

An assessment of posture and gait in *Iguanodon bernissartensis*

BOULENGER, 1881

by Pierre BULTYNCK

Abstract

The original mounting of specimens of *Iguanodon bernissartensis* at the museum of the Royal Institute of Natural Sciences of Belgium in Brussels, in an upright bipedal position is widely considered to represent the only posture accepted by DOLLO, late last and early this century. However, DOLLO also recognized a bipedal running gait, in which the back and tail were held more horizontally, corresponding to that now generally accepted for most ornithopods. Quadrupedality, proposed by NORMAN (1980) as the predominant posture for adults of *I. bernissartensis*, was probably only adopted when stationary or moving slowly. A newly-mounted recent cast shows the species in the latter posture. "Semibipedal" (LEONARDI, 1987) seems to be the most appropriate term to describe the resting position and locomotion of this dinosaur.

Key-words: Dinosauria, *Iguanodon bernissartensis*, posture, gait.

Résumé

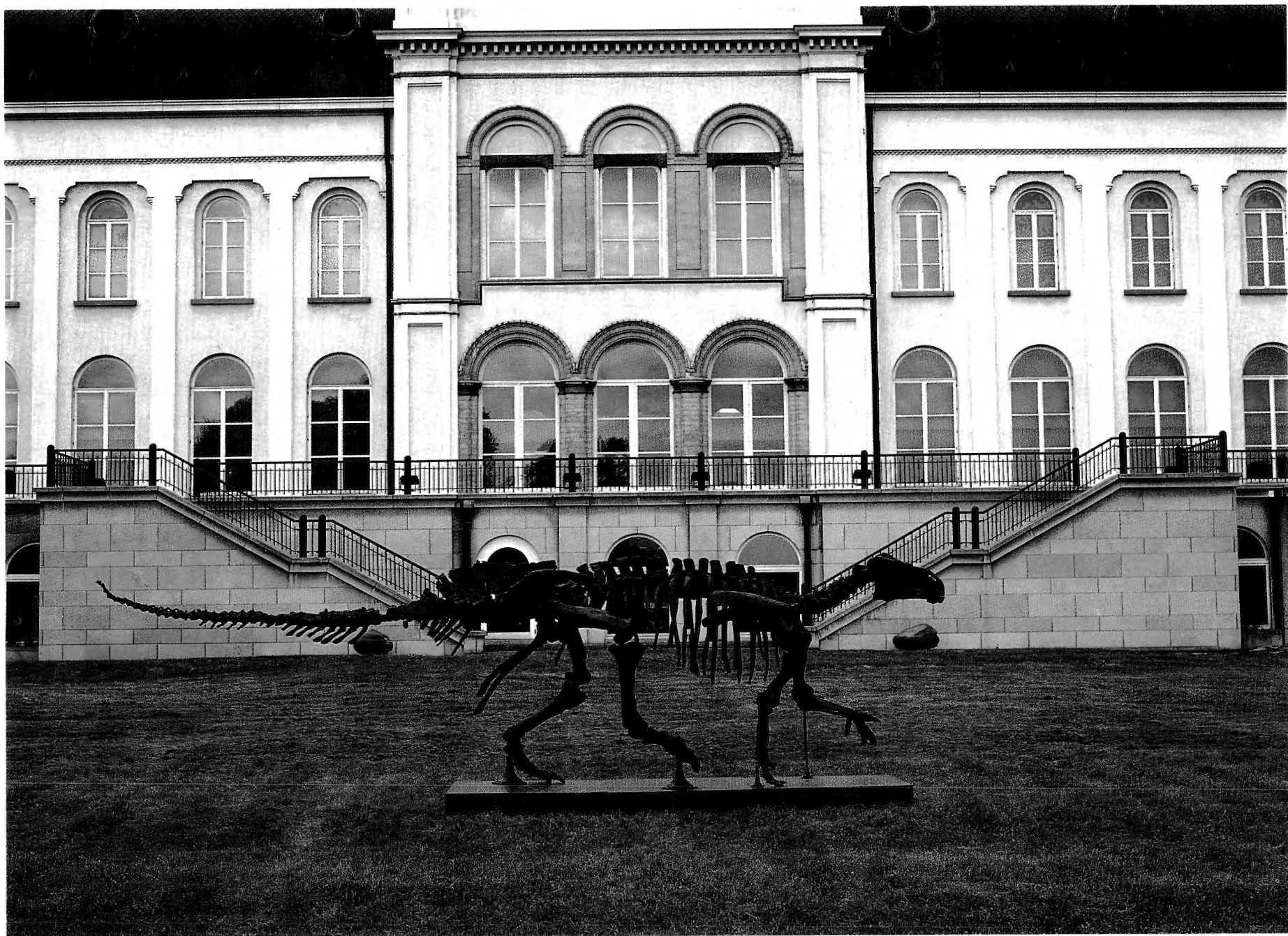
Au musée de l'Institut Royal des Sciences Naturelles de Belgique, les squelettes d'*Iguanodon bernissartensis* sont, dans leurs montages originaux, en position redressée et bipède. D'après l'opinion la plus répandue, DOLLO, à la fin du siècle dernier et au début de ce siècle, leur attribuait uniquement cette position. Toutefois, il admettait également une course bipède, le dos et la queue étant plus horizontaux comme dans les reconstitutions actuelles de la plupart des ornithopodes. La station quadrupède, prédominante chez les adultes d'*I. bernissartensis* selon NORMAN (1980), était sans doute adoptée uniquement lors du repos et d'une marche lente. Cette dernière est représentée dans un nouveau montage d'un moulage récent. Le terme "semi-bipède" (LEONARDI, 1987) semble le plus approprié pour caractériser le repos et la locomotion de ce dinosaure.

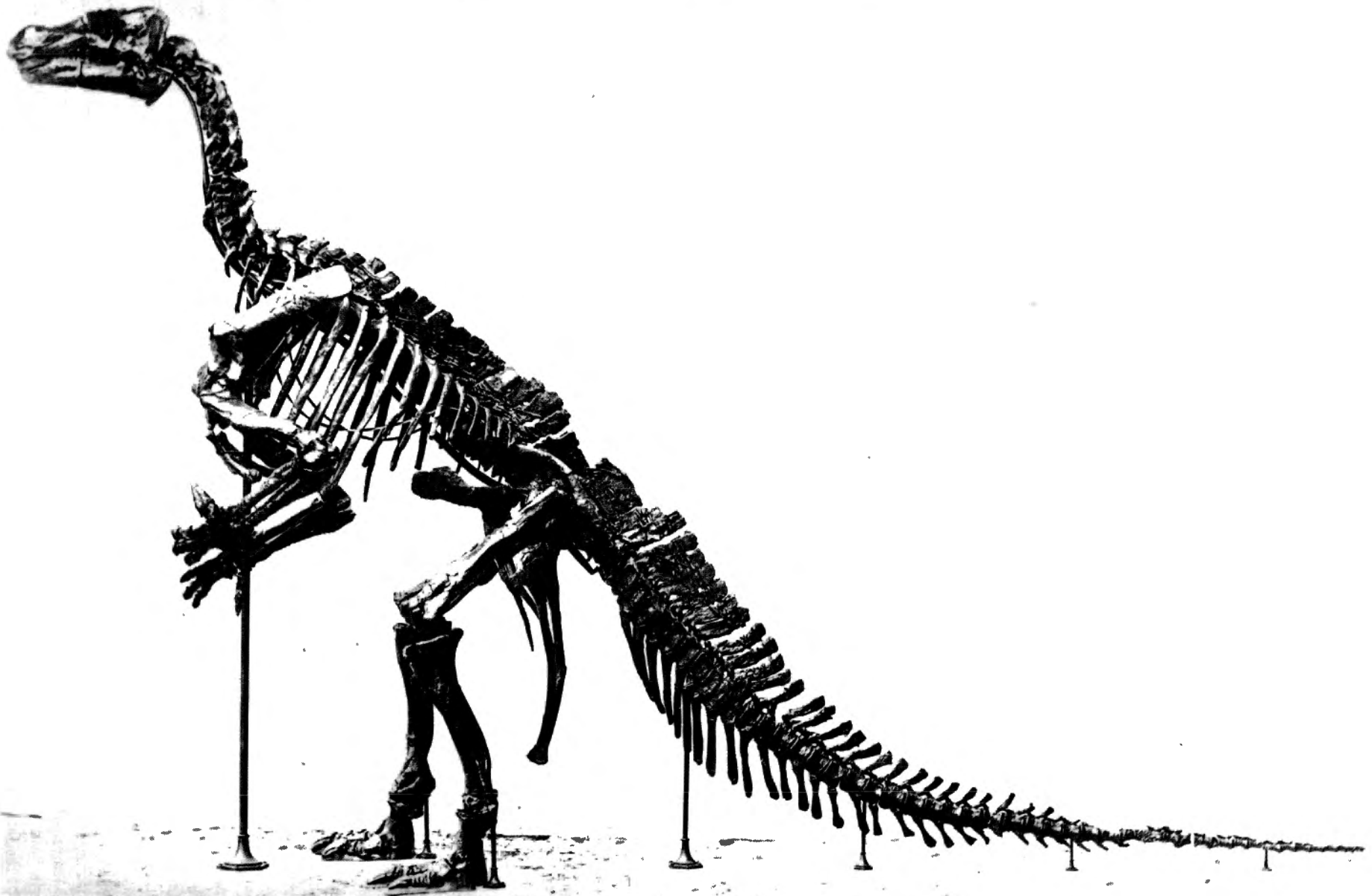
Mots-clés: Dinosauria, *Iguanodon bernissartensis*, positions.

A new cast of one of the original specimens of *I. bernissartensis* (Paratype IRScNB-R52; catalogue n° 1536) discovered at Bernissart (Belgium) in 1878 has been mounted in the museum in a quadrupedal, slowly walking position (Fig.1). The original skull, being incomplete, has been replaced by a cast of one of the best preserved (Paratype IRScNB-R55; catalogue n° 1535). Missing phalanges of the left manus have been completed using those from another specimen (IRScNB catalogue n°1558). The new mounting has been carried out

jointly by members of the technical staff of the Institute, J.-J. BLAIRVACQ, H. DE POTTER and L. TREVELS.

This new way of mounting conforms with the discussion by NORMAN (1980) of DOLLO's 1883 reconstruction of the skeleton of *I. bernissartensis* in an upright, bipedal position. The backbone is at an angle of 40°-50° to the horizontal and the tail rests on the ground so that the vertebral column is strongly curved between the sacrum and the distal part of the tail. In 1882-1883 DE PAUW, the chief museum preparator, assembled and mounted the first complete skeleton of *I. bernissartensis* (Holotype IRScNB-R51; catalogue n° 1534) in this position (Fig.2), following the instructions of DOLLO (1883), who stated clearly that it shows a bipedal walking gait, excluding quadrupedality. DOLLO was also aware of the fact that, due to deformation during fossilisation, the articulation between some skeletal elements is unsatisfactory. His reconstruction was based on the arrangement of pelvic girdle and hindlimbs comparable with that found in cursorial birds, especially in ratites, on the reduction of the forelimbs, on the different number of digits in manus and pes corresponding, to their different functions, and on tridactyl footprints reported from Wealden Beds in England and the Lower Cretaceous of northern Germany, interpreted by DOLLO as marks of the hindfeet of *I. mantelli*, VON MEYER, 1832. DOLLO, being the first to have complete *Iguanodon* skeletons to work with, provided more solid arguments for the upright bipedal or kangaroo-like posture of some ornithopods, advanced previously by LEIDY (1858) for *Hadrosaurus* and by HUXLEY (1870) and HULKE (1876) for *Iguanodon*. DOLLO (1905) recognized two additional bipedal postures for *Iguanodon* based on footprints and "tail marks" discovered in the Wealden Beds near Hastings (England) by DAWSON (unpublished): a running gait (= "course") and a stationary or at rest posture (= "temps de halte" ou "repos"). When *Iguanodon* was at rest, it could raise its trunk while the tail was used to support the body's weight; this was made possible by the presence of ossified tendons along the major part of the vertebral column. While running, the body was held for-



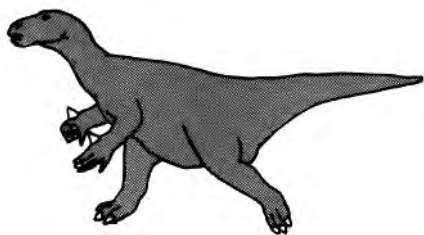


Posture and gait in *Iguanodon bernissartensis*

Fig. 1. — New cast of *Iguanodon bernissartensis* BOULENGER, 1881 (based on Paratype IRScNB/KBIN-R52) mounted in a quadrupedal, slowly walking position. In the background the “Convent Wing” of the Museum, built between 1857 and 1860. Photography by I. BACHY and T. HUBIN, © IRScNB/KBIN.

Fig. 2. — Holotype IRScNB-R51 of *Iguanodon bernissartensis* BOULENGER, 1881 mounted in 1882-1883 by DE PAUW according to DOLLO's first interpretation of the life posture of this species.

ward and the tail was raised at some distance from the ground. DOLLO illustrated the running gait by a picture from BEECHER (1902) showing the reconstruction of a skeleton of *Hadrosaurus annectens* (MARSH, 1892) in a running, bipedal posture, most of the vertebral column was mounted straight, at an angle of about 20° to the horizontal, with the tail being at more or less 1.20 m above the ground. That DOLLO accepted a similar posture for *Iguanodon* has been overlooked by all subsequent authors. HEILMANN (1926) figured two running iguanodonts in a posture clearly resembling that shown by BEECHER, but did not provide anatomical arguments for his restoration.

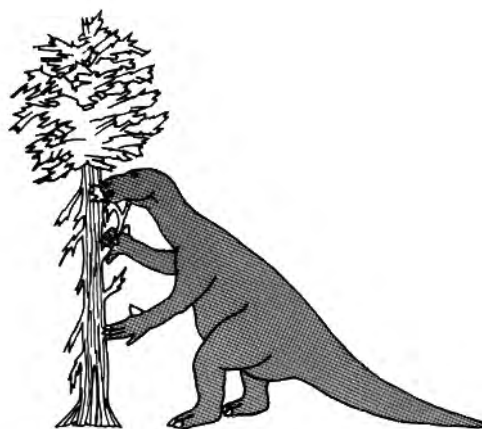


LULL & WRIGHT (1942) were the first to discuss anatomical observations in favor of a more or less horizontal posture of *Hadrosaurus* during bipedal running; their conclusions, too, were based on iguanodon material from Bernissart. The structure of the bones of the pelvic girdle shows that the ilium must have been held horizontal, limiting the erectness of the animal, “except possibly for very brief periods of time”. The ossified tendons along the dorsal and the proximal two-thirds of the caudal vertebrae gave a certain dorso-ventral rigidity and consequently this part of the vertebral column was held straight. This conclusion is supported by the position in which most naturally articulated skeletons of hadrosaurs as well as the Bernissart iguanodon skeletons were found. Figures 27 to 33 in LULL & WRIGHT (1942) represent hadrosaurs in both a bipedal and a quadrupedal posture. During normal progression on land, the total weight of the body was supported by the hindlimbs; the forelimbs were only used for “occasional resting, but neither for progression nor prehension”.

GALTON (1970) reassessed the conclusions of LULL & WRIGHT (1942). Hadrosaurs, and probably all ornithomorphs, were bipedal and the straight part of the vertebral column was probably held more or less horizontal while running. Bipedality is demonstrated by, amongst others, the length of the hindlimb in comparison to that of the trunk and forelimb, and the non-graviportal structure of the latter and the manus, more precisely the elonga-

ted radius, ulna and metacarpals. In these aspects hadrosaurs and *Iguanodon* differ from undoubtedly quadrupedal dinosaurs such as sauropods and ceratopsians, and from graviportal mammals such as *Mastodon*, *Elephas*, and *Loxodonta*.

LULL & WRIGHT (1942) and GALTON (1970) did not specifically discuss the mounting of *I. bernissartensis* in the museum of the IRScNB figured by DOLLO (1883, pl. 5). On the other hand, NORMAN (1980), revealed some specific errors in the same reconstruction of the skeleton. The curvature of the tail has been artificially exaggerated in order to produce the kangaroo-like posture. This anomaly disappears if the vertebrae of the trunk and the tail are placed in a more horizontal position, the latter forming a counterbalance to the rest of the body, with the pelvis functioning like the point of equilibrium between the two arms of a balance. The sacral vertebrae would be submitted to opposing tractional forces, explaining the progressive development of the vertebrae and ossified tendons on either side of the sacrum. Contrary to LULL & WRIGHT (1942) and GALTON (1970), NORMAN accepted that the structure of the pelvic girdle in *Iguanodon* and other ornithomorphs enabled these animals to raise the thorax easily so that the vertebral column was at an angle of 40° to 50° to the horizontal “when stationary and



feeding, or when moving slowly”. On the other hand he also believed that *I. bernissartensis* rested on its forelimbs, because of the strongly fused carpal bones, able to support its weight. The structure of the pectoral girdle, the ratios of the hind- and forelimb lengths, the structure of the latter and the presence of “flattened, hoof-like unguals” on the middle three digits of the hand suggest that the adult *I. bernissartensis* “spent most of its time in a quadrupedal posture”, though juveniles had a predominantly bipedal mode of life.

Using dimensions of leg bones and estimates of body mass, obtained from volumes of plastic models, ALEXANDER (1985) studied the posture and gait of some large dinosaurs, a.o. *I. bernissartensis*, and compared the measurements with those obtained from modern animals. Discussing NORMAN's (1980) drawing of *I. bernissartensis* in a quadrupedal walking gait and taking into account that the centre of mass would lie midway between the two hindlegs, ALEXANDER concluded that "the animal would have balanced on the hind feet alone and would not have needed support from the forefeet".

From the comparison of a trackway of *Iguanodon*, which according to NORMAN (1980) shows both fore and hind footprints, with those of large quadrupedal mammals, "it seems unlikely that the fore feet of *I. bernissartensis* supported more than a very small fraction of body weight, in normal walking". In an upright, bipedal position the body must have been supported partly by the tail.

NORMAN (1986) modified his earlier opinion on the quadrupedality of *I. bernissartensis*, "which appears to be on the threshold between being a conventionally bipedal ornithomimid and an obligate quadruped. However, these species have not yet developed the extremely massively constructed forelimb and the stout, frequently fused scapulo-coracoid, both of which seem to be characteristic of the obligate quadrupedal ornithomimids (the ceratopsians, stegosaurs and ankylosaurs)".

NORMAN & WEISHAMPEL (1990) clearly stated that iguanodonts were primarily bipedal and that, when running, the long tail was in a more or less horizontal position and counterbalanced the weight of the anterior part of the body, but they were more ambiguous when discussing the posture of *I. bernissartensis*. Several anatomical characteristics of the forelimbs and the pectoral girdle suggest a weight-bearing function in conjunction with quadrupedality. The latter gait was probably adopted by adults "while standing or during slow locomotion".

Conclusions

After the many arguments put forward for several years in favor of the more or less straight, rigid pose of the backbone and the tail in hadrosaurs and iguanodonts, I was surprised to see a recent reconstruction of an iguanodont in a quadrupedal pose, with its forward curling tail on the ground, in CZERKAS & OLSON (1987, p.i-iii).

It has been demonstrated by several authors that the part of the vertebral column with the ossified tendons was held more or less straight during life in most ornithomimids, but whether or no it was held more or less horizontal, as suggested by the structure of the ilium and the pelvis, is still a matter for discussion. The recurrent argument that most naturally articulated skeletons of hadrosaurs and iguanodonts in situ show the back and the tail in a horizontal position, may be considered as a

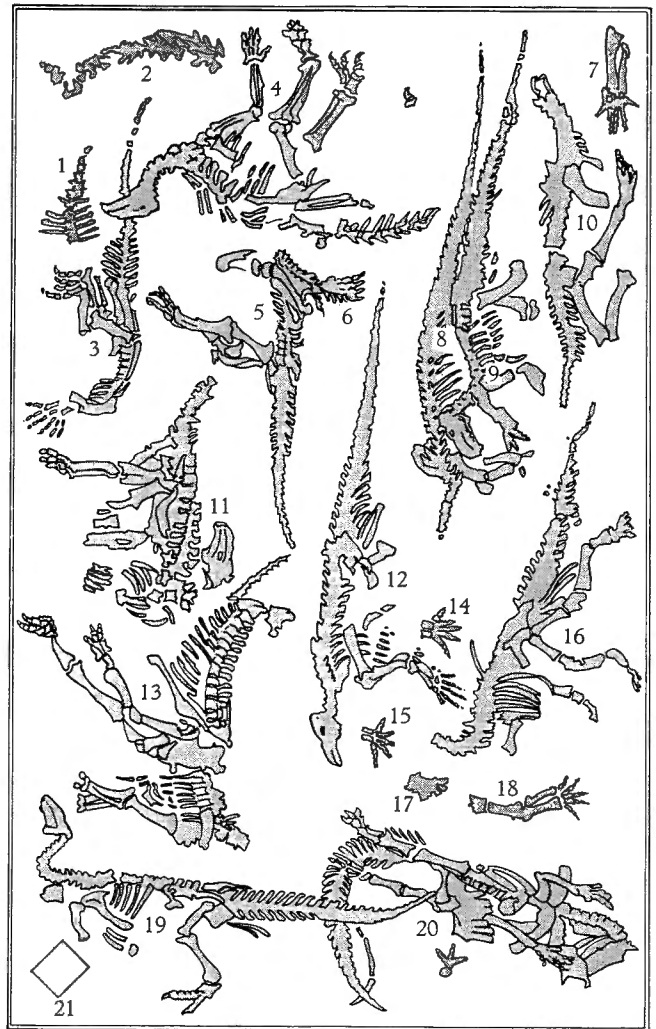


Fig. 3. — Plan of the cage with twenty *Iguanodon* specimens, complete and incomplete, each lying as found at Bernissart. The back and the tail of specimen n° 19 are more inclined than shown in the drawing.

selective observation in the case of the Bernissart material. In at least three specimens discovered at Bernissart the straight part of the vertebral column forms an angle of about 30° to 50° to the horizontal. Two are exhibited in this position at the museum, in the cage with iguanodonts in situ (n°s 16 and 19 on the plan, Fig.3; IRScNB catalogue n°s 1724 and 1726). The third (IRScNB catalogue n°1716) was the first skeleton to be discovered at Bernissart and a drawing by LAVALETTE (unpublished) shows it as it appeared when extracted from the matrix (Fig.4); this was also the first specimen to be reassembled, in 1878. The original photo of this mounting is well known from the literature (DE PAUW, 1902, pl.1; CASIER, 1960, pl.5, right part, but note that it is not the holotype as stated in the explanation of the plate; NORMAN, 1985, p.28; BULTYNCK, 1987 and 1989, fig.12; MARTIN & BULTYNCK, 1990, p.20). The mounting in life position was visibly influenced by the position in which the specimen was found. These observations sup-

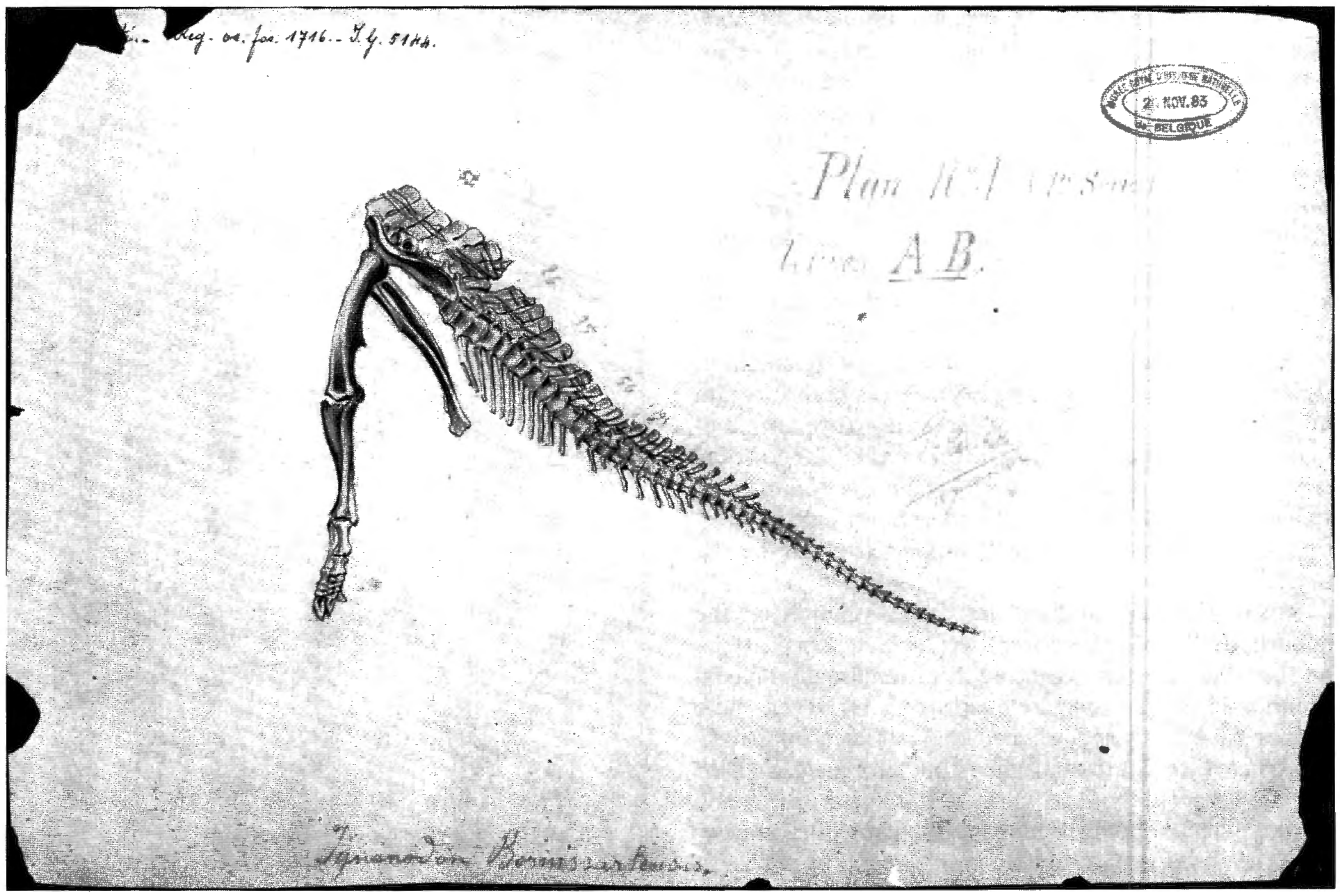


Fig. 4. — Unpublished drawing by LAVALETTE in 1883 of IRScNB catalogue n° 1716 of *Iguanodon bernissartensis* as discovered at Bernissart in 1878.

port NORMAN's (1980) conclusion that *I. bernissartensis* was able to raise the trunk, and the mounting of the skeletons in an erect posture, as shown in the museum, is considered to correspond to one of the various positions possible during life. The animals may have done so when feeding on high vegetation, when defending themselves with the sharp spur of the manus or when at rest. However, I agree with NORMAN's (1980) criticism that the curvature of the tail has been exaggerated in the holotype (DOLLO, 1883, pl.5; Fig.2) and in a second exhibited specimen (IRScNB catalogue n°1715). On the other hand, in several mounted, exhibited specimens (IRScNB catalogue n°s 1562, 1639, 1713 and 1714) the part of the vertebral column with ossified tendons is in a straight position.

Quadrupedality, first proposed by NORMAN (1980) as the predominant posture for adults of *I. bernissartensis*, was probably adopted only when stationary, moving



slowly, or browsing on low vegetation. This agrees with ALEXANDER's (1985) conclusions that the species did not need to use its fore feet for normal walking.

"Semibipedal" (LEONARDI, 1987) seems to be the most appropriate term to characterize the posture and gait of *I. bernissartensis*, meaning that "it was generally bipedal, but the forelimbs were sometimes placed on the ground during slow gait or when stationary".

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P. BULTYNCK
 Departement Paleontologie,
 Koninklijk Belgisch Instituut
 voor Natuurwetenschappen,
 Vautierstraat 29,
 B-1040 Brussel - België

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