本稿は，昨年11月11日に，京都で開かれた第77回化石研究会例会の折に配られた Dr. Beverly Halstead の講演の要旨です。演者の了解を得て全文を掲載します。演者は1984年10月～12月，学術振興会の交換教授として，京都大学の地鉱教室に来られていました。イギリスの Reading 大学で，専門は古生代における脊椎動物の硬組織の起源の研究です。（編 集 係）

DINOSAURS THEIR LIFE AND TIMES

- a discussion of their physiology and behaviour

by Beverly Halstead

The dinosaurs dominated life on Earth for a period of some 140 million years. From 200 to 64 million years ago dinosaurs ruled. Dinosaurs represented the very peak of the evolution of reptiles but there never was a genuine type of reptile named a dinosaur. The name meaning "terrible lizard" was first coined by richard Owen to designate a highly developed type of reptile that, unlike all living forms, had the stance and gait of a mammal. This condition in which the limbs were held vertically below the body and not sticking out sideways as in the sprawling posture of the reptiles (whose name comes from the Latin word repere, reptilis to crawl). This parasagittal gait, characteristic of birds and mammals, is also the hallmark of the dinosaurs, and was achieved independently by two major divisions of the archosaurian reptiles. Even today the living crocodiles show an approach to such an advanced method of locomotion, when they progress by means of the so-called "high walk".

Perhaps the first question to be asked is how and why did this improvement in limb posture come about. The ancestors of the dinosaurs, the very first archosaurs, from the early Triassic, seem to have been semiaquatic carnivores, filling the ecological niche currently occupied by the living crocodiles. The main organ for propelling themselves through the water was a thick muscular tail, flattened from side to side. However, the initial thrust or acceleration was provided by the limbs and in particular the hind limbs. Again as with crocodiles - this led to the hind limbs being longer and stronger than the forelimbs and such limb disparity is again characteristic of most dinosaurs. The power of the initial thrust depends on the amount of the limb that is actually moved - with a normal reptile this is only from the knee or elbow joint, so that only the distal part of the limb is effectively used. With movement from the glenoid and acetabulum the entire length of the limb can be used to generate thrust. Such developments seems to have arisen primarily as adaptations for a semiaquatic mode of life. With the emergence of such animals from the water, the effective stride would be much longer than with any animal with a sprawling gait and, by the same token, would be capable of a much greater speed. There would, however, be one major problem: the limb disparity would mean that the hind limbs were capable of producing a greater maximum speed than the forelimbs. The solution to this problem was simply that the forelimbs were lifted out of the way and a bipedal posture and gait achieved. The heavy muscular tail acted as a conterbalance to the trunk and head.

The first dinosaurs were bipedal carnivores between 1 m and 2 m in length. There were the theropods, lightly built coelurosaurs and the ,ore heavily built carnosaurs, both classed in the order Saurischia, on the grounds of the structure of the pelvic girdle. From the lightly built coelurosaurs, there evolved the prosauropods which marked an important evolutionary stage, in that they increased considerably in size; some of the late Triassic prosauropods reaching 12 m in length. This lineage, which culminated in the brontosaurs, marked a major evolutionary development in the saurischians, in that there was now established a herbivorous lineage, which meant that a completely dinosaurian terrestrial food web could become established.

At much the same time, there appeared a number of small bipedal herbivores again about 1 m in length but from an unknown ancestry and with the pelvic girdle with the pubis aligned posteriorly and parallel to the ischium. As this appears somewhat birdlike this group was designated the bird-hipped dinosaurs or Ornithischia. A number of primitively quadrupedal ornithischians with a well developed bony armour are known from the earliest Jurassic rocks and these seems to represent a primitive structural stage. From these armoured forms there evolved the later squat ankylosaurs and the spiked and plated stegosaurs. The major evolutionary development, however, was among the bipedal forms that evolved in two directions: a line that increased in size culminating in the hadrosaurs or duckbilled dinosaurs, the largest being the Chinese Shantungosaurus, and a line that remained relatively small, but nevertheless, gave rise to groups, which themselves evolved into large forms such as the pachycephalosaurs or bone-heads and the ceratopians such as the familiar Triceratops.

Perhaps the most notable features of the dinosaurs were their large size as well as their success on the Earth for a very long period of time. These two features are not unrelated. One of the reasons for the success of the higher vertebrates is their ability to maintain a constant internal temperature, that is not subject to the diurnal fluctuations of the environment. The dinosaurs achieved this in a quite unique way: they became homeothermic or "warmblooded" simply by virtue of their size, they became inertial or ectothermic homeotherms. The mere fact of their surface to volume ratio ensured a constant internal temperature. One of the major problems encountered by large animals is the need to prevent overheating. Although the interior may be of a relatively constant temperature, the skin and more importantly the brain could be subject to severe diurnal changes. Many dinosaur skulls had exceptionally large evaporative surfaces of the nasal passages, seen in their most extreme among the hadrosaurs, as well as large venous sinuses which would have served as heat sinks.

Birds and mammals have achieved the same constancy of internal environment by means of having a high metabolic rate and they are termed endotherms, and they possess a variety of adaptations for controlling the temperature: feathers and fur, shivering, sweating etc.. Such mechanisms require a high metabolic rate and the food requirements are similary enormous, for example a crocodile requires aproximately one tenth of the food a comparably sized mammal needs. The food requirements of the large 100 tonne dinosaurs would be beyond the capacity of such animals, if they were endotherms. The tempo of life of ectotherms and endotnerms are easily distinguished. Some years ago, it was suggested from a study of the proportions of the limbs, that the speed of the large dinosaurs was similar to that of living elephants and rhinoceroses. It is, however, possible to determine accurately from their footprints, the exact speed at which dinosaurs moved. This cannot establish the maximum speed, although the recent study of a dinosaur stampede from Australia probably approached this. Nevertheless, the strength of bone can be calculated and this establishes the natural safety factor of the skeleton and this in turn determines the maximum speed above which the skeleton will fail. From all this it transpires, that the giant sauropods, brontosaurs and their allies, walked at about 4kph, the large carnosaurs normally about 5kph and when moving at maximum speed at some 8kph. In contrast, the later lightly built coelurosaurs were capable of bursts of speed up to 20kph. On the evidence of footprints, it seems that the dinosaurs were ectothermic in their abilities and energy requirements.

Taking the energy budget on a wider scale, it is possible to show that with present day endothermic animals, mammals and birds, the energy consumption requirements are such that in terms of biomass a population of herbivores can suport only some 3 % of carnivores; with an ectothermal population this is nearer 30 %. To date only a single study has been done on this aspect of dinosaur ecological energetics, from an Upper Cretaceous horizon in Alberta, Canada, and it was evident that the proportion of carnivores present demonstrated that the entire ecosystem was an ectothermic one.

It is possible to calculate a great deal regarding the functioning of dinosaurs and to extrapolate from this, to outline some of the major features of their internal physiology. Fortunately, it is possible to go further than this and to establish a number of aspects of the behaviour of dinosaurs. Again the evidence of footprints is crucial. Among the more striking facts to have emerged in recent years is that many groups of herbivorous dinosaur lived in herds. This was true of the giant sauropods as well as the latest and most advanced the duckbilled dinosaurs. Furthermore, the carnivorous dinosaurs similarly hunted in small packs. The social nature of dinosaur communities throws a new light on our understanding of the nature of the life of the dinosaurs. Perhaps one of the more remarkable aspects of the herding nature of the herbivorous dinosaurs is the realization that such herds were structured, in that the subadult individuals walked in the middle of the group and the larger and presumably more powerful adults kept to the periphery. One can only assume that this was to provide protection for the more vulnerable yonger members of the herd.

One of the more surprising facts to have emerged is that the large carnivorous such as Tyrannosaurus could not have been active hunters. They were very slow moving and were fundamentally scavengers. One brontosaur corpse would have provided sufficient sustenance for a tyrannosaur for about three years; one large carnosaur needed about the equivalent of one duckbilled dinosaur per year for its survival.

The advanced coelurosaurs, in particular the clawed-dinosaurs or deinonychosaurs and the ostrich-dinosaurs, were notable for the relatively large size of their brains. Their brain-body ratio gave them brains some 6 times better than crocodiles, some clearly had binocular vision and they were agile and speedy and with an excellent sence of balance. It was the development of the cerebellum, the part of the brain concerned with muscular coordination and balance, that produced a type of brain comparable to that of living flightless birds. These carnivorous dinosaurs were well outside the normal range of ability considered appropriate for a reptile - they were undoubtedly the most advanced reptiles so far recognised.

The contemporary herbivorous dinosaurs, similarly possessed an array of characters not usually associated with typical reptiles. The structure of the skull suggests that they possessed muscular cheeks exactly as in mammals, the dentition especially that of the duckbilled dinosaurs, with some 2000 teeth in their jaws, provided strong evidence of these dinosaurs being able to process tough plant material by chewing. Furthermore, these dinosaurs possessed a secondary palate, so that they could process food in their mouth and still continue to breathe, again a feature normally considered to be characteristic of mammals. By far the most unexpected information to have come to light during the past few years is data which implied a much higher level of behavioural patterns that was ever previously imagined with regard to the dinosaurs. It was suggested that the only reasonable interpretation of the thickening on the summits of the skulls, of the pachycephalosaurs, was that they served as battering rams and were used in trials of strength among individuals of the same species. Subsequently detailed analysis of the head ornament of the ceratopians led to the same conclusions. In fact, the healed lesions or wounds on the bony frills of Triceratops were made by the horns of fellow Triceratops. There thus emerged indirect evidence of the social structure of dinosaur herds. The existence of dinosaur nurseries and major nesting sites where the adults clearly protected the nests and moreover cared for their young, during the early stages of their development, still further extended our knowledge of dinosaur behaviour patterns.

All these modern studies of dinosaurs have lead to a complete re-evaluation of the lives of the dinosaurs. The pattern of inferred behaviour and many aspects of their physiology now present a picture of an exceedingly advanced group of reptiles, which have much more in common with the behavioural pattern of birds and mammals than was previously imagined. However, it is not quite as simple as this. Most zoologists inhabit temperate climates and their views of reptiles are generally coloured by their experience of the lives of reptiles in temperate regions and they contrast dramatically with the behaviour of mammals and birds. In the tropics, in marked contrast, reptiles have a much more interesting repertoire of behaviour and in this respect are not dissimilar to what we now infer about the life of dinosaurs.

The life and times of the dinosaurs were certainly varied but we should be happy that they are no longer here because it was not until they quit the stage that modern mammals and eventually ourselves were able to emerge to rule the Earth.