and nasals; from its position it can surely only be an ethmoid.

Nyrania (see FRITSCH, Fauna der Gaskohle etc., II, 1, 1885, p 34): N (and *Gaudryia*, which BROILI (loc. cit. p 13) combines with it) does not have a very large otic notch. The nasals are as large as in D, the parietals certainly much larger. Intertemporals are present as in *Cochleosaurus*, the supratemporals are much larger than in all other genera of this group and the squamosals infinitesimally small (Fig. 8). The jugal only reaches the orbit with one edge; between it and the lachrymal a puzzling small piece is articulated. The rather long lachrymal does not reach the orbit.

From this comparison it arises that *Dasyceps* fits well in the family Melosauridae. In this family it is the only possessor of a "facial pit". Also the very far backwards position of the nasal openings and the form of the posterior skull angles isolate it from the other genera. *Dasyceps* is the largest melosaurid. *Cochleosaurus* probably shows the greatest number of similarities in the skull roof with *Dasyceps*.

Of other genera, *Eryops* and *Archegosaurus* stand very near this group. *Eryops* differs particularly by the large backwards-projecting condyles and the deep downwards and backwards running temporal region as well as by the extraordinarily long jugal. *Archegosaurus* stands nearer the Melosauridae according to the upper side of skull; the skull is certainly more strongly perforated than in the latter.

I cannot hold the "facial pit" of *Dasyceps*, so striking by its size, as a characteristic of systematic importance since it occurs in quite different families and orders of Hemispondyli and even in the Microsauria (according to JAEKEL's recent classification: Ueber die Klassen der Tetrapoden. Zoolog. Anz. 34, 1909, 193-212), but always only in isolated species. Therefore I hold it for a physiological feature which is connected with a particular way of life. It is found (according to JAEKEL's figures, 1909, loc. cit. Fig. 10) in *Microbrachium pelicani*, a microsaur; then in *Acanthostoma vorax* (see JAEKEL loc. cit. Fig. 7-8, e.g.), a branchiosaur; WILLISTON has described it recently in *Trematops milleri*, a genus related to *Eryops*; it is also observed in a recently found well preserved skull of *Telerpeton* (see 1912A p. 85-86 "internasal opening not present in *Telerpeton*), a cotylosaur from Elgin, by Mr. WILLIAM TAYLOR. *Dasyceps bucklandi* is the fifth form known to me (New or little-known Permian vertebrates, *Trematops* new genus. Jour. of Geol. 17, 1909, 636-658, Fig. 7). Here and in *Acanthostoma* it is largest.

In order to understand the purpose of the "facial pit" one must turn to recent forms. Unpaired sunken sense organs in the area of the snout occur in the chimaeras as a mating organ and in several deep-sea fishes (Teleostei) with long appendages as a taste organ, but these can give no explanation of the case in question. My attention was drawn to the similarly placed pit in the salamander skull by Mr. WILLIAM TAYLOR of Elgin, and Dr. J. VERSLUYS of Giessen and Prof. BLOCHMANN of Tübingen were kind enough to refer me to the important literature, for which I thank them.

From the literature I found a median opening in the bony skull between the premaxillae and nasals, or frontals (in some cases) in:

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| *Amblystoma* | *Salamandrina perspicillata* |
| *Anaides lugubris* | *Siredon* |
| *Batrachoseps attenuatus* | *Spelerpes fuscus* |
| *Chioglossa* | *Triton cristatus* |
| *Desmognathus fuscus* | " *viridescens* |
| *Ellipsoglossa naevi* | " *platycephalus* |
| *Gyrinophilus porphyriticus* | " *subcristatus* |
| *Plethodon glutinosus* | " *toronus* |
| *Salamandra maculosa* | *Amphiuma tridactylum* |
| " *atra* | *Salamandrella* |

In the named Urodela (the list is in any case incomplete) a gland is found in the pit. The gland is the glandula intermaxillaris. It is found in the terrestrial Urodela but not the aquatic. These internasal glands expand from the palate to the upper surface of the skull under the integument and in *Plethodon*, *Chioglossa*, *Batrachioseps* and others (GEGENBAUR, Vergl. Anatom. II, 1901, 118) extend to the orbits and behind them. The canals of the internasal glands, leading into the oral cavity, are lined with cilia like the oral cavity mucous membrane (GEGENBAUR loc. cit.). The glandula intermaxillaris is the most important of all gland organs of the anterior head [3]. R. WIEDERSHEIM has shown (Die Kopfdrusen der geschwänzten Amphibien und die Glandula intermaxillaris der Anuren. Zeitschr. f. wissensch. Zool. 27, 1876, 42 and Das Kopfskelett der Urodelen. Morpholog. Jahrb. 3, 1877, 515) "that it must be of the greatest use for the type of food intake of the animals, in that the secretion supplied by it moistened the tongue like a type of fly lime, on which the insects to be seized remain very readily stuck." The stickiness of the secretion is quite extraordinary in e.g. *Spelerpes fuscus*: a fly taken in by the furthest joint of only one leg cannot free itself again even with the greatest exertion. It is thus doubtless not a saliva-secreting but a mucous gland. The tip of the tongue touches the exit of the gland on folding back and darting out and thus picks up each time some of the sticky material in order to seize insects for food. "It is not surprising that this organ is found in no Phanerobranchiate or Cryptobranchiate when one considers that these salamanders are adapted exclusively to water life, in which they could not use such a device." (WIEDERSHEIM loc. cit. 1877, 515). Certainly the gland and a skull perforation are found in the aquatic Axolotl, which might be surprising if one does not regard it, like WIEDERSHEIM (loc. cit. 1877, 516) as an atavistic form; "it is interesting that a roomy internasal opening is found only in young axolotls, filled in with connective tissue, but which fills up more and more with cartilage in the adult animal. Thus exactly the same cavity is adhered to in the young stage which plays such a large role in the construction of the anterior head of all Salamandridae and which is always filled by that secretory organ". This indicates a degeneration in forms which go into the water.

On the contrary, K. PETER regards the internasal septum as primitive and the internasal cavity as secondary (Entwicklung ind funktionelle Gestaltung des Schädels von *Ichthyophis glutinosus*. Morphol. Jahrb. 25, 1898, 578), for he holds the gill-bearing Urodela as simply organised and more primitive than the "more highly developed" terrestrial forms. But it is not so easy to be certain about this latter point. A simplification of organisation occurs in the transition of terrestrial forms to water life, if the latter condition remains permanent.

In Anura the intermaxillary gland is also well developed. In several, e.g. *Rana esculenta*, the skull roof is even perforated in the same place as in the Urodela.

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[3] See further PARKER, Structure and development of the skull in Urodelous Amphibia. Pgilos. Trans. 1877 and Trans. Zool. Soc. XI. 1880. P. REICHEL, Beiträge zue Morphologie der Mundhöhlendrüsen der Wirbeltiere. Morpholog. Jour. Bd. 8. 1882.

“The position of the intermaxillary gland is represented in the Reptilia by the glandulae palatinae which are probably derived from that. They are partly paired, partly unpaired (median), consisting of individual glands. They are least developed in the Amphisbaenidae, clearest in *Chamaeleo*.” (GEGENBAUR loc. cit. 118).

In order now to return to the fossil forms provided with an intermaxillary cavity in the bony skull, so it can be gathered with certainty from what has been said that they were not water dwellers but thoroughly terrestrial forms which probably fed on insects (which indeed reached very considerable size in the Permian and Carboniferous). Naturally the intermaxillary gland was not only present in the 5 named fossil forms but (as today) also in those that do not show that gap in the skull roof.

From the fact that the intermaxillary gland was already distributed in Microsauria[4], different families of Stegocephalia (Hemispondyli) and Cotylosauria as early as the Carboniferous, Permian and Triassic, indicate it must be regarded as a very ancient organ. And the case of *Microbrachium* shows a parallel to the axolotl, in which the internasal cavity is also strongly developed, while the limbs and the whole body shape show that it is derived from terrestrial ancestors but is now a form entirely transferred to water or to a chosen way of life, for the limbs are extremely rudimentary and trunk and tail very elongated.

<u>On the comparative anatomy of the “epiotic” and the “supraoccipital” of the Stegocephalia and other Sauropsida</u>

The medially placed bone pair at the posterior edge of the stegocephalian skull is named by the majority of authors supraoccipital and that following laterally, epiotic. More cautious designations like “supraoccipital plates” indeed also occur. JAEKEL is of the view that the so-called epiotic is identical with the opisthotic (= paroccipital OWEN = processus paroticus HUXLEY).

First of all let us consider the occiput of two well-described Stegocephalia. One is *Capitosaurus stantonensis* (Fig. 10) (Proc. Zool. Soc. 1904, II, Pl. 11 Fig. 2). There the exoccipitals are clearly marked off; each of them has a vertical and an oblique laterally upwards-directed process. On each of them a vertically rising small piece runs upwards. On the lateral process a separate small bone piece is also placed. The skull roof follows immediately on this small bone with the above-mentioned so-called supraoccipitals and epiotics (WOODWARD uses a different system of naming). The occiput of *Mastodonsaurus giganteus* appears almost exactly the same, according to E. FRAAS (Palaeontographica 36, 1889, 69, Fig. 2) (Fig. 11). The lateral processes of the exoccipitals are quite rudimentary and the vertically rising bone piece is certainly constricted but not separated by a suture; the latter is probably obliterated. Without again entering into the significance of the bones, I might compare the occiput of *Pareiasaurus bombidens* (SEELEY, Phil. Trans. Roy. Soc. 182 B, 1892, Pl. 18 Fig. 2) (Fig. 12) with *Capitosaurus* and *Mastodonsaurus*. Here also in the middle of the posterior edge of the skull roof both the bone pairs of the Stegocephalia, the so-called epiotics, are present. Below these so-called supraoccipitals (and clearly marked off from them) and above the foramen magnum lie the vertically rising true supraoccipitals of the Reptilia that meet roof-like. Laterally the foramen magnum is bordered by the exoccipitals, which, as in most Reptilia,

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[4] The gaps are found as well as in *Microbrachia*, according to FRITSCH (Fauna der Geskohle I, Pl. 16 and Pl. 20, Fig. 1) in lesser degree in *Melanerpeton falax* and *Keraterpeton crassum*.

pass sutureless into the processus paroticus (= opisthotic). In the one skull described by HUXLEY (belonging to the complete skeleton) the natural upper end surface of the opisthotic is uncovered in the original. It is a smooth, rather curved contact surface. Directly on it lies the so-called epiotic of the skull roof. And it is similar for the so-called supraoccipitals (which border the foramen magnum). Before drawing further conclusions, I might also compare the occiput of *Pareiasaurus* with that of the Ichthyosauria as iknown through OWEN, BAUER (Anatom. Anz. 18, 1900, 586 Fig. 17) and ANDREWS[5]. Probably no doubt can exist that the elements in the attached figures in *Pareiasaurus* and *Ichthyosaurus* (Fig. 13), named according to BAUER as exoccipital, supraoccipital and opisthotic, are really identical. In the Ichthyosauria the opisthotic is made completely certain by the impression of the inner ear, also the true epiotic fused inseparably with the supraoccipital here. In the place where the opisthotic ends laterally, in the Ichthyosauria, a bone corresponding to the so-called epiotic of the skull roof no longer lies on it but the supratemporal (= squamosal of most authors) does. But the opisthotic of the Ichthyosauria is also doubtless homologous to the similar-looking and positioned bone of the Placodontia (Fig. 14), from which JAEKEL started off ("*Placochelys placodonta*" Ref. wiss. Erf. d. Balatonsees, I, 1, Anh. 1907, p 14, Pl. 2 Fig. 1). In order now to return to the starting point, the laterally branching bone elements from the exoccipitals of the Stegocephalia *Capitosaurus* and *Mastodonsaurus*, I hold definitely for homologues of the opisthotics of the named Reptilia and the small elements in the Stegocephalia rising vertically from the exoccipitals and fused with them or isolated may be homologues to the supraoccipitals including epiotics (e.g. of the Ichthyosauria). And the so-called supraoccipitals and so-called epiotics in the Stegocephalia and Pareiasauria, found in the skull roof and provided with sculpture, generally do not belong in the auditory bulla but are covering bones. The names opisthotic, epiotic (still never shown isolated) and prootic are given for the 3 primary skull bone pairs, which form the auditory bulla as primary ossifications in the skull; the remaining bones and particularly the covering bones appear later ontogenetically. As the single exception, to my knowledge, the epiotics seem to be separated from the supraoccippital by a suture in a *Phytosaurus* skull soon to be described by me.

It was my first task then to establish that the bones in Stegocephalia named epiotic and supraoccipital of the posterior skull roof are covering bones and not otic bones (replacement bones) and that hence they must not be named as they usually are. I might therefore recall on this that COPE named the so-called epiotic of the skull roof, <u>intercalary</u> (Trans. Amer. Phil. Soc. N. S. 17, 1892, Pt. I, p 13; later, 1896, he used the term "tabular bone") and that MIALL named the so-called supraoccipital of the skull roof, <u>dermo-supraoccipital</u>[6].

The second question is the assessment of this covering element which is certainly probably not to be clothed in any definite form. These bone pairs are the most inconstant in the skull of Sauropsida. The supratemporal is a little more constant; the intertemporal appears quite sporadically. Analogous characteristics in the skull roof are found e.g. in the Ganoidei. Different numbers of smaller and larger skull elements occur there, particularly behind, which are named supraoccipitals, supratemporals and posttemporals; in the older forms they are often found in more than only one pair of each. The more primitive a form of tetrapod is, the higher the number of skull elements it seems to possess. JAEKEL considers "as a primitive starting point…a uniform roof which was first divided into regions and definite bone plates under the stress and strain of the roofed-over parts of the head. The agreement in principle in the layout

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[5] I do not believe that ANDREWS gives the position of the opisthotic quite correctly (Geol. Mag. 1907, p 204, Fig. 2).

[6] B. C. MIALL, Studies in comparative anatomy. No. I. The skull of the Crocodilia. MACMILLAN, London, 1878, p 12.

of the roofed-over parts of the head has then also brought independence over the more important and more constant parts of more constant elements, while making itself felt in other greater differences also in the formation of the skull roof." (Klassen der Tetrapoden. Zool. Anzeiger, XXIV, 1909, p 198).

Plate I: *Dasyceps bucklandi* LLOYD sp. from the Permian sandstone of Kenilworth, Central England. 2/3 natural size. Original in the museum at Warwick.
More detailed explanation, see Textfig. 1, p. 32 (324). Inner view of the skull roof and in part a cast of it.

Plate II: *Dasyceps bucklandi* LLOYD sp. from the Permian sandstone of Kenilworth, Central England. 2/3 natural size. Original in the museum at Warwick.
Upper view of the skull roof and palatal view of the anterior and left half.
More detailed explanation, see Textfig. 3, p. 35 (327).

Fig. 1: *Dasyceps bucklandi* LLOYD. Dorsal view of the skull, 2/3 nat. size, cf. Pl. I (XLIV). In the middle in front lies the large "facial pit", to both sides of which the small nasal openings.

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| E = so-called epiotic (dermal bone) | Pm = premaxilla |
| F = frontal | Pn = lachrymal |
| J = jugal | Po = postorbital |
| L = prefrontal | Qj = quadratojugal |
| M = maxilla with teeth | S = so-called supraoccipital (dermal bone) |
| N = nasal | Sq = squamosal |
| P = parietal (between both P the parietal fossa) | Sq? = probably belonging to the Sq |
| Pf = postfrontal | St = supratemporal |

Fig. 2: *Dasyceps bucklandi* LLOYD. Dorsal view with mucus canals in ¼ nat. size.

Fig. 3: *Dasyceps bucklandi* LLOYD. Part of the palate and the skull roof in 2/3 nat. size. cf. Pl. II (XLV).

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| Gz = palate teeth on premaxilla and palatine | Pt = pterygoid |
| M = maxilla (with teeth) | Q = quadrate |
| P = palatine | ?Tr = perhaps a transversal |
| Pm = premaxilla | V = vomer |
| PO = inner nasal opening | |

Where palatal teeth are shown, it is their impression under the chipped off palate bones. The posterior part of the skull shows the skull roof in poor condition.

Fig. 4: *Cochleosaurus bohemicus* FR. (After BROILI). Names mostly as Fig. 1.
It? = intertemporal
C = condyle

Fig. 5: *Chalydosaurus vranii* FR. (After FRITSCH). Names as Fig. 1.

Fig. 6: *Melosaurus uralensis* H. v. M. (After H. v. MEYER).
C = condyle. Other names as Fig. 1.

Fig. 7: *Osteophorus roemeri* H. v. M. (After H. v. MEYER).
Et? = probable ethmoid. . Other names as Fig. 1.

Fig. 8: *Nyrania trachystoma* FR. (After FRITSCH.) Names as Fig. 1.

Fig. 9: Dorsal view of the skull of *Salamandrina perspicillata*. (After WIEDERSHEIM fide GADOW.) Shows the large internasal opening (= “facial pit”) in the skull.

Fig. 10: Occiput of *Capitosaurus stantonensis* WOODW. (After A. S. WOODWARD).
Bo = basioccipital
E = so-called epiotic (dermal bone)
Eo = exoccipital
G = rock
Op = opisthotic
Pt = pterygoid
Q = quadrate
Qj = quadratojugal
S = so-called supraoccipital (dermal bone)
So = supraoccipital (replacement bone)
Sq = squamosal

Fig. 11: Occiput of *Mastodonsaurus giganteus* IG. (Copy E. FRAAS).
Ex Occ lat = opisthotic
S Temp = squamosal

Fig. 12: Occiput of *Pareiasaurus bombidens* OWEN. (After SEELEY and completed from my own observations.)
E = so-called epiotic (dermal bone)
S = so-called supraoccipital (dermal bone). Other names as Fig. 10.

Fig. 13: Occiput of *Ichthyosaurus* sp. (after F. BAUER).
Pro = prootic (must be rather differently placed according to my view)
Stap = stapes

Fig. 14: Occiput of *Placochelys placodonta* JKL. (After JAEKEL, however with different bone names.) 2/3 nat. size. Letters as above.