Diet of prosauropod dinosaurs from the late Triassic and early Jurassic

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Prosauropods were not scavenger-predators, rather they were the dominant large terrestrial herbivores during the late Triassic and early Jurassic. The herbivorous adaptations of anchisaurids include spatulate teeth with anteroposteriorly expanded crowns (maximum width apical to base of crown) which are obliquely inclined with respect to the jaws so each slightly overlaps the tooth behind it, and which have coarse marginal serrations at 45° to the cutting edges. Most of the teeth of yunnanosaurids lack serrations and resemble those of sauropod dinosaurs in form and in having self-sharpening surfaces, formed by tooth-to-tooth wear, which increased the efficiency of dealing with more resistant plant material. Anchisaurids and yunnanosaurids had a ventrally set jaw articulation; the teeth and skull of melanorosaurids are unknown. All prosauropods were high browsers that extended the feeding range with a long neck and tripodal feeding (long hindlimbs and stout tail for support). They used herding and the enormous claw on the pollex for defense, and probably had a muscular gastric mill with stones that was used for grinding the food. They account for at least 95% of the biomass in their respective faunas. ☐ *Saurischia, Prosauropoda, Triassic, Jurassic, functional anatomy, diet.*

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Prosauropod dinosaurs (Fig. 1A, B) were the dominant medium- to large-sized dinosaurs of the Late Triassic, with maximum lengths as adults of about 2.5 m for *Anchisaurus* (Fig. 1E) up to about 10 m for *Riojasaurus,* with an 'average' length of about 6 m (Fig. 1A, B). Prosauropods have been found on all continents except Antarctica and terrestrial faunas rich in prosauropods are known from Europe (Huene 1908, 1932), Asia (Young 1951), South America (Bonaparte 1971, 1978a) and Africa (Haughton 1924; Charig *et al.* 1965; van Heerden 1979; Cooper 1981). In addition, prosauropods have been described from North America (Galton 1976) and Australia (Galton & Cluver 1976). The dominant position of prosauropods has been further emphasized by two developments during the last twenty years. Firstly, Walker (1964) and Charig *et al.* (1965) pointed out that most of the postcranial material thought to represent Triassic members of the theropod infraorder Carnosauria is actually prosauropod. Secondly, Olsen & Galton (1977) showed that the age of the prosauropods from the upper part of the Newark Supergroup of eastern United States and of the Glen Canyon Group of Arizona, U.S.A. was Lower Jurassic (Pliensbachian) rather than Upper Triassic (Fig. 2). Consequently, prosauropods did not become extinct at the end of the Triassic. Other 'Triassic' prosauropods that are now regarded as Early Jurassic in age (Hettangian to Pliensbachian) include those from the Upper Stormberg fauna of South Africa and the upper Lower Lufeng Series of China (Fig. 2, see Olsen & Galton 1977, 1984).

I provisionally recognize three families of prosauropods: the Anchisauridae (= Plateosauridae, Thecodontosauridae, Mussauridae Bonaparte & Vince 1979) for most prosauropods (Fig. 1B, E) following Galton (1971) and Cooper (1981); the Yunnanosauridae Young 1942 for *Yunnanosaurus* Young 1942, the teeth of which are unique among prosauropods in lacking denticles and possessing occlusal wear surfaces (see p. 117); and the Melanorosauridae for the large graviportal forms (*Melanorosaurus, Riojasaurus* Fig. 1A) following van Heerden (1977, but not 1979) and Cooper (1980). I excluded the carnivorous Herrerasauridae and Staurikosauridae from the Prosauropoda (Galton 1977) and now follow Bonaparte (1978a) and include them in the Theropoda.

Prosauropods are usually considered to represent the first radiation of dinosaurs adapted for eating plants (Colbert 1962; Charig *et al.* 1965; Romer 1966; Bakker 1975; Galton 1976; Gow 1978; Bonaparte 1982; Benton 1983), but relatively little has been said concerning why pro-

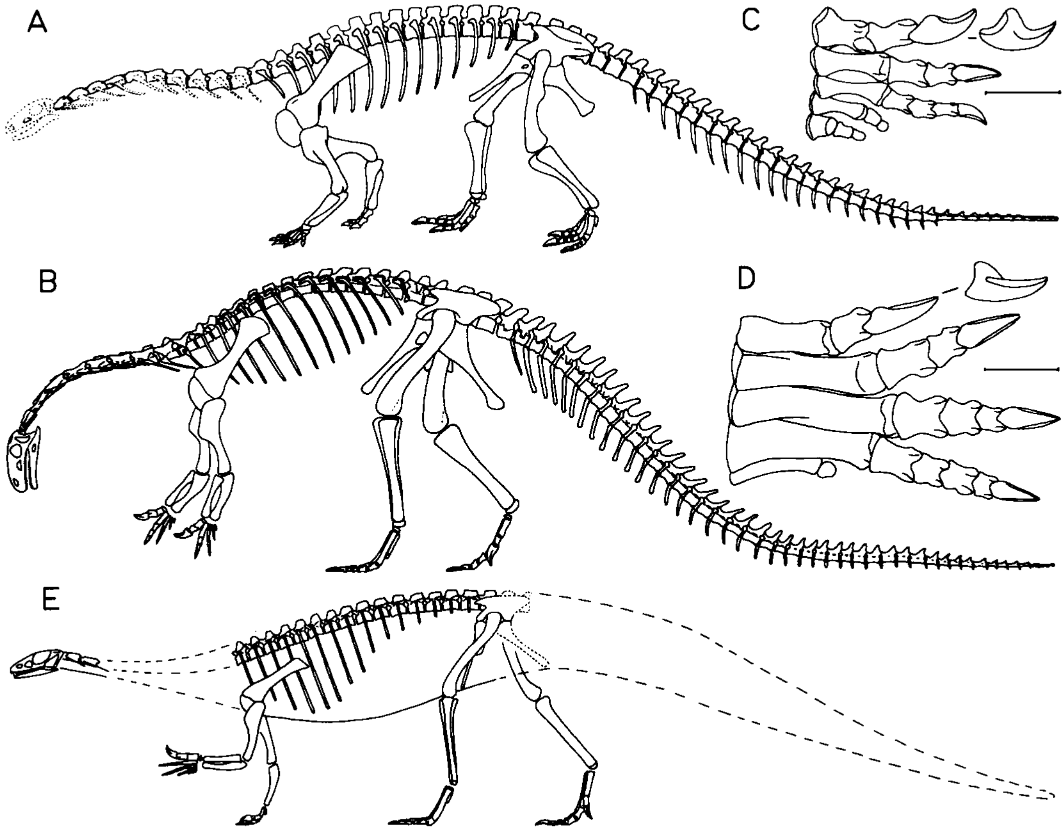

Fig. 1. Skeletal reconstructions of prosauropod dinosaurs. □ A. Melanorosaurid *Riojasaurus* from the Upper Triassic of Argentina, from Bonaparte (1971), total body length of this specimen about 6 m, maximum up to about 10 m. □ B. Anchisaurid *Plateosaurus* from the Upper Triassic of West Germany, based on AMNH 6810 and modified from Galton (1971), total body length of this specimen about 6.5 m, maximum up to about 9 m. □ C. Left manus of *Plateosaurus*, SMNS 13200. □ D. Left pes of *Plateosaurus*, SMNS 13200 at same reduction as C. □ E. Anchisaurid *Anchisaurus* from the Lower Jurassic of Connecticut, U.S.A., YPM 1883 and modified from Galton (1976), estimated total body length about 2.5 m. Scale lines represent 10 cm (C, D).

sauropods are regarded as herbivores. However, they have not always been so regarded. Lull (1953: 118) noted that *Anchisaurus* from the Connecticut Valley, U.S.A. preyed upon smaller vertebrates 'as the powerful grasping claws and well developed teeth imply'. Swinton (1970: 162) noted that the teeth of *Plateosaurus* 'were ideally suited for the capture of slippery prey, and associated with clawed fingers and toes' and large size, he visualized *Plateosaurus* as 'an enemy of unusual power and terrifying aspect'. Cooper (1981) discussed the diet of anchisaurid prosauropods, with particular reference to *Massospondylus* from southern Africa, citing several characters of anchisaurids which show that they should be regarded as carnivores or carrion feeders rather than as herbivores. In addition, Seeley (1894) included as part of the type of *Euskelosaurus browni* from southern Africa, a large maxilla with theropod-like teeth of carnivorous aspect. This referral is accepted by Charig *et al.* (1965) and Cooper (1980), who both note that such teeth are ubiquitously associated with the postcranial remains of melanorosaurid prosauropods from southern Africa.

The purpose of this paper is to provide a detailed discussion of the various lines of evidence concerning the diet of prosauropod dinosaurs. A preliminary discussion of the diet of prosauropods is given by Galton (1984). Institutions mentioned in this paper are abbreviated as follows: AMNH – American Museum of Natural History, New York; BCM – Bristol City Museum, England; BMNH – British Museum (Natural Histo-

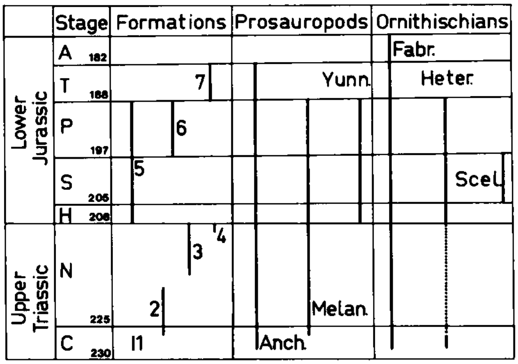

Fig. 2. Stratigraphic correlations of the Upper Triassic and Lower Jurassic beds containing prosauropods and the stratigraphic ranges for the families of prosauropod and early ornithischian dinosaurs, data mostly from Olsen & Galton (1977, 1984) and Olsen *et al.* (1982). European standard stages with age of boundaries in m.y. (from Armstrong 1982) in left hand column: A, Aalenian; C, Carnian; H, Hettangian; N, Norian; P, Pliensbachian; S. Sinemurian; T. Toarcian. □ 1–8, estimated ages for prosauropod bearing rocks (with genera involved): 1, Argana Formation (T6) of Argana, Atlas Mountains, Morocco (*Azandohsaurus*); 2, Fossiliferous lower level of Lower Stormberg Series - lower Elliot Formation - of South Africa (*Euskelosaurus, Melanorosaurus*); 3, upper Los Colorados and El Tranquilo formations of Argentina [*Coloradia* (? = *Mussaurus*), *Riojasaurus*]; Stubensandstein (*Sellosaurus*) plus Knollenmergel and Rhät (*Plateosaurus*) of West Germany; 4, Rhaetian beds of England [*Thecodontosaurus*, melanorosaurid postcrania described by Seeley (1898) and Huene (1908)]; 5, Upper Lower Lufeng Series of Yunnan, China [*Lufengosaurus, Yunnanosaurus*, ?melanorosaurid postcrania originally referred to *Sinosaurus* by Young (1948, 1951)]; Upper Stormberg Series - upper Elliot and Clarens formations of South Africa (*Massospondylus*); 6, Kayenta Formation of Arizona, U.S.A. (*Massospondylus*); 7, Portland Formation of Connecticut and Navajo Sandstone of Arizona, U.S.A. (*Ammosaurus, Anchisaurus*). Families of prosauropods with earliest and latest genera: Anch., Anchisauridae, earliest - *Azandohsaurus, Euskelosaurus*, latest - *Ammosaurus, Anchisaurus*; Melan., Melanorosauridae, earliest - *Melanorosaurus*, latest - ? postcrania originally referred to *Sinosaurus* by Young (1948, 1951); Yunn, Yunnanosauridae, only *Yunnanosaurus*. Families of early ornithischians with earliest and latest records: Fabr., Fabrosauridae (Fig. 4N), earliest - unnamed teeth from Morocco (Figs. 5N, O, 7X, Y), latest - undescribed teeth from Upper Cretaceous of Montana (Galton in prep.); Heter., Heterodontosauridae, earliest - maybe *Pisanosaurus* Casamiquela 1967 from Ischigualasto Formation of Argentina, referred to this family by Bonaparte (1976) but to the Hypsilophodontidae by Galton (1972), latest - *Heterodontosaurus* (Fig. 4O) and other genera (Hopson 1980) from Upper Stormberg Series of South Africa and Lesotho; Scel., Scelidosauridae, *Scelidosaurus* (Fig. 4P) from the Lower Liassic of England. This family does not include *Sarcolestes* from the Middle Jurassic of England (Galton 1983).

ry), London; FMNH - S.V.D. Catholic University of Peking, China housed at Field Museum of Natural History, Chicago; IGS - Geological Society Collection, housed at Institute of Geological Sciences, London; MGSP - Museum of Geological Survey of Portugal, Lisbon; MNHN - Muséum National d'Histoire Naturelle, Paris; MSF - Museum Saurierkommission Frick, Townwerke Keller AG. Frick, Switzerland; SMNS - Staatliches Museum für Naturkunde in Stuttgart, West Germany; UT - Museum für Geologie und Paläontologie, Universität Tübingen, West Germany; YPM - Peabody Museum of Natural History, Yale University, New Haven, CT., U.S.A.

Diet of anchisaurid prosauropods

Supposed carnivorous adaptations

Presence of carnivorous teeth. – Isolated teeth of carnivorous aspect i.e. with a transversely compressed and slightly recurved crown that tapers continually to a point with fine serrations set perpendicular to the anterior and posterior edges, have been referred to the Anchisauridae (Figs. 3A, 5T–V). These include a couple of the earliest records of prosauropods: the holotype of *Thecodontosaurus subcylindrodon* Huene (1908, Fig. 268) from the Schilfsandstein (Lower Keuper, Carnian) of Stuttgart, West Germany and a referred tooth of *T. antiquus* (Fig. 3A) from the Bromsgrove Sandstone (Lower Ladinian) of Warwick, England [only specimen accepted as *Thecodontosaurus antiquus* by Walker (1969) of those from the Lower Keuper which were referred to this species by Huene (1908)]; plus the holotypes of *Palaeosaurus cylindrodon* Riley & Stutchbury, 1836 (see Riley & Stutchbury 1840, Pl. 29: 4) from the Rhaetic (Upper Triassic) of Bristol, England (family Palaeosauridae included in the Thecodontosauridae [= Anchisauridae] by Charig *et al.* 1965) and three Rhaetic species of *Plateosaurus*: *P. cloacinus* (Quenstedt) (see Huene 1908, Fig. 274), *P. elizae* (Sauvage) (see Huene 1908, Fig. 278) and *P. obtusus* (Henry) (see Huene 1908, Fig. 276). I agree with Charig *et al.* (1965) that any taxon based on an isolated tooth from the late Middle or Upper Triassic should be regarded as *incertae sedis* because such teeth could have come from any large carnivorous group present at that time. These include rauisuchid, ornithosuchid and par-

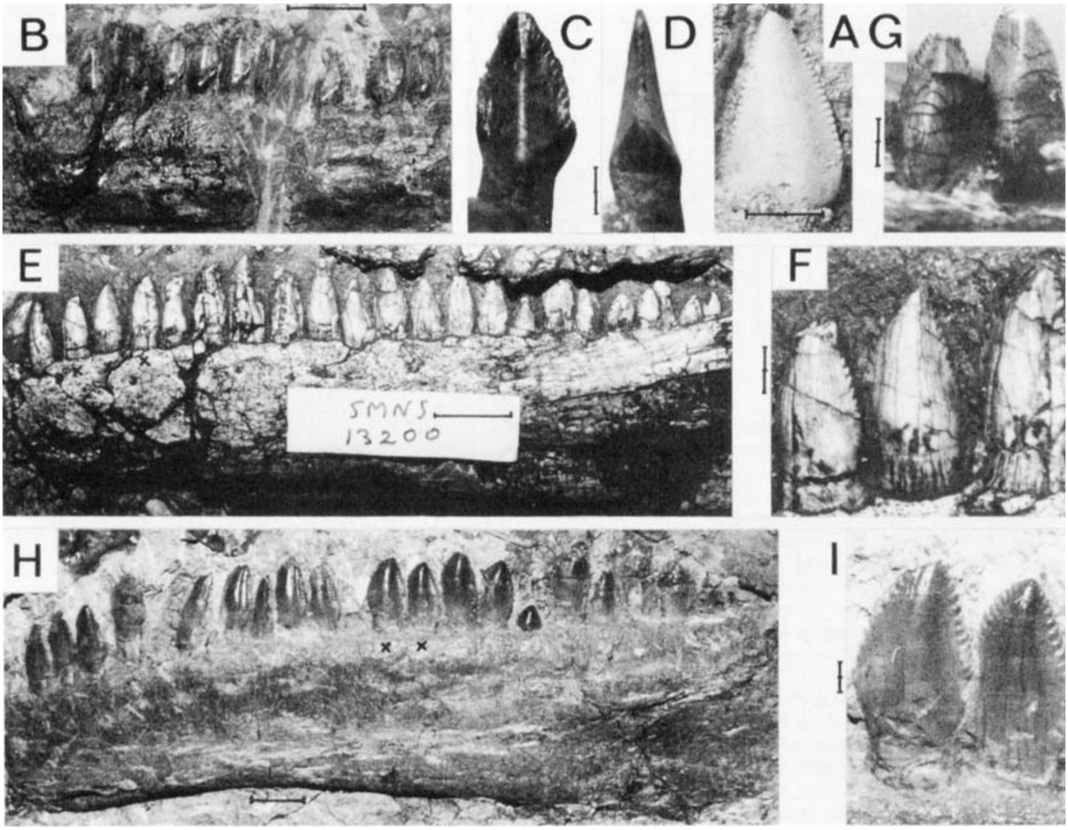

Fig. 3. Left dentaries (B, E, H) and teeth in lateral view of theropod (A) and anchisaurid prosauropods from the Middle (A) and Upper Triassic. □ A. Isolated tooth from the Bromsgrove Sandstone of Warwick, IGS GSC-4873, incorrectly referred to *Thecodontosaurus antiquus* by Huene (1908) and Walker (1969). □ B–D. *Azandohsaurus laaroussi* Dutuit 1972 from the Atlas Mountains, Morocco (see Fig. 5A, B). □ B. Holotype MNHN MTD-XVI.1. □ C, D. Referred isolated tooth MNHN ALM-508 in lateral or medial (C) and anterior or posterior views (D). □ E–G. *Sellosaurus gracilis* from the Stubensandstein of Nordwürttemberg, West Germany. □ E, F. SMNS 12685. □ G. Lateral view of two teeth in left maxilla of SMNS 4388, the holotype of *Thecodontosaurus hermannianus* Huene 1908 (see Fig. 5E). □ H, I. *Plateosaurus engelhardti* from Frick, Switzerland, MSF 2. Scales represent 2 mm (A, ×5; C, D, F, G, ×3; I ×2) and 10 mm (B, E, ×1; H, ×0.66).

asuchian thecodontians plus herrerasaurid, staurikosaurid and podokesaurid theropod dinosaurs. Consequently, the referral of the isolated teeth cited above with a carnivorous aspect to the Anchisauridae is not accepted, and they are best regarded as belonging to carnivorous archosaurs of uncertain affinities.

Cooper (1980) described a rather large, bilaterally compressed tooth, biconvex in section with finely serrated edges, that was found associated with a specimen of *Euskelosaurus* from the Mpandi Formation (Norian, Upper Triassic) of Zimbabwe, southern Africa. He cited Charig *et al.* (1965) concerning the almost ubiquitous association of carnivorous teeth of this type with melanorosaurid bones and noted that one from the lower Elliot (Norian) of Lesotho (formerly Basutoland) was named *Basutudon ferox* Huene 1932 (Fig. 5T). However, Raath (*in* Cooper 1980: 6) questioned whether these were genuine or fortuitous associations because 'such teeth frequently lack roots and may have been lost during predation'. This appears to be the case for the carnivorous teeth found close to the pelvic girdle of *Vulcanodon karibaensis* Raath 1972, a supposed melanorosaurid from the Lower Jurassic of Zimbabwe that Cruickshank (1975) referred to the Sauropoda. Ostrom (1969: 144) records that isolated teeth (but no other remains) of the carnivorous theropod *Deinonychus* have been

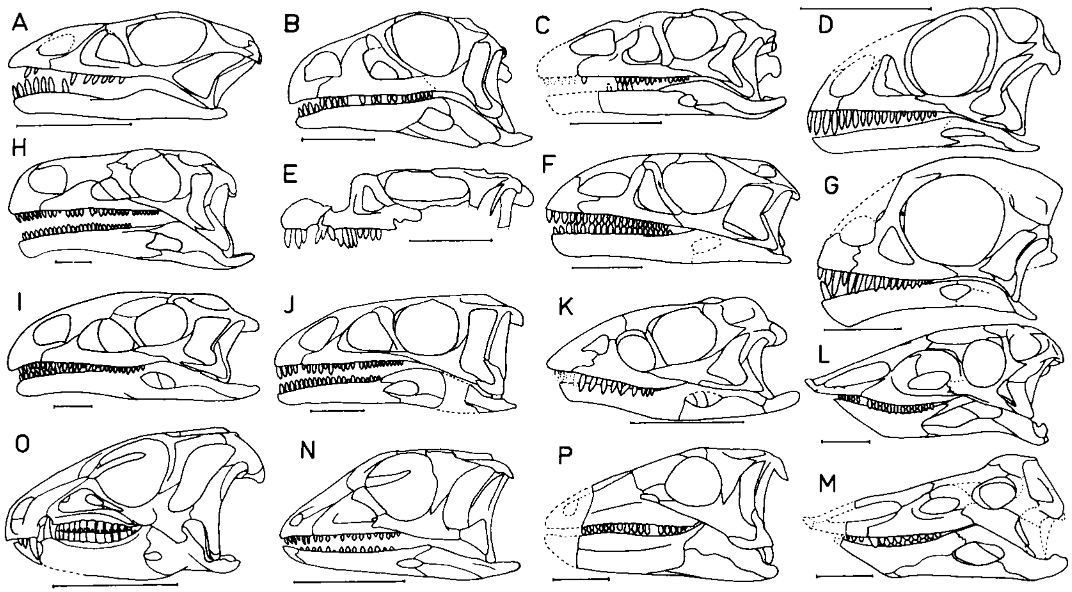

Fig. 4. Reconstructions of skulls in left lateral view of anchisaurid (A–J) and yunnanosaurid (K) prosauropods, aetosaurian thecodontians (L, M) and ornithischian dinosaurs from the Upper Triassic (B, G–J, L, M) and Lower Jurassic (A, C–F, K, N–P). ☐ A. *Anchisaurus polyzelius* from Connecticut, U.S.A., YPM 1883, from Bakker & Galton (in prep.). ☐ B. *Coloradia brevis* Bonaparte from Argentina, holotype, from Bonaparte (1978b). ☐ C. *Lufengosaurus huenei* Young from Yunnan, China, holotype, adapted after figures in Young (1941). ☐ D, E. *Massospondylus carinatus* from South Africa, juvenile (D) and larger individual (E, as preserved), from Cooper (1981). ☐ F. *Massospondylus* sp. from Arizona, U.S.A., from Attridge *et al.* (in press). ☐ G. *Mussaurus patagonicus* Bonaparte & Vince from Argentina, holotype, from Bonaparte & Vince (1979). ☐ H, I. *Plateosaurus engelhardti* from West Germany, SMNS 13200 (H, see Huene 1926, Romer 1966, Galton 1984) and AMNH 6810 (I, see Galton 1984). ☐ J. *Sellosaurus gracilis* from West Germany, based on UT 18318a (see Huene 1915) and SMNS 12216, 12685 (see Huene 1932). ☐ K. *Yunnanosaurus huangi* Young from Yunnan, China, holotype, adapted from figures in Young (1942). ☐ L. *Aetosaurus* from Nordwürttemberg, West Germany, from Walker (1964). ☐ M. *Typothorax* from Texas, U.S.A., from Walker (1964). ☐ N. Fabrosaurid *Lesothosaurus* from Lesotho, southern Africa, from Thulborn (1970). ☐ O. Heterodontosaurid *Heterodontosaurus* from Lesotho, from Charig & Crompton (1974). ☐ P. Scelidosaurid *Scelidosaurus* from Dorset, England, adapted from figures in Owen (1861). Scale lines represent 10 mm (G) and 50 mm.

found associated with skeletons of *Tenontosaurus,* a medium sized herbivorous ornithopod for which the skull and teeth are well known (see Ostrom 1970), and that this association occurred at 14 separate excavation sites in the Cloverly Formation (Lower Cretaceous) of Montana, U.S.A. Consequently, I regard all the associations of isolated carnivorous teeth with prosauropod postcranial bones as fortuitous. Therefore, as such, they provide no information on the diet of prosauropods.

Seeley (1894) described a large (more than 400 mm long) maxilla with replacement teeth *in situ* that was found at the same excavation site in the lower Elliot Formation as the lectotype femur of *Euskelosaurus browni.* Charig *et al.* (1965: 206–207) noted that the dental alveoli of this specimen 'are broken open and show two fairly well preserved successional teeth which are much broader and less pointed than those of a typical Jurassic carnosaur; they are very compressed labio-lingually with sharp crenulate anterior and posterior margins; and one is slightly recurved, while the apex of the other appears to be directed straight downward'. Cooper (1980: 15) notes that this bone could hardly have been lost during predation, but that the fortuitousness of this association remains to be determined. This maxilla is similar to those of rauisuchid thecodontians (see Bonaparte 1978a, 1981; Charig *et al.* 1976), and the partial dentary of a rauisuchid has been identified from the Lower Elliot Formation of South Africa by Hopson (1984). Another specimen (SAM K1497) that is listed from the Clarens Formation of South Africa by Cooper (1981: 821) as a form allied to *Teratosaurus* (Upper Triassic, West Germany, see Huene 1908) is probably also a rauisuchid because Bonaparte (1981) refers

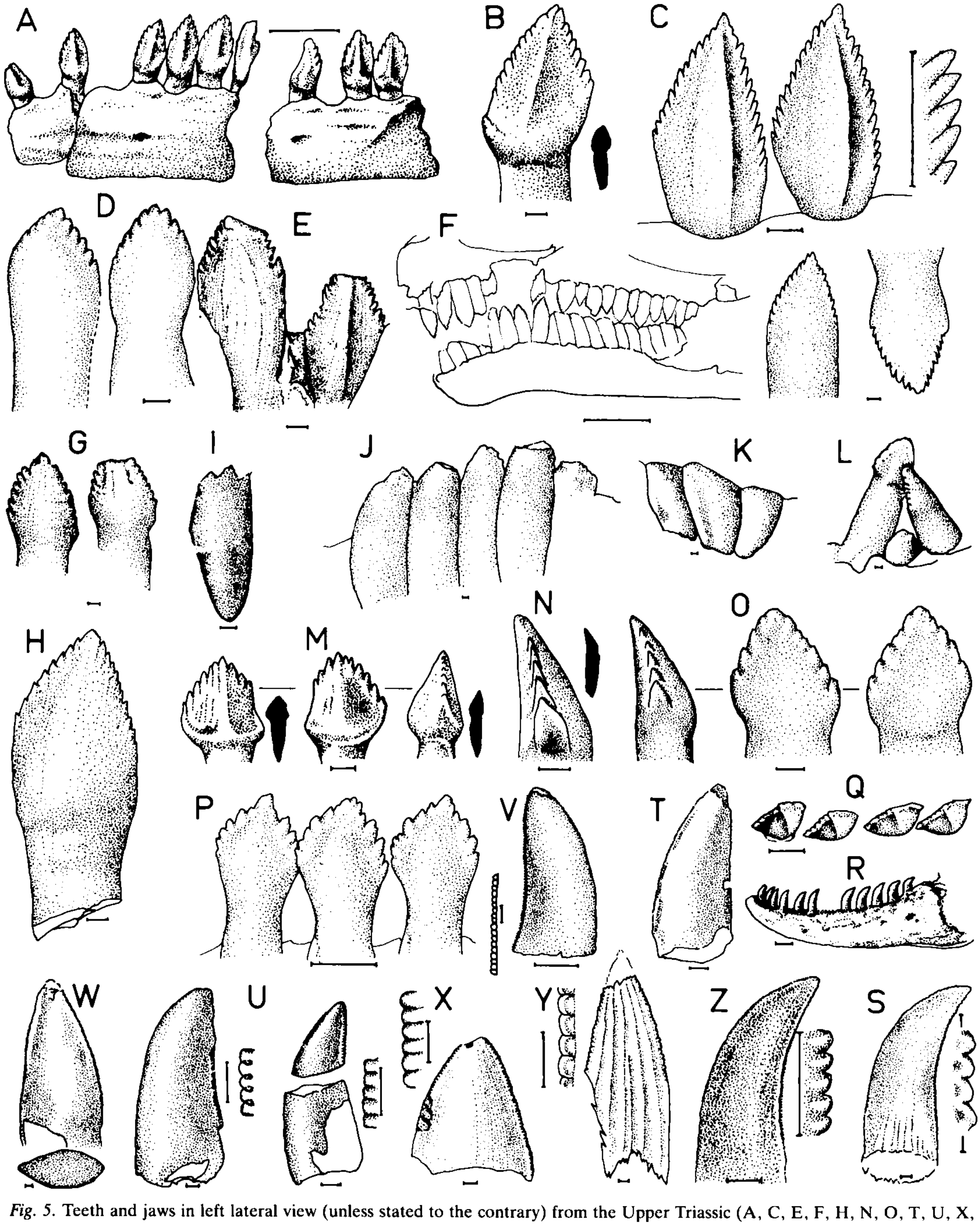

Fig. 5. Teeth and jaws in left lateral view (unless stated to the contrary) from the Upper Triassic (A, C, E, F, H, N, O, T, U, X, Y), Lower (D, G, I–M, V) and Middle Jurassic (Z), Eocene (W) and Recent (P–S). □ A, B. *Azandohsaurus laaroussi* Dutuit from Atlas Mountains, Morocco, after Dutuit (1972) (see Fig. 3B, C). □ A. Holotype dentary MNHN MTD-XVI 1. □ B. Cotype tooth MNHN MTD-XVI 2. □ C. *Thecodontosaurus antiquus* Morris 1843 from near Bristol, England, neotype two dentary teeth BCM 2 with detail of edge, after Huene (1908). □ D. *Massospondylus carinatus* from Rhodesia, two maxillary teeth in medial view, after Cooper (1981). □ E, F. *Sellosaurus gracilis* from West Germany. □ E. Two maxillary teeth of SMNS 4388 (see Fig. 3G), holotype of *Thecodontosaurus hermannianus* Huene, after Huene (1908). □ F. Tooth rows of UT 18318a with details of a maxillary and dentary tooth, after Huene (1915). □ G. *Lufengosaurus huenei* from Yunnan, China, two isolated teeth, after Young (1947). □ H. *Plateosaurus engelhardti* from East Germany, isolated tooth, after Jaekel (1913). □ I–L. *Yunnanosaurus huangi* from Yunnan,

Teratosaurus to the Rauisuchidae. The large lower jaw (BMNH R2790) referred to *Euskelosaurus browni* by Seeley (1894: 338, Fig. 6) was referred by Huene (1911, Figs. 19, 20) to the erythrosuchid thecodontian *Erythrosuchus africanus*, the holotype of which came from the same locality (see also Charig *et al.* 1976: 30) in the Upper Beaufort Series (*Lower* Triassic).

Relatively long teeth. – Cooper (1981) notes that the maximum ratio of tooth length to skull length in the two skulls of *Massospondylus* (Fig. 4D, E) are almost 7% and almost 10%, respectively, which is more than in extant carnivorous reptiles such as the Nile Crocodile (*Crocodilus niloticus*) at 7.6% and the Nile Monitor (*Varanus niloticus*) at 6%. However, crocodiles are characterized by an extreme elongation of the snout, which would lower this ratio, and the ratio is not as high in other anchisaurids, e.g. *Anchisaurus* 5% (Fig. 4A), *Coloradia* 5.4% (Fig. 4B), *Lufengosaurus* 6% (Fig. 4C), *Massospondylus* from Arizona 5.3% (Fig. 4F), and *Plateosaurus* 4.7% (Fig. 4H). In addition, this ratio is probably not very useful in deducing the diet because it is even higher in some sauropods, such as *Diplodocus* (8.9%) and *Camarasaurus* (9.8%), the diet of which was undoubtedly herbivorous (Bakker 1971, 1978; Coombs 1975; Romer 1966; Weaver 1983).

Serrated edges of teeth indicate a cutting function. – Carnivorous archosaurs do have serrated anterior and posterior edges to the teeth, but these are fine serrations perpendicular to the edge, as in rauisuchid thecodontians (Charig *et al.* 1976; for *Teratosaurus* see Huene 1908, Pl. 98), parasuchian thecodontians (Fig. 6X; Huene 1921, Figs. 1–12), the crocodile *Sebecus* (Fig. 5W), coelurosaurian theropod dinosaurs (Fig. 5Y), and carnosaurian theropods (Fig. 5Z; for teeth of Upper Jurassic theropods *Allosaurus* and *Ceratosaurus* see Madsen 1976, Fig. 9C, D; Janensch 1925, Pls. 9, 10; for other Jurassic and Cretaceous theropod teeth see Steel 1970, Figs. 1–8, 10–15). The proportionally larger denticulate edges of the teeth of anchisaurid prosauropods (Figs. 3B–I, 5A–H, 6P, R, 7A–F) are apically inclined at an angle of about 45° to the edge and are much more like those of the extant herbivorous lizard *Iguana iguana* (Fig. 5P) and, as Hotton (1955) has shown, there is a strong correlation between tooth form and diet in extant lizards. In another context, Cooper (1981: 826, 827) draws attention to the similarities between the teeth of anchisaurids and herbivorous fabrosaurid ornithischian dinosaurs (Figs. 5M–O, 7X, Y; see Galton 1978). The teeth of the two groups were confused by Dutuit (1972), who described a jaw with teeth and an isolated tooth of a prosauropod (Figs. 3B–D, 5A, B) plus an isolated fabrosaurid tooth (Fig. 5N; see also Figs. 5O, 7X, Y) *together* as *Azandohsaurus laaroussi* Dutuit 1972, a new ornithischian from the Upper Triassic of Morocco, north Africa. The presence of serrations on the teeth of anchisaurid prosauropods indicates a cutting function, but the coarseness of the serrations and their 45° orientation indicate that it was plant material that was being cut rather than flesh.

Shearing planes of teeth aligned along jaws as in all carnivores. – Cooper (1981) notes that the shearing planes '"... worked on the principle of concentrating all the power of the bite on a small area with very deep shearing surfaces so large pieces can be cut with one stroke" (Crompton & Hiiëmae 1969: 27). These are all features of a carnivore masticatory apparatus (Crompton & Hiiëmae 1969)'. However, Crompton & Hiiëmae

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China, after Young (I, 1942; J–L, 1951). ☐ I. Tooth from anterior end of maxilla (1942). ☐ J. Right dentary teeth in medial view. ☐ K. Teeth from middle of right maxilla in lateral view. ☐ L. Teeth from middle of left dentary in medial view. ☐ M. *Lesothosaurus* from Lesotho, isolated right dentary tooth in medial, lateral and anterior views, after Thulborn (1970). ☐ N, O. Isolated fabrosaurid teeth from the Atlas Mountains, Morocco. ☐ N. Anterior or posterior edge of MNHN MTD-XVI 3, after Dutuit (1972). ☐ O. MNHN ALM-509 in anterior or posterior, lateral and medial views (see Fig. 7X, Y). ☐ P, Q. Herbivorous lizard *Iguana iguana*. ☐ P. Right dentary teeth in medial view, after Montanucci (1968). ☐ Q. Dentary teeth in occlusal view, after Throckmorton (1976). ☐ R, S. Carnivorous lizard *Varanus komodensis*. ☐ R. Dentary, after Mertens (1942). ☐ S. Tooth, after Burden (1928) with detail of posterior edge, after Auffenberg (1981). ☐ T. *Basutudon ferox* Huene, holotype tooth, from Lesotho, after Huene (1932). ☐ U. Isolated teeth from Somerset, England, after Huene (1908), holotype teeth of *Avalonia sanfordi* Seeley 1898 (BMNH 2869) and *Picrodon herveyi* Seeley 1898 (BMNH 2875). ☐ V. Isolated tooth of *Sinosaurus triassicus* from Yunnan, China, after Young (1948). ☐ W. Maxillary tooth of crocodile *Sebecus* from Argentina, after Colbert (1946). ☐ X. Isolated tooth of parasuchian (phytosaurian) *Rutiodon* from North Carolina, U.S.A., after Huene (1921). ☐ Y. Isolated tooth of coelurosaurian theropod *Halticosaurus* from France, after Larsonneur & Lapparent (1966). ☐ Z. Isolated tooth of carnosaurian theropod *Megalosaurus* from Oxfordshire, England, after Owen (1857). Scale lines represent 10 mm (A, R, T, V, W, Z) and 1 mm (other teeth and detail of edges).

(1969) were referring specifically to the specialized and anteroposteriorly elongated carnassial teeth of the mammalian order Carnivora in which the single occlusal surface of the one carnassial tooth in the dentary slices past that of the opposing tooth in the maxilla. The teeth of anchisaurid prosauropods do not have opposing occlusal surfaces, although they are present in herbivorous ornithischian dinosaurs (some ankylosaurs, and in all pachycephalosaurids, heterodontosaurids, ceratopsians, and ornithopods except fabrosaurids) in which the shearing planes are aligned along the jaw (Galton 1973). Ornithischian dinosaurs were undoubtedly herbivorous so this criterion for carnivory in mammals is not relevant in assessing the diet of dinosaurs.

Closure of maxillary teeth outside those of dentary provided an efficient shearing plane for cutting. – The self-sharpening leading edges of the undoubtedly herbivorous ornithischian dinosaurs listed in the previous section had an even more efficient shearing plane for cutting (see Galton 1973) so this feature is not exclusive to carnivorous tetrapods.

Relatively small, grasping hands armed with enormous trenchant claw. – Cooper (1981) notes that the enormous trenchant claw of digit I of the manus (Fig. 1C cf. 1D) was as rapacious as that found in the most carnivorous of dinosaurs. The skull is relatively small in *Plateosaurus* (Fig. 1B) in which the length of the mandibular ramus is about 50% of femoral length (Huene 1926) as against over 100% in the contemporaneous and undoubtedly carnivorous theropod *Halticosaurus* (Huene 1934). In *Massospondylus* as reconstructed by Cooper (1981, Fig. 94), this ratio was 44%, whereas in the contemporaneous carnivorous theropod *Syntarsus* (Raath 1969, 1980), the value is similar to that for *Halticosaurus* (Bakker 1975:59). The proportionally small skull of anchisaurids was borne on a slender neck (Fig. 1B), and it was probably not very effective for defense. When attacked prosauropods probably reared up, supporting their weight on the hindlimbs and stout tail, and used the massive first ungual of the manus as a defensive weapon (Galton 1971, 1976). An enormous first ungual phalanyx also occurs in the manus of the herbivorous sauropod dinosaurs (see Coombs 1975). The herbivorous ornithopod *Iguanodon* (Lower Cretaceous, Europe) bore a very large spike on digit I of the manus (Norman 1980, Fig. 78). Chalicotheres and ground sloths are examples of herbivorous mammals with large claws on the manus, and the herbivorous homalodotheres had small claws (see Romer 1966).

Carnivorous ancestry of prosauropods. – Cooper (1981) notes that prosauropods were carnivorous because they were descended from the carnivorous proterosuchian theocodonts. If this argument was correct then herbivory would never have evolved in any group of vertebrates. The diet of an ancestral group is not relevant in considering the diet of its descendants. The Proterosuchia are restricted to the Proterosuchidae and Erythrosuchidae, neither of which left any known descendants (Charig *et al.* 1976; Chatterjee 1982).

Why anchisaurids were not predators on large prey

Cooper (1981) concluded that anchisaurids were not predators on large prey because of:

(1) The small size of the skull relative to the body length (Fig. 1B).

(2) The lateral inflexibility of the axial skeleton that was deduced from the presence of accessory articulations (hyposphene-hypantrum) in the dorsal vertebrae and the plane of the pre- and postzygapophysial articular surfaces of the cervical and dorsal vertebrae which are at 45° to the vertical.

(3) The relatively weak dentition (see Fig. 4A–J).

Supposed adaptations for carrion feeding

Large trenchant claw of manus for ripping apart carcasses. – Cooper (1981) notes that the teeth were unable to cope with ripping apart carcasses and, in addition, if *Massospondylus* spent its time chasing small prey, then it is difficult to explain the development of the large ungual on the pollex (see Fig. 1C) because, with its long neck, the skull would have reached any potential prey long before the hands (Fig. 1B). However, none of this is a problem if prosauropods were herbivores that used the manus for defense while supported on a tripod formed by the large hindlimbs and the elongate, stout tail.

Bypassing food chain by cannibalism. – Cooper (1981:814) notes for *Massospondylus* that 'cannibalism would have formed a major part of its diet, and it would not have been strictly dependent upon food-chain cycles'. This concept would work for only a relatively short period of time during conditions of extreme stress, but it is ecologically impossible for an extended period of time because it would lead to extinction. This is certainly not an appropriate ecological strategy for a group that was successful for at least 45 my (Fig. 2).

Explanation of herding. – Cooper (1981:815) notes that 'as active predators in arid wastelands and deserts, flocking might be a major handicap and self-defeating, as the animals would be perpetually in direct conflict over the same prey. Such a problem might not, however, arise if they were carrion-feeders, and it could be argued that with such a diet, as with modern hyaenas and vultures, flocking would be an advantage'. However, vultures are an inappropriate modern analog to use in considering the diet of prosauropods because the power of flight for aerial surveying, and especially the development of low energy gliding, added a new dimension to carrion feeding. It should be noted that hyaenas of Africa usually scavenge during the day but hunt in packs at night and that at least 80% of the kills are made by the hyaenas themselves in the Spotted Hyaena (*Crocuta crocuta*) and the Brown Hyaena (*Hyaena brunnea*) while the Striped Hyaena (*Hyaena hyaena*) kills a variety of domestic animals (Ewer 1973). Consequently, even hyaenas, the most highly adapted of living mammals for a scavenging diet, catch most of their own prey. Thus hyaenas fall into the carnivore category known as the scavenger-predator type, which includes many large vertebrates of today such as some species of felines, jackals, raptorial birds, and the Komodo Monitor.

The adaptations to a scavenger-predator type of diet are different for each class of tetrapod, and this is certainly the case for birds and mammals. The Komodo Monitor or ora, *Varanus komodensis*, of the Lesser Sunda Islands group of Indonesia is the largest living lizard, and it reaches a maximum length of 3 m. Auffenberg (1981: 193) has made a detailed study of the ora and presents data to show that 'an individual ora may be a successful predator one moment and an effective scavenger the next ... Where carcasses are not abundant, even full-grown oras become pure predators of a very resourceful and successful type'. The most important feeding adaptations are the teeth that 'bear a greater resemblance to those of flesh-eating carcharid sharks and carnosaurian dinosaurs than to the teeth of living reptiles and mammals' (Auffenberg 1981: 209). The teeth are laterally compressed with a progressive taper to a recurved distal end, the posterior edge bears fine serrations that are perpendicular to the edge, and there is a prominent gap between adjacent teeth (Fig. 5R, S; Auffenberg 1981, Figs. 2–4, Pl. 1). Consequently in the ora, the adaptations of the teeth for a scavenging diet are the same as for a carnivorous diet, and the same would be expected for anchisaurids if they were scavengers. However, the teeth of anchisaurids are adapted for an herbivorous rather than a carnivorous diet (see below, *herbivorous adaptions*), so it is concluded that anchisaurids were not carrion feeders but were herbivores instead. Herding would not be a problem if anchisaurids were herbivorous because this occurs in many different species of herbivorous mammals, and it has also been postulated for sauropods (Bakker 1971) and it probably also occurred in ornithischians.

Supposed reasons why anchisaurids were not herbivores

Teeth without flattened, opposing crowns. – Cooper (1981) notes that the form of the teeth of anchisaurids means that the food could not have been pulped prior to swallowing. However, no archosaurs, including the herbivorous ornithischians, have flattened, opposing crowns for pulping food as occur in some mammals, such as man, and in early to middle Triassic herbivorous reptiles such as procolophonids and gomphodont cynodonts (Gow 1978).

Virtually no lateral movement of the jaws so no mastication of plant material. – Cooper (1981) deduced the lack of lateral movement from the closure of the maxillary teeth outside those of the dentary but, in addition, such movement would have been largely precluded by the large pterygoid flange, formed by the ectopterygoid and pterygoid and, in *Plateosaurus* at least, by the form of the articular surfaces between the quadrate and the articular of the lower jaw (see Galton 1984). Cooper (1981) cites Crompton & Hiiëmae (1969) that the sideways movement of the jaw is the most important movement in the chewing stroke of an herbivore, but he fails to note that they were discussing the situation in *mammals*. Throckmorton (1980) concludes that the mammalian chewing cycle developed from the reptilian chewing cycle by the *addition of transverse movement of the lower jaw*. Consequently, the lack of transverse movement shows that anchisaurids are reptiles which lacked the specialization of mammals and provides no information concerning the diet.

Shearing planes of teeth aligned along, not across jaw. – Anchisaurids lack the specialized transversely oriented wear surfaces present in herbivorous mammals because such surfaces would have been useless in the absence of any transverse motion of the lower jaw. Occlusal surfaces are best developed amongst archosaurian reptiles in the herbivorous ornithischians but the surfaces are parallel to the long axis of the jaw. The absence of transversely oriented shearing planes on the teeth merely shows that anchisaurids did not have mammalian herbivorous adaptations and provides no information on the diet.

Inefficient masticatory apparatus could not cope with resistant plant material. – Cooper (1981: 705) quoted Galton (1976: 89–90) that '... in *Plateosaurus* the teeth are straight in anterior view, and there are no signs of any wear surfaces on the crowns and, as far as I can determine, this is the case for all prosauropod teeth [not now true for yunnanosaurids, see below p. 117]. Prosauropods probably could not chew very resistant plant material ... even with the help of a gastric mill, prosauropods were probably not very efficient herbivores *when compared with the ornithischians that replaced them* ... I believe that part of the reason for the elimination of the prosauropods was the relative inefficiency of the masticatory apparatus *with respect to that of most ornithischians*' [italics are mine to indicate sections from Galton (1976) included above that were *not* quoted by Cooper (1981)]. It should be noted that, although anchisaurids were not as specialized for an herbivorous diet as were most ornithischians, this does not mean that they were not herbivores.

Herbivorous diet unsuitable for desert habitat. – Cooper (1981) notes that an herbivorous diet would make *Massospondylus* dependent on the two scarcest commodities in the desert, viz. non-resistant plant material and fresh water. He discusses the environments in southern Africa and notes that a few major rivers must have cut across the arid Stormberg Desert, at least during its early development, as indicated by the abundance of the freshwater fish *Semionotus*. Nash (1975) discusses the mode of life of the early crocodilian *Orthosuchus* (Upper Elliot Beds, Lesotho) and concludes that it spent much of its life in water as do living crocodiles. Raath (1980) discusses the paleoecological conditions at two sites where *Massospondylus* and the carnivorous theropod *Syntarsus* were discovered together in the Lower Jurassic: one in the upper part of the Elliot Formation of South Africa, and the other in the Forest Sandstone Formation of Zimbabwe. He concludes that both genera could tolerate a considerable ecological range, but that they were fundamentally dependent on the occurrence of surface water in their environments. Herbivorous lizards are quite diverse in extant arid environments.

Herbivorous adaptations of anchisaurids

Prosauropods are reptiles so the adaptations of anchisaurids to an herbivorous diet should be assessed on this basis rather than by comparison with herbivorous mammals which show specialization in the teeth and skull that occur only in the class Mammalia.

Shape of teeth. – The spatulate crowns of the maxillary and dentary teeth of anchisaurids are expanded anteroposteriorly, so the maximum width of the crown is greater than that of the root (Figs. 3B–K, 5A–H, 6P, R, 7A–F) and are laterally compressed with the lateral surface being slightly more convex anteroposteriorly than the medial surface. This crown shape is similar to those of the herbivorous fabrosaurid ornithischians (Figs. 5M–O, 7X, Y; Galton 1978) and of the herbivorous lizard *Iguana iguana* (Fig. 5P, Q; Throckmorton 1976, Fig. 7A, C; Montanucci 1968, Fig. 2D). In herbivorous lizards of the families Iguanidae and Agamidae, the shearing edge of the crown is expanded anteroposteriorly so, with a reduction of the space between adjacent teeth in the tooth row, there is a more nearly continuous cutting edge than occurs in insectivorous lizards (Fig. 5Q) (Ray 1956; Montanucci 1968; Throckmorton 1976). This is in contrast to the situation in the carnivorous archosaurs cited above (p. 111) plus the Komodo Monitor (see p. 113) in which the crowns of the maxillary and dentary teeth are subconical with a steady taper from the root, so the maximum width of the crown equals that of the root (Figs. 3A, 5W–Z) with prominent gaps between adjacent teeth (Fig. 5R; for carnivorous thecodontians see Charig *et al.* 1976, for theropod dinosaurs see Steel 1970, Figs. 6, 10), and the lateral and medial surfaces show an equal degree of anteroposterior convexity. In the extant carnivorous crocodiles and some carnivorous varanid lizards (Fig. 5R, S; Mertens 1942), the well spaced teeth are robust and conical, whereas those of carnivorous snakes are elongate, slender, sharp pointed and conical (Edmund 1960).

Form of the serrations. – The serrations of the maxillary and dentary teeth are prominent (high notches or *Spitzkerbung* of Huene 1926) and are set at an angle of about 45° to the anterior and posterior cutting edges (Figs. 3B–I, 5A–H, 6P, Q, 7A, C, D, F). This is also the case in the herbivorous fabrosaurids and *Iguana iguana* (Figs. 5M–P, 7X), whereas in the carnivorous archosaurs cited above (see p. 111), and the Komodo Monitor (see p. 113), the serrations are much finer and are perpendicular to the edge (Figs. 3A, 5S, W–Z). The teeth of the herbivorous sauropods usually lack serrations but Janensch (1935, Pl. 12: 2, 3) figures two premaxillary teeth of *Brachiosaurus* with several prominent 45° serrations similar to those of anchisaurids.

Orientation of crowns. – The cutting edges of the crowns are obliquely inclined with respect to the long axis of the maxilla and dentary, so the anterior and posterior edges are slightly more medial and lateral, respectively (Figs. 3B–K, 5A, E, F; for ventral views of maxillary tooth rows of *Lufengosaurus* and *Plateosaurus* see Young 1951, Fig. 11 and Galton 1984). The teeth of fabrosaurid ornithischians (Galton 1978, Fig. 6B) and of *Iguana iguana* (Fig. 5P, Q) have the same arrangement. Throckmorton (1976: 387) notes that, because of the oblique orientation of the teeth in *Iguana*, '... the anterior end of the perforation made by one tooth lies medial to the posterior end of the one preceding it. If the food item is thin, then the perforations of the upper and lower dentition will overlap, freeing the piece of food item in the mouth. If the food item is thicker, the perforations, although not overlapping, still allow the food item to be torn by a quick movement of the head'. He also notes that the amount of head movement increases with the difficulty of cropping the food. In the carnivorous archosaurs cited above (see p. 111), the cutting edges of the crowns are orientated along the long axis of the maxillary and dentary (see Madsen 1976, Pl. 2B for *Allosaurus*; Steel 1970, Fig. 4.3 for *Tyrannosaurus*) as is also the case in the Komodo Monitor (see Mertens 1942, Fig. 120).

Herbivorous adaptations of dentition more marked posteriorly. – In *Sellosaurus* (Fig. 3E) and *Massospondylus* (Attridge *in* Charig *et al.* 1965: 207) '... the teeth in the front of the lower jaw are high and recurved while those at the back are of the spatulate type characteristic of prosauropods'. In *Sellosaurus* (Fig. 3E), the lateral asymmetry continues until at least tooth 14 and on tooth 16 the denticles still extend further down on the posterior edge than on the anterior edge. In teeth 18 to 22 the crown appears to be symmetrical with the denticles equally developed on both edges. In *Thecodontosaurus* (BCM 2) tooth 15 is still asymmetrical and the condition of the remaining six teeth cannot be determined. In *Plateosaurus* (Fig. 3H), the denticles are symmetrical by at least tooth 13 (Fig. 3I, situation for more anterior teeth is not clear).

In carnivorous theropods (Steel 1970) and thecodontians (Charig *et al.* 1976), the teeth are uniform for the length of the tooth row of the maxilla and most of the dentary except for the most anterior ones that may be slightly asymmetrical because the denticulate edges are not directly opposite each other. In most genera of iguanid lizards, the conical anterior teeth grade into the cuspate posterior ones. Hotton (1955) showed that the more plant material a species included in its diet, the more anteriorly the cuspate teeth begin in the tooth row. Montanucci (1968) continued this work on the neotropical genera *Basiliscus, Enyaliosaurus, Ctenosaura* and *Iguana.* He showed that the dentition becomes more highly modified as the amount of plant material in the diet increases, and that *Iguana iguana*, the most herbivorous, has all its teeth cuspate and the highest degree of lateral compression.

Low-set jaw articulation. – In anchisaurids, the jaw articulation is set below the line of the tooth row (Fig. 4A–J). In herbivorous mammals, the jaw articulation is set dorsally, but Galton (1976) considered that the system in anchisaurids was functionally analogous. However, Cooper (1981) discounted the ventral articulation of prosauropods as an herbivorous adaptation because he considered the primary function of an offset articulation to allow for a more effective sideways movement to the jaw. Greaves (1980: 439) has shown for ungulates with a dorsally offset articulation that '... the same set of bilaterally symmetrical muscles, with relatively fixed directions of pull and without any forces in the wrong direction, are not only able to bring the teeth together but can also move the lower jaw in two different directions (i.e. medially from either side)'. Transverse movements of the jaws were not possible in anchisaurids, but two other functions proposed for the dorsally offset articulation of mammals are also applicable to the ventrally offset articulation of anchisaurids, viz. it increases the angle between the lever arm of the bite force and the plane of the teeth which is important in dealing with resistant plant material (Crompton & Hiiëmae 1969), and it allows for a more even distribution of the biting force by ensuring that the tooth rows are almost parallel at occlusion so contact is made along the complete length of the tooth row by a 'nutcracker' like action (Colbert 1951: 89). I consider that the ventrally offset jaw articulation of anchisaurids is a herbivorous adaptation that is analogous with respect to these two functions to the dorsally offset jaw articulation of herbivorous mammals. The correctness of this conclusion is reinforced by comparisons with the undeniably herbivorous ornithischian dinosaurs that, with the exception of the fabrosaurids (Fig. 4N), all have a ventrally offset jaw articulation (Fig. 40, P; Galton 1973) as do the herbivorous aetosaurian thecodontians (Fig. 4L, M; Walker 1961; Charig *et al.* 1976). The amount of ventral offset is small in *Anchisaurus* (Fig. 4A) and quite large in *Plateosaurus* (Fig. 4H, I), and a comparable difference occurs in ornithischians and aetosaurs between primitive members of the group and those more highly adapted for an herbivorous diet (Fig. 4L–P; Galton 1973; Walker 1961). In contrast, the jaw articulation of carnivorous thecodontians (see Charig *et al.* 1976) and of theropod dinosaurs (see Steel 1970, Figs. 6, 10) are all in line with the tooth row as in carnivorous mammals and all living reptiles.

Supplementary action of gastric mill. – The lack of wear facets on the teeth of anchisaurids indicate that the teeth did not come into contact with each other, so there was no tooth-to-tooth occlusion as occurs in the teeth of most herbivorous ornithischians except fabrosaurids (Galton 1973). *Iguana iguana* also lacks wear facets and Throckmorton (1976) shows that this lizard uses its teeth to bite off a piece of a plant and that no further mechanical breakdown of the food occurs once it is in the oral cavity. Presumably, the situation was similar in anchisaurids. However, a gastric mill may have provided for a supplementary mechanical breakdown of the plant material, once it was ingested (Galton 1976). A well-preserved gastric mill consisting of a concentrated mass of small stones has been found associated with the stomach contents of several specimens of *Massospondylus* (Bond 1955; Raath 1974) and Cooper (1981: 824) notes that the main function of the gastroliths 'was certainly the trituration of food'. Similar masses of 'gizzard stones' or gastroliths found associated with the rib cage of sauropod dinosaurs are interpreted as representing a gastric mill by Bakker (1971). There are plenty of herbivorous birds alive today, none of which has teeth, and these use the gizzard for the further mechanical breakdown of the food. Welty (1975: 92) notes that 'the grit in the gizzards of seed eaters may not be indispensible but, at least in the Domestic Chicken, it increases the digestibility of whole grains and seeds by 10%'. He also noted that 'a Turkey will grind up in its gizzard 24 English walnuts in the shell in four hours' and 'could grind to pieces 12 steel needles in 36 hours, and 16 surgical lancets in 16 hours'. The presence of a gastric mill in anchisaurids would have enabled them to break down resistant plant material after it was bitten off and swallowed.

Adaptations for high browsing. – Bakker (1978: 662) notes that 'from the Late Carboniferous until the early Late Triassic, all the big herbivores were short-necked, short-limbed, low-browsers (diadectids, edaphosaurs, deinocephalians, pareiasaurs, dicynodonts, rhynchosaurs, gomphodonts and aetosaurs). But in the mid-Late Triassic this trophic role was taken over by prosauropod dinosaurs – long-necked forms with long hindlimbs, powerful pelvis and tail. Prosauropods could probably feed tripodally – supporting their weight on the hindlimbs and stout tail, much as modern varanid lizards do when threatened'. The long neck extended the vertical feeding range so that vegetation at higher levels could be reached as in giraffes. The proportionally small size of the skull would have reduced its leverage effect on the long neck, especially when held horizontally (Fig. 1B). These two characters are even more prominently developed in the dominant large terrestrial herbivores of the Jurassic and Cretaceous, the sauropod dinosaurs (Bakker 1971, 1978; Coombs 1975; Romer 1966).

Represent largest biomass in respective faunas. – Apart from the fauna of the Los Colorados Formation of Argentina, in which the anchisaurid *Coloradia* Bonaparte 1978b is smaller than the melanorosaurid *Riojasaurus* (Fig. 1A), anchisaurids are the largest animals present in adequately known faunas. This is true for *Sellosaurus* (Stubensandstein, West Germany), *Plateosaurus* (Knollenmergel, Germany) and *Euskelosaurus* (Lower Elliot Formation, South Africa) of the Upper Triassic and *Massospondylus* (Upper Elliot Formation and Clarens Formation, South Africa) and *Lufengosaurus* (Lower Lufeng Beds, China) of the Lower Jurassic. In terrestrial mammalian faunas of the Tertiary and Recent, the largest animals in a fauna are always herbivores. This is also true for dinosaur faunas from the Middle Jurassic to the Late Cretaceous.

There is always a preponderance of herbivores over carnivores in fully terrestrial faunas (Bakker 1975) and anchisaurids are relatively abundant in the Late Triassic and Early Jurassic faunas considered by Benton (1983, see appendix for details) to provide statistically significant percentage faunal compositions. Thus *Plateosaurus* (with junior synonym *Gresslyosaurus*) represents at least 75% of the individual animals from the Knollenmergel of Germany; *Euskelosaurus* represents 86% of the fauna of the lower Elliot Formation (Upper Triassic) and *Massospondylus* represents 21% of the fauna from the upper Elliot Formation (Lower Jurassic; most common element is small herbivorous mammal-like reptile *Tritylodon* at 51% with ornithischians representing 7%) and 40% from the Clarens Formation; *Massospondylus* represents 57% of the fauna of the Forest Sandstone Formation of Zimbabwe (discounting *Euskelosaurus* that is incorrectly included in this fauna although it is from the underlying Mpandi Formation, see Cooper 1980); and *Lufengosaurus* (together with *Yunnanosaurus*) represents 82% of the fauna of the upper Lower Lufeng Series of China.

Prosauropods are the largest and most common elements in adequately know faunas so their biomass must have greatly exceeded that of the rest of the fauna combined. Thus Bakker (1975) calculated that the biomass of prosauropods from the Knollenmergel of Germany (*Plateosaurus*) and the upper Lower Lufeng Series of China (*Lufengosaurus, Yunnanosaurus*) to be 98.4% with the remaining 1.6% as carnivorous coelurosaurian theropods. If prosauropods are regarded as predator-scavengers, then this would give a predator-prey ratio of 100%, an ecological impossibility. However, if prosauropods were herbivores, then this would give a normal terrestrial food pyramid with a predator–prey ratio of 1.6%. This figure may be too low because Béland & Russell (1978) have increased the predator–prey ratio calculated by Bakker (1975) for the fauna of the Oldman Formation (Upper Cretaceous) of Alberta, Canada from 3.25% to 6%. This ratio was more probably about 5% for the faunas of the Knollenmergel and Lower Lufeng Series with the prosauropods accounting for at least 95% of the biomass.

Diet of the Yunnanosauridae

Many of the herbivorous adaptations discussed above for anchisaurids also occur in *Yunnanosaurus huangi* viz. the teeth are spatulate (Fig. 5I–L), the crowns are obliquely inclined with respect to the long axis of the maxilla and dentary (Young 1951, Fig. 12.2) so the posterior edge of each tooth is lateral to the anterior edge of the tooth behind it (Fig. 5J, K); the jaw articulation is offset ventrally (Fig. 4K); the skull is proportionally small with a proportionally long neck (see Young 1942, 1951); and, with the slightly larger *Lufengosaurus, Yunnanosaurus* constitutes about 82% of the fauna from the upper Lower Lufeng Series (Benton 1983) and at least 95% of the biomass.

Simmons (1965) catalogued several isolated teeth of *Yunnanosaurus* from the upper Lower Lufeng Series of Lufeng, China. These isolated teeth (Figs. 6A–O, 7G–O) resemble those of sauropods (Fig. 7P–W; Lull 1911; Janensch 1935; Ostrom 1970) rather than those of *Lufengosaurus* (Figs. 5G, 6P–R, 7A–F) and the teeth of other anchisaurid prosauropods (Figs. 3B–I, 5A–F, H). In *Lufengosaurus*, the crowns are denticulate and symmetrical in anterior or posterior views (Figs. 6P, Q, 7A–F; see also Fig. 3D) but adenticulate and asymmetrical in *Yunnanosaurus* (Figs. 6B, D, F, H, J, M, O, 7I, L, M, O) and sauropods (Fig. 7Q, S, U, W). From the similarities in wear to the teeth of some sauropods (see below), it is assumed that in *Yunnanosaurus* the apicies of the maxillary and dentary teeth were directed medioventrally and medio-

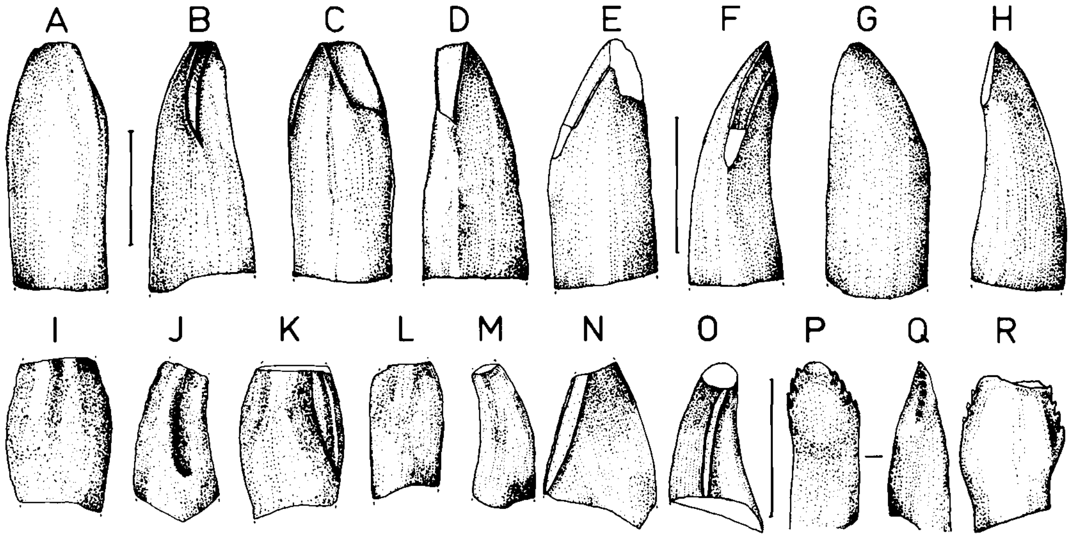

Fig. 6. Isolated teeth of yunnanosaurid (A–O) and anchisaurid prosauropods from the Lower Jurassic. □ A–O. *Yunnanosaurus huangi*, referred teeth FMNH CUP-2051 (A–D, Fig. 7M–O), FMNH CUP-2047a (E–H, from Hei Koa Peng), FMNH CUP-2056 (I–K, Fig. 7J–L, from Ta Ti), FMNH CUP-2340c (L, M, Fig. 7G–I) and FMNH CUP-2047b (N, O) in lateral (A, G, I, L), medial (C, E, K, N), anterior (B, F, J, M, O) and posterior views (D, H). □ P–R. *Lufengosaurus huenei*, isolated teeth FMNH CUP-2340a (P, Q from end of tooth row, Fig. 7A–C) and FMNH CUP-2340b (R, Fig. 7D–F) in lateral, anterior and lateral views. Unshaded areas represent broken bone. Scale lines represent 10 mm (A–D × 1.5, E–H × 1.7, I–R × 1.8).

dorsally, respectively. In *Lufengosaurus* (Fig. 7A, C, D, F) and other anchisaurids, the lateral and medial surfaces of the crowns are very similar. However, in *Yunnanosaurus* and sauropods, the lateral surface of the crown is usually uniformly convex (Figs. 6A, G, I, L, 7G, J, P, T), whereas the medial surface is concave dorsoventrally except near the root (Figs. 6C, E, K, N, 7H, K, N, R, V), and there is a variably developed depression on either side of the anteroposteriorly convex central part. The overall form of the teeth of *Yunnanosaurus* (Figs. 6A–O, 7G–O) is similar to those referred to the Lower Cretaceous sauropods *Astrodon* and *Pleurocoelus* (Fig. 7P–W; Lull 1911; Ostrom 1970).

The teeth of anchisaurids lack wear surfaces (Figs. 3B–I, 5A–H), whereas wear surfaces are well developed on several teeth of *Yunnanosaurus*. On two of the teeth shown (Fig. 6E, F, N, O) there is a single wear surface along one edge. Another tooth has two wear surfaces (Figs. 6B–D, 7M–O); comparisons with the teeth of the sauropod *Brachiosaurus* (Janensch 1935) indicate that this tooth is from the right maxilla. The wear surface on the posterior edge is slightly curved (Fig. 7N), and the smooth enamel border forms a slightly raised rim around the dentine (Fig. 7M); comparable wear surfaces are present on the teeth of *Astrodon* (Fig. 7Q, U; Lull 1911) and were probably formed by contact with the food. The larger wear surface on the anterior edge is flat and obliquely inclined, facing anteromedially and ventrally, and the enamel is minimally raised with respect to the dentine (Fig. 7N, O). Similar flat and obliquely inclined wear surfaces occur on the anteromedial surfaces of the maxillary teeth of *Brachiosaurus* (Janensch 1935), and they resulted from wear against the opposing dentary teeth that have corresponding posterolateral wear surfaces.

The edges of the flat and obliquely inclined wear surface on the maxillary tooth of *Yunnanosaurus* would have been self-sharpened by wear against the corresponding surface on the opposing dentary tooth. Consequently, a series of relatively coarse, 45° inclined marginal serrations were no longer necessary for cutting plant material and vestiges of this system are retained on only a few teeth (Fig. 5I, L; see also Young 1942, 1951). The pattern of wear is comparable to that on the teeth of some of the large sauropods such as *Brachiosaurus* (Janensch 1935) which were undoubtedly herbivorous (Bakker 1971, 1978; Coombs 1975; Weaver 1983). The maxillary and

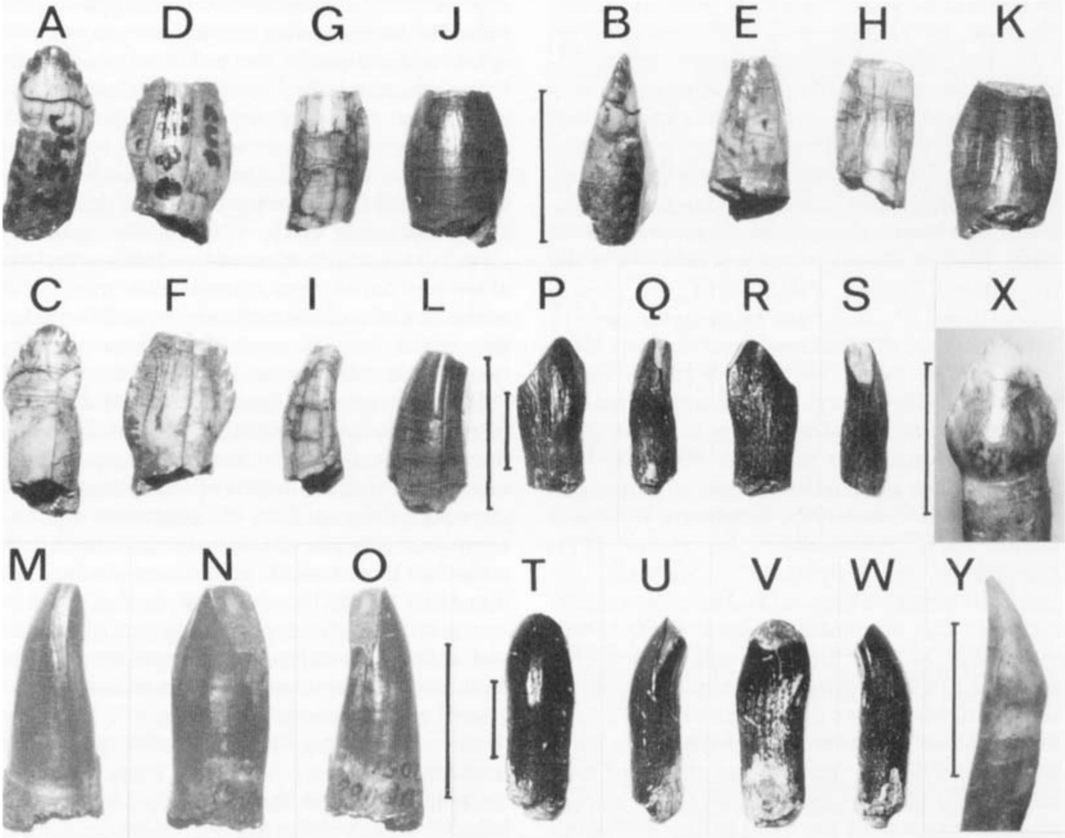

Fig. 7. Isolated teeth of anchisaurid (A–F) and yunnanosaurid prosauropods (G–O), sauropods (P–W) and fabrosaurid ornithopods (X, Y) from the Upper Triassic (X, Y), Lower Jurassic (A–O) and Lower Cretaceous (P–W). ☐ A–F. *Lufengosaurus huenei* from Yunnan, China, FMNH CUP-2340a (A–C) and 2340b (D–F) in lateral (A, F), anterior (B, E) and medial views (C, D). ☐ G–O. *Yunnanosaurus huangi* from Yunnan, China, FMNH CUP-2340c (G–I, Fig. 7L, M), CUP-2056 (J–L, Fig. 7I–K) and CUP-2051 (M–O, Fig. 7A–D) in lateral (G, J), medial (H, K, N), anterior (L, M) and posterior views (I, O). ☐ P–W. Isolated teeth of *Pleurocoelus valdensis* from Portugal, MGSP, in lateral (P, T), medial (R, V), anterior (Q, U) and posterior views (S, W). ☐ X, Y. Isolated tooth MNHN ALM-509 (Fig. 5O) from Morocco in lateral (X), and anterior or posterior views (Y). Scale lines represent 10 mm (A–L × 2, M–O × 1.5, P–W × 1) and 5 mm (X, Y × 4).

dentary teeth of sauropods have also lost the marginal serrations, but two premaxillary teeth of *Brachiosaurus* (Janensch 1935, Pl. 12: 2, 3) have coarse, 45° inclined serrations comparable to those of anchisaurids. *Yunnanosaurus* is the prosauropod most highly adapted for dealing with resistant plant material because it is the only prosauropod whose teeth had self-sharpening wear surfaces that were maintained by tooth-to-tooth wear. However, the rest of the anatomy of *Yunnanosaurus* is comparable to that of anchisaurids so this genus is definitely not referable to the Sauropoda.

Diet of the Melanorosauridae

The isolated tooth crowns of carnivorous aspect that have been found with the postcranial remains of melanorosaurids in South Africa (p. 108; Charig *et al.* 1965), China (Fig. 5V) and England (Fig. 5U) were most probably shed by a carnivorous archosaur (a thecodontian or a theropod dinosaur) while it preyed on the carcass prior to burial. Similar association of isolated theropod tooth crowns and the skeletons of theropod prey were cited above (see p. 108). Consequently, the teeth of melanorosaurids are unknown and no skull bones have been described. However, the elongate neck in *Riojasaurus* (Fig. 1A), the only adequately known melanorosaurid, indicates that the skull was probably proportionally small as in anchisaurids and yunnanosaurids (lower jaw about half femoral length) rather than proportionally large as in carnivorous theropod dinosaurs (lower jaw longer than femur). The length of the limbs relative to the rest of the body in *Riojasaurus* is less than it is in the facultatively bipedal *Plateosaurus* and *Anchisaurus* (Figs. 1A, B, E) and more comparable to the situation in the sauropods (see Colbert 1962; Romer 1966; Steel 1970). As a result, *Riojasaurus* probably always walked quadrupedally. This is in marked contrast to the situation in all saurischian carnivores that were obviously fully bipedal forms, even in the Triassic (e.g. *Herrerasaurus, Staurikosaurus,* see Bonaparte 1978a and Galton 1977; *Halticosaurus*, see Huene 1934; *Coelophysis*, see Colbert 1962; *Syntarsus*, see Raath 1969 and Bakker 1975). Bonaparte (1982) estimates that specimens of *Riojasaurus* constitute about 38% of the total number collected from the Los Colorados Formation of Argentina with small herbivores totaling another 18% (aetosaurian thecodontians 12%, tritylodonts 6%). Bonaparte (1981) notes that the estimated total body length of the preserved individuals of *Riojasaurus* ranges from 2 m to 10 m. It is difficult to envision such a large quadrupedal animal with sauropod-like proportions and which formed such a large proportion of the total biomass of vertebrates in the fauna as anything other than a herbivore. Although the skull and teeth are unknown, I agree with Bonaparte (1971, 1982) and Benton (1983) in regarding *Riojasaurus* as a herbivore.

Summary and conclusions on the diet of prosauropods

Some of the arguments used by Cooper (1981) to show that *Massospondylus* and other anchisaurid prosauropods were adapted for a scavenger-predator type of diet with the possibility of cannibalism are irrelevant or inaccurate. These include the presumed origin of prosauropods from carnivorous proterosuchian thecodontians, the referral of isolated carnivorous teeth to anchisaurids, the proportionally long teeth, the presumed shortage of plants and water in the Stormberg Desert, and the possibility of bypassing the food chain by cannibalism. Other arguments involve the inappropriate comparisons of prosauropods with mammals, the results of which show that anchisaurids had reptilian feeding systems rather than providing any information on their diet. These arguments include the presence of carnivorous mammal characters, such as the alignment of the shearing surface of the crowns along the length of the jaws and the maxillary teeth biting outside those of the dentary, and the absence of herbivorous mammal characters, such as the lack of any lateral movements of the lower jaw and of any flat crushing surfaces or transversely orientated wear surfaces on the teeth.

Comparisons with the dentitions of undoubtedly carnivorous reptiles, such as most thecodontians (except aetosaurs) and all theropod dinosaurs, show that the dentition of anchisaurid prosauropods does not have the characters of a carnivorous reptile viz. subconical shaped teeth with maximum crown width at the root-crown junction and a steady taper distally, cutting edges of crown orientated along the long axis of maxilla and dentary, prominent gaps between adjacent teeth, lateral and medial surfaces with equal degree of anteroposterior convexity, and the serrations on the cutting edge fine and perpendicular to the edge.

Comparisons with the dentition of undoubtedly herbivorous reptiles such as *Iguana iguana* and ornithischian dinosaurs show that the dentitions of anchisaurid prosauropods have the characters of herbivorous reptiles, viz. spatulate teeth with anteroposteriorly expanded crowns, the maximum width of which is apical to the crown-root junction, the crowns obliquely inclined with respect to the long axis of the maxilla and dentary with only small gaps between adjacent teeth and, in most cases, the posterior edge of one tooth being lateral to and slightly overlapping the tooth behind it. In addition, the lateral surface of the crown is slightly more convex anteroposteriorly than the medial surface, and the serrations on the cutting edges are coarse and at an angle of 45° to the edge. As is also the case in herbivorous lizards, the teeth in the posterior part of the toothrow are more highly adapted for an herbivorous diet than are those more anteriorly. The mechanical breakdown of plant material was probably aided by stones in a muscular gastric mill after it was swallowed, as in herbivorous birds today.

The jaw articulation of anchisaurid prosauropods is ventrally offset with respect to the tooth row, as in all herbivorous ornithischians except the fabrosaurids and in advanced herbivorous aetosaurian thecodontians. The offset articulation did not facilitate the transverse movement of the lower jaws as does the dorsally offset jaw articulation of herbivorous mammals. However, it probably did increase the amount of force that could be applied to the food and allowed for a more even distribution of the force along the tooth row as also occurs in herbivorous mammals.

An herbivorous diet for anchisaurid prosauropods helps to explain some other characters of the group. The long neck would have increased the available vertical feeding range for vegetation, especially when feeding tripodally using the hindlimbs and stout tail for support, and the proportionally small skull would have reduced its leverage – comparable adaptations were developed to an even greater degree in the very large and herbivorous sauropod dinosaurs of the Jurassic and Cretaceous. However, a small skull on a long neck provides relatively little defense against predators, a potential weakness that was compensated for by the enormous trenchant claw on digit I of the manus that would have been a formidable defensive weapon when the animal supported itself tripodally. Herding would also have provided additional protection against predators, and it occurs in many species of larger herbivorous mammals. An herbivorous diet would also explain why anchisaurids represent at least 95% of the biomass of their respective vertebrate faunas, a result of their being the largest and most common animals, in adequately known terrestrial faunas from the late Triassic and early Jurassic.

Most of the arguments for herbivory summarized above also apply to *Yunnanosaurus*, the only genus of the family Yunnanosauridae. In addition, the form of the teeth with occlusal wear facets, some of which were self-sharpened by tooth-to-tooth wear, is comparable to those of sauropod dinosaurs. The arguments for herbivory in anchisaurids that relate to the postcranial skeleton and relative biomass of anchisaurids also apply to *Riojasaurus*, the only adequately known member of the family Melanorosauridae, which attained a maximum body length of about 10 m. However, neither the skull nor the teeth are known for any melanorosaurid.

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In *Plateosaurus* at least (Galton in press), there was probably a soft secondary palate and cheeks as were subsequently developed independently in herbivorous ornithischian dinosaurs other than fabrosaurids (Galton 1973). The soft secondary palate was supported by the maxillae, vomers, and the ventromedially directed and peg-like process on each palatine (Galton 1984, Pl. 6, Fig. 1). A diagonally inclined ridge that extends from the base of the coronoid process along the lateral surface of dentary (Galton 1984, Pl. 1, Figs. 1, 2) was for the attachment of cheeks, but a corresponding attachment region on the lateral surface of the maxilla is not recognizable (see Galton 1984, Pl. 1, Figs. 1, 2).