ART. XI. — *The Typical* ORNITHOPODA *of the American Jurassic;* by O. C. MARSH. (With Plates IV–VII.)

THE herbivorous Dinosaurs now known from the Jurassic deposits of this country consist mainly of the gigantic *Sauropoda* and the huge *Stegosauria*, both quadrupedal forms. A third group is the bipedal *Ornithopoda*, which contains the genus *Camptosaurus* as well as various smaller and more bird-like types. The first two groups have been investigated by the writer, and the main results published in this Journal. The third group also received considerable attention during the above investigation, but a recent study both of the type specimens and additional material has revealed new points of interest, and some of these are given in the present article.

Camptosaurus, Marsh, 1885.

The large Dinosaur described by the writer as *Camptosaurus dispar*, of which a restoration also has recently been published,* is now so well known that it may be taken as a form typical of the group. It is exceeded in size by *Camptosaurus amplus*, Marsh, but there are at least two smaller species of the genus (*C. medius* and *C. nanus*, noticed below). So far as at present known, these species are found in successive deposits of the same general horizon, the smallest below and the largest above.

Camptosaurus amplus is represented by remains which show that this reptile when alive was about thirty feet in length. The type specimen of *C. dispar* was about twenty feet in length, and ten feet in height. *C. medius* was about fifteen feet long. The smallest species of the genus, *C. nanus*, was not more than six feet in length, and perhaps four feet in height when standing at rest. One of the striking features of this diminutive species is its long sigmoid scapula shown in figure 3, Plate V. This is in strong contrast with the short, straight scapula of *C. dispar*, seen on the same plate, figure 2. The limb bones of all the species of this genus are very hollow.

* This Journal, vol. xlvii, p. 245, March, 1894. See also, vol. xviii, p. 501, December, 1879; and vol. xxix, p. 169, February, 1885

The skull, brain, and teeth, of *C. medius* are shown on Plate IV. The peculiar peg and notch articulation in the sacral vertebræ of this genus, already described, is indicated on Plate VI, figure 2, and a summary of the principal characters of the genus, and of the nearest allied genera, will be found in the text below.

Dryosaurus, gen. nov.

Another genus of Jurassic Dinosaurs, allied to *Camptosaurus*, but differing from it in many important respects, is *Dryosaurus*, the one here established. The type was described by the writer in 1878, under the name *Laosaurus altus*, and a tooth, the pelvis, and a hind leg, were also figured.* Additional material since received shows that this genus is quite distinct from *Laosaurus*, to which it was at first referred, and is intermediate between *Camptosaurus* and that genus, as is shown in a summary of the characters of these genera given later in the present article.

The European representative of *Dryosaurus* is *Hypsilophodon*, Huxley, from the Wealden of England. That genus, however, differs from the nearest allied forms of this country in several well-marked characters. Among these, the presence of teeth in the premaxillary bones and a well-ossified sternum are features not seen in American Jurassic forms. The fifth digit of the manus, moreover, in *Hypsilophodon* is almost at right angles to the others, and not nearly parallel with them as in *Dryosaurus*. It agrees with the latter genus in having the tibia longer than the femur.

The only species of *Dryosaurus* at present known is the type first described, and in future this may be called *Dryosaurus altus*. Several specimens of this Dinosaur are preserved in the Yale Museum, and they show it to have been in life about twelve feet long, and one of the most slender and graceful members of the group. The known remains are all from the Atlantosaurus beds of Colorado and Wyoming.

Laosaurus, Marsh, 1878.

The present genus includes several species of diminutive Dinosaurs, all much smaller than those above described, and possessing many features now seen only in existing birds, especially in those of the ostrich family. The two species of the genus first described by the writer (*Laosaurus celer*, the type, and *L. gracilis*)† show these avian features best of all,

* This Journal, vol. xvi, p. 415, plate ix, November, 1878.
† *Ibid.*, vol. xv, p. 244, March, 1878.

and it would be difficult to tell many of the isolated remains from those of birds. A larger species, which may be called *Laosaurus consors*, is now known by several skeletons nearly complete. The type specimen, here figured in part on Plates V–VII, is the most perfect of all, and this was collected by the writer in 1879. The animal when alive was about eight or ten feet in length. The known remains are from the Atlantosaurus beds of Wyoming.

One of the distinctive features of this genus, which separates it at once from those above described, is the pubis. The prepubis, or anterior branch of this bone, which was very large and broad in *Camptosaurus*, still long and spatulate in *Dryosaurus*, is here reduced to a pointed process not much larger than in some birds. These differences are shown in Plate VII, figures 1, 2, and 3.

Nanosaurus, Marsh, 1877.

The smallest known Dinosaur, representing the type species of the present genus, was described by the writer in 1877, under the name *Nanosaurus agilis*.* The type specimen consists of the greater portion of the skull and skeleton of one individual, with the bones more or less displaced, and all entombed in a slab of very hard quartzite. The whole skeleton was probably thus preserved in place, but, before its discovery, a part of the slab had been split off and lost. The remaining portion shows on the split surface many important parts of the skeleton, and these have been further exposed by cutting away the matrix, so that the main characters of the animal can be determined with considerable certainty.

A study of these remains shows that the reptile they represent was one of the typical *Ornithopoda*, and one of the most bird-like yet discovered. A dentary bone in fair preservation (Plate VI, figure 3) indicates that the animal was herbivorous, and the single row of pointed and compressed teeth, thirteen in number and small in size, forms a more regular and uniform series than in any other member of the group. The ilium, also, shown on the same plate, is characteristic of the *Ornithopoda*, having a slender, pointed process in front, but one much shorter than in any of the larger forms. The posterior end is also of moderate size. All the bones of the limbs and feet are extremely hollow, strongly resembling in this respect those of birds. The femur was shorter than the tibia. The metatarsals are greatly elongated and very slender, and there were probably but three functional toes in the hind foot.

* This Journal, vol. xiv, p. 254, September, 1877.

A second form referred by the writer to this genus, under the name *Nanosaurus rex*, may perhaps belong to the genus *Laosaurus*. The femur is shown on Plate VI, figure 5. The animal thus represented was considerably larger than the present type species, and from a somewhat higher horizon in the Atlantosaurus beds.

The type specimen here described, which pertained to an animal about half as large as a domestic fowl, was found in Colorado. This reptile was a contemporary of the carnivorous *Hallopus*, likewise one of the most diminutive of Dinosaurs, and one of the most remarkable.

The various Dinosaurs thus briefly referred to under their respective genera have many other points of interest that cannot be here discussed, but their resemblance to Birds is worthy of some notice. This is apparent in all of them, but, in the diminutive forms, the similarity becomes more striking. In all the latter, the tibia is longer than the femur, a strong, avian character, and one seen in Dinosaurs only in the small bird-like forms.* In *Nanosaurus*, nearly all, if not all, the bones preserved might have pertained to a bird, and the teeth are no evidence against this idea. In the absence of feathers, an anatomist could hardly state positively whether this was a bird-like reptile or a reptilian bird.

The main characters of the four genera above discussed are as follows:—

Camptosaurus.

Premaxillaries edentulous, with horny beak. Teeth large, irregular, and few in number. A supra-orbital fossa. Cervical vertebræ long and opisthocœlous. Lumbars present. Five free vertebræ in sacrum, with peg and notch articulation. Limb bones hollow. Fore limbs small. Sternum unossified. Five functional digits in manus. Prepubis long and broad; postpubis elongated. Femur longer than tibia. Metatarsals short. Three functional digits in pes; the first rudimentary, and the fifth wanting.

Dryosaurus.

Premaxillaries edentulous, with horny beak. Teeth of moderate size. A supra-orbital fossa. Cervicals long and biconcave. No lumbars. Six coössified vertebræ in sacrum, without peg and notch articulation. Limb bones hollow. Fore limbs very small. Sternum unossified. Five digits in manus. Prepubis long and narrow; postpubis elongate and slender. Posterior limbs very long. Femur shorter than tibia. Metatarsals long and hollow. First digit in pes complete; fifth metatarsal represented by short splint only.

* Besides the genera here mentioned, *Cœlurus*, *Compsognathus*, and *Hallopus* also possess this character.

Laosaurus.

Premaxillaries edentulous. Teeth small and irregular. Cervicals short and flat. Six vertebræ in sacrum; no peg and notch articulation. Sternum unossified. Fore limbs small. Limb and foot bones hollow. Prepubis very short and pointed; postpubis slender. Femur shorter than tibia. Metatarsals elongate. First digit in pes functional; fifth rudimentary.

Nanosaurus.

Teeth compressed and pointed, and in a single uniform row. Cervical and dorsal vertebræ short and biconcave. Sacral vertebræ three (?). Anterior caudals short. Ilium with very short, pointed front, and narrow posterior end. Fore limbs of moderate size. Limb bones and others very hollow. Femur curved and shorter than tibia. Fibula pointed below. Metatarsals very long and slender.

The genera thus defined contain all the known forms of the the typical *Ornithopoda* from the American Jurassic. They are, moreover, the earliest representatives of this group known in this country from osseous remains, as such fossils have not yet been found in the Triassic, where the oldest Dinosaurs occur. Some of the bird-like footprints in the Connecticut river sandstone may indeed have been made by Dinosaurs of this group, but there is no positive evidence on this point. The American Cretaceous forms of the typical *Ornithopoda*, so far as at present known, are all of large size, and highly specialized, and this appears to be true, also, of the Old World species.

In considering the relations of this well-marked group, here called the typical *Ornithopoda*, with the other two nearest allied suborders, the quadrupedal *Stegosauria* and *Ceratopsia*, it becomes evident, as previously shown by the writer, that all three belong in one great group, which may be regarded as an order. Although differing widely from each other in many notable features, they have a few characters in common, which are important enough to bind them together, and perhaps to indicate a common origin. The most significant of the characters shared by all is the predentary bone, which no other vertebrates possess. Another common character of importance, although sometimes nearly obsolete, is a postpubic bone which is present in all Birds, although in some recent forms it is rudimentary. A comparative series showing the relative development of the anterior and posterior branches of the pubis in six genera of American Predentate Dinosaurs is shown in Plate VII.

In recognition of the manifest relations of the three groups, *Ornithopoda* as here restricted, *Stegosauria*, and *Ceratopsia*, sharply defined as suborders, they should be placed together in a single order, which may appropriately be named the PREDENTATA. This order should be regarded as of equal rank with the *Sauropoda*, the *Theropoda*, and perhaps also the *Hallopoda*, as defined by the writer, the whole constituting the subclass known as the *Dinosauria*.

Yale University Museum, New Haven, Conn., June 15, 1894.

EXPLANATION OF PLATES.

PLATE IV.

FIGURE 1.—Skull of *Camptosaurus medius*, Marsh; seen from the left side.

FIGURE 2.—The same skull, with brain-cast in position; seen from above. Both figures are one-fourth natural size.

FIGURE 3.—Tenth upper tooth of *Camptosaurus medius*.

FIGURE 4.—Fifth lower tooth of same species. Both figures are natural size. *a*, outer view; *b*, posterior end view; *c*, inner view.

PLATE V.

FIGURE 1.—Pelvis of *Camptosaurus dispar*, Marsh; seen from the left. One-twelfth natural size.

FIGURE 2.—Left fore leg of same species. One-twelfth natural size.

FIGURE 3.—Left fore leg of *Camptosaurus nanus*, Marsh. One-fourth natural size.

FIGURE 4.—Left hind leg of *Laosaurus consors*, Marsh. One-sixth natural size.

PLATE VI.

FIGURE 1.—Lower tooth of *Laosaurus consors*. Natural size. *a*, outer view; *b*, posterior end view; *c*, inner view.

FIGURE 2.—Posterior sacral vertebræ of *Camptosaurus dispar*; showing peg and notch articulation; top view. One-fourth natural size.

FIGURE 3.—Dentary bone of *Nanosaurus agilis*, Marsh; seen from the left.

FIGURE 4.—Ilium of same individual; left side. Both figures are natural size.

FIGURE 5.—Left femur of *Nanosaurus rex*, Marsh. One-half natural size. *a*, front view; *b*, side view; *c*, back view; *d*, proximal end; *e*, distal end.

PLATE VII.

FIGURE 1.—Left pubis of *Laosaurus consors*; outer view. One-fourth natural size.

FIGURE 2.—The same bone of *Dryosaurus altus*, Marsh. One-eighth natural size.

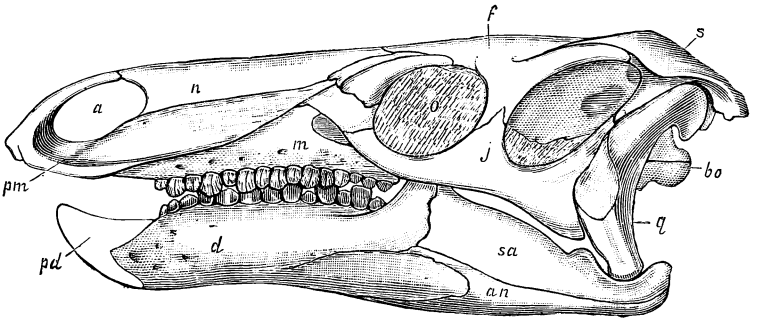
FIGURE 3.—The same of *Camptosaurus dispar*. One-twelfth natural size.

FIGURE 4.—The same of *Triceratops prorsus*, Marsh. One-twentieth natural size.

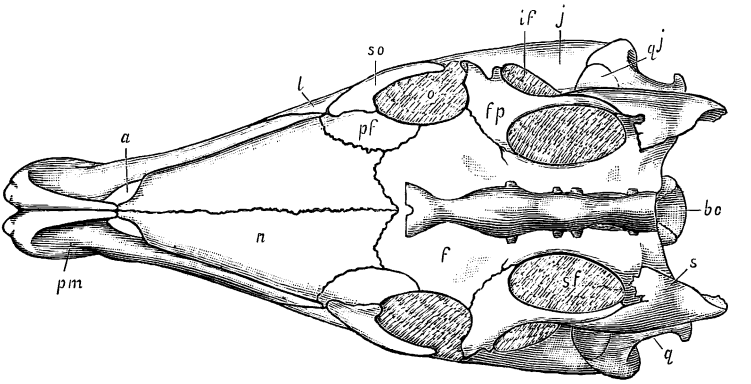
FIGURE 5.—The same of *Claosaurus annectens*, Marsh. One-sixteenth natural size.

FIGURE 6.—The same of *Stegosaurus ungulatus*, Marsh. One-twelfth natural size. *p*, prepubis; *p'*, postpubis.

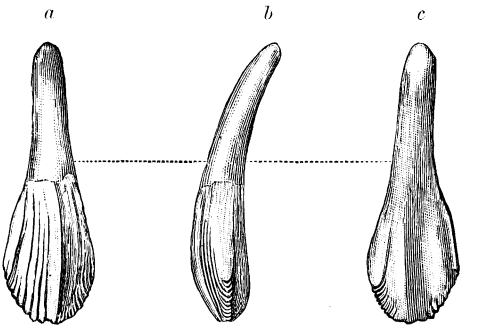
1.



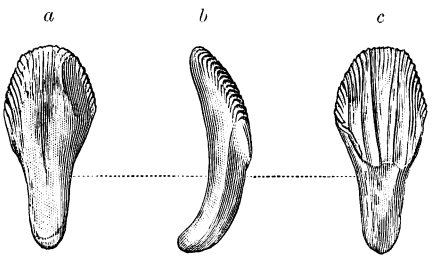
2.



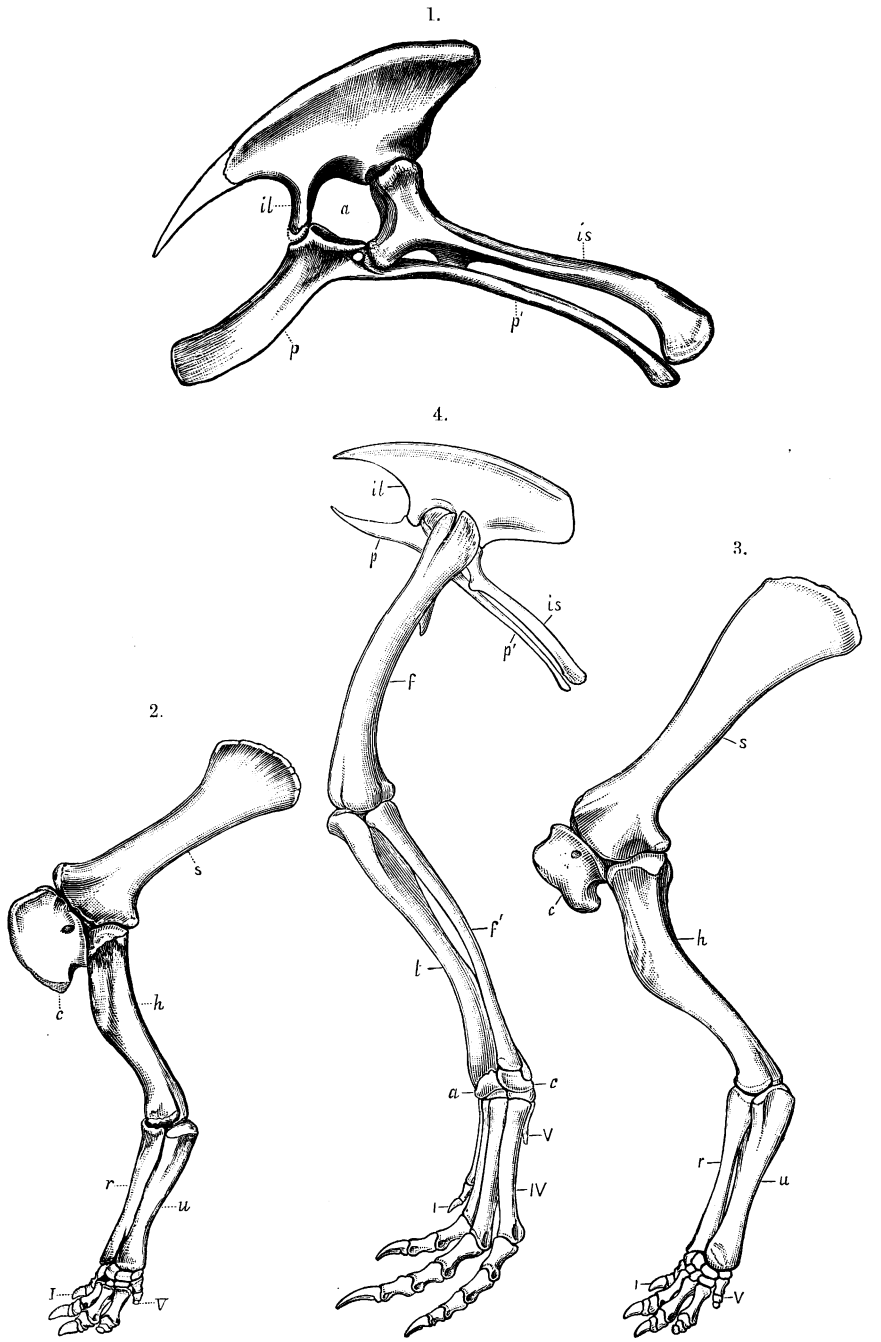
3.



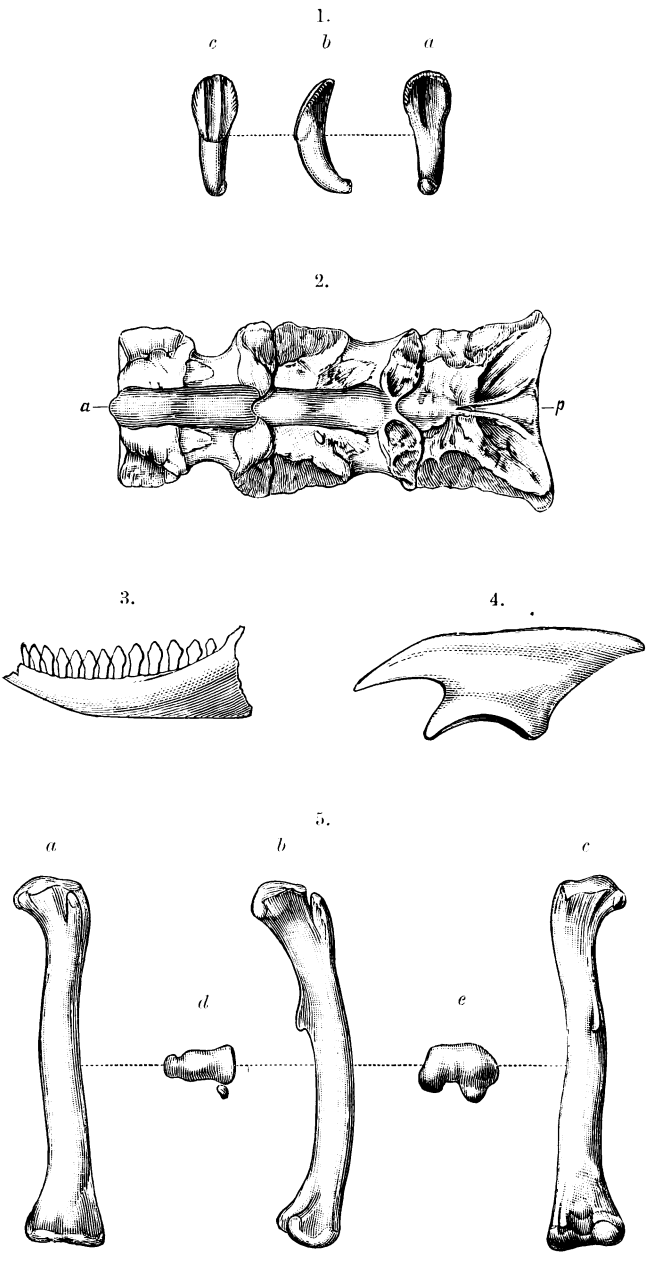
4.



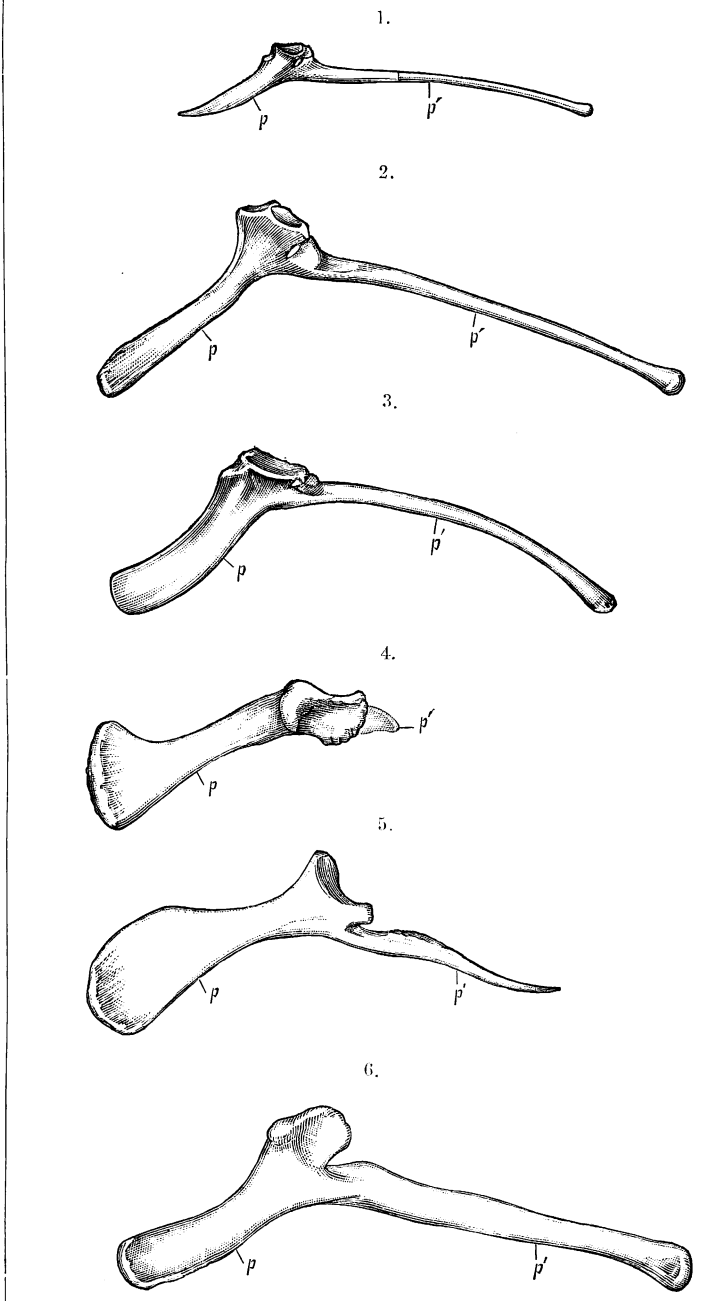
SKULL AND TEETH OF CAMPTOSAURUS MEDIUS. Marsh.



1–3. Camptosaurus. 4. Laosaurus.



1. Laosaurus. 2. Camptosaurus. 3–5. Nanosaurus.



PUBES OF PREDENTATE DINOSAURIA.