Phylogenetical and morphological Notes on the primary and secondary Dermal Bones of the Skull.

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(With 6 Figs. in the Text.)

Explanation of the figures.

Fig. 1 (p. 74). Upper view of skull of *Pelobates fuscus* Laur., showing the secondary dermal ossifications; prootical region not overroofed. — ad. ♂ from Esztergom (Hungary), 30. III. 1920. Leg. Mr. L. Véghelyi. (Mus. Hung. Amph. No. 2570/1.) — 2 × nat. size. — Ad nat. del. Baroness A. M. de Fejérváry-Langh, Ph. D.

Fig. 2 (p. 74). Upper view of skull of *Pelobates cultripes* Cuv., showing the secondary dermal ossifications; an osseous bridge above the prootical region, from the frontoparietals to the tympanic, enclosing the fenestra posttemporalis. — ad. ♀ from Lisbon, 1912. Leg. Dr. J. de Bethencourt-Ferreira. (Roy. Hung. Geological Inst.) — 2 × nat. size. — Ad nat. del. Baroness A. M. de Fejérváry-Langh, Ph. D.

Fig. 3 (p. 75). Upper view of median and hind part of skull of a nearly metamorphosed larva of *Pelobates syriacus* Bttgr.; no trace of secondary exoskeletal elements. — Asia minor, 1911. Leg. Mr. L. de Náday. (Mus. Hung. Amph. No. 2511). — Strongly magnified. — Ad nat. del. Baroness A. M. de Fejérváry-Langh, Ph. D.

Fig. 4 (p. 78). Nasal bone of *Ophisaurus apus* Pall. and the secondary dermal bone-plate attached to its dorsal surface. — old ♂ from Zelenika (Dalmatia). (Roy. Hung. Geol. Inst.) — Strongly magnified. — Ad nat. del. Baroness A. M. de Fejérváry-Langh, Ph. D.

a: dorsal view, with the secondary dermal bone-plate (corresponding to the praefrontal shield) adhering to it.

b: ventral view of the same.

c: dorsal view, after the removal of the secondary dermal bone; that part of the secondary dermal ossification which corresponds to one half of the frontonasal shield rests upon the nasal bone under the form of a crusta calcarea.

d: dorsal view of the isolated secondary dermal bone-plate which corresponds to the praefrontal shield.

Fig. 5 (p. 78). Supraciliary lamina and a part of the crusta calcarea (*), detached from the roof of the skull, of *Tiliqua scincoides* White. — ad. ♀, Australia, 1908. (Mus. Hung. Rept. No. 2290/15.) — Strongly magnified. — Ad nat. del. Baroness A. M. de Fejérváry-Langh, Ph. D.

Fig. 6 **a** (p. 88). Upper view of skull of a fontanelliferous *Lacerta*. (*Lacerta muralis* Laur. var. *Bocagei* Seoane, ad. ♂ from Alcochête [Portugal], 1912. — Leg. Dr. J. de B.-Ferreira. — Coll. Fejérváry-Langh.) — About 6·06 × nat. size. — Ad nat. del. Dr. C. Szombathy.

Fig. 6 **b** (p. 83). Fully ossified supraciliary lamina of an old ♂ of the same variety. (From La Coruna [Spain]. — Leg. Don V. L. Seoane. — (Mus. Hung.) — 9·35 × nat. size. — Ad nat. del. Baron G. J. de Fejérváry. (Only the II. & III. supraocularies are cleanly prepared, whilst the surrounding parts, covered with scales, are marked with dots.) — Both Figs. from G. J. de Fejérváry, Ann. Mus. Nat. Hung., XIII, Budapest, 1915, Pl. II, Figs. 1 & 6.

Within the Vertebrate Skeleton anatomists distinguish two main kinds of bones: the „membrane" bones or dermal bones, called „Deckknochen", „Hautknochen" or „Belegknochen" by the

German authors, and the cartilaginously preformed „cartilage bones", known under the name of „Ersatzknochen" or „Knorpelknochen" in the German anatomical Literature.

The former ones, which are designated as „Allostoses", must be looked upon as phylogenetically derived from an ancestral exoskeleton, whilst the latter ones — the „Autostoses" — constitute the primary elements of the endoskeleton, i. e. the primordial or chondroskeleton. Phylogeny has teached us that the first ossifications are represented by the elements originated from the ancestral exoskeleton, whilst the ossification of the different parts of the undoubtedly more ancient cartilaginous (primordial) skeleton occurred but in a somewhat later phase of Vertebrate Evolution.

It cannot be my intention to enter into details concerning the autostotic and allostotic mode of development of the various skeletal and especially cranial elements, nor to deal with the principles of their often so difficult homologization in the different Classes and Orders, a problem the difficulty of which may be still increased by cases of fusion or by complicated coenogenetical phenomena. I shall merely confine myself to the statement that, as regards the development of dermal and chondral ossifications, the evidence of three types has been established, which are represented by: the **cartilage bones, the dermal bones**[1]) including s. lat. the odontogenous bones („Zahnknochen") as well, and the socalled **mixed bones.**[2])

It is but the second of the three mentioned types which shall be here discussed.

As stated above, the dermal (or „membrane") bones, which, nowadays, represent integrant components of the Vertebrate skull (i. e. of the endoskeleton), are the offspring of ancient exoskeletal elements. I will designate this ancestral exoskeleton as the **primary exoskeleton,** in opposition to the **secondary exoskeleton** occurring in phylogenetically younger forms, i. e. in some Fishes and in various representants of the Classes of Batrachians, Reptiles and Mammals.[3])

In the **Fishes,** which present the greatest complexity with respect to their osteological features, the distinction between primary and secondary exoskeletal elements constitutes a very difficult problem. In a very large number the dermal bones of

[1]) The term „membrane" bone, by which the „Deckknochen" of the skull are generally designated, though corresponding to their embryological development, is rather inadmissible from a phylogenetical point of view. I prefer to use, therefore, the expression „dermal bone".

[2]) The ossifications of ligaments and muscles will not be here considered.

[3]) Birds are devoid of exoskeletal ossifications; in this Class it is but the sclerotical ring which might be looked upon as constituting an „exoskeletal" element; at present, however, this special formation shall be left out of consideration.

the skull seem to be throughout the offspring of a primary exoskeleton. There are, however, representatives of the Class in which the presence of secondary exoskeletal elements (bone-plates) can be established.

Such secondary exoskeletal plates are present on the skull of *Ostracion* for instance, and the bony gular plates of the ancestral representants of the *Dipneusti* may probably also be referred to this kind of elements. The praedental bone, occurring in some Fishes (*Onychodontidae, Aspidorhynchidae*), referred to by Prof. Abel as constituting a „sekundäre . . . Bildung"[4]) and the praeethmoideum (present in *Cyprinus* for instance) are probably also belonging to the secondary exoskeletal ossifications. Future investigations, leading to a more exact knowledge of the phylogenetical evolution of the single elements constituting the Fish-skull, will surely enrich this series by many other examples.

With respect to the Fishes it is important to point out the fact that in most of the cases in which the presence of secondary exoskeletal elements could be established, the mentioned ossifications occur, on the skull, but under the form of single „supernumerary" bones, and the occurrence of numerous bony plates, united to a coherent (secondary) exoskeletal armour overroofing the „membrane" bones (like in *Ostracion*), must be considered as a rather exceptional feature.

The most ancient representatives of the Orders *Osteostraci*[5]), *Antiarchi* and *Arthrodira* present a highly developed exoskeleton. The structure of the exoskeletal elements of the *Anaspida*, which are the oldest Vertebrates we know of, could not be established, though it is probable that their dorsal (?) crest[6]) might be looked upon as containing dermal ossifications. The elements of the exoskeleton of the *Osteostraci* and *Antiarchi* cannot be homologized with the dermal bones of the skull in any other Vertebrate. There is no proof as yet of the exoskeleton of these two Orders being a secondary one — like in *Ostracion* —, and that, below it, the presence of an ossified skeleton, containing homologizable primary dermal bones (i. e. so called „membrane" bones) ought to be presumed. It is, at least for the present, more reasonable to consider these two groups as constituting extinct side-branches, the endoskeleton of which was probably merely cartilaginous, whilst their exoskeletal elements may presu-

[4]) O. Abel, D. Stämme d. Wirbeltiere, Berlin u. Leipzig, 1919, p. 54—55.

[5]) Including the „*Heterostraci*". (Cf. O. Abel, op. cit. p. 71.)

[6]) Mr. Traquair and other palaeontologists consider this crest as ventral, whilst Jaekel, and recently Freiherr Stromer v. Reichenbach, suggested it to be dorsal. Such an orientation of the body would make the general topography of its morphological structures decidedly more comprehensible. In this case the tail would represent, of course, the hypobatic type, instead of the epibatic by which all palaeozoic Fishes, known up to now, are characterized.

mably be regarded as primary and very specialized features, unhomologizable with the skeletal elements of any higher Vertebrate. The dermal bones of the skull of the fourth Order, the *Arthrodira*, are much like those of the more recent Fishes, with which they may, to a certain extent, be successfully homologized. They are, as may be stated for the dermal bones of the skull in the great majority of the forms belonging to this Class, elements of a primary exoskeleton.

On account of this far-reaching morphological and phylogenetical dissociation existing between the Orders *Osteostraci* and *Antiarchi* on one hand and the Orders *Arthrodira, Elasmobranchii, Acanthodei* and *Teleostomi* on the other, I propose to conserve, for the formers, the ancient Subclass *Placodermi* (Agassiz), to which, provisionally, the *Anaspida* might also be referred, whilst establishing for the latter 4 Orders the new Subclass **Coinocrania.**[7])

In the **Batrachians** the dermal ossifications of the skull are, with relatively rare exceptions, represented by derivatives of a primary exoskeleton. The skull of the *Stegocephalia*, which are the prototypes of „armoured" Batrachians, presents easily homologizable dermal bones, which seem to be all of a primary exoskeletal origin. There exists, however, in this Order, an important osteological feature which must be here taken into consideration. The roof of the skull of numerous Stegocephalians is very rough. The asperities occurring on it are often very like a **„crusta calcarea".** As the corium of the Stegocephalians secreted lime in large quantities, it is not impossible that, at least in some cases, such asperities were formed by lime-concretions of the derm, having been deposed upon the primary dermal bones of the skull. In this case the asperities would effectively result in being a true „crusta calcarea", which would represent, on the skull, the primitive stage of the formation of secondary exoskeletal elements.

We must not forget, however, that the „sculptures" observable on the cranial bones do not always necessarily represent a crusta calcarea, i. e. a complex of secondary lime concretions, but are often retraceable to the osteogenesis of the respective bones themselves, constituting thus their proper structural feature. This sculpture is radial, or concentric, or rather both.[8]) It is very important to point out the fact that structural sculptures may be present on both the primary and secondary dermal bones, so that the mere presence or absence of sculptures offers no clue to a distinction of these two skeletal components.

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[7]) From *κοινός* = common, and *τὸ κρανίον* = the skull. — Not to confound with the lacertilian group „Kionokrania" (from *τὸ κίων* = column, pillar).

[8]) Cfr. F. Leydig, Üb. d. allgem. Bedeckungen d. Amphibien, Arch. f. mikr. Anat. XII, Bonn, 1876, p. 77 of the Separate, dealing with the exoskeletal ossifications of *Tarentola* (Reptilia, *Geckonidae*).

As regards the crusta calcarea, it always occurs under the form of most differently shaped, though well defined „sculptures", often presenting small pits, which are the traces of the „Bindegewebskörper",[9]) or small spinous rugosities.

Thus we must take care not to confound the „structural" sculptures of the primary dermal bones with the crusta calcarea, representing the primitive stage of the secondary exoskeletal ossifications and formed by the corial lime deposits. The crusta calcarea constitutes, in its very first stage, a complex of rather independent lime concretions, coossifying later on with the subjacent bones of the skull. For those who are in the lucky position to dispose over a large material it will not be too hard a task to establish in which forms a true crusta calcarea occurs, definitively elucidating hereby the origin and evolution of the two different kinds of „sculptures", so unperfectly known as yet and although so often referred to in the various descriptions.

In the Coecilians, some of which are provided with a „degenerated" exoskeleton, hidden under the smooth epiderme, and which are asserted to derive from Stegocephalian predecessors, the skull seems to be devoid of secondary exoskeletal elements.

The Urodeles or Tailed Batrachians are devoid of conspicuous secondary exoskeletal elements, the dermal bones occurring on their skull deriving from a primary exoskeleton.

The same thing occurs with almost all the Anura or Tailless Batrachians. There are, nevertheless, some interesting exceptions, very instructive from the standpoint of the development of the exoskeleton in general. With respect to this subject Mr. G. A. Boulenger[10]) writes as follows: „On trouve une plus ou moins grande quantité de substance calcaire dans la peau du Crapaud commun; ces dépôts calcaires peuvent être très développés dans la peau du dos de certaines espèces des genres *Megalophrys*, *Nototrema*, *Phyllomedusa* et *Lepidobatrachus*; d'autres Anoures possèdent un bouclier dorsal osseux, libre (*Ceratophrys*) ou ankylosé aux vertèbres (*Brachycephalus*)." These dermal ossifications constitute a secondary exoskeleton — just like the osseous plates occurring in *Ostracion* — in opposition to the ancestral primary exoskeleton, from which the socalled „membrane bones" of the skull derived. Thus **it is advisable to distinguish within the dermal bones** of the **skull,** in general, **two** phylogenetically **different kinds,** i. e. **primary** and **secondary dermal bones.** Such secondary dermal bones are also present on the skull of a European Genus, viz. on that of *Pelobates*.[11]) The secondary dermal bones are in-

[9]) Cfr. Leydig, op. cit. p. 74.

[10]) Les Batraciens &c., Encycl. Sc., Bibl. de Zool., Paris, 1910, p. 18—19.

[11]) Cfr. Gadow, in: The Evol. of Horns and Antlers, Proc. Z. Soc. London, 1902, p. 208: „In *Pelobates* the skin of the upper surface of the head is partly co-ossified with the underlying cranial bones, giving them a pitted" (? rather spinous!) „appearance. Now, frontal and parietal being

separably attached to or fused with the primary dermal bones in both the European species pertaining to this Genus (*P. fuscus* Laur., and *P. cultripes* Cuv.)[12]), so that the shape of the primary dermal bones can only be examined in young specimens, a mechanical removal of the secondary exoskeletal elements, occurring in the adult, being quite impossible. As shown in Figs. 1—2 the secondary exoskeletal bones attained in *P. cultripes* Cuv. a considerably higher development than in *P. fuscus* Laur.

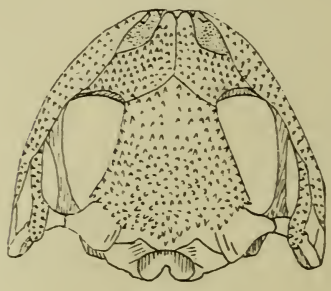

Figure 1.

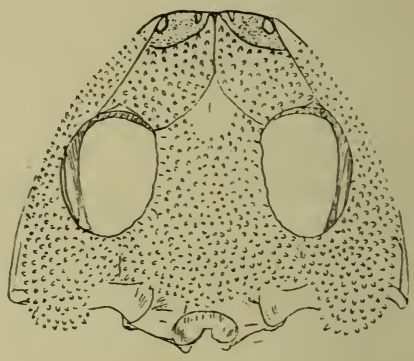

Figure 2.

The course of the development of this secondary exoskeleton seems to be most simply explainable. The lime of the derm (cutis or corium) forms at the beginning smaller concretions, which, in the lapse of time, coalesce between each other, forming larger plates. The shape of these plates depends on the local anatomical structures of the respective regions of the corium, as well as on the mechanical action produced by the kinesis of the animal, and on the effects produced by oecological conditions, i. e. by the environment. At the beginning the dermal ossifications occurring on the skull seem to be limited to those regions of the derm which cover osseous surfaces, i. e. which are immediately superposed to the bones constituting the roof of the skull. Almost all of these latter bones are primary dermal bones, and only very few pertain to cartilaginously preformed bones, as the ethmoid for instance. It is a well known fact that in Batrachians and Reptiles the skin generally very closely adheres to the roof of the skull, and so the lime-concretions formed by the derm on these parts coalesce very soon with the bones immediately beneeth them, constituting thus a socalled „crusta calcarea".

If the secondary dermal ossification continues to a higher degree, it may form osseous bridges, connecting various prominent points or edges of oppositely neighbouring bones. In *P. fuscus*,

membrane bones, or at least membranes which have received their bone from the cutis, this superimposed ossifying mass of *Pelobates* is a second instalment, or second generation of dermal bone."

[12]) And surely also in the Asiatic *P. syriacus* Bttgr.

for instance, the prootics are freely visible from above, whilst in *P. cultripes* a bridge is to be found connecting the secondary dermal bones which overroof the frontoparietal on one hand, and the tympanic, quadratojugal and maxillary on the other. This frontoparietalo-tympanic bridge encloses, with the prootic, the fenestra posttemporalis (Fig. 2).

That these formations occurring in *Pelobates* are not ancestral markings, inherited from some Stegocephalous predecessors, as assumed by Boas with respect to the *Hemiphractidae*[13]), seems to be proved by their late ontogenetical appearance. I examined large, nearly metamorphosed larvae of *Pelobates* (also of *P. syriacus* Bttg.), where no trace of secondary dermal ossifications could be found; the surface of the frontoparietals and tympanic is in such young individuals (Fig. 3) quite smooth, presenting well defined outlines, and resembling the type observable in *Alytes* for instance; a large fontanelle separates the frontoparietals from each other. The mentioned smoothness of the bones in question proves also that the „incrustation" later occurring on them is certainly not a primary structural particulartiy.

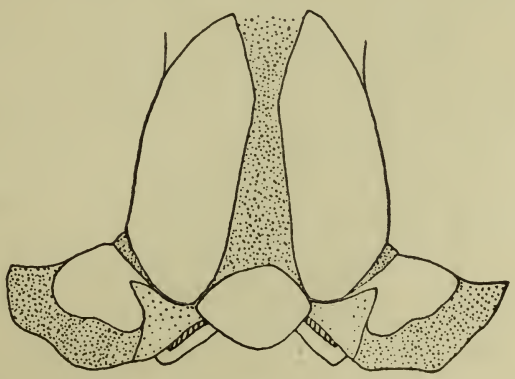

Figure 3.

On the body the development of the secondary exoskeletal plates is not as limited as on the head, and so the corium might secrete larger osseous plates there, which, simply by means of their anatomical topography, are generally not connected with any endoskeletal elements. In some cases, however, (*Brachycephalus*) the components of the secondary exoskeleton of the body may also ankylose to more superficial endoskeletal elements, in the same way as the primary dermal bones coalesced with the elements of the ancestral endoskeleton, i. e. with the chondroskeleton. The roof, i. e. the outer surface of these „body-plates" is generally very rugose (cfr. Stegocephalians and *Ceratophrys*), but this incrustation is not a „tertiary", viz. not a later stratum of lime settled upon the phylogenetically secondary exoskeletal plates, but merely represents the structural „sculpture" of the respective secondary

[13]) Die Schläfenüberdachung u. d. Palatoquadr. i. ihr. Verhältn. z. übr. Schädel b. d. Dipnoern u. d. terr. Wirbelt., Morph. Jahrb., Bd. XLIX, 2. Heft, 1914, fide O. Abel, op. cit. p. 316.

dermal plates themselves. That means that the crusta calcarea overroofing the skull in some Batrachians and Reptiles,[14]) in a similar way as in *Pelobates* or *Ceratophrys* for instance, is morphologically equivalent, i. e. homologous with the whole of any secondary dermal bone-plate of the body, the difference between their mode of occurrence, i. e. their independency from or connexion with the endoskeleton, being simply retraceable to the above mentioned aberrant topographical conditions.

With respect to the phylogenetical development of the secondary exoskeleton we can distinguish, as within each Evolution, a phase of ascension and a phase of culmination, which are then often followed by a third phase, represented by degeneration. There is no difficulty to approximately establish the phase of culmination, but to decide whether certain characters of an organism are developing or degenerating, may be, in some cases, a very hard task.

P. cultripes is, with respect to its secondary dermal ossifications, surely in the phase of culmination, whilst the application of the biogenetical law allows the supposition that the secondary dermal ossifications of *P. fuscus* are not, as Prof. Abel[15]) seems to presume, in the phase of degeneration, but, on the contrary, in that of ascension. It remains naturally an open question whether this species will ever reach, or not, the same culmination as *P. cultripes*.

The rugged bony stratum covering the skull in *Hemiphractus* and some other Tailless Batrachians belongs also to the category of secondary dermal ossifications, even if it were inherited from Stegocephalian ancestors, as supposed by Boas.

If, however, as I presume, the ontogeny of these forms would prove that the secondary dermal ossification appears also in these cases as late as in *Pelobates*, and if the skull of the young animal would present also here the typically specialized anurous features of the frontoparietals, tympanic and other bones, — and I am afraid that future investigations will prove it to be so — Mr. Boas' mentioned supposition ought to be decidedly rejected.

Let us now examine the **Reptiles.** With respect to the absence or presence of a secondary exoskeleton the youngest Order, the *Lacertilia*, offer the most manifest conditions. Thus we shall begin with the examination of the latter ones. Within this Order we may distinguish two main Types. The first is represented by forms in which the body is generally devoid of exoskeletal plates, the roof of the skull, i. e. the surface of its primary dermal bones, is generally smooth, and the upper surface of the Orbits is not protected by a lamina supraciliaris. Such conditions are present in the *Varanidae*, *Agamidae*, &c. I will designate this Type as the nudorbital. The second main Type is represented by forms in which the body very often bears

[14]) Cfr. *Heloderma*, *Ophisaurus*, *Trachysaurus*, *Tiliqua*, &c.
[15]) op. cit. p. 314.

an exoskeletal armour, formed by osseous plates, which occur also on the roof of the skull, either under the form of a thick and prominent „crusta calcarea", or under that of a mosaic of more or less detachable bone-plates; the outlines of each „incrusted surface", or of each bone-plate, correspond to those of a pilear shield; the dorsal surface of the Orbits is covered with a lamina supraciliaris. Such forms are *Ophisaurus*, *Trachysaurus*, *Tiliqua*, &c. I propose to designate this Type as the tectorbital. These two main Types are those to which all other more or less complicated exoskeletal formations, occurring in the Lacertilia, are to be retraced.

From the phylogenetical point of view the nudorbital type is the more ancient, whilst true representatives of the tectorbital are, up to now, only known from the palaeogene, and so will probably have existed at least as soon as at the End of the Mesozoic.

With respect to the morphological conditions in which we are interested at present, the **tectorbital** Type is by far the more important. For its characterization let us choose the Anguinid Genus *Ophisaurus* and the Scincid Genus *Trachysaurus* as examples. The body of these animals is provided with an armour of osseous plates — constituting the exoskeleton — the skull presenting, on its surface, convex bony elements, corresponding to the pilear shields. In consequence of this osseous scutellation the shape of and the limit between the single „membrane" bones, i. e. primary dermal bones of the skull cannot be seen. The temporal, gular and loreal region and in *Trachysaurus* the mandibles are covered with osseous plates, which correspond to the lepidotical elements. If we examine these exoskeletal bones on the skull of *Trachysaurus* we will find that some of them are rather easy to be detached from the endoskeleton (i. e. from the subjacent primary dermal bones), so on the lateral regions of the parietal, on the postfrontals and on the mandibles. The anterior lower part of the maxillaries, the lower part of the praemaxillary and the immediate area around the outer nareal openings corresponding to the nasal shields is devoid of osseous plates. On some parts, however, i. e. on the frontal bone and on the anterior median part of the parietal bone (corresponding to the interparietal shield), as well as on the region corresponding to the frontonasal and praefrontal shields, the dermal armour adheres very strongly to the subjacent primary dermal bones („membrane" bones), in a way as to occur rather under the form of an „incrustation" than under that of separable elements. In some special cases, however, they might be isolated, as in the nasal region of *Ophisaurus* for instance. Baroness A. M. de Fejérváry-Lángh, Ph. D., has shown in her Monograph of fossil Ophisaurs,[16]) which is about to be published, that the os nasale of *Ophisaurus* can only be examined, with respect to its shape, if the large and dilated exoskeletal plate, adhering to its

[16]) Beiträge zu einer Monographie der fossilen Ophisaurier.

posterior part, and corresponding to the praefrontal shield, is detached from it (cfr. Fig. 4). This very often happens quite simply in the course of maceration. Its ventral surface indicates always very well the true outlines of the bone, because the mentioned exoskeletal plate adheres to its upper surface. The secondary formation which occurs on the anterior part of its dorsal surface under the form of an „incrustation", corresponding to one half of the frontonasal shield, adheres so much to the roof of the nasal bone that a detachement of it seems to be impossible (see Fig. 4c).

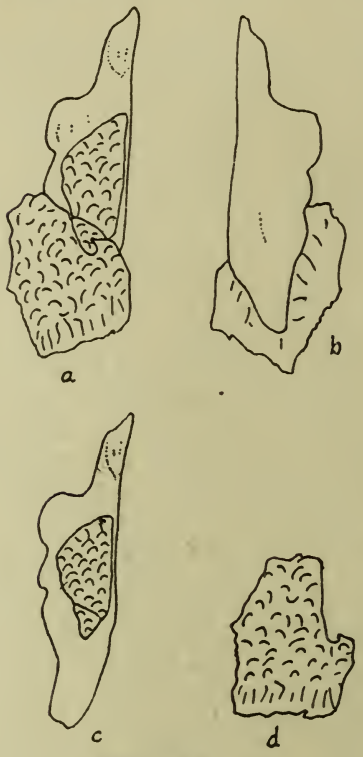

Figure 4a—d.

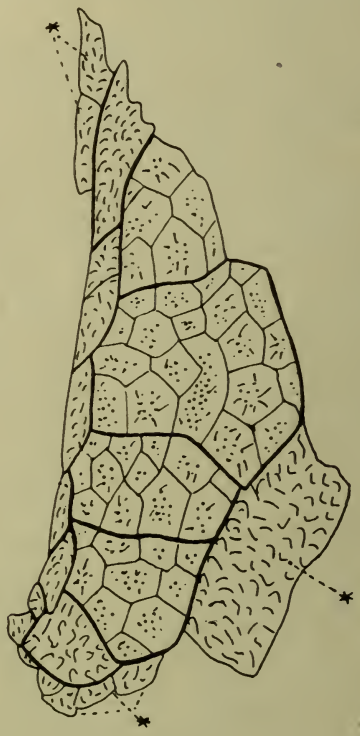

Figure 5.

As regards the lamina supraciliaris, it is homologous with the mentioned „exoskeletal" elements, representing thus a throughout secondary formation. Its bionomical rule is certainly very important because it protects the eye. Its anterior part closely adheres to (*Ophisaurus*), or rather coossifies with (*Trachysaurus*), the supraorbital bone (a primary dermal bone). The upper surface of this supraciliary lamina, — consisting of large plates, the supraoculars, and a lateral series of smaller plates, the socalled supraciliaries — is rough; its ventral (orbital) surface is rather smooth and on this side the morphological structure of the single plates can be very well established. If we examine the ventral (orbital)

surface of the lamina supraciliaris in *Trachysaurus, Tiliqua* (Fig. 5) or *Zonurus* for instance, we will find, especially in younger specimens, that the osseous substance constituting the single plates is not uniform, each plate consisting of small polygonous elements.[17]) These polygonous elements may be looked upon as representing single areas of ossification, being retraceable to the single centres of ossification from which the development of the larger plates originally proceeded. This very clearly proves that the larger osseous plates were built up by the fusion of smaller dermal bones, a fact which is in full accordance with the natural course of the formation and gradual extension of dermal lime concretions.[18])

The statement of the lamina supraciliaris belonging to the secondary exoskeleton, as well as its above sketched composition, throw fresh light upon the phylogeny of this cranial element, elucidating thus, especially if correlativity is simultaneously taken into consideration, the following disputed points of the origin of Lacertian forms.

The one group of the Genus *Lacerta*, designated by Mr. G. A. Boulenger as „Massive Lizards" (*Lacerta ocellata* Daud., *L. Simonyi* Stdr., *L. viridis* Laur., *L. agilis* L., &c.), possesses a strongly ossified skull and, in many species, a completely ossified temporal „armour". These features are also present in the other Group, the more or less „*muralis*-like" Lizards, but the ossification is there, generally,[19]) considerably weaker, and the number of the osseous plates of the temporal region is generally very much reduced and in many forms the whole temporal armour is wanting. Thus, on account of the secondary dermal bones of the skull, the Genus must be referred, like all the members of the family, to the tectorbital Type. — We have no proof at all of the *Lacertidae* having derived from Scincoid ancestors, i. e. from forms in which not only the skull, but also the body was provided with secondary dermal bone-plates. It must be admitted, however, that the body of most Lacertilians presenting the same cranial construction as the *Lacertidae*, i. e. agreeing with them in the presence of a supraciliary lamina and some temporal bone-plates, is provided with an exoskeletal armour and thus it may be presumed that the procedure, which gave rise to the formation of the dermal ossification on the head in the predecessors of the *Lacertidae*, was not limited to

[18]) A similar procedure has been observed with respect to the development of the primary dermal bones constituting the upper surface of the skull in the Dipneust and Crossopteryg Fishes (cfr. Abel, Stämme d. Wirbeltiere, p. 178).

[19]) In *L. peloponnesiaca* D. & B. the skull is strongly osseous, the temporal region is provided with „einem fast geschlossenen Hautknochenpanzer", and even the mandibularies bear dermal bone-plates (cfr. Méhely, Ann. Mus. Nat. Hung., V, Budapest, 1907, p. 479).

[17]) In *Tiliqua* these elements are even to be demonstrated on the rugose dorsal surface of the lamina supraciliaris (cfr. Fig. 5).

the corium of this part only, but took place in other parts of the body as well. It is not quite impossible, therefore, that the predecessors of the *Lacertidae* possessed a more extended secondary exoskeletal armour. I would like to emphasize, however, that such a supposition is not corroborated by any ontogenetical or embryological fact and could be supported but in a purely theoretical way, merely on the strength of the above cited physiological consideration. Thus, for the present, it might appear more probable that in the *Lacertidae* it is only on the head where the formation of secondary dermal bones took place; we saw that on the roof of the skull, where the skin very closely adheres to the (actually) endoskeletal bones, exoskeletal, i. e. corial ossifications are easily formed,[20]) by means of the cells of the connective tissue, which may function in a similar way as the true osteoblasts. But how to explain the presence of the temporal armour? Under that no bony parts are to be found, as it covers only deep muscular layers. A satisfactory answer with respect to this question could, at present, hardly be given. Maybe that mechanical irritations, due to the mode of life of these larger animals, which use their head when boring themselves into an earthy-stony ground, ought to be here taken into consideration.

Some years ago Prof. de Méhely[21]) has proved that within the Lacertian forms referred by most authors to the species *Lacerta muralis* Laur., some rather heterogeneous species exist, which cannot be looked upon as constituting mere races of one and the same species. In the quoted publications Mr. Méhely has also dealt with the supraciliary lamina of the „*muralis*-like" Lizards, and demonstrated that with respect to this element two aberrant features occur. In one part of these forms the supraciliary lamina is composed of fully ossified „supraocularies" and a more or less complete series of „supraciliaries", whilst in the other the supraciliary lamina is rather weak, and bears a more or less large membraneous fontanelle; in the latter forms the number of supraciliary elements is much reduced, and may even be represented by a unique element, i. e. the first supraciliary (supraciliare principale). The skull of the Lizards presenting a completely ossified supraciliary lamina, is strongly osseous, its roof is rather strongly incrusted, and the temporal region generally bears at least some „supratemporal" dermal bones. The skull of the other group is weak, rather membraneous, generally more depressed, being, in its temporal region, devoid of any dermal ossification. The species

[20]) Cfr. the discussion of the secondary dermal bones in *Pelobates*.

[21]) Cfr.: Zur Lösung d. „Muralis-Frage", Ann. Mus. Nat. Hung., V, Budapest, 1907, p. 84—88, Taf. III; Archaeo- und Neolacerten (Erwiderung an d. Herren G. A. Boulenger F. R. S. u. Dr. F. Werner), ibid. V, 1907, p. 469—493, Taf. X; Materialien zu e. Syst. u. Phyl. d. muralis-ähnlichen Lacerten, ibid. VII, 1909, p. 409—621, Taf. X—XXV, Textfig. 1—8; Weitere Beitr. z. Kenntn. d. Archaeo- u. Neolacerten, ibid. VIII, 1908, p. 217—230, Taf. VI.

pertaining to this latter type were designated by Mr. Méhely, the discoverer of this interesting osteological feature, as „*Archaeolacertae*", whilst those with na osseous lamina as „*Neolacertae*".

As proved by the denominations, Mr. Méhely considered his „Archaeolacertae" as a phylogenetically ancestral group, in opposition to his „Neolacertae", which, according to him, ought to represent the modern stage. Mr. Boulenger[22]) who criticized Mr. Méhely's papers, pronounced a contrary opinion: according to him, just the forms bearing an ossified supraciliary lamina are ancestral, whilst those presenting membraneous supraocularies are modern types, having degenerated with respect to their cranial ossification. It would lead us much too far from our subject to discuss all the different arguments and contra-arguments[23]) emitted by these authors in the course of their very interesting polemics. I shall merely confine myself to some evidences offered by the study of the skull.

All ancestral Vertebrate Types, the Fishes excepted, present a strongly ossified robust endoskeleton, this ossification generally decreasing in the course of phylogenetical development.[24]) An Increase of ossification occurs only in rare and special cases, often through the formation of secondary exoskeletal elements, i. e. secondary dermal bones. This is quite natural, because the higher Classes of Vertebrates, — among which the Batrachians are the direct offspring of Fishes, whilst the Reptiles being again retraceable to Stegocephalous Batrachians, — did not recommence the procedure of their skeletal ossification within each younger phyletical branch. The Fishes, being the first Vertebrates which existed, are quite naturally retraceable to ancestors with a cartilaginous endoskeleton. Now, if we take into consideration the fact that the family *Lacertidae*, as such, is one of the most recent branches of the Reptilian Stem, the membraneous structure of their skull must be admitted to represent, eo ipso, a secondary, i. e. a degenerated feature. It could be presumed, from a purely theoretical standpoint, that ossification may decrease in a branch, and that after this decrease a secondary increase may take place, but in the present case there is no reason or proof at all for such a supposition. The primordial (chondro-) skeleton of the „Archaeolacertae" is not a bit more cartilaginous, i. e. less extensively ossified, than in the „Neolacertae", and though it would precisely be the unossified (cartilaginous) state of the chondroskeleton and not the „membraneous" structure of the primary and secondary dermal bones, which could prove

[22]) Remarks on Prof. L. v. Méhely's Paper „Zur Lösung der Muralis-Frage", Ann. & Mag. Nat. Hist., XX, London, 1907, p. 39—46.

[23]) See Méhely, opp. ccit., and Boulenger, op. cit. and: Remarks on Prof. L. v. Méhely's recent Contrib. to the knowledge of the Lizards allied to L. muralis, Ann. & Mag. N. H., (8), V, 1910, p. 247—256, fig. 5.

[24]) Cfr. Bolkay, Addit. to the Foss. Herpetol. of Hungary &c., Mitteil. a. d. Jahrb. d. kgl. Ungar. Geol. R. A., XXI, Budapest, 1913, p. 229.

primitivity. We know that the first ossifications are phylogenetically represented by primary dermal bones and not by chondrial ossifications. Thus, if a well developed chondrial ossification occurs in a form in which the dermal bones are rather „membraneous", it is most probable that these latter ones are in a phase of degeneration and not of ascension! Therefore the discrimination between the phase of ascension and that of declension, i. e. between a beginning development and a degeneration, is not so difficult in this case. And even if the chondroskeleton would prove to be more cartilaginous in the „Archaeolacertae" than in the „Neolacertae", this cartilaginous state would undoubtedly represent its degeneration and not its primitivity, as no adult Reptile exists in which the chondroskeleton would be in a primary cartilaginous state. And now, as regards especially the secondary dermal bones, the whole construction of the skull of the „Archaeolacertae" proves that, as stated above, also these Lizards are undoubtedly typical representants of the cranial type designated by me as tectorbital. The morphological structure of the lamina supraciliaris in the „Archaeolacertae", and its segmentation (cfr. Fig. 6a), which corresponds to the modern Lacertian pileus, prove that this element has degenerated from an osseous lamina, and does not represent, by any means, the primitive beginning phase of lime-concretions.[25]) The roof of the primary dermal bones of the skull in the Archaeolacertae is predominantly smooth, so that in this case, on account of the mentioned preliminaries, a reduction, i. e. a degeneration of the secondary exoskeletal „crusta calcarea" must be admitted.

Mr. Méhely believes that the apical „knobs" he found on the caudal scales of the „Archaeolacertae" are „sensorial knobs". I examined the histological structure of these formations, and I was, up to now, unable to find any structure justifying this arbitrary enunciation. If, however, future investigations would yet prove Mr. Méhely's supposition to be right, this fact would only support the justness of the phylogenetical views pronounced, with respect to this subject, by Mr. G. A. Boulenger and presently by myself. A more perfect sensorial apparatus always indicates a development, which, in spite of that, might result in being a degeneration of some characters, and not primitivity. According to Mr. Méhely

[25]) Cfr. p. 74 & 78—79 of this publication & Fig. 5. It is true that, in some cases, allostotic bones might really be formed by the calcination of membranes, though comparative anatomical research and correlativity clearly prove in this case that the supraciliary membrane may be considered as a product of degeneration and not as an „orimental" bone. Besides, the mentioned structure of the lam. sup., observed in the more ancestral families *Scincidae* and *Anguinidae*, does not make it probable at all that this secondary exoskeletal element is due to the calcination of a membrane, the other secondary dermal bones of the Lizard-skull not being either retraceable to membrane-ossifications. In this case the membrane, which might calcify during the ontogenetical development (Fig. 6b), seems to be a phylogenetical extreme, and not a starting point.

the „Archaeolacertae" are smarter and more prudent than the „Neolacertae", and if it is really so, they would prove to be psychically, i. e. with respect to their nervous system, decidedly higher developed than the „Neolacertae". The discussed osteological features, as well as the phylogenetical age of this young Reptilian branch, directly forbid to think of the possibility of a heterepistasis which ought to result in the development of the sensory system on one hand and the „soit-disant" primitivity of the skull on the other. With respect to this latter character I must point out again the stated phylogenetical absurdity of such a supposition.

That the supraciliary membrane („fontanelle") calcifies, i. e. ossifies in old males of species which are generally characterized by a fontanelle (Fig. 6a & b), does not represent a biogenetical recapitulation, but is purely due to an individual physiological procedure, which, as a rule, does not occur in females, in which the fontanelle seems to be persistent. I should like to observe, furthermore, that such species are, with respect to their cranial characters, mostly intermediate between the „Neolacertae", constituting the afonanellous older type, and the degenerated, fontanelliferous „Archaeolacertae", i. e. they represent the as yet less degenerated forms of the fontanelliferous type.

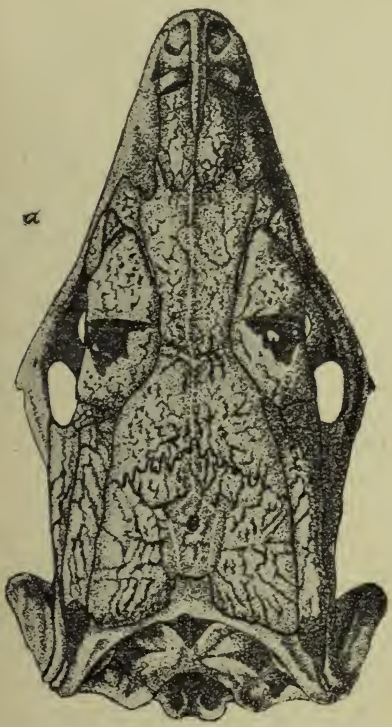

Figure 6a.

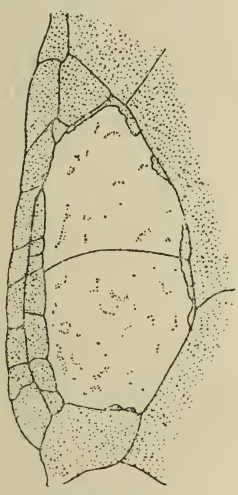

Figure 6b.

The Genus *Lacerta* encloses thus a very interesting Series, demonstrating the course of degeneration followed by the secondary exoskeletalel elements[26]) of the cranium, whilst the more ancestral Lacertilian families, referred to above, offer

[26]) We saw (cfr. footnote 19) that in *L. peloponnesiaca* D. & B. the bony dermal armour is not limited to the temporal region, but extends even upon the mandibularies. This feature is decidedly ancestral in the case of the genus *Lacerta*, which is one of the youngest representants of the tectorbital type.

fine examples illustrating some important points with respect to the formation (phase of ascension) and culminating development of the treated dermal ossifications.

Before terminating this brief sketch of the secondary dermal ossifications in the Lacertilia, I should like to draw attention to some spare literary references regarding this subject.

As far as I am informed, Mr. Calori was the first who, in 1858, discussed the „scudetti o squame ossee cutanee" occurring on the Saurian skull. According to this author these bony scutes are „cosi saldate alle ossa sottoposte che non vale ingengno, nè destrezza a sollevarle, e formano sopra quelle ossa come una incrostazione."[27])

A few years later Prof. Leydig[28]) also deals with the „crusta calcarea" of Saurians. He very judiciously recognized its (corial) genesis, and refers to it under the term of „Verknöcherte Schädelhaut". He also recognized the difference which exists between the lamina supraciliaris and the temporal armour on one hand, and the other bones constituting the roof of the skull on the other. As regards the supraciliary lamina and the temporal armour, Prof. Leydig writes as follows: „Ferner aber gibt es . . . echte für sich bleibende Hautknochen, welche nicht mit einem aus der häutigen, embryonalen Schädelwand entstandenen Knochen verschmolzen sind." — He seems to make a difference between the „calcareous crusta" and the independent „echte . . . Hautknochen" just referred to, and though, as stated above,[29]) this difference is not a meritorious one, it is but a quantitative and not qualitative difference, the dependency or independency of these secondary dermal ossifications being, as already mentioned, merely due to their different topographical conditions. On p. 49 we find the following observation: „Die Knochenkruste am Schädel erhält eine fernere Bedeutung für uns dadurch, dass sie es ist, welche durch ihre grösseren Gefässfurchen die Abgrenzung der sogenannten Kopfschilder bedingt, letztere sonach keineswegs ganz und überall mit dem Umriss der darunterliegenden Knochen zusammenfallen." And further on: „Es genügt das Auftreten einer neuen Gefässfurche, um ein Schild weiter zu gliedern oder umgekehrt, es kann ein Schild, das sonst für sich besteht, bei Mangel einer solchen Trennungsfurche in ein anderes aufgenommen sein." It would lead us to far to enlarge upon the formation and

[27]) L. Calori, Sulla Scheletografia de'Saurii. Nota II. Sullo Schel. della *Lacerta viridis* L. Sulla riprod. d. coda nelle Lucertole e s. ossa cutanee del teschio de'Saurii, Bologna, 1858. (Fide F. Siebenrock, D. Skelet d. Lacerta Simonyi Steind. u. d. Lacertidenfamilie überhaupt, Sitzungsber. d. Kais. Akad. d. Wiss. in Wien, Math. naturw. Cl., Bd. CIII, Abt. I, 1894, p. 224).

[28]) Die in Deutschl. leb. Arten d. Saurier, Tübingen, 1872, p. 47—50.

[29]) Cfr. the discussion of the secondary dermal bones and the crusta calcarea, on p. 75—76.

genesis of the pilear shields in general, and to discuss it, and to what an extent, their shape might be dependent on blood-vessels. I should merely like to suggest that the outlines of the elements of the secondary dermal ossifications agree, as a rule, with those of the pilear shields, and that just the contrary of Prof. Leydig's statement seems to occur: it is not the shape of the pilear scutes or shields, occurring in all Reptiles, which depends on that of the corial ossification, present on the skull of certain groups, but these latter ones are secreted (by the corial tissue) within the separate fields of the single shields, the morphology of which draws, in a quasi mechanical way, the limit between the settling groups of lime-concretions, i. e. between each secondary exoskeletal plate or surface of ossification.

In 1886 Prof. Brühl[30]) dealt with the elements here discussed. Mr. Siebenrock[31]) resumes Brühl's respective views in the following terms: „Wie aus seiner Darstellung zu schliessen ist, hält er die Knochenkruste oder den Hautknochenpanzer der Lacertiden für ein Gefüge von selbständigen Knochenplatten, welche nicht mit der Oberfläche des Schädels verwachsen, sondern ihr nur angeklebt sind. Sie können daher, wie Brühl glaubt, wenn auch nicht leicht und nicht immer gleich gut, vom Schädel lospräpariert werden."

In 1894 the famous Vienna Anatomist, Mr. F. Siebenrock, of the k. k. Naturhistorisches Hofmuseum, published the result of his observations on the skeleton of *Lacerta Simonyi* Steind. and on that of the *Lacertidae* in general.[32]) In this highly valuable paper the author devotes p. 223—225 to the description of the crusta calcarea. According to him this incrustation, which is present in some Saurian families, as „bei den Scincoiden, Anguiden und Gerrhosauriden", would be especially developed in the *Lacertidae*. I cannot agree with this opinion, because, as stated above, the secondary dermal ossifications are much more developed in *Ophisaurus* (*Anguinidae*), *Trachysaurus*, *Tiliqua*, *Egernia* (*Scincidae*), *Zonurus* (*Zonuridae*) or *Heloderma* (*Helodermatidae*) than in the younger representants (*Lacertidae*) of the same (i. e. tectorbital) Type.

Mr. Siebenrock emits the opinion that, with respect to the interpretation of the exoskeletal ossifications, Brühl's statement is wrong. He writes as follows[33]): „Alle Versuche, die Knochenkruste oder nur einen Theil derselben von der Schädeloberfläche loszutrennen, bleiben erfolglos. Dass man die Knochennähte am Schädel deutlicher hervortreten sieht, wenn man die schrundigen Erhabenheiten mit dem Messer oder Schaber entfernt, ist ausser

[30]) Zootomie aller Thierclassen, Taf. p. CLI, with Explanation, Wien, 1886.

[31]) l. c.

[32]) Op. cit. — In his earlier publication „D. Kopfskel. d. Anguiniden, Scincoiden u. Gerrhosauriden", appeared in the Annals of the Vienna Natural History Hofmuseum, M. Siebenrock does not deal with the elements we are discussing.

[33]) Op. cit. p. 224—225.

Zweifel. Aber nach Brühl's Anschauung müsste man von einem Lacertidenkopf zuerst die loslösbaren Knochenschilder entfernen, um sich die eigentlichen Schädelknochen vorführen zu können: «Alle Darstellungen von Dorsalsichten der *Lacerta*-Köpfe mit Hautschildern, wie sie Herr Leydig, Herr Calori u. a. bringen, sind osteologisch ungenügend und irreführend, da in ihnen die eigentliche Zusammensetzung des Schädeldaches nicht zum Ausdrucke kommen kann.»

Vergleicht man die Schädel in verschiedenen Altersstadien, so sieht man, dass an jenen der jungen Individuen die Nähte gut unterscheidbar sind, weil die noch dünne Knochenkruste wenige Unebenheiten besitzt. Wenn aber mit dem fortschreitenden Wachsthum des Thieres die Knochenkruste stärker wird, so nimmt sie auch an Rauhigkeit zu und macht dadurch die Nähte unklar. Man kann aber trotzdem an sehr rein präparirten *Lacerta*-Köpfen, wenn sie auch von den grössten Arten stammen, die einzelnen Nähte ganz genau unterscheiden. Hiefür liefert der Kopf von *Lacerta Simonyi* den besten Beweis, welcher nicht nur durch seine Grösse, sondern auch durch die bedeutenden Rauhigkeiten der Schädeloberfläche ausgezeichnet ist und dennoch alle Nähte deutlich erkennen lässt."

Now, as regards Mr. Leydig's figures, they do, effectively, not present the true limits of most of the primary dermal bones constituting the roof of the skull; it must be thus established that Mr. Brühl is absolutely right in affirming that such figures are inadequate to show the outlines of the true (i. e. actually endoskeletal) cranial bones. On the other part Mr. Siebenrock was not mistaken in asserting that these secondary dermal ossifications cannot be, in the Genus *Lacerta*, detached from the roof of the skull, and that on a very clean, exactly prepared skull the true outlines of the primary dermal bones, constituting its roof, might, however, be observed. But, as stated above, the secondary dermal bones, and thus the „crusta calcarea" also, degenerated in the modern *Lacerta*, having been reduced to a relatively feeble incrustation, whilst in the more ancestral *Ophisaurus* or *Trachysaurus* for instance, which represent the phase of the culmination of the exoskeletal development, some of these elements are really „independent", and may be detached from the primary dermal bones on which they occur. In such cases we are fully entitled to speak with Brühl about independent bone-plates.

As regards the large series belonging to the **nudorbital** Type, it encloses but a few forms provided with secondary exoskeletal bones. These elements present, with respect to their morphological and topographical conditions and to their relations, much diversity, and, in some cases, even more or less transitory formations. In the Central American Toad-Lizard (*Phrynosoma*), for instance, the skull bears osseous horn-like spines, which, at first sight, seem to form a part of the primary dermal bones

of the skull, from which they cannot be detached[34]). They — or at least some of them — might have originated, however, from corial lime-deposits, belonging thus to the category of the secondary exoskeletal elements.

The body of this Iguanid Genus is not provided with any exoskeletal armour, and even in the larger spines I was unable to find — at least macroscopically — traces of calcination. — Among the noumerous forms belonging to this Type it is but the *Geckonidae* which I will as yet refer to. The skin of some Geckonians (*Tarentola mauritanica* L. for in stance) exhibits lime-concretions, occurring under the form of „Kalkschuppen";[35]) Prof Leydig found them in the corium of nearly the whole body and even on the head. With respect to the occurrence of these secondary exoskeletal elements he writes as follows: „Sie lassen sich in Hautstücken des Rückens so gut wie in jenen der Bauchfläche erkennen, ebenso am Scheitel und Gesicht, an den Gliedmassen bis zu den Zehenspitzen hinaus; selbst die Nickhaut ist an den Stellen, welche noch den Charakter schuppiger Haut haben, nicht frei davon. Dagegen vermisse ich sie im den Querfalten an der Unterseite der Zehen und in den Schildern der Oberlippe, während in die grossen Schilder der Unterlippe doch wieder einzelne Kalkschüppchen aus der Umgebung hereintreten." Their shape is „rundlich oder rundlich-eckig", on the lateral parts of the body „annähernd rhombisch"; in the latter region they are ranged „nach Art der Schuppen eines Fisches, des *Polypterus* etwa, in Schräglinien", with „einen etwas hervorstehenden Hinterrand". „Dort wo sie ihren Platz in den Hautwarzen finden, können sie kreisförmig um ein Mittelstück gestellt sein; wieder an anderen Orten schliessen sie ohne sonderliche Ordnung aneinander." As regards the construction of these elements, Prof. Leydig writes: „Indem wir auf den Bau Rücksicht nehmen, erblicken wir sofort echte Knochenkörperchen in kreisförmiger Lagerung; ausserdem eine concentrische Schichtung und radiäre Streifung, letztere wohl herrührend von der Menge und Richtung der feinsten Ausläufer der Knochenzellen.[36]) Die Oberfläche der Schuppen ist, gewissermassen in Wiederholung des ganzen Schuppenkleides, dachziegelig-höckerig. Wenn man genau zusieht, zeigt sich als etwas Durchgreifendes, dass nur die Mitte der Einzelschuppen Knochenkörperchen besitzt, hingegen die Rinde diese Elemente nicht mehr aufweist. Letztere geht in eine warzige Oberfläche aus, in ähnlicher Weise wie das am Zahnbein höherer und niederer Wirbeltiere vor-

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[34]) Prof. Abel's statement, according to which the „Stacheln" of the *Phrynosoma*-skull would represent „reine Hornbildungen", devoid of a „knöcherne Unterlage" (op. cit. p. 347), is decidedly due to a mistake.

[35]) Cfr. F. Leydig, Üb. d. allgem. Bedeck. d. Amph., p. 77 of the Separate.

[36]) These are, presumably, not „true" Osteoblasts, but cells of the corial (connective) tissue, functioning in the same way as the „true" Osteoblasts.

kommt,[37]) und ebenso an den Kalkschuppen von *Coecilia*. Man könnte sich dies so erklären, dass der Kalk, jetzt nicht mehr unter der unmittelbaren Herrschaft der Zellen oder Knochenkörperchen stehend, nur den rein physikalisch-chemischen Gesetzen folgt und daher hier in der Haut des Reptils in der gleichen Weise die Ablagerungen erzeugt, wie draussen in einer Tropfsteinhöhle."[38]) —

Another African species, *Tarentola annularis* Geoffr., presents, according to Prof. Leydig, the same conditions as the preceding one.[39]) In a series of tropical and subtropical *Geckonidae*, examined by Prof. Leydig, no trace of secondary exoskeletal ossifications were found, and the same thing has been stated in the Tyrrhenian *Phyllodactylus europaeus* Gené.[40]) — The relatively feebly developed secondary exoskeleton occurring in *Tarentola*, — the elements of which are independent from the skull, i. e. they are not ankylosed to the cranial bones, — represents, with respect to this latter character, a particular specialization, not observable, as a rule, in other Lacertilians. Its development may be designated as having reached the phase of culmination of the evolution of the secondary exoskeleton within the phylogenetically rather isolated, heterepistatic Geckonian branch, as there is no morphological feature we know of, making allowance for the supposition of the *Geckonidae* being the „degenerated" offspring of armoured predecessors.

On the cranial roof of the Order *Rhiptoglossa* (comprising the unique Family *Chamaeleontidae*) a strong, granulated crusta calcarea occurs. The „horns" exhibited by several species are generally devoid of a bony „axis"; in some forms, however, the horns are provided with „eine knöcherne, von der Schnauze ausgehende Stütze . . . , die entweder nur die Wurzelhälfte des Gebildes oder das ganze bis zur Spitze stützt; oder es können zwei solcher beschuppter knöcherner Schnauzenfortsätze nebeneinander auftreten, die seitlich zusammengedrückt oder gar dreikantig sind, mit den Spitzen auseinanderweichen oder sich nähern, bei anderen Arten wieder am Grunde miteinander verwachsen können, so daß ein gabelförmiges Gebilde entsteht, oder sie verschmelzen der ganzen Länge nach und bilden ein einziges Schnauzenschwert, das nur durch eine Längsfurche an der unteren Schneide seine ursprüngliche Paarigkeit verrät ".[41]) It is possible that at least the distal portion of the longer horns represents a secondary dermal ossification (an „epiphytic" element), whilst the short osseous stumps and the basal part of the longer horns may constitute an

[37]) „Man vgl. z. B. Czermack's Aufsatz über die menschlichen Zähne und meine Darstellung des Zahnes der Salamandrinen." (Footnote[1]) of Leydig's Text.)

[38]) Op. cit. p. 77.

[39]) l. c.

[40]) Op. cit. p. 78.

[41]) F. Werner, in: Brehms Tierl., 4. Aufl., Bd. V, Leipzig u. Wien, 1913, p. 221—222.

„apophysis" of the primary dermal bones on which they occur.[42]) This is, however, but a presumption or rather supposition on my part, and the question remains to be settled by future, careful investigations, in the course of which special attention ought to be paid to the, as yet unknown, ontogenetical or osteogenetical development of the mentioned armaments.

In the Ophidian Order no secondary dermal ossifications are known.

Let us now throw a glance upon the bony dermal armour of some other, more ancestral Reptilian Orders.

Some Dinosaurs present exoskeletal elements on the body, which either form a more or less extensive closed armour, or consist but of isolated plates. As regards the skull, the distal portion of the „horns" of *Ceratopsidae* will presumably prove to represent secondary dermal bones, and practically to belong only in their proximal (basal) part to the primary dermal bones („membrane" bones) of the skull.[43]) The smaller ossicles on the periphery of their parietal and squamosal bones are surely secondary exoskeletal elements. — It is most probable that the praedental bone of the *Praedentata* („*Ornithischia*") will also prove to be a secondary dermal bone, just like in the case of the homonyme bone occurring in some Fishes.

Among the Crocodilians it is especially the palpebral bones (very strongly developed in *Caiman palpebrosus* Cuv. and *C. trigonatus* Schn. for instance) which are to be mentioned as representing typical secondary dermal bones. These elements are formed by the corial tissue of the upper eyelids; Cuvier[44]) records them, with respect to the two Caimans mentioned, as follows: „L'épaisseur de la paupière supérieure est entièrement remplie d'une lame osseuse divisée en trois pièces par des sutures; dans tous les autres *caïmans* et *crocodiles*, il n'y a qu'un petit grain osseux vers l'angle antérieur." This element has been figured by Prof. Brühl[45]) as „supraorbital", and by Prof. Gadow[46]) (in *A. missisipiensis* Daud.) as „lacrymal" (!),[47]) both homologizations being absolutely inadmissible. The same palpebral bone is also present in some fossil forms, as in *Nannosuchus* for instance. The sculptures, thoroughly obliterating in old specimens the outer (superficial) limit of the single primary dermal bones, must be considered as a crusta calcarea, i. e. a secondary dermal

[42]) Cfr. the following statements set forth in the discussion of the Mammalian horns and antlers.

[43]) Cfr. the preceding footnote.

[44]) S. les diff. esp. de Crocod. viv. &c., Ann. Mus. d'Hist. Nat., Paris, T. X, 1807, p. 37.

[45]) Das Skelet der Crocodilinen, Wien, 1862, and Zoot. all. Thierel., Wien, Taf. p. VI, 1874 & Taf. p. CXXXIII, Fig. 7, 1886.

[46]) Rept. and Amph., in: Cambr. Nat. Hist., London, 1901, p. 468, Fig. 112. — NB. The „true" lacrymal lies between the praefrontal and the maxillary!

[47]) What about the true lacrymal then?

ossification. I found the roof of the skull to be smooth in quite young specimens,[48]) the ridges observable on the horny plates of the „pileus" being confined to the integument, which can be easily detached from the skull. Later on the calcareous substance secreted by the derm settles upon the subjacent cranial bones, forming a crusta calcarea, which, in old specimens, uniformly invests the whole cranial surface, obliterating, as stated above, the superficial limits of the primary dermal bones.[49]) In such individuals the deeper corial layers adhere, in consequence of the absolute synostosis of their lime-concretions with the cranial bones, very strongly to the roof of the skull, so that the skin cannot be perfectly „stripped off", as is the case in young specimens. — I am uncertain about the occurrence of a „structural" sculpture of the cranial bones themselves. If such a sculpture occurs it could only be observed in those forms, in which the calcareous investment of the cranial roof is very feebly developed.

With respect to the cranial „sculptures", present in a very large number of gigantic fossil Reptilia (*Cotylosauria, Theriodontia, Sauropterygia* &c. &c.), I can only refer to what has been established on p. 72, when dealing with the same formation in the Batrachians.

In the Placodontian *Placochelys* it seems that we may be entitled to look upon the cone-like osseous elements occurring in the squamosal and quadratal region, as constituting secondary dermal ossicles.

The „horns" (at least in their distal part) and the tuberosities present on the skull of the Cotylosaurian *Elginia* might be presumably also referred to secondary dermal bones.

In the Chelonians the dorsal roof of the skull seems to be devoid of noteworthy secondary dermal ossifications, the one *Miolania* excepted, in which the „horns" belong perhaps to this latter category.[50])

With respect to the trunk I should like to observe that the chelonian plastron and carapace undoubtedly represent secondary exoskeletal features. In some forms a tertiary exoskeleton has been formed, protecting the degenerated secondary exoskeleton, as in *Psephophorus* and *Dermochelys coriacea* L. The tertiary exoskeleton of this latter form seems to be a degenerated offspring of that occurring in *Psephophorus*. The median boss-like os-

[48]) I examined only *Alligator*, but I presume the same conditions to be present in other Crocodilians as well.

[49]) As regards the ontogenetical development of the crusta calcarea, the same course has been traced in the Batrachians as well (cfr. p. 75).

[50]) The cranial roof of *Miolania* is sculptured. The question whether this sculpture might be attributed to the presence of a crusta calcarea, or merely to the osteogenesis of the respective primary dermal bones themselves, remains to be decided by an immediate examination of the original specimens.

sicles present on the carapace of *Toxochelys* are also tertiary exoskeletal elements.[51])

In **Mammalians** two kinds of exoskeletal elements are, as a rule, distinguished: the horns — which are looked upon by most authors as elements originally independent from the frontal bone, i. e., using our present terminology, constituting true secondary dermal bones, — and the dermal bone-plates. Not all horn-like features are, however, due to ossifications. It is a well known fact that the „horn" of the *Rhinocerotidae* is purely corneous, and does not contain any osseous „axis". This, corneous horn is supported by a slight, hyperostotic elevation of the nasal bones, faintly projecting into its hollowed base. Thus the osseous substance of the low basal „stump" apparently belongs to the actual endoskeleton, i. e. to primary dermal bones (the nasals). In opposition to this the horns and antlers of all other Mammals contain or purely consist of an osseous material. The *Cavicornia* possess an osseous cone, protruding from the frontal bone, which is covered by a horny substance produced by the epiderm. The mentioned cone is proved to originate in the Cavicornia from a separate corial i. e. dermal bone, its centre of ossification being originally independent from the frontal bone. This secondary dermal bone, the os cornu, fuses already in early ontogenetical stages, i. e. in the juvenile individual, with the antagonistic protuberances sent off by the frontal (= frontal apophyses). This palingenetic mode of development throws light upon the relatively recent corial origin of this element, i. e. on its phylogenetical independency from the primary dermal bones.

As far as I am acquainted with the mammalogical literature, the ontogenetical development of the simple (monostyle) or monaxone osseous cone of the bifurcated and thus antlers-like horns of *Antilocapra* has not as yet been established. Prof. Nitsche[52]) pronounced the very plausible opinion that the osteogenesis of the osseous horn-cones of this Genus will probably be the same as in other *Cavicornia*, and so the cranial element in question ought to be, also in this case, looked upon as constituting a secondary dermal bone („Cutisbildung und Epiphyse"), having, later on, fused with the frontal.

In the *Giraffidae* the three horns are also typical secondary dermal bones. [53])

In the *Cervidae* the origin and homologization of the antlers constitutes a very difficult problem. Prof. Nitsche assures that these bony appendages are not „dermal bones". Using our present terminology, this would mean that the antlers do not represent

[51]) Cfr. O. Abel, Grundz. d. Paläobiol. d. Wirbelt., Stuttgart, 1912, p. 611—614. For *Toxochelys* see Abel, Stämme d. Wirbelt., p. 395.

[52]) Studien über Hirsche (Gattung *Cervus* im weitesten Sinne), Heft I, Unters. üb. mehrstangige Geweihe u. d. Morph. d. Hufthierhörner i. allgem., Leipzig, 1898, p. 78.

[53]) Op. cit. p. 68 & Textfig. 8.

secondary dermal bones, but constitute, according to Mr. Nitsche, the product of a hyperossification of the frontal bone itself. He writes as follows [54]): „Die Geweihe der Cerviden sind bei ihrer erstmaligen Entstehung vom behaarten Integumente verhüllte Apophysen des Stirnbeines . . . , deren späterbin von dem vertrocknenden Integumente . . . entblösster und daher absterbender, apicaler Abschnitt . . . sich durch Nekrose von der persistierenden Apophysenbasis, dem Rosenstocke, löst . . . und schliesslich abfällt . . . Der schon verloren gegangene apicale Abschnitt, das Erstlingsgeweih . . . , wird nun unter Überwallung der so entstandenen Wundfläche vom Integumente aus . . . durch einen vom Periost des Rosenstockes ausgehenden Regenerationsprocess . . . unter Zufügung der bisher fehlenden Rose . . . und meist auch unter Zufügung neuer Enden . . . in hypertropher Weise ergänzt. Auch diese Neubildung wird nach Vertrocknung und Abstossung des Integumentes . . durch Nekrose vom Rosenstocke gelöst und sofort wieder regenerirt: ein Wechsel, der rhythmisch durch das ganze Leben des Hirsches fortdauert."

Thus, according to this author, the secondary exoskeletal os cornu would be absent in the *Cervidae*. Mr. Gadow [55]) combats this opinion. According to him the separate occurrence of the os cornu is a pathological phenomenon[56]), and does not represent, neither ontogenetically nor phylogenetically, the primitive starting point. He homologizes the „pedicle and antler" of the *Cervidae* with the os cornu, and proves that both the horns and antlers develop in the same way. This os cornu is, however, according to Mr. Gadow, an apophytic, and not epiphytic, portion of the frontal bone itself.

His investigations clearly demonstrate that the antlers and the osseous cone of the horns present, with respect to their development, the same essential points [57]) and — a strange fact — are cartilaginously preformed. The statement that „hyaline cartilage, which, together with rapidly proliferating connective tissue, makes up the apical portion of the pedicle and forms the growing point of the future pricket" seems, to my mind, very important, again proving the fact that also dermal bones might be cartilaginously preformed, and thus making, merely on the base of the presence or absence of cartilaginous preformation, an infallible distinction between the „cartilage bones" (i. e. those belonging to the chondrocranium) and the „dermal bones" rather illusorious. [58])

[54]) Op. cit. p. 63—64. — The references to the Textfigures contained in Mr. Nitsche's work, are left out in the citation; the omissions are marked by points (. . .).

[55]) The Evolution of Horns and Antlers, Proc. Z. Soc. London, 1902, p. 206—222. [56]) p. 212. [57]) Cfr. op. cit. Textfig. 25.

[58]) Prof. Gadow is perfectly right in affirming that one will have to get accustomed „to the existence of cartilage in places where text-books carefully abstain from mentioning it." (Cfr. op. cit. p. 222).

Mr. Gadow believes the Giraffid horns to represent rudimentary elements, which are also but frontal apophyses, having been, later on, detached from this bone, their independency not representing thus, according to him, an ancestral feature. [59]) The „frontal bosses" of the Okapi are looked upon by Gadow as „remnants", representing an „apparent loss of all these armaments."[60])

If the opinion pronounced by Prof. Gadow would prove right, viz. if the horns and antlers of Mammals would really constitute apophyses sent off by the frontal bone: they could in no wise be considered as secondary, but exclusively as primary dermal bones, that is to say they could not even be designated as being of an exoskeletal origin, practically representing phylogenetically young exostoses of bones which are retraceable to an ancestral i. e. primary exoskeleton, but which nowadays constitute, under the form of primary dermal bones, integral components of the modern Vertebrate endoskeleton.

Prof. Max Weber pleads, with respect to the development of horns and antlers, a standpoint which is intermediary between the two antagonistic opinions mentioned above. [61])

Regarding the origin of the antlers of the *Cervidae* he emphasizes the evidence of the close connexion existing between the antlers and the derm, resuming his conclusions in the following terms: „Sein [62]) von der Haut entblößtes Endstück, die Stange, wird im nächsten Jahre gewechselt: d. h. Osteoklasten erweichen dasselbe nekrotisch an seiner Basis, so daß weite Räume entstehen, seine Verbindung lockernd, bis es schließlich abfällt. Die entstandene Wundfläche überwuchert die Haut. Unter ihrem Schutz hat nun Regeneration statt, indem sich auf der Spitze des Stirnzapfens (Rosenstock) osteoblastisches Gewebe bildet, das in den meisten Fällen zur endlichen Bildung einer verknöcherten komplizierteren Stange führt, indem an ihr zackige Verästelungen, sog. Enden oder Sprossen auftreten. Wenn auch diese Neubildung vom Periost des Rosenstockes ausgeht, und damit als Epiphyse des Skeletes sich dokumentiert, so ist die Beteiligung der Haut nicht zu leugnen, und hat damit die Behauptung, daß die Stange eine Hautverknöcherung, ein Cutisknochen sei, eine gewisse Berechtigung. Nur so läßt sich die Periodizität des Abwerfens und der Regeneration erklären, die mit der Periodizität der Geschlechtsfunktion zusammenfällt, mit der sich ja auch anderwärts periodische stärkere Betätigung der Haut (Drüsen, Haarwechsel) verbindet."[63])

The pedicle constitutes, according to Weber, an apophysis[64]) of the frontal bone, whilst the antlers („Stange") are looked upon

[59]) Op. cit. p. 214.
[60]) Op. cit. p. 219.
[61]) Die Säugetiere, Jena, 1914, Footnote on p. 23.
[62]) Referring to the „Spieß" or „Erstlingsgeweih".
[63]) Op. cit. p. 19—20.
[64]) Op. cit. p. 18.

by him as rather epiphytic. This is contrary, indeed, to both the respective views of Nitsche and Gadow, as, according to these authors, the (basal) pedicle and (its distal outgrowth) the antlers are likewise apophytic elements. As regards the development of the cavicornian horn, Weber's views essentially agree with those emitted by Gadow, which are diametrically opposed to Nitsche's interpretation. He pretends the os cornu to derive from the frontal bone, considering its independent centre of ossification as a secondary — though evidently not „pathologic" — phenomenon, by which „. . . das Os cornu der Cavicornia . . . den Charakter eines Cutisknochens annimmt; deutlicher die ihm inkomplet homologe „Stange" der Hirsche, die gleichfalls aus kleinen Anfängen der Periodizität sexueller Prozesse unterworfen wurde . . ." [65] I dare say that this „intermediary" standpoint has been very nebulously drawn up. The opinion pronounced in this latter sentence with respect to the cervid antlers, does not harmonize much with the preceding one.[66] On p. 22 the author homologizes the cavicornian os cornu, designated by him at this place as an epiphysis, with the „Rosenstock (Stirnzapfen)" i. e. the pedicle of the *Cervidae*, a statement again containing a contradiction.

This illogical and vacillating mode to discuss such a complicated problem, even neglecting to undertake any argumentation of the quoted „statements", is not adapted indeed to further the desirable solution of the question.

The Giraffid horns are simply referred to by Weber as ossa cornuum.

According to Prof. Wiedersheim[67] the „Stange" (antler) of the *Cervidae* is homologous with the cavicornian os cornu (i. e. the osseous cone of the horn), whilst the cervid „Rosenstock" (pedicle) being homologous with the frontal apophysis (basal „stump" of the horn) of the *Cavicornia*. Up to this point Wiedersheim agrees with Gadow. Whilst, however, this latter author considers the pedicle and antler of the *Cervidae* as well as the os cornu of the *Cavicornia* and *Giraffidae* as frontal apophyses, i. e. using our present nomenclature, as belonging to primary dermal bones, Prof. Wiedersheim looks upon both the horns and antlers as built up by two different elements, viz. the apophytic „Stirnzapfen" and „Rosenstock" and the epiphytic „os cornu" and „Stange". These latter elements are, according to him, „dermal bones" („Hautknochen"). This might be the fundamental idea the author wanted to express, but, unfortunately, the different terms are not always exactly, i. e. logically used. The explanation of his Fig. 95 gives us a precise idea of his conception; but the text of the same page (p. 137) is not clear at all, and even contains a grave mistake. Prof. Wiedersheim writes there as follows:

[65]) Op. cit. p. 23.
[66]) On p. 20 of op. cit.
[67]) Vergl. Anat. d. Wirbeltiere, 6. Aufl., Jena, 1906, p. 137.

„Bei diesen[68]) entsteht um die von den Stirnbeinen auswachsenden Knochenzapfen („Stirnzapfen") eine verhornende Epidermis-Schicht. Bei den Geweihträgern (Cervidae) dagegen bildet sich in engstem Konnex mit dem Geschlechtsleben und unter exzessiver Beteiligung der Gefässe des Koriums ein Hautknochen, welcher als Stirnzapfen („Rosenstock") dem Os frontale aufsitzt . . ." Now, the cavicornian „Stirnzapfen", which is precisely the „Knochenzapfen" sent off by the frontal bone — and which is accurately designated in the explanation of Fig. 95 as „HZ Hornzapfen, d. h. der vom Os frontale ausgehende Stirnzapfen, welchem das sogenannte Os cornu (OC) wie eine Epiphyse aufsitzt" — represents, according to the absolutely reliable explanation of the textfigure, only the basal „stump", i. e. the apophytic portion of the osseous horn, whilst its much longer distal portion consists of an other, epiphytic element: the os cornu, which is provided with the mentioned horny epidermal investment.

As Wiedersheim admits the existence of a genetical difference between the proximal and distal portion of the osseous part of the horn, it would have been suitable to clearly keep throughout the description to this important distinction, paying heed to it by means of an exact terminology. This unprecise use of technical terms led Wiedersheim to commit, in the few lines cited above, a further error, the importance of which cannot be overlooked nor neglected. This grave mistake, alluded to above, consists in his statement that in the *Cervidae* „bildet sich . . . unter exzessiver Beteiligung der Gefässe des Koriums ein Hautknochen, welcher als Stirnzapfen („Rosenstock") dem Os frontale aufsitzt . . ." The homologous „Stirnzapfen" and „Rosenstock", i. e. the basal „stump"[69]) of the osseous cone and the pedicle of the antlers are not separate dermal bones which „lay upon" the frontal, but they are practically an exostotic part of the frontal itself. It is evident that Wiedersheim does not mean the pedicle („Rosenstock") here, but the antler („Stange"), homologized by him, in the explanation of Fig. 95, with the epiphytic os cornu. This erroneous exchange of the two quoted terms („Stange" and „Rosenstock") is also proved by the fact that the pedicle („Rosenstock)" has no „coroniform swollen base („rose") " from which it would be periodically detached and renewed, the pedicle being persistant. Thus it is as clear as possible that it is the antler („Stange") which is looked upon by Prof. Wiedersheim as an epiphytic „Hautknochen", i. e. applying our present terminology: a secondary dermal bone, and not, as he wrote in the text, the pedicle, what would result in being a pure non-sense.

[68]) i. e. in the *Cavicornia*.

[69]) I must point out the fact that Wiedersheim's interpretation (op. cit. Fig. 95) of the German term „Stirnzapfen" does not correspond to the English osseous „cone"; the „Stirnzapfen" are the frontal apophyses, i. e. the basal „stumps" of the horns, whilst the (osseous) cone means the (epiphytic) os cornu.

Thus both, Gadow and Wiedersheim, very correctly look upon the antlers and horns as constituting homologous elements, departing herein from Nitsche's theory. Whilst, however, Gadow considers both armaments as a genetical unity, representing a simple apophysis, Wiedersheim distinguishes two portions within them, viz. an apophytic, belonging to the frontal (primary dermal bone according to our present terminology), and an epiphytic, retraceable to an originally independent corial ossification (secondary dermal bone).

In footnote [1]) of p. 137 the latter mentioned author pronounces the following opinion with respect to the primary starting point of the horns' and antlers' development: „Überhaupt ist bei allen Hörner- und Geweihbildungen der innige Konnex derselben mit dem Integument, welches stets als der primäre Ausgangspunkt zu betrachten ist, wohl im Auge zu behalten."

Finally there is yet an author whose important observations must be recorded, having thrown some fresh light upon the morphology and development of the cervid antlers. This author is Mr. L. Rhumbler, who published, in 1913, a valuable paper bearing the title „Fehlt den Cerviden das Os cornu?" [70]) We saw that Prof. Nitsche believed that the cavicornian ossa cornuum — which represent, according to Mr. Rhumbler „. . . ganz sicher, wie geeignete Jugendzustände . . . ohne weiteres zeigen, Epiphysen, d. h. sie sind in ihrer knöchernen Grundlage mit dem Schädel erst nachträglich verwachsende . . . Cutisknochen" — are wanting in the *Cervidae*. Mr. Rhumbler examined a fine series of anomalous roebuck (*Capreolus capreolus* L.) antlers, which prove that also in the *Cervidae* the antlers are composed of two different elements. The conclusion of his inquiries is summarized in the following sentences: „Die Hirsche besitzen ebenso wie alle anderen mit Stirnwaffen ausgestatteten Wiederkäuer ein epiphytales Cornu; sie tragen aber einen apophytalen Mantel um diesen Knochenzapfen, [71]) der in anormalen Fällen gesondert bleiben kann, in normalen Fällen dagegen zu einer nicht scharf abgesetzten, sondern untrennbar angeschmiegten Rinde dem Os cornu fest aufschmilzt. Die eigentümlichen Lagerungsverhältnisse des Os cornu im innern eines Apophysenmantels erklären mehr oder weniger direkt oder indirekt auch alle übrigen Besonderheiten, die das Geweih der Cerviden den sonstigen Hornbildungen bei andern Wiederkäuern gegenüber voraus hat, nämlich das Spitzenwachstum der Geweihe, ihre Verzweigung, das Absterben und die Beseitigung des Bastes, und schließlich das jährliche Abwerfen der bloßgelegten Geweihstangen. Die einfache Änderung, das zu dem

[70]) Zool. Anz., Bd. XLII, p. 81—95, Figs. 1—15.

[71]) Mr. Rhumbler uses the expression „Knochenzapfen" and also „Stirnzapfen" for the epiphytic distal portion, i. e. the antler, corresponding to the os cornu. His terminology differs thus from that followed by Prof. Wiedersheim in op. cit. Fig. 95.

Os cornu ein apophytaler Umhüllungsmantel hinzutrat, hat alles andere zur Folge gehabt." [72]) The fundamental idea of this statement pretty well agrees with Landois' opinion: „Bei den Cerviden hat sowohl die Knochenhaut (Periost) des Schädeldaches als auch die Lederhaut daselbst die Fähigkeit erlangt.. Knochen zu erzeugen, welche sich als sekundäre Geweihstangen ausgestalten können." [73])

Mr. Rhumbler agrees with Gadow and Wiedersheim up to the point to homologize, by the bulk, the horns and antlers. Nevertheless the views pronounced by these three authors with respect to the identification, i. e. homologization, of the single elements composing the armaments, are very different. Mr. Rhumbler's statement pleads the rightness of the views of authors who, on the contrary to Mr. Gadow's opinion, considered horns and antlers as consisting of two genetically different elements, united by a phylogenetically later fusion. The element described by Mr. Rhumbler as the cervid os cornu is most probably retraceable to a purely corial ossification, bearing in anomalous, i. e. at least actually anomalous, cases no intimate relations to the osseous tissue constituting the frontal bone. It must be here remarked that Mr. Rhumbler is decidedly mistaken pretending that the „Rosenstock, der das Geweih trägt ist . . . ein epiphytaler Hautknochen, ein Os cornu also .."; [74]) again a wrong expression, a wrong application of the term: pedicle. The figure he refers to (op. cit. Fig. 5), clearly demonstrates that the „Rosenstock", i. e. the pedicle itself, is undoubtedly a frontal apophysis. That is to say that the term pedicle can only be used for the basal part below the „rose" (designated by „M" on his Figs. 5 & 6), supporting, or in the special cases represented by the mentioned Figures (1—6) rather peripherically enclosing the os cornu. The outer layers („Umhüllungsmantel") of the antlers represent, according to Rhumbler, merely the continuation of the pedicle, i. e. frontal apophyses, and would thus be retraceable to a strangely specialized frontal exostosis, whilst the inner „axis" of the antlers would consist of the epiphytic os cornu. Supposed this hypothesis proves to be right, the whole of the antlers („Stange") could in no wise be homologized with the cavicornian os cornu, as interpreted by Wiedersheim. Mr. Rhumbler's latter statement, i. e. the purely apophytic character of the „antlers-sheet", appears, to my mind, somewhat improbable. This is, however, on my part, merely an impression; maybe that I am mistaken, but I must confess not being able to depart that far from the supposition that the antlers — their „sheet" included — are of a dermal origin. Their

[72]) Op. cit. p. 94.

[73]) H. Landois, Eine dritte Edelhirsch-Geweihstange &c., Arch. f. Entw. mech., Bd. 14, 1908, p. 289—295, with 3 Textfigs. Quoted sentence on p. 294 (fide Rhumbler, op. cit. p. 94).

[74]) Op. cit. p. 82.

annual renewment and their intimate relation with the integument are circumstances pointing very much indeed towards a more recent corial origin. It is not impossible that the specimens described by Mr. Rhumbler are more or less pathologic monstruosties, and that the axial element, considered by Mr. Rhumbler as the os cornu proper, is merely an anomalously detached part of the external „sheet", in which case the antlers ought to be considered, to their whole extent (i. e. the „sheet" as well as the „axis"), as homologa of the ossa cornuum in other Ruminants. Mr. Rhumbler's valuable investigations prove, at any rate, that the portion above the pedicle may, in some way, be genetically independent from the latter, i. e. from the frontal bone, a fact which could easily be considered as proving its independent origin, especially if the other well known morphological and physiological peculiarities of the cervid antlers are simultaneously taken into consideration. Thus, it is not impossible that both the axis and the sheet of the antlers correspond to the os cornu, the histogenesis of the „sheet", viz. of the outer layers, being, however, supplied — by means of their apparently more intimate connexion with the hollow, tube-like pedicle — by cells sent off by the frontal tissue, i. e. especially by those of the pedicle. In this case the antlers ought to be considered as having a mixed histogenetical origin, in which both, primary and secondary dermal bones, played their rôle. As regards the anomalously detached „axis", the natural course of the antlers-sheet's „mixed osteogenesis" might have been, in some way, altered or modified, this alteration resulting in the separate occurrence of „axial" and „sheet" elements. All these combinations are, however, thoroughly hypothetical and theoretical. Only palaeontology and embryology could offer the necessary details on the base of which the problem could be definitively solved. And such suitable researches are as yet wanting. — For the present only the following establishments could be taken for granted: horns and antlers are, by the bulk, homological armaments, both consisting of a proximal apophytic portion, derived from a primary dermal bone (the frontal), and a distal epiphytic portion, represented by a secondary dermal bone (the os cornu); the true starting point of the development of Ruminant armaments has to be searched for in the derm, as stated by Wiedersheim, and not in an exostosis proceeding from the primary dermal bones of the skull, as suggested by Gadow.

An ethological and bionomical analysis of the natural course of the formation of horn-like elements alone will prove the correctness of Wiedersheim's standpoint. The external mechanical irritation to which the first origin of horns and antlers must have been due, acted, eo ipso, in an extero-interior direction, and not contrarily. Thus, if we accept for the origin of the horn-like formations the Lamarckian mechanical cause, it is natural that the epidermal and corial tissues were the first to react upon the

external irritation, the effect of this latter reaching the osseous cranial surface at last. And so it is clear that the cranial bones were only indirectly attained by the effect of the (external) irritation which acted upon the complexion, and it is very probable that their apophytic growth has been a mere consequence of an other, immediate irritation caused by budding ossicles (the ossa cornuum) formed by and lying in the derm.[75])

The evolution of the horns of other cornigerous Mammalians, (*Sivatheriidae* [Order *Artiodactyla*], *Dinoceradidae* [O. *Amblypoda*], *Arsinotheriidae* [O. *Embrithopoda*], *Titanotheriidae* [O. *Perissodactyla*] and *Mylagaulinae* (Family: *Castoridae*, Order *Rodentia*]), and thus the homologization of their elements, could only be cleared up by future special investigations.

Finally the horns of the Dasypodid Genus *Peltephilus* (O. *Xenarthra*) shall be mentioned, which seem to be the horn-like modifications of the foremost plates of the secondary exoskeletal armour overroofing the upper parts of the skull.

Let us see now the dermal bone-plates of the Mammalia. Such are present in the fossil Xenarthran *Mylodon* (family *Megatheriidae*), the corium of which contained numerous dermal bone-plates, representing the secondary exoskeleton. A powerful secondary exoskeleton is present in the Xenarthran *Glyptodontidae*, consisting of sculptured polygonous dermal bone-plates, which acquire a rather spinous aspect on the tail. The head is covered with a cap-like mosaic of exoskeletal elements (cfr. *Glyptodon*, *Doedicurus*); these elements are, in the same way as on the body, quite independent from the primary dermal bones of the skull, i. e. they are not ankylosed to them. The same phenomenon occurs in the recent *Dasypodidae* (Order *Xenarthra*) and *Manidae* (Order *Pholidota*), in which the secondary dermal bones of the head, covered by a horny epidermal layer, are not connected by any osseous tissue to the primary dermal bones of the cranium. It is only the above mentioned fossil Dasypodid Genus *Peltocephalus* in which the secondary exoskeletal plates, overroofing the upper surface of the skull and the upper part of the temporal region, seem to be more intimately attached to the subjacent primary dermal bones. In all the Mammalians, however, the primary dermal bones are clearly distinguishable from the secondary exoskeletal plates, so that the homologization of these elements is beyond all doubt. This state of things, due to the relatively loose connexion existing between the secondary and

[75]) We saw that in the horn of the *Rhinocerotidae* a bony distal element, corresponding to the os cornu, seems to be absent; yet the question arises, if this absence is primary and not secondary, due to a later suppression of an osseous oriment of yore by the „hypertrophic" development of the corneous layers constituting the horn. May be also that the special structure of the integument of these „Pachydermes" prohibited, ab initio, the formation of an epiphytic dermal ossicle.

primary dermal bones, is a natural consequence of the skin in the Mammalians not adhering as closely to the roof of the skull as in Fishes, Batrachians and Reptiles.

Among other Mammalian groups secondary dermal ossifications have not as yet been observed, „unless it were in the Cetacea where Kuekenthal has found traces of a dermal armour."[76])

In the fossil *Archaeoceti* some forms (*Zeuglodon, Delphinopsis*) possess secondary dermal ossifications, and Kükenthal, having found such bone-plates in *Neophocaena phocaenoides* Cuv., pronounced the opinion that the „. . . Vorfahren der Zahnwale hautpanzertragende Landtiere gewesen sind . . . Die Zahnwale haben sich zu einer Zeit von landbewohnenden Vorfahren abgezweigt, als diese noch einen Hautpanzer trugen, wie ihn z. B. ein Teil der Edentaten vielleicht als altes Erbstück noch jetzt besitzt",[77]) a presumption, which has not been supported, up to now, by any phylogenetical fact. The integument of other *Phocaenidae* presents but horny (corneous) tubercles.

Resumé.

1° The Vertebrate exoskeleton is formed by dermal i. e. corial bones.

2° With respect to the dermal bones we must distinguish two kinds: the primary and secondary dermal bones.

3° The „membrane" bones of the skull are phylogenetically dermal bones, and derived from an ancestral exoskeleton. They represent the phylogenetically oldest osseous elements.

4° This ancestral exoskeleton is the primary exoskeleton.

5° The ancestral endoskeleton is represented by the chondroskeleton.

6° The elements of the primary exoskeleton, i. e. the primary dermal bones, withdrew from the corial i. e. connective tissue, by the cells of which they were built up, and entered into a close connexion with the ancestral endoskeleton (i. e. the chondroskeleton), forming with the latter a new skeletal unity: the (more or less) osseous endoskeleton.

7° The corium, after the loss of its primary ossifications, secreted, in various Vertebrates, new osseous elements: the secondary dermal bones, which form the secondary exoskeleton.

8° Such secondary dermal bones occur on the skull of numerous forms, and, especially in some Batrachians and Reptiles, in which Classes the skin very closely adheres to the roof of the skull, may coalesce, i. e. coossify with the subjacent primary dermal bones or, in some cases (*Anura*), with the cartilage bones as well.

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[76]) Cf. Gadow, op. cit. p. 208.

[77]) Fide Hilzheimer, Handbuch d. Biologie d. Wirbelt., II, Stuttgart, 1913, p. 629—630.

9° In the Fishes the primary dermal bones, though practically forming a part of the osseous endoskeleton, preserved their ancient exoskeletal charakter to a higher degree than in the other Vertebrates. The secondary dermal ossifications of the skull generally occur, in this Class, under the form of rather single elements; in some cases (*Ostracion*) they may, however, form a coherent armour, overroofing the primary dermal bones.

10° The exoskeletal plates occurring on the head of the *Placodermi* are probably also primary dermal bones — and not secondary as in *Ostracion* —, but they are not homologizable with the primary dermal bones of the coinocranian Fishes.

11° The „sculpture" of the cranial bones in the Batrachians and Reptiles may be retraced to the presence of a crusta calcarea, or it may represent a structural particularity of the respective cranial bones themselves.

12° The structural sculpture is radial or concentric, or rather both. It may occur on both the primary and secondary (and also on the dermal bones tertiary ones).

13° The crusta calcarea — which is formed by the corium — appears as a pitted or spinous incrustation, constituting, in its very orimental phase, a complex of rather independent lime-concretions, which coossify later on with the subjacent bones of the skull.

14° The crusta calcarea of the skull is morphologically homologous with the whole of any secondary dermal bone-plate of the body.

15° The crusta calcarea of the Batrachian and Reptile skull may represent either the first stage of the formation of secondary exoskeletal ossifications, or the remnants (rudiments) of degenerated secondary exoskeletal elements.

16° In the recent Anura some forms are provided with bony „stegal" elements, i. e. secondary dermal ossifications; these do not represent ancestral features, inherited from some Stegocecephalian predecessors, but they are later acquisitions of the Anuran Stem.

17° Among the Lacertilians two main Types could be distinguished with respect to the dermal bones of the skull: the nudorbital Type, in which a supraciliary lamina is absent, and in which the skull is generally devoid of secondary dermal ossifications, and the tectorbital, in which a lamina supraciliaris and other secondary dermal ossifications are present.

18° The lamina supraciliaris is formed by the fusion of small polygonous plates, a fact especially well expressed in the young specimens of some more ancestral representatives of the tectorbital Type.

19° In some cases the secondary dermal bones covering the upper surface of the Lacertilian skull may be detached from the primary dermal bones to which they adhere.

20° In the Genus *Lacerta* the secondary exoskeletal ossifications are decidedly degenerating in the course of evolution.

21° Prof. de Méhely's „*Archaeolacertae*" are phylogenetically younger than his „*Neolacertae*", the membraneous resp. weak structure of the „archaeolacertian" skull being due to a decrease of ossification („degeneration").

22° The evolution of the osseous Reptilian horns, and the homologization of the elements by which they are composed, remains to be established by future investigations; some of them might consist of an apophytic basal part, pertaining to primary dermal bones, and an epiphytic distal portion, represented by a secondary dermal ossification.

23° Secondary dermal ossifications occurring under the form of well defined bones are relatively rare and few in number on the skull of the non-lacertilian Reptiles. Such secondary dermal bones are present on the periphery of the parietal bone in *Ceratopsidae* (O. *Dinosauria*, Suborder *Praedentata*); the praedental bone of the *Praedentata* will probably also prove to belong to the same category of ossifications. A crusta calcarea is often present.

24° In some cases a tertiary dermal ossification may occur on the trunk, as in the chelonian *Psephophorus*, *Dermochelys* and *Toxochelys*.

25° In Mammals the secondary dermal bones may be represented by horns and antlers, or by exoskeletal bone-plates.

26° The osseous, but often cartilaginously preformed, distal portion (i. e. the os cornu) of the cavicornian horns and cervicornian antlers is epiphytic, belonging thus to the category of the secondary dermal bones. The basal part of the horns and antlers is apophytic and belongs always to primary dermal bones. Horns and antlers are — by the bulk — homologous armaments.

27° The exoskeletal bone-plates (secondary dermal bones) protecting the skull in some Mammalians are not as closely attached, i. e. ankylosed to the subjacent primary dermal bones as in the lower Vertebrates.

Budapest, the 16 th of July 1921.