

# SEXUAL DIFFERENCES IN ORNITHOPODOUS DINOSAURS.

By  
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With 3 Textfigurs.

Altogether very little is known on the sexual characters of fossil Reptiles. Apart of some papers by SEELEY, BROOM, HOOLEY and ABEL nearly nothing has been written on this subject<sup>1)</sup>. As already emphasised by DOLLO sexual characters can be recognised in fossil Reptiles by analysing those characters that can be ornaments or arms, those that occur in the pelvis and may thus be considered to be in correlation with the genitory organs and finally those, that are met with in the parts used for clasping the female during the act of mating.

As far back as 1915<sup>2)</sup> I pointed to the frequent occurrence of two „species“ of the same genus of Dinosaurs in the same locality. Bernissart furnished us with *Iguanodon bernissartensis* and *Iguanodon mantelli*, by Wiener-Neustadt *Struthiosaurus austriacus* and *Struthiosaurus pawlowitschi* were found together, Szentpéterfalva supplied us with *Rhabdodon suessi* and *Rhabdodon priscum*, Valiora with *Orthomerus transylvanicus* and *Orthomerus transylvanicus* var. *sulcata*. From the Tendaguru JANENSCH described *Brachiosaurus brancai* and *Brachiosaurus fraasi* and *Dicraeosaurus hansemanni* and *Dicraeosaurus sattleri*. Already then this occurrence in pairs was considered to be due to sexual dimorphism.

Two years later it was discovered<sup>3)</sup> that in those North-American Trachodonts, that show especially long neurapophyses or an ornamented skull, the ischium is always hammershaped and the pseudopectineal process abbreviated. Accordingly the Trachodonts known till then were divided in two groups, one of which included only males:

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<sup>1)</sup> The whole literature prior to 1926 is given in my “book” *Osteologia Reptilium fossilium et recentium*. Berlin 1926.

<sup>2)</sup> NOPCSA, Fr., Über Geschlechtsunterschiede bei Dinosauriern. *Centralbl. für Min., Geol., Paläont., Stuttgart* 1915.

<sup>3)</sup> NOPCSA, Fr., Neues über Geschlechtsunterschiede bei Dinosauriern. *Centralblatt f. Min., Geol., Paläont., Stuttgart* 1917.

I	II
<i>Saurolophus</i>	<i>Diclonius</i>
<i>Corythosaurus</i>	<i>Kritosaurus</i>
<i>Hypacrosaurus</i>	<i>Hadrosaurus</i>
	<i>Claosaurus</i> (= <i>Thespesius</i> )

The later discoveries confirmed this distinction for the newly discovered genera could be grouped according to the same principle:

I	II
<i>Stephanosaurus</i>	<i>Edmontosaurus</i>
<i>Cheneosaurus</i>	
<i>Parasaurolophus</i>	

The single exception is made by *Prosaurolophus*, for in this „genus“ on the top of the skull a small ornament is present, but in spite of this the ischium is slender. In all genera having a hammershaped ischium this thickening was considered to be a sexual mark. The reasons were: first because in *Rhea* and in *Anas* the retractor muscles of the penis insert at this place, secondly because in Crocodiles the penis is likewise applied against the anterior margin of the ischiadic symphysis, thirdly because the occurrence of a strong os penis in *Diplodocus* and *Camarasaurus* shows that Dinosaurs had a well developed penis. Regarding the os penis of Dinosaurs, it is enough to mention that the assymetry, the individual variation and the sporadic occurrence of the bone in question are all arguments that prevent one from locating the long and bent bone found sometimes in the skeletons of *Diplodocus* and *Camarasaurus* elsewhere than in the penis.

Similar differences as among the Trachodons could be established in 1917 also among the Camptosaurians. According to the principle adopted for dividing the Trachodons the Camptosaurians could be divided as follows

I	II
<i>Camptosaurus dispar</i>	<i>Camptosaurus browni</i> <i>medius</i>

In 1923<sup>4)</sup> I could point out that the *Rhabdodon* supposed to be a male (*Rhabdodon priscum* = *Rhabdodon robustum*) likewise had a hammershaped ischium, while the so called female (*Rhabdodon suessi*) had a slender ischium.

The chronological sequence of the Trachodons in North America favors in no way the idea that the ornamented forms are only more specialised

<sup>4)</sup> NOPCSA, Fr., On the geological importance of the primitive Reptilian fauna etc. Quart. Journ. Geol. Soc., Vol. LXXIX, London 1923.

genera than the others, for *Stephanosaurus* shows rather primitive teeth but never the less a hammershaped ischium and an ornamented skull and besides this ornamented and not ornamented Trachodonts occur as well in the Judith and Belly River formations as in the Edmonton and the Laramie.

In 1928 in the genera *Orthomerus* and *Rhabdodon* following sexual differences could be fixed.

	M a l e	F e m a l e
<i>Orthomerus</i>		
	caudal vertebrae with furrow	without furrow
<i>Rhabdodon</i>		
	caudal vertebrae with furrow	without furrow
	mandible strong	slender
	ischium hammershaped	slender

At the same time it could be pointed out that also in the genus *Camptosaurus* the species *Camptosaurus dispar*, that was considered to be a male, has furrowed caudal vertebrae, while such a furrow is absent in the so called female *Camptosaurus browni*<sup>5)</sup>.

About the same time in the genus *Thespesius* two species were described<sup>6)</sup> the one of which had an elongated skull and an abbreviated pseudopectineal process, the other a shorter skull and a longer pseudopectineal process. In 1929 WIMAN described the Trachodontid genus *Tanius*<sup>7)</sup> that is closely allied to *Orthomerus* and that has a hammershaped ischium. The jugal of *Tanius* is quite unlike the one of the true Trachodonts, but identical with the jugal in *Orthomerus*. So hammer shaped ischia are known to occur in three different systematic units (Camptosaurians, Protrachodonts and Trachodonts)!

The discovery of two fused and ornamented frontals of an Ornithopodous Dinosaur in the collection of Dinosaur bones coming from Valiora and belonging to the Roy. Geological Survey of Hungary sheds a good deal of fresh light on the important question of sexual differences in fossil Reptiles.

A photograph of this new bone from above and from the side is given in fig. 1, a and b. For comparison the figure of the frontal of a juvenile Ortho-

<sup>5)</sup> NOPCSA, F., Dinosaurierreste aus Siebenbürgen IV. Palaeontologia Hungarica, Budapest 1926 (published 1928).

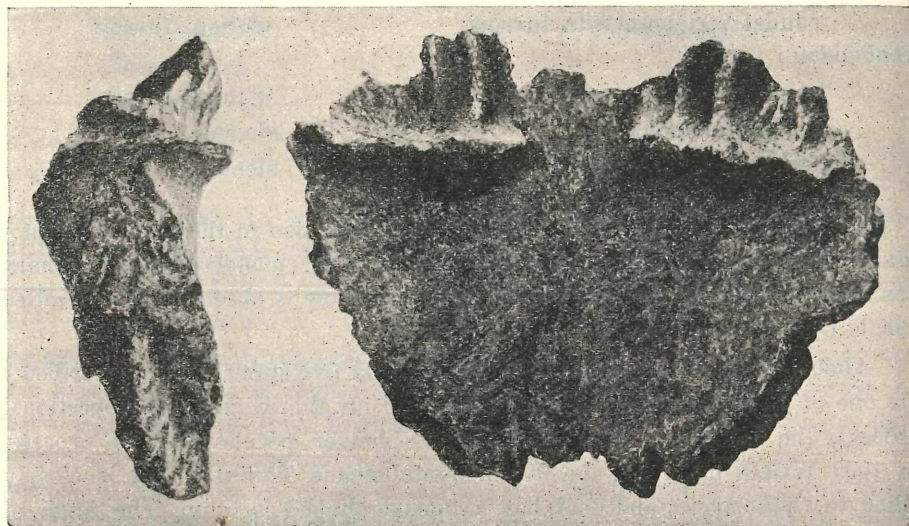
<sup>6)</sup> GILMORE, Ch. W., Contribution to vertebrate Palaeontology. Department of Mines; geol. Surv. Bullet., No. 38, Ottawa 1924.

STERNBERG, C. M., A new species of *Thespesius* from the Lance. Department of Mines; geol. Surv. Bullet., No. 44, Ottawa 1926.

<sup>7)</sup> WIMAN, C., Die Kreide-Dinosaurier aus Shantung. Palaeontolog. Sinica (ser. C), Vol. VI, Peking 1929).

merus (R 3842) described and figured under the name *Mochlodon*<sup>8)</sup> may be referred too.

The greatest breadth of the new ornamented piece is 8,8 cm, its greatest length 6,3 cm. Below it shows, as the frontals of all Orthopoda, two longitudinal ridges, that converge markedly in the middle. Behind the point, where the two ridges come nearest to each other, each ridge shows a rough suture for the alisphenoid bone. In front of this point the ridges are sharp and to the greater part smooth; in this part an indication of a suture is only met



a)

b)

Fig. 1. Frontals of male *Orthomerus* (nat. size) (nasal suture at the top of the figure) a) exterior view; b) superior view.

with on the anterior end of each ridge, where the orbitosphenoid touched the frontal.

The upper aspect of the new piece (fig. 1b) is most peculiar. Instead of having, as all the frontals of *Rhabdodon* and *Orthomerus* hitherto known, a flat fronto-nasal suture, this suture turns abruptly upward so that the nasal met the frontal in nearly a right angle. On account of this the upper surface of the nasal looked backwards and not upwards. A similar, but much more exaggerated turning up of the nasal suture has been described by GILMORE in the frontal of *Lambeosaurus*. This feature, that comes also out very well in the side view of the specimen (fig. 1a) shows that the skull, to which the

<sup>8)</sup> NOPCSA, Fr., Dinosaurierreste aus Siebenbürgen III. (Weitere Schädelreste von *Mochlodon*.) Denkschr. d. k. Akad. d. Wiss., math.-naturw. Kl., Vol. LXXIV, Wien 1903; Taf. I, Fig. III u. IV.

new piece belongs, must have born a horn, crest or helmet as in the ornamented North American Trachodonts. A comparison with the single frontal known to belong surely to *Rhabdodon* (R 3815 Nat. Hist. Mus. London) and with those known just as surely to belong to *Orthomerus* (R. 4915) shows that the new piece has more affinities to the latter than to the former. The piece figured in 1903 on Plate I, fig. 3, 4 as belonging to *Rhabdodon* belongs to the *Orthomerus* (R 3842 Nat. Hist. Mus. London). It is more elongated than the larger piece. The principle difference between the typical, not ornamented frontals of *Orthomerus* and the new ornamented piece consists in the still more marked abbreviation of the latter, for it is shorter than any not ornamented pieces but this is again the same sort of difference as established for the frontals of the different North American Trachodonts.

To this difference one may not attribute too much weight. Such an abbreviation is not only observable in the growth of *Orthomerus* and in the phylogenetical evolution of the bipedal *Orthopoda* (*Hypsilophodon*, *Camptosaurus*, *Kritosaurus*, *Saurolophus*) but also during the individual growth of recent Reptiles. According to drawings given by LÜTKEN<sup>9)</sup> in *Crocodylus intermedius* the ratio of the length of the frontal (without its nasal projection) to its breadth is 10 : 8 in the young, but 10 : 13 in the adult. Drawings given by BRÜHL<sup>10)</sup> and DESLONGCHAMPS<sup>11)</sup> show that in *Gavialis* the same ratio is 10 : 7 in the young and 10 : 11 in the adult. Rather unclear photographs published by MOOK<sup>12)</sup> show that analogous changes occur also in *Crocodylus americanus*, *Caiman sclerops* and *Alligator mississippiensis*. Apart from this, as in *Orthopoda* the chronologically older, more primitive, short snouted Crocodiles (as *Atoposaurus* and *Notosuchus*) have comparatively longer frontals than the newer types and so these Reptiles repeat the same evolution as the *Orthopoda*. According to information gained from Baron G. FEYERVÁRY in *Varanus salvator* the ratio of the dimensions of the frontal are 10 : 3 in the young, but 10 : 4 in the adult. Thus it is evident that the shortening of the frontal is a character that occurs independently in the ontogenetical and phylogenetical evolution of very different reptilian units, and thus the abbreviation of a frontal alone can not be considered as generic character. As no other trachodontid teeth are known from the Danian of Transylvania than those belonging to *Orthomerus*, everything goes to show that the ornamented frontal must at

<sup>9)</sup> LÜTKEN, Ch., On *Crocodylus intermedius*; Vidensk. Meddel. fra den naturh. Foren, Kjobenhaven 1884.

<sup>10)</sup> BRÜHL, C. B., Das Skelett der Krokodilinen, Wien 1862.

<sup>11)</sup> DESLONGCHAMPS, Eu., Le Jura Normand. Études paléontologiques, Caen u. Paris 1878.

<sup>12)</sup> MOOK, Ch. C., Individual and age variations in the skulls of recent Crocodylia. Bull. Amer. Mus. Nat. Hist., New York 1921.

least belong to a „genus“ closely allied to the type (R 3841 Nat. Hist. Mus. London).

Of course the discovery of an ornamentation on the top of the skull in a Dinosaur, having mandibular teeth utterly unlike those of the true Trachodons, is of far reaching importance. It shows that the development of ornamental excrescences supported by underlying bone does not only occur in *Theropoda* (*Ceratosaurus*, *Tyrannosaurus*) but also in different *Orthopoda*. This analogy is all the more important as elongated neural spines as in *Hypacrosaurus*, have likewise been found in the *Theropoda* (*Spinosaurus*, *Altispinax*)<sup>13</sup>.

Bearing now in mind that, with the single exception of *Prosaurolophus*, the highly ornamented skulls are only found in animals having a hammer-shaped ischium or at least an abbreviated but broadened pseudopectineal process and bearing further on also in mind, that only a correlation due to sex can explain this parallelism, it becomes a priori highly probable that the excrescences on the skull are but sexual ornaments.

As far as we know at present on the skulls of the Trachodons three types of ornaments can be distinguished. The most primitive is a solid bony horn (*Saurolophus*), the second seems to have been a tube reaching to the posterior end of the skull, the third a helmet springing from the upper part of this tube. The long tube visible in *Parasaurolophus* can be considered to be an exaggeration of the second type. In *Lambeosaurus* a remnant of the primitive short tube is yet visible under the helmet, in *Corythosaurus* this remnant has finally been perfectly suppressed by the helmet. Just as interesting as these outgrowths on the top of the skull are the changes of the nostrils that accompany these outgrowths (fig. 1)<sup>14</sup>. The most primitive stage in the development of the nostrils is the stage seen in *Iguanodon bernissartensis*, *Prosaurolophus* or *Thespesius* (fig. 1a). A slight modification is visible in *Iguanodon mantelli* (fig. 1b), for in this „species“ the nares are already somewhat elongated backwards and a further degree of modification is visible in *Saurolophus* (fig. 1c). In this „genus“ already an indication of that sort of narrowing is visible, as is attained fully developed in the ornamented Trachodons. It consists in a narrowing of the posterior part of the nares, that finally goes so far as to form, even in semiadult males as „*Cheneosaurus*“, a long tube (fig. 1d).

<sup>13</sup>) HUENE, Fr., The carnivorous Saurischia in the Jurassic and Cretaceous; Revista Museo la Plata, Vol. XXIX, Buenos Aires 1926.

<sup>14</sup>) Being incapable to draw, Prof O. ABEL was so kind as to redraw these figures and thereby sacrificed some of his most precious time for the benefit of my paper. What this kindness means only those can appreciate, who had in similar experience.

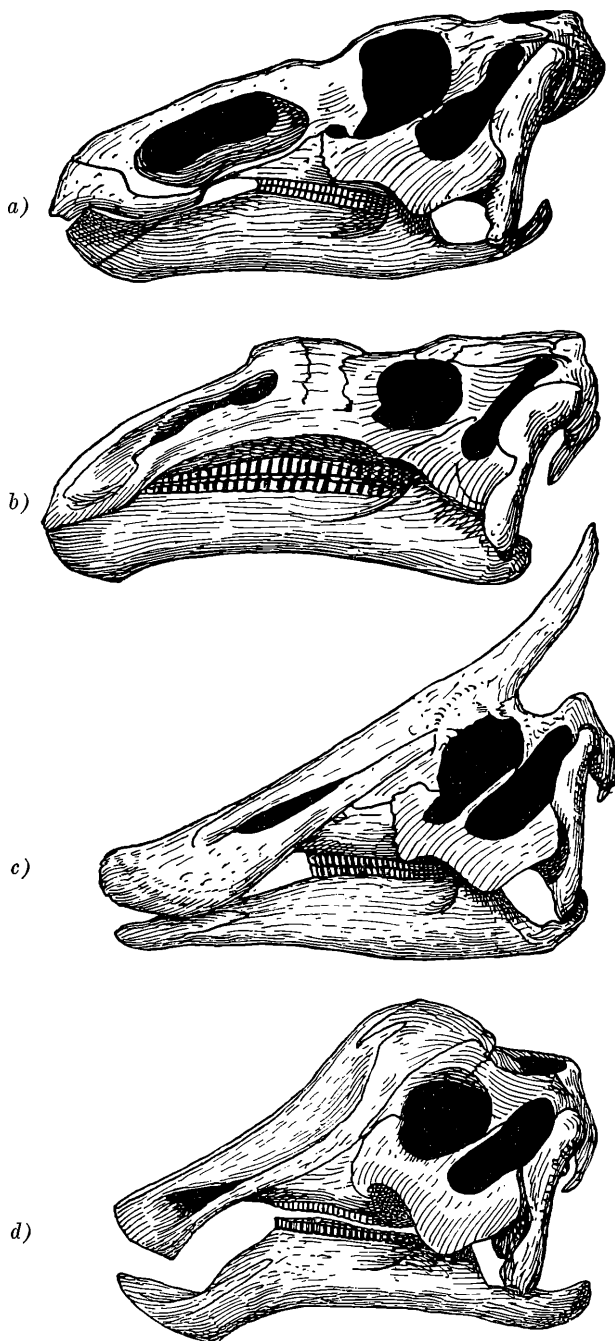


Fig. 2. a) skull of male *Thespesius*; b) skull of male *Iguanodon*; c) skull of *Saurolophus*; d) skull of some semiadult *Corythosaurian* („*Cheneosaurus*“).

The origin of different lacunae on the sides of the supracranial excrescences in those types, that bear a helmet, shows that the helmet did not serve for mechanical purposes and therefore we may suppose that the excrescence was only covered by skin. This allows one to make a guess regarding its function. As the excrescence begins with a backward prolongation of the nares, one may suppose that primarily this part was in connection with some airsacks, that served to inflate — somewhat as in *Chameleo*<sup>15)</sup> — two lateral sexual ornaments meeting on the top of the skull and that furtheron, as this ornament or, as ABEL<sup>16)</sup> suspected, organ of smell grew, a thin bony support developed. This hypothesis can equally account for the thinness of the excrescence, its great variety and its connection with pelvic modifications.

The validity of this theoretical speculation can be gathered from a study of living animals. Quite analogous cranial outgrowths as in the Trachodons occur sometimes in the *Lamellirostres*, where they are, as a rule, limited to the males and only rarely turn up in females (*Biziura*).

As far back as 1872 MARSCHALL<sup>17)</sup> pointed out that in some birds belonging to this order, as *Cygnus olor* and *Anas tadorna*, the males are characterised by an outgrowth of tissue at the root of the beak. In others, as in *Cygnus musicus* and *Cygnus coscoroba*, this outgrowth is replaced by a swelling of the facial bones, that contain a pneumatic cavity. In *Cygnus musicus* this cavity is yet traversed to some extent by diploe and opens by a small foramen into the orbit, in *Cygnus coscoroba* the inside of the cavity is smooth and opens into the nasal cavity. In the variety *Anser cygnoides* a similar cavity occurs as in *Cygnus coscoroba*.

Still more interesting are *Fuligula nigra* and *Fuligula spectabilis*. In the males of *Fuligula spectab.* on each side of the skull, posteriorly of the root of the beak and under the skin a large pneumatic swelling is observable, that is covered by very thin bone. This swelling is situated exactly at the place where the airsacks were supposed to have existed in *Iguanodon mantelli*. In *Fuligula nigra* the males have similar swellings, but besides this they bear above these swellings yet another high, median outgrowth arising abruptly on the top of the skull (fig. 2 a, b). It is largely formed by the nasals, it is likewise pneumatic, it is divided by a median septum, finally it is in internal communication with the lateral swellings. All these cavities are lined in this case inside with thick epithelium and in almost each of the points mentioned they are analogous to the pneumatic crest of *Corythosaurus* that is also in con-

<sup>15)</sup> TORNIER, G., Bau und Betätigung der Kopflappen und Halsluftsäcke bei Chamäleon. Zoolog. Jahrbücher (Abt. f. Anatomie), Vol. XXI, Jena 1904.

<sup>16)</sup> ABEL, O., Die neuen Dinosaurierfunde in der Oberkreide Kanadas. Die Naturwissenschaften, Berlin, Vol. XII, 1924.

<sup>17)</sup> MARSHALL, W., Über die knöchernen Schädelhöcker der Vögel. Niederländ. Archiv f. Zoolog., Vol. I, 1872.



nection with the nares. The function of this cavity can be found out by a study of *Anas clangula*. Although not visible as outgrowth, on the top of the skull in this bird likewise two pneumatic cavities are present, that are likewise divided by a median septum, but below they communicate in this bird with two smaller cavities, that are supplied with nerves. These lower cavities form a part of the olfactory organ and are separated by a series of valves from the rest of the narial cavity. The separation is such, that the air quitting the body during the act of by expiration shuts the valves automatically, while the fresh air taken up at the beginning of the inspiration opens them

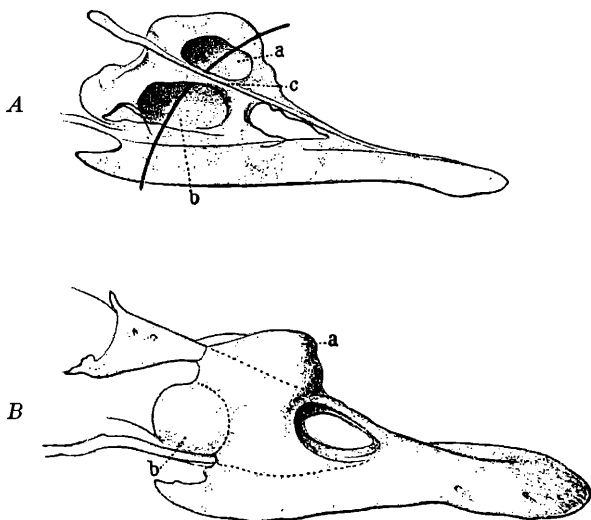


Fig. 3. A) Median section of skull of male of *Fuligula nigra* showing the two pneumatic cavities; B) lateral view of the skull showing the median outgrowth and the pneumatic cavities as swellings (reproduced from Marshalls original paper) a) median outgrowth, b) swelling of the maxillary; c) ascending process of the premaxillary.

again. This arrangement shows beyond all doubt that these sexual outgrowths serve for smelling.

A curious point worth mentioning is, that the same sexual ornament as in the Trachodons is just found in the Lamellirostres and not in other birds, thus in such birds that are not only semiaquatic as the Trachodons, but to which the Trachodons have already several times also been compared on account of their bill. Probably one will have to consider the aquatic mode of life of Trachodons and Lamellirostres as the primary cause of this double convergence.

In all the so called femals of *Orthopoda* the number of sacral vertebrae is generally greater than in the males:

♂		♀	
<i>Iguanodon mantelli</i>	5	<i>Iguanodon bernissartensis</i>	6
<i>Parasaurolophus</i>	7	<i>Kritosaurus</i>	9
<i>Corythosaurus</i>	8	<i>Diclonius</i>	9
<i>Saurolophus</i>	8	<i>Prosaurolophus</i>	9
<i>Camptosaurus dispar</i>	5	<i>Camptosaurus browni</i>	7

An exception is only made by *Thescelesaurus*, for *Thescelesaurus warreni*<sup>18)</sup>, that many be considered a male, has 6 sacral vertebrae, while the *Thescelesaurus neglectus*<sup>19)</sup> has but 5. Unfortunately it is not known whether parallel changes do not occur in birds.

The reasons why *Parasaurolophus* is placed in this list against *Kritosaurus* and *Corythosaurus* against *Diclonius* will be discussed later on.

A fine corroboration of the hypothesis according to which the ornamented Trachodons are males can be found in the study of their limb bones. If the occurrence of excrescences and pelvic modifications are actually only due to sexual differences, modifications may be expected to occur also in the anterior limb, that must have served, during the act of mating, for clasping the female.

In order to get a clear view of the proportions of the limb bones of different bipedal *Orthopoda* Dr. SIEBER was so kind as to count out on my request the relative dimensions of these bones, by taking the femur to be the unit (= 1000). The table shows the results:

Name of „genus“ and „species“	Femur = 1000		
	tibia	humerus	ulna
<i>Corythosaurus</i>	926	—	—
<i>Hypacrosaurus</i> No. 8501	885	475	619
7948	966	—	647
<i>Lambeosaurus</i>	954	—	—
<i>Parasaurolophus</i>	—	591	659
<i>Edmontosaurus</i> No. 2289	—	561	612
„ Francfort specimen <sup>20)</sup>	977	561	561
<i>Saurolophus</i>	887	530	591
<i>Prosaurolophus maximus</i>	866	529	545
<i>Diclonius mirabilis</i>	837	482	481
<i>Hadrosaurus foulkei</i>	887	543	560

<sup>18)</sup> PARKS, W. A., *Thescelesaurus Warreni*. University of Toronto, geol. Series No. 21; Toronto 1926.

<sup>19)</sup> GILMORE, Ch. W., loc. cit. 1924.

<sup>20)</sup> The length of the femur, that is missing in the Francfort specimen, has been calculated on base of the relative length of humerus and femur known in the *Edmontosaurus* specimens No. 2288 and No. 2289.

Name of „genus“ and „species“	Femur = 1000		
	tibia	humerus	ulna
<i>Thespesius saskatchewanensis</i>	790	—	—
<i>edmontoni</i>	832	525	586
<i>annectens</i>	896	557	566
<i>Kritosaurus</i>	—	603	584
<i>Tanius</i>	945	513	[614] <sup>21)</sup>
<i>Iguanodon mantelli</i>	926	580	556
<i>bernissartensis</i>	944	606	521
„ <i>atherfieldensis</i> (not full grown!)	877	560	501
<i>Camptosaurus dispar</i>	982	597	460
<i>medius</i>	911	575	405
„ <i>nanus</i>	911	554	395
<i>Thescelesaurus neglectus</i>	1183	[800] <sup>22)</sup>	513
„ <i>warreni</i>	1193	807	796
<i>Hypsilophodon</i>	1298	724	663

This table shows first of all that in the bipedal *Orthopoda* a general increase of the femur can be detected when compared to the tibia, for the proportion rises from 1000 : 1298 in *Hypsilophodon* to 1000 : 837 in *Diclonius*. The second feature, that comes out clearly, is a relative decrease of the humerus, for the proportion drops from 1000 : 724 in *Hypsilophodon* to 1000 : 482 in *Diclonius* and to 1000 : 475 in *Hypacrosaurus*. Other regularities can not be detected in the table, but the proportions of the humerus to the ulna show such changes, as might be attributed to sexual dimorphism. Taking the humerus to be the unit (= 100) the proportions of the ulna show as follows:

<i>Camptosaurus dispar</i>	Ul = 77	<i>Camptosaurus medius</i>	Ul = 70
—		„ <i>nanus</i>	71
<i>Thescelesaurus warreni</i>	98	<i>Thescelesaurus neglectus</i>	64
<i>Iguanodon mantelli</i>	96	<i>Iguanodon bernissartensis</i>	86
<i>atherfieldensis</i>	89	—	
—		<i>Kritosaurus</i>	97
—		<i>Diclonius</i>	100
—		<i>Hadrosaurus foulkei</i>	103
—		<i>Prosaurolophus</i>	103
—		<i>Edmontosaurus</i> (Frank-	
—		fort spec.)	100
—		No. 2289	

<sup>21)</sup> Calculated from the length of the radius by assuming the proportion of the ulna to the radius to have been, as generally in Trachodons, 100:92.

<sup>22)</sup> Calculated by assuming the proportion of the humerus to the tibia to have been the same as in *Thescelesaurus warreni*. —

<i>Thespesius edmontoni</i>	112	<i>Thespesius annectens</i>	102
<i>Saurolophus</i>	112	—	
<i>Parasaurolophus</i>	112	—	
<i>Tanius</i>	118?	—	
<i>Hypacrosaurus</i>	130	—	

This list shows at a glance that there exists a general tendency to elongate the ulna but that in corresponding types the longer ulna is always met with in those „species“ or „genera“ in which either the pseudopectineal process is short as in *Thespesius edmontoni* or *Iguanodon mantelli*, or the ischium is hammershaped as in *Tanius* or *Camptosaurus dispar*, or besides this even the skull is ornamented as in *Saurolophus*, *Prasaurolophus* and the *Corythosaurians*. The shorter ulna always goes with a pointed ischium.

This coincidence ist all the more surprising as the elongation of the ulna is not paralleled or compensated by a corresponding elongation of the humerus. In comparison to the femur the humerus is long in the „male“ *Camptosaurus dispar*, but short in the „male“ *Iguanodon mantelli*. This shows that is the ulna that is affected by the sexual dimorphism and not the humerus.

As it is quite impossible to find any connection between the development of an ornament on the skull, the modification of the pelvis and the modification of the antibrachium except such as due to sex, the occurrence of a strong sexual dimorphism in the bipedal *Orthopoda* may be considered as proved.

Of course it is much more difficult find out which females belong to the different male *Orthopoda*, than merely to establish their existence. To a certain extent however even this problem can be solved. First of all it is evident that the two „species“ of *Iguanodon* belong together and than it seems just as sure that *Thespesius edmontoni* is the male of *Thespesius saskatchewanensis*. *Thespesius edmontoni* has not only got an abbreviated pseudopectineal process, but in many points it is in the same relation to *Thespesius saskatchewanensis* as *Iguanodon mantelli* to *Iguanodon bernissartensis*. This parallelism goes even so far as to extend to the scapula, for in both genera it is more slender in the one sex than in the other.

*Saurolophus* and *Prosaurolophus* also belong together. While the relation of the humerus to the femur is much the same in *Saurolophus* as in *Prosaurolophus*, the outline of the skull of *Saurolophus* is in the same relation to the outline of the skull of *Prosaurolophus* as is the outline of the skull of *Thespesius edmontoni* to the one in *Thespesius saskatchewanensis*. As this ist the same relation as existing also between the outlines of the skulls in both Iguanodons, it seems quite safe to consider *Prosaurolophus* to be the female of *Saurolophus*. Of course in this case *Prosaurolophus* must be considered as such a female, to which the sexual ornament was transmitted in a

slight degree, numerous quite analogous cases are however also known in recent animals. It is enough to refer to *Biziura*.

Having eliminated *Thespesius*, *Saurolophus* and *Prosaurolophus* from the rest of the Trachodons, only *Diclonius*, *Edmontosaurus* and *Hadrosaurus* can be considered as females of *Parasaurolophus*, *Lambeosaurus* and the Corythosaurians. Guided by the evidence afforded by *Saurolophus* and *Prosaurolophus*, *Diclonius* might be the female of some Corythosaurian, for the proportion of the humerus to the femur is somewhat the same in both, and the difference observable in the relative length of the tibia might be explained by the different position of the centre of gravity in the two sexes. This difference may also explain, why the femur is sometimes relatively long in animals considered as females, but sometimes relatively short. At the same time this independance of the relative length of the femur from the relative length of the pseudopectineal process indicates that the stronger or weaker development of the latter is independant of the muscular attachments important in locomotion. So this again tends to show that this elongation is due to some other obscure factor that can only be sexual dimorphism.

Unfortunately it can not yet be definitely decided in what relation *Edmontosaurus*, *Parasaurolophus*, *Kritosaurus* and *Lambeosaurus* are, but perhaps *Kritosaurus* is the female of *Parasaurolophus* for the relation of the humerus to the femur is in both about the same. This would bring it about that *Lambeosaurus*, in which the skull is less specialised than the Corythosaurians, would have to be considered as the male of *Edmontosaurus*. As the skull is less flattened, therefor yet less specialised in *Edmontosaurus* than in *Diclonius*, all this seems to agree quite well.

The correctness of this grouping can be deduced from the formula of the cervical and dorsal vertebrae in some Trachodons:

	$\delta$		$\text{♀}$
<i>Parasaurolophus</i>	· { cerv. 13 dors. 17 } 30	<i>Kritosaurus</i>	· { cerv. 13 dors. 16 } 29
<i>Saurolophus</i>	· { cerv. 12? dors. 20 } 32?	<i>Prosaurolophus</i>	· { cerv. 11 dors. 19 } 30
<i>Corythosaurus</i>	· { cerv. 15 dors. 19 } 34	<i>Diclonius</i>	· { cerv. 16 dors. 18 } 34

Summing up all together it can be safely stated, that in the bipedal *Orthopoda* an elongation of the anterior and an abbreviation of the posterior part of the skull, the development of protuberances on the skull, elongated neurapophyses, the elongation of the antibrachium, few sacral vertebrae, the persistence of a short pseudopectineal pro-

cess and the developement of a hammer on the ischium characterise the males.

According to the rules of nomenclature this demands already the elimination of the following names: *Iguanodon bernissartensis* DOLLO (1882), *Prosaurolophus* B. BROWN (1915) and *Thespesius sasketchwanensis* STERNBERG (1926). As *Hypacrosaurus* has the priority over *Corythosaurus*, but as *Diclonius* precedes both and as *Kritosaurus* has the priority over *Parasaurolophus*, all the „generic“ names of the Trachodons will probably with the time have to be reduced to *Diclonius*, *Edmontosaurus* (= *Lambeosaurus*) and *Kritosaurus*.

Surely similar characters as in the male *Orthopoda* will be found in the male *Theropoda* and so these, as well as all the *Sauropoda*, will naturally also have to be revised. The difference observable on the distal ends of the ischia of the *Sauropoda* pleads for such a revision. This end ist slender in *Camarasaurus*, *Haplocanthosaurus* and *Helopus*<sup>23)</sup>, but thickend in *Diplodocus*, *Apatosaurus* and *Ornithopsis*. In the other *Sauropoda* it is hithertoo unknown, although it would be especially interesting to know for example something about the ischium of *Barosaurus*.

The occurence of one male *Iguanodon* among 23 females at Bernissart, the much more frequent occurrence of not-ornamented frontals of *Orthomerus* at Szentpérterfalva and Valiora (ratio 6 : 1), and the more frequent occurrence of female Camptosaurians may perhaps be taken as indications ,that some *Ornithopoda* lived in herds and were polygamous, this can however definitely only be setteld by means of North-American statistics. *Agama colonorum* affords a parallelism among recent Reptiles. That the female *Ornithopoda* defended their offsprings may be gathered from the stronger development of the spine on the thumb in the female *Iguanodon* and this again goes to show, that the young ones stayed a good while near their mother.

Thus in spite of the fragmentary state of preservation of fossil Reptiles one manages never the less, step by step, to gather a fair amount of information about their structure and their mode of life.

<sup>23)</sup> WIMAN, C., loc. cit. 1929.

**Addendum:**

Severe illness having prevented me from revising the proof sheets of my paper „The Genera of Reptiles“ (Palaeobiologica, Vol. I) several misprints occurred that need rectification:

pag. 168, line 19 from below: omit comma between the words „— pus“ and „cleft“;

pag. 168, last line: stroke out „†*Pantelosaurus*“;

pag. 169, last line: read „*Dvinia*“ instead of „*Doinia*“;

pag. 170, line 6 from above: read „T-shaped“ instead of „shaped“;

pag. 170, line 8 from above: stroke out „†*Galaeops*“;

pag. 170, line 10 from above: read „*Galeopidae*“ instead of „*Galaeridae*“;

pag. 170, line 11 from above: read „*Galaeops*“ instead of „*Galerus*“;

pag. 173, line 10 from above: read „*Psilotrachelosaurus*“ instead of „*Philotrachelosaurus*“;

pag. 183, footnote 1 does not refer to *Saurornithoides* (line 19 from below) but to *Teinurosaurus* (last line of text). Footnote 2 to *Aublysodon* (before last line of text);

pag. 185, line 13 from below: read „*Euoplocephalus*“ instead of „*Erroplcephalus*“.

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