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Gorgonopsidae from the North Dvinsky excavations of V. P. Amalitsky.*

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170 & 3 pages; 26 figures; 13 plates. Footnotes signified by brackets.

Gorgonopsidae from the North Dvinsky excavations of Prof. V. P. Amalitsky.

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> "The Gorgonopsians are probably the ancestors of both Anomodonts and Cynodonts, and being thus on the direct mammalian line all new facts concerning their morphology are extremely important." (Broom and Haughton, *Ann. S. Afric. Mus*., vol. XII, pt. 1, 1913, p. 27)
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> "The Gorgonopsids are plainly the central group of the Theriodonts." (Watson, *Proc. Zoolog. Soc. London*, 1921, p. 80)

In the great amount of material from the North Dvinsky excavations that was left after the death of Prof. V. P. Amalitsky are a number of skeletal remains that may be considered as belonging to forms of Gorgonopsia Lyd. At the time two nearly complete

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skeletons of these remains were mounted by the late Professor and exhibited in Saint Petersburg, one in 1900 (during the XII Congress of Russian scientists and M.D.s) (GR no. 29); another a few years later (GR no. 97). Both examples were called by the same name: *Inostrancevia alexandri* Amal. There also remained an unfinished work of the late Professor with the early descriptions of both skeletons, also of one more skull (GR no. 70) and a few different bones, which Amalitsky considered as belonging to the same species of *Inostrancevia*. He prepared a number of corresponding photographs and three phototype plates, which are presented here (Plates I, II, III).

As is known, Owen, when studying the skull of this animal that was sent to him, came to the conclusion that its temporal fossae were roofed over by bone as in alligators of today or in extinct Labyrinthodontia. But the structure of the skull as a whole, and in particular the structure of the dental apparatus, did not leave Owen any doubt that the animal should be considered as belonging to the highest reptiles, and that its characteristics were "rather those of a carnivorous marsupial than any Crocodilian reptile" (*Ibid*, p. 27). Owen put this form into the order Theriodontia, the representation of which he characterized as follows: "the dental apparatus of carnivorous animals differ in regard to their position and are separated from the molars by large caniniform fangs in the upper and lower jaws; the lower fang overlaps with the upper, projecting as in Mammalia" (*Ibid*, p. 15, "Theriodontia"). Osborn wrote later: "represents a group which possesses truly all the primitive characteristics of Mammalia, both in the structure of the skeleton and the dental apparatus. No other group of Reptilia or Amphibia comes so close to the hypothetical Promammalia" (Osborn, *Amer. Naturalist*, 1898, 32, p. 333).

In 1890, while systematizing the material of the British Museum, Lydekker took *Gorgonops torvus* Ow. from the order Theriodontia and assigned it to the special family Gorgonopsidae and put the latter in the group *incertae sedis* among Anomodontia. He supposed that "in roofing of the temporal fossa" *Gorgonops* was the connecting link between typical Theriodontia and Pareiasauria (Lydekker, *Catalogue of the Fossil Reptilia and Amphibia in the British Museum*, pt. IV, 1890, p. iii).

In exactly the same way, Seeley, in his *Classification of the Fossil Reptilia* in 1894, separated *Gorgonops* from Theriodontia into the special suborder Gorgonopsia, and supposing that their "temporal vacuities roofed over" put it between Pareiasauria and Dinocephalia. Thus in Theriodontia, Seeley left only: 1) Lycosauria, 2) Cynodontia, and 3) Gomphodontia.

In 1909 Broom studied anew the skull of *Gorgonops torvus* described by Owen, and came to the conclusion that although *Gorgonops'* parietal region is wide, its temple openings are the same as in the rest of Therapsida. After a short time, the statement of Broom was proven to be true by the discovery of a nearly complete skull of *Gorgonops torvus* by Whaits (*cf*. Broom, *Proc. Zool. Soc. London*, 1913, p. 225)

At first Broom thought that *Gorgonops*, together with *Titanosuchus*, belonged to Dinocephalia (Broom, *Geol. Magaz. London*, 1909, p. 401, *cf. Proc. Zool. Soc*., 1913, p. 225), but he later referred it to Therocephalia (*cf. Proc. Zool. Soc. London*, 1913, p. 225). He also considered that *Inostrancevia alexandri* from North Dvina belonged to it. It had become known at that time through the photographs of Amalitsky. In the latter Broom saw similarity to the South African *Scylacosaurus* (Broom, The reptiles of the Karroo Formation, *An Introduction to the Geology of Cape Colony* by Rogers and Toit, 1909, p.

250). But already in 1913 the collected material of Theriodontia made Broom insist that it was time to re-establish the order Gorgonopsia for *Gorgonops* and forms close to it as a special suborder of Therapsida. “It is possible to say, without any danger of magnifying the fact,” wrote Broom, “that *Gorgonops* differs from the typical Therocephalia more than Carnivora from Marsupialia” (Broom, On the Gorgonopsia, a suborder of the mammalial-like reptiles, *Proc. Zool. Soc. London*, 1913, P. 225). Their skulls in many respects are close to the skulls of Anomodontia, themselves standing between Therocephalia on the one hand, and Cynodontia on the other. According to Broom the characteristics of their skulls are (*Ibid*, p. 229):

1. Wide parietal region;
2. Presence of preparietals;
3. Large postfrontals;
4. Large postorbitals; they form the upper temporal edge and meet in the back with the squamosal;
5. The development of the real odd-numbered vomer;
6. Transpalatines (ectopterygoids) closely united with pterygoids;
7. Left and right halves of the lower jaw united by a strong symphysis;
8. Angular with a deep groove.

In the postcranial skeleton to be noticed are (for example in *Scimnognathus tigriceps* Broom) (Broom, On the Gorgonopsia, p. 229):

1. First cervical vertebrae, proatlas, and atlas are very similar structurally with such in Anomodontia and Dinocephalia; both halves being free and not forming a single arch as in cynodonts;
2. Large scapula, without a special acromion;
3. Coracoid and precoracoid, as in Therocephalia;
4. Cleithrum, large clavicles and interclavicles, and ossified sternum present, at least in some forms (*Scylacops*);

5. Carpus is represented by the large radiale and ulnare, and a small intermedium. Centralia consists of 2 bones, the external being smaller. Distal part of the carpals consists of 4 bones; of them the fourth, the longest, probably represents the united 4th & 5th carpals;
6. Digital formula: 2, 3, 4, 5, 3; the third finger has one and the fourth two phalanges, as in Therocephalia (Broom, *ibid*, p. 229, *cf. Philosoph. Transact. R. Soc. London*, vol. 206, 1915, p. 18).

On the whole "the most striking characteristic of the carpus of the Gorgonopsia", wrote Broom, "is the similarity with the Pelycosauria to a greater degree than with Anomodontia or Dromasauria." The digital formula of Pelycosauria, as in Gorgonopsia, is 2, 3, 4, 5, 3, and in Dromasauria, Anomodontia, and Cynodontia it is 2, 3, 3, 3, 3 (Broom, *Annals S. African Mus*., 1913, vol. Xii, pt. I, p. 33).

Broom gave such a scheme for the systematic position of the given forms (see fig. 1) (*Annals S. Afric. Mus*., vol. XII, pt. I, 1913, p. 12).

Fig. 1, p. 6

Thus, according to Broom, the Gorgonopsia are the ancestors of Anomodontia and Cynodontia, and form a direct branch to Mammalia. Stratigraphically they appear in South Africa before Anomodontia, and even may be before Therocephalia (Broom, On the Gorgonopsia, p. 230). But Broom brought such forms as *Titanosuchus, Scapanodon, Archaeosuchus, Cynosuchus,* and others into the group Gorgonopsia, together with *Gorgonops torvus* Ow. (*l.c.*).

In 1914 Watson showed by the structure of the base of the skull, occipital and auditory regions that Gorgonopsidae represents a number of stages between the pelycosaur type of *Dimetrodon* and the cynodont *Diademodon*.(Watson, Notes on some carnivorous therapsids, *Proc. Zool. Soc. London*, 1914, Pt. IV, pp. 1021-1038). In the structure of the lower surface of their skull he noticed: (*Ibid*, p. 1031).

1. Long region in front of basisphenoid, in which both pterygoids, together with the parasphenoid between them, form a narrow partition behind their strongly descending branches;
2. Interpterygoid vacuities, if present, very small and located between the descending branches of pterygoids;
3. In the middle of the rear part of the palate is a groove;
4. Suborbital vacuities are absent;
5. Choanae very large; divided by partition, and not reaching the level of the lower edges of the maxillae. The latter have a tendency to come closer.

But while Broom considered this partition as single, something like a vomer of Anomodontia, Watson insisted that it consists of two ingrown prevomers, between which in some forms of *Arctops* it is possible to trace a line or the dividing furrows. The posterior part of the palate of Gorgonopsidae has, according to Watson, the wide vomer of Mammalia (Watson, Notes on some carnivorous therapsids), for the homologue of which he considers the parasphenoid. "Dr. Broom is quite correct in his contention," wrote Watson in 1913, "that the mammalian vomer is homologous with the reptilian parasphenoid, and that the reptilian vomers, the prevomers are lost in the majority of recent mammals (Watson. *Annals and Magazine of Nat. History*, vol. XI, 1913, p. 74).

In comparison with the closest of the theriodonts to Mammalia—Cynognathidae—the palate of Gorgonopsidae is different, according to Watson, only by

the absence of the so-called secondary hard palate. In Gorgonopsidae it only begins to appear, with the development of this palate, the reduction of the prevomers continues.

Watson divided all Theriodontia into four suborders:

1. Therocephalia;
2. Gorgonopsia;
3. Bauridae;
4. Cynodontia (including Nythosauridae and Cynognathidae) (*Proc. Zool. Soc. London*, 1914, Pt. IV, p. 1038).

About the question of the vomer (prevomer) of Gorgonopsidae, in 1915 Broom declared that up to date it was difficult to be sure about the right homologue of this bone. "In the youngest Gorgonopsia, *Scylacognathus parvus*," wrote Broom, "the structure and the relationships of it are such as in the real vomer. In the later Gorgonopsia vomer shows an odd structure, although it is possible that it is the result of the union of both of its parts. Watson sees it as a union of the praevomers; I described it as a real odd vomer" (Broom, Origin of mammals, *Philosoph. Transactions R. Soc. London*, v. 206, 1915, p. 29).

An even more definite view on the same subject was expressed by Haughton, who studied the skulls of some Gorgonopsia (*Gorgonognathus longifrons*, *Galesuchus gracilis*, *Gorgonops* sp., *Scymnognathus seratidens*): "Although a middle suture line can be seen on the praemaxillaria," he wrote, "on the praevomer such is not noticeable. This is a singular and not a double united bone, as was supposed by Broom and Watson" (Haughton, *Annals S. Afric. Mus*., vol. XII, pt. III, 1913, pp. 86-87).

In 1917, Watson, giving the classification of the whole group Anomodontia, left the order Theriodontia with the past subdivision into: 1) Gorgonopsia, 2) Cynodontia, 3)

Therocephalia, 4) Bauriamorpha; and characterized it as follows: these are "the Anomodontia with specialization for carnivorous life and with reduced quadratum and qu.-jugal; their glenoid is located on scapula and coracoid" (Watson, A sketch classification of the pre-Jurassic tetrapod vertebrates, *Proc. Zool. Soc. London*, 1917, p. 176).

1. Gorgonopsia, according to Watson, are theriodonts, "The parietalia of which do not reach temporal hollows, and the bony palate has no suborbital vacuities" (*l.c.*). Here, together with *Gorgonops* Ow., he also referred *Inostrancevia amalitzici*.
2. Cynodontia—Theriodontia with a narrow intratemporal partition, formed by parietals. The secondary hard palate is absent; on the surface of the palate are no suborbital vacuities.
3. Therocephalia—with a narrow intratemporal partition, for the most part formed by parietals. The secondary hard palate is absent; on the surface of the palate are wide suborbital vacuities.
4. Bauriamorpha—with short temporal hollows, divided by the parietals. The secondary hard palate and the large suborbital vacuities are present (*Ibid*, p. 177).

In 1918, Haughton gave a few facts about the internal structure of the braincase of some Gorgonopsia (*Scymnognathus tigriceps*, *Gorgonognathus longifrons*, *Scylacops capensis*) in comparison with Dinocephalia and Therocephalia (Haughton, Some new carnivorous Therapsida, with notes upon the brain case in certain species, *Annals S. Africa Mus*., vol. XII, pt. VI, 1918). Considering the corresponding views of Watson about *Dimetrodon* and *Diademodon*, Haughton came to the conclusion that a striking similarity of the main characteristics is present in the construction of the braincase of all carnivorous Therapsida. "All have the inner ear lying well down in the brain & not up in

the side-wall, thus showing a mammalian affinity rather than one with modern reptiles" (*Ibid*, p. 214). But, by the internal structure of the braincase of Gorgonopsia, wrote Haughton, it is not so closely related to Cynognathidae as should be expected judging by the external characteristics. They are closer in that respect to Pelycosauria and Dinocephalia than to any other suborder, which was already noticed by Broom and others on the basis of the external characteristics with Dinocephalia. Their similar characteristic is the epipterygoid, "a rod-like bone with an expanded base," while in Cynognathidae (*Diademodon*) the epipterygoid is in the shape of the plates (Haughton, Some new carnivorous Therapsida).

In 1919 Abel, in "Die Stamme der Wirbelthiere," again divided Theriodontia into the following suborders: 1) Therocephalia, 2) Dromasauria, 3) Dinocephalia, 4) Dicynodontia. *Gorgonops* he referred to Dinocephalia together with *Delphinognathus*, *Tapinocephalus*, *Moschops*, and *Moschognathus*, joining in this respect to the former point of view of Broom. Abel referred *Inostrancevia* to Therocephalia and also referring to it , Abel referred to Therocephalia and also referred *Scylacosaurus, Cynognathus, Bauria, Gomphognathus, Diademodon, Sesamodon*, and others to it (Abel, Oth., Die Stamme d. Wirbelthiere, 1919).

Abel considered the opinion of Watson that the vomer (prevomer) of *Gorgonops* must not be mixed with the vomer of mammals to be incorrect. Such opinion, he thought, is based on the supposition that the parasphenoid of stegocephalians and reptiles is identical with the vomer of mammals, the prevomer of the latter being absent. But in reality the parasphenoid is absent in mammals and the prevomer of reptiles is therefore homologous to their vomer (*Ibid*, p. 435).

In 1921, Watson began to study anew a number of known up-to-date Gorgonopsidae from the *Endothiodon* Zone of the Lower Beaufort of South Africa (*Arctops willistoni* Watson, *Gorgonops torvus* Ow., *Scymnognathus whaitsi* Broom, *Leptotrachelus eupachygnathus* Watson). He tried to follow the position of each of them between the most primitive Pelycosauria, for which form, following Case and Williston, he accepts *Varanosaurus* as a morphological ancestor of *Dimetrodon* (through *Dicopeus*) on the one hand, and the most progressive—Anomodontia, exactly—*Diademodon* and *Trirachodon*, on the other (Watson, The bases of classification of the Theriodontia, *Proc. Zool. Soc. London*, 1921). Referring to it the much later Gorgonopsidae from the *Cistecephalus* Zone from the Lower Beaufort described by Owen (*Lycosaurus pardalis, Arctognathus (Lycosaurus) curvimola*) (Owen, *Catalogue Foss. Reptilia of S. Africa*, pp. 15-17, 71), Broom, and Haughton (*Scymnognathus tigriceps* Br. and Haugh., *Scymn. parvus* Br., *Scymn. minor* Br., *Scymn. angusticeps* Br., *Scymn. serratidens* Haugh., *Scylacops capensis* Br., *Gorgonognathus longifrons* Haugh.) (*Annals of the S. Afric. Mus*., 1913, vol. XII, pt. 1, III; *Bullet. Americ. Mus. Natur. History*, 1913, vol. 32, p. 559; 1915, vol. 25, p. 128; *Proc. Zool. Soc. London*, 1913, p. 227; 1915, p. 171 and others), Watson came to the conclusion that Gorgonopsidae by the structure of their skull represent a number of forms, more or less distant in evolution from the species Pelycosauria in the direction toward *Diademodon* from Cynodontia and the latter to Mammalia. The most primitive, like *Arctops*, are linked by a number of intermediate forms with cynognathid(s). Also that "each form is advanced in certain features while retaining a more primitive structure in others, so that an imaginary animal, built up by throwing together the most advanced features in all the actual animals, would be far more

advanced than any one is on the average; although in no point would it be more advanced than a known form" (Watson, The bases of classification of the Theriodontia, p. 77). The changes, thought Watson, went on in the same direction, in which pelycosaurs like *Varanosaurus* evolved into theriodonts of the species *Gorgonops*, and the animal of the species *Gorgonops* into the form like *Arctognathus*. The last (*Arctognathus*) "which is technically a Gorgonopsid is structurally closer to *Cynognathus* than it is to *Gorgonops*" (*Ibid*, p. 79).

Returning to the question about the classification of Theriodontia, Watson believed that Gorgonopsidae are representative of the central group of the named order, its main stem, which evolved in a straight direction to Cynognathidae and through them to Mammalia. From them the other groups of Theriodontia were formed as side branches. But the classification of Theriodontia, remarked Watson, in the same form as it was offered by him at one time; exactly: Gorgonopsia, Cynodontia, Therocephalia, and Bauriamorpha (*Ibid*, p. 88). But Watson also said that the groups named, at least Gorgonopsidae and Therocephalidae, unite a great number of forms not of a common direct origin, and are common only in two or three general characteristics (*Ibid*., p. 88).

Thus is determined at the present time the place and the importance of Gorgonopsia Lyd. in the realm of Theriodontia and their relationship to Mammalia.