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Abstract: In the 169 years since Owen named a tooth as *Cardiodon*, the study of sauropod dinosaurs has gone through several distinct periods. In the early years, a sequence of descriptions of isolated skeletal elements gave rise to a gradually emerging understanding of the animals that would later be known as sauropods. The second phase began in 1871 with Phillips's description of *Cetiosaurus oxoniensis*, the first reasonably complete sauropod, and continued with the Marsh-Cope Bone Wars and the description of the nearly complete sauropods *Camarasaurus* and '*Brontosaurus*' (= *Apatosaurus*). As these and other genera became better known, a third phase began, exploring not just the remains but the lives of these giants, with arguments about posture and habitat to the fore, and with the public becoming increasingly aware of sauropods owing to skeletal mounts. A 'dark age' followed during and after World War II, with sauropods considered uninteresting evolutionary dead ends and largely ignored. This was brought to an end by the 'dinosaur renaissance' that began in the late 1960s, since when work has recommenced with new vigour, and the public has been introduced to a more vigorous and terrestrial image of sauropods through film and television. Both diversity and disparity of sauropods continue to increase through new descriptive work, and the group is now seen as more fascinating and worthy of study than ever before.

Sauropod dinosaurs are the terrestrial superlative: they were not just the largest animals ever to have walked on land, but an order of magnitude heavier than their nearest rivals – the hadrosaurid dinosaurs, and the proboscidean and indricotherian mammals. Although the first genera now recognized as sauropods were named in 1841, the nature of the animals was not understood for some time, and many aspects of their palaeobiology remained controversial for considerably longer; some, including habitual neck posture, remain unresolved to this day. Throughout the 169 years of research into sauropods, an increasingly clear picture has gradually emerged. This paper traces the process of discovery through five distinct eras: an initial period of studies restricted to isolated elements; the period in which near-complete specimens first became available; the age of interpretation and controversy; the 'dark ages'; and the modern renaissance.

Institutional abbreviations: AMNH, American Museum of Natural History, New York, NY, USA; BMNH, Natural History Museum, London, UK; CM, Carnegie Museum of Natural History, Pittsburgh, PA, USA; HMN, Humboldt Museum für Naturkunde, Berlin, Germany; OUMNH, Oxford University Museum of Natural History, Oxford, UK; USNM, National Museum of Natural History, Washington, DC, USA; YPM, Yale Peabody Museum, New Haven, CT, USA.

Stage 1: early studies, isolated elements (1841–1870)

It was only 17 years after the naming of the first dinosaur recognized by science, *Megalosaurus* Buckland 1824, and a year before the coinage of the name Dinosauria Owen 1842, that the first sauropods were named: *Cardiodon* Owen 1841*a* and *Cetiosaurus* Owen 1841*b*. The former was named on the basis of a single tooth crown from the Middle Jurassic Forest Marble Formation of Bradford-on-Avon, Wiltshire. It was later figured by Owen (1875*a*, plate IX, figs 2–5), but has since been lost (Fig. 1a). A second tooth crown, BMNH R1527, was referred to this genus by Lydekker (1890, p. 236), and was later figured by Barrett (2006, fig. 2a,b). These two teeth are the only elements to have been assigned to *Cardiodon*, and this genus – the first sauropod – is now all but forgotten. Various workers have suggested that *Cardiodon* might be a senior synonym of *Cetiosaurus*, but this putative synonymy was refuted by Upchurch & Martin (2003, pp. 214–215).

It is with the genus *Cetiosaurus*, named later that same year, that the story of sauropods really begins. Owen (1841*b*) used a wide variety of specimens from six different localities as the basis for the new genus *Cetiosaurus*, for which no specific name was initially given. Despite the large amount

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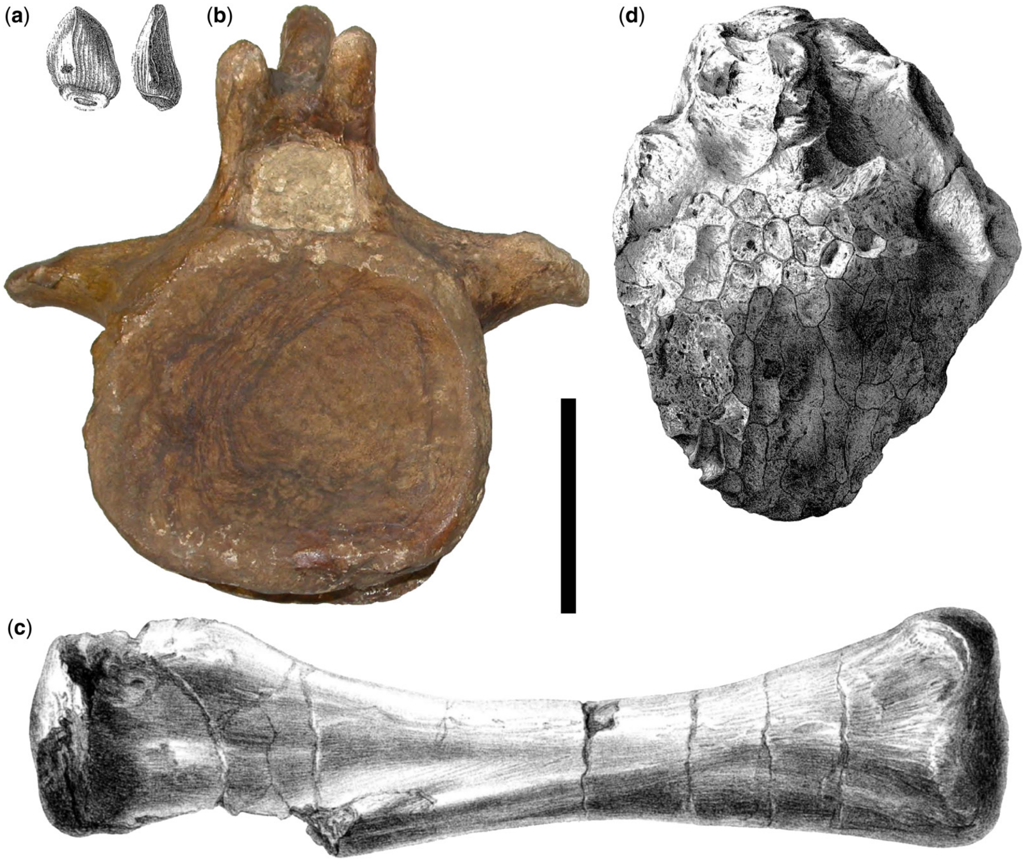

Fig. 1. Historically significant isolated sauropod elements. (**a**) The holotype tooth of *Cardiodon* in labial and distal views, modified from Owen (1875*a*, plate IX, figs 2 and 3); (**b**) anterior caudal vertebra of *Cetiosaurus brevis* in anterior view, part of the holotype, photograph by the author; (**c**) holotype right humerus of *Pelorosaurus* in anterior view, modified from Mantell (1850, plate XXI, fig. 1b); and (**d**) lectotype dorsal vertebra of *Ornithopsis* (see Blows 1995, p. 188) in anterior view, exposing pneumatic cavities owing to erosion of the anterior articular surface, modified from Owen (1875*a*, plate IX, fig. 1). The scale bar is 5 cm for (a), 10 cm for (b) and (d), and 30 cm for (c).

of material most of it was rather poor, consisting largely of partial caudal vertebrae and appendicular fragments. Owen noted that in their size, and in the size and proportions of their neural spines and chevron articulations, the vertebrae resembled those of whales; but that the concavity of their articular surfaces and high position of the transverse processes suggested a reptilian affinity. Accordingly, he named the new genus *Cetiosaurus* or ‘whale lizard’ (Fig. 1b).

It is often said that Owen (1841*b*) described *Cetiosaurus* as a gigantic crocodilian, but in fact this assignment came later. In his initial description, Owen (1841*b*, p. 462) explicitly separated his new animal from crocodiles, concluding that ‘the surpassing bulk and strength of the *Cetiosaurus* were probably assigned to it with carnivorous habits, that it might keep in check the Crocodilians and Plesiosauri’. What is certain is that when, a year later, Owen (1842, p. 103) created the name Dinosauria, he omitted *Cetiosaurus* from it; limiting its initial content to ‘the gigantic Crocodile-lizards of the dry land’, *Megalosaurus*, *Iguanodon* Mantell 1825 and *Hylaeosaurus* Mantell 1833. *Cetiosaurus*, then thought aquatic, was explicitly excluded.

In subsequent years, a total of 13 species of *Cetiosaurus* were named by Owen and others on the basis of British material, although nearly all of these are now considered nomina nuda or nomina dubia (Upchurch & Martin 2003, pp. 209–215). It was not until 1871 that truly informative *Cetiosaurus* remains would be described. Before this, though, several more historically important sauropods would be named on the basis of isolated elements.

The first of these, and the first sauropod to be named on the basis of appendicular material, was

Pelorosaurus Mantell 1850 (Fig. 1c), based on a humerus from the Early Cretaceous Wealden Supergroup that at the time seemed 'stupendous' (p. 379) at a length of 4.5 ft – although this is little more than 60% the length of the humeri of the subsequently described brachiosaurids *Brachiosaurus altithorax* Riggs 1903*a* and *Brachiosaurus brancai* Janensch 1914, animals which if they were isometrically similar to *Pelorosaurus* would have weighed four times as much as it did. The significance of *Pelorosaurus* is that it was the first-named sauropod that was recognized by its describer as being terrestrial – ironically, owing to its possession of a medullary cavity, a feature that seems to be unique among sauropods. Although Owen (1859*a*, p. 40) tried to portray Mantell as having mistaken the 'anterior for the posterior of the bone', it is clear from Mantell's description, and particularly his correct identification of the deltoid process (deltopectoral crest), that he oriented the humerus correctly and that the error was only in the caption of Mantell's plate XXI. Mantell subsequently described a second species, *Pelorosaurus becklesii* Mantell 1852, which in fact is not closely related to the type species (Upchurch 1995, p. 380). The type specimen of '*Pelorosaurus*' *becklesii*, BMNH R1868, is important because as well as a humerus, radius and ulna, it includes a skin impression – the first known from any sauropod, and still one of only very few sauropod skin impressions. Because Mantell referred to *Pelorosaurus* the same caudal vertebrae that Owen (1842) used as the type specimen for *Cetiosaurus brevis* Owen 1842, the taxonomy of *Cetiosaurus* and *Pelorosaurus* is complex and intertwined. This situation is being addressed by a petition to the International Commission on Zoological Nomenclature (ICZN) (Upchurch *et al.* 2009). *Pelorosaurus*, including the misassigned species '*Pelorosaurus*' *becklesii*, is being restudied to better determine its affinities but the type material appears to represent a basal titanosauriform, possibly a brachiosaurid (Upchurch & Martin 2003, p. 210).

As with dinosaurs in general, England was very much the home of sauropods during the early days of their study. The first sauropod named from outside England was *Aepisaurus* Gervais 1852, based on a subsequently lost humerus of which the proximal part has since been found; it is now considered a nomen dubium. The first sauropod from outside Europe was *Astrodon* Johnston 1859 from the USA, which, like *Cardiodon*, was named on the basis of a single tooth crown and not initially given a specific name. Six years later, the tooth was referred to the new species *Astrodon johnstoni* Leidy 1865, although this is often misspelled as A. *johnsoni* (e.g. Carpenter & Tidwell 2005). (*Pleurocoelus* Marsh 1888, based on mostly juvenile vertebral centra, has sometimes been considered separate from *Astrodon*, but is now generally considered a junior synonym of that genus despite the inadequate *Astrodon* type material – see the overview in Carpenter & Tidwell 2005.)

Another significant find was *Ornithopsis* Seeley 1870, named on the basis of two partial presacral vertebrae from different localities that are now known to belong to sauropods (probably two different sauropod taxa) but thought by Seeley (p. 279) to be 'of the Pterodactyle kind' (Fig. 1d; see Martill 2010). Seeley's mistake was based on his recognition of pneumatic features in the bones – internal air spaces giving rise to a honeycombed internal structure, and lateral foramina through which air entered these spaces from the sides of the bones. At the time of Seeley's writing, almost all animals known to have pneumatized bones in their postcranial skeletons were birds and pterosaurs, the only exception being the theropod *Becklespinax altispinax* Paul 1988*b*, then thought to belong to *Megalosaurus* (Naish 2010). As both birds and pterosaurs are flying vertebrates, Seeley's assumption that an animal with postcranial skeletal pneumaticity (PSP) was closely related to, or even intermediate between, the flying vertebrate groups was perfectly sensible. We now know that PSP also occurs in sauropods, non-avian theropods and in some basal sauropodomorphs (Wedel 2006), and possibly also in some crocodile-line archosaurs (Gower 2001; Nesbitt & Norell 2006, p. 3). Sauropod pneumaticity has been subsequently studied by Longman (1933) and Janensch (1947), but thereafter remained largely overlooked until the more recent work of Britt (1993) and Wedel (2003*a*, *b*, 2005). A picture has now emerged of a complex range of vertebral pneumatic features, encompassing everything from gentle lateral depressions in basal sauropods such as *Barapasaurus* Jain *et al.* 1975, via large internal spaces in basal neosauropods such as *Camarasaurus* Cope 1877*a*, to the dense, irregularly honeycombed, internal structure of derived titanosaurs such as *Saltasaurus* Bonaparte & Powell 1980.

Stage 2: the emerging picture (1871–1896)

Understanding of sauropods took a giant leap forward with the description of *Cetiosaurus oxoniensis* Phillips 1871 (Fig. 2), a Middle Jurassic sauropod from England, described and illustrated in detail by Phillips in 50 pages of his book on the geology of Oxford and the Thames Valley. Phillips described remains from several localities, all near Oxford, and there is no compelling reason not to accept his assessment that they all belong to the same species. Most important are the associated remains of several individuals from Kirtlington Station, north of Oxford, of which the largest is

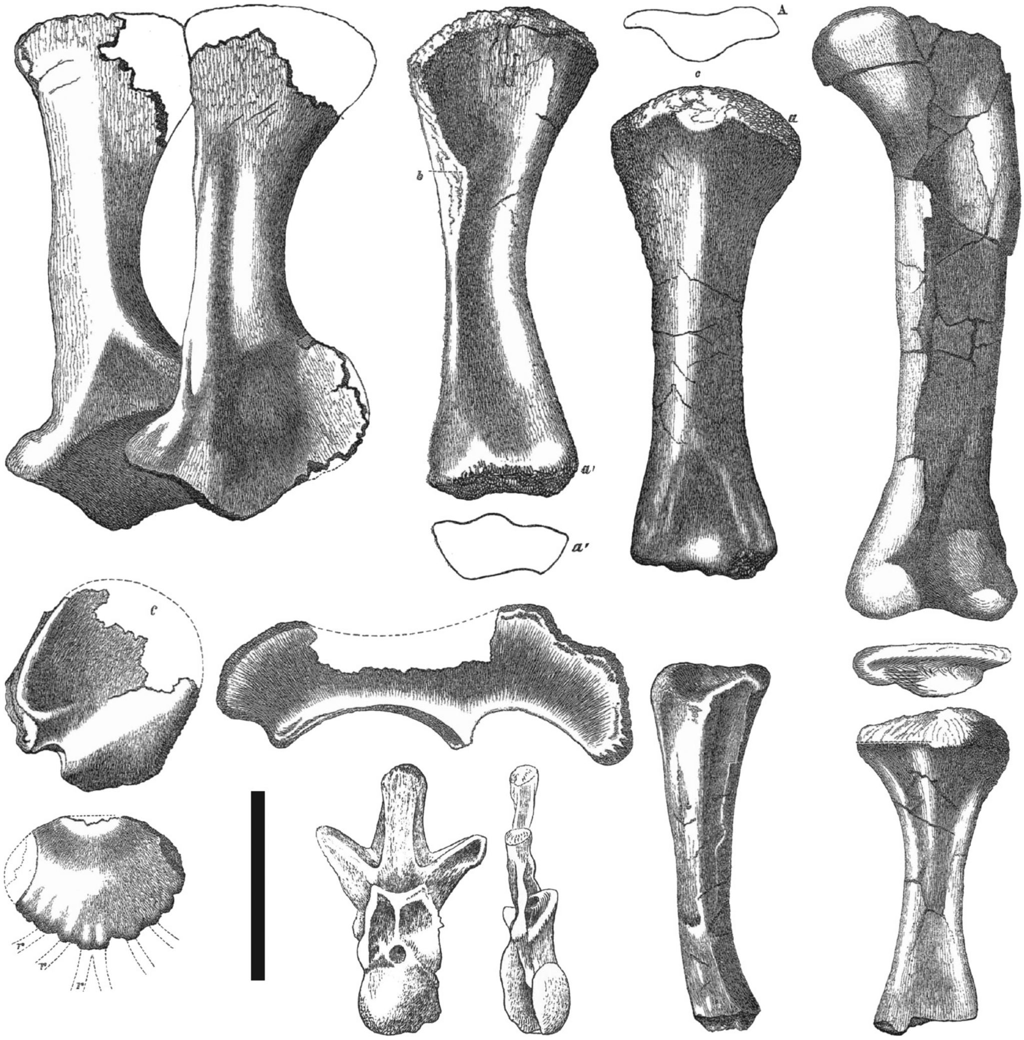

Fig. 2. Elements of *Cetiosaurus oxoniensis*. Top row, left to right: right scapula in lateral view and left scapula in medial view; right humerus in anterior and distal views, and left humerus in proximal and posterior views; left femur in anterior view. Bottom row, left to right: left coracoid in medial view and ?left sternal plate in ?dorsal view; right ilium in lateral view and ?fourth dorsal vertebra in anterior and right lateral views; ?right ulna in ?posterolateral view; right tibia in proximal and posterolateral views. Dorsal vertebra modified from Phillips (1871, fig. 86), other elements modified from Owen (1875*b*, figs 1–9), which were reproduced from Phillips (1871). The scale bar is 50 cm.

also the best represented and was accordingly nominated by Upchurch & Martin (2003, p. 216) as the lectotype. Material described and figured by Phillips included: a tooth; dorsal, sacral and caudal vertebrae; dorsal ribs; sternal plate, coracoids and scapulae; humeri and ulnae; ilium, pubis and ischium; femora, tibiae and fibula; metatarsals and pedal phalanges. The only parts of the skeleton not represented were the skull, cervical vertebrae, radius and manus – although recent work by Galton & Knoll (2006) has tentatively agreed with Woodward's (1910) and Huene's (1926) assignment of the isolated saurischian braincase OUMNH J13596 to *Cetiosaurus oxoniensis*. Given the lack of prior information about sauropods, Phillips's identification of the various bones was impressively accurate. He made only two errors: he interpreted the sole recovered sternal plate as a median element rather then as one of a pair; and he interpreted the ischiadic and pubic articular surfaces of the pubis and ischium, respectively, as articulating with the ilium. Phillips did not attempt a skeletal reconstruction – unfortunately, as it would have been of great historical importance.

Armed with all of this material, Phillips was able to envisage the sauropod body plan for the first time (although he could not have known about the long neck and small head), recognizing it as capable of terrestrial locomotion and possessing erect posture:

> all the articulations [of the limb bones] are definite, and made so as to correspond to determinate movements in particular directions, and these are such as to be suited for walking. In particular, the femur, by its head projecting freely from the acetabulum, seems to claim a movement of free stepping more parallel to the line of the body, and more approaching to the vertical than the sprawling gait of the crocodile.
>
> (pp. 293–294)

However, Phillips hedged his bets with regard to lifestyle, concluding that 'we have, therefore, a marsh-loving or river-side animal' (p. 294). Phillips was also first to suggest the dinosaurian affinities of *Cetiosaurus*, albeit tentatively:

> The [femur] is nearly straight, in this respect differing much from the crocodilian, and approaching towards the deinosaurian type
>
> (p. 280)

> 'a lizard of such vast proportions would seem to claim easy admission to the deinosaurians, and to take its place naturally with megalosaurus or iguanodon … but its fore-limbs are more crocodilian, its pelvic girdle more lacertilian, while its vertebral system is of a peculiar type'.
>
> (p. 291)

Phillips's work on *Cetiosaurus* marked a significant step forward, giving the first meaningful window on the morphology and ecology of a sauropod dinosaur. However, his work was to be largely superseded just six years later by a sequence of important announcements in 1877: the first recognized Gondwanan sauropod, *Titanosaurus* Lydekker 1877; the onset of the Bone Wars, with the descriptions of the sauropods *Camarasaurus*, *Apatosaurus* Marsh 1877*b*, *Atlantosaurus* Marsh 1877*b*, *Amphicoelias* Cope 1877*b* and *Dystrophaeus* Cope 1877*c*; and the first skeletal reconstruction of a sauropod.

Titanosaurus was named by Lydekker (1877) on the basis of a partial femur and two incomplete caudal vertebrae, and was diagnosed by only a single character – procoelous caudal vertebrae (i.e. having centra that are concave anteriorly and pronouncedly convex posteriorly). Although the original *Titanosaurus* material was from India, similar procoelous caudal vertebrae from other countries were subsequently referred to the genus, eventually resulting in a total of 14 species! It has since been shown by Wilson & Upchurch (2003, p. 152) that the type species of *Titanosaurus*, *T. indicus* Lydekker 1877 is invalid as it can no longer be diagnosed: the single diagnostic character identified by Lydekker, procoelous caudal vertebrae, is now recognized as synapomorphic of the much larger clade Titanosauria, which at the last count encompasses more than 50 valid genera. Lydekker's initial naming of *Titanosaurus* on the basis of this morphology remains historically significant, however, as not only the first recognition of the important group now known as Titanosauria but also as the first sauropod recognized from the Gondwanan supercontinent (Table 1).

The year 1877 also marked the beginning of the Bone Wars – a period of intense, aggressive competition between Othniel Charles Marsh and his great rival Edward Drinker Cope to find and name dinosaurs from the newly discovered Morrison

Table 1. *First sauropods named from each continent*

Continent	First named genus Earliest still valid	Author and date	Clade
Europe	*Cardiodon**	Owen (1841*a*)	?Cetiosauridae
	Cetiosaurus	Owen (1841*b*)	Cetiosauridae
North America	*Astrodon*	Johnston (1859)	Titanosauriformes
Asia	*Titanosaurus*[†]	Lydekker (1877)	Titanosauria
	Tienshanosaurus[‡]	Young (1937)	Eusauropoda
South America	*Argyrosaurus*	Lydekker (1893)	Titanosauria
Africa	*Algoasaurus*[§]	Broom (1904)	Sauropoda
	Tornieria	Sternfeld (1911)	Diplodocinae
Australasia	*Rhoetosaurus*	Longman (1926)	Sauropoda
Antarctica	(None named)		

*The type specimen of *Cardiodon* is lost and the referred specimen is not diagnosable.

[†] *Titanosaurus* was diagnosed by a character that now characterizes the large clade Titanosauria (see the text).

[‡] The Chinese genus *Helopus* Wiman 1929 predates *Tienshanosaurus*, but because the name *Helopus* was preoccupied by a bird, the genus was renamed *Euhelopus* Romer 1956.

[§] *Algosaurus* is not diagnosable.

Formation of the western United States (Colbert 1997). Besides such well-known non-sauropod dinosaurs as *Allosaurus* Marsh 1877*b* and *Stegosaurus* Marsh 1877*c*, this year saw the establishment of two classic sauropods in *Apatosaurus* and *Camarasaurus*, as well as the less well known sauropod genera, *Amphicoelias*, *Atlantosaurus* (probably synonymous with *Apatosaurus ajax* Marsh 1877*b*; Berman & McIntosh 1978, p. 11) and *Dystrophaeus* (probably a nomen dubium). Unfortunately, in their haste to beat each other to press, both Marsh and Cope published rushed and inadequate descriptions, often without illustrations, most of which would not be considered taxonomically valid if published today. Synonymies also abounded: for example, Marsh's genus *Atlantosaurus* was first published under the name *Titanosaurus montanus* Marsh 1877*a*, until Marsh became aware of Lydekker's slightly earlier use of this generic name, and so renamed it *Atlantosaurus*; and this is now thought to be probably synonymous with *Apatosaurus*, as is the slightly later *Brontosaurus* Marsh 1879. While the Marsh–Cope rivalry undoubtedly benefited palaeontology by catalysing work that would not otherwise have been done so quickly, the net results of this race were negative, yielding a set of specimens with very poor locality documentation and a trail of shoddy scientific work that had to be redone subsequently (Barbour 1890): so while, for example, Marsh is credited with the names *Apatosaurus* and *Brontosaurus*, most of his publications on these animals are now of purely historical interest, while the subsequent monographs on this genus by Riggs (1903*b*) and Gilmore (1936) are still widely used.

The year after the initial Morrison 'Dinosaur Rush', *Camarasaurus* became the first sauropod to be adequately figured (Cope 1878), but prior to this it had already been made the subject of the first attempt to reconstruct the skeleton of a sauropod: that of Dr John Ryder, executed in 1877 under the direction of Cope (Fig. 3a). Astonishingly, the reconstruction was life sized, 'over fifty feet in length' (Osborn & Mook 1921, p. 252), and was based on material from several individuals. Although it was exhibited at a meeting of the American Philosophical Society on 21 December 1877, and subsequently exhibited at the AMNH, it was not published until 37 years later (Mook 1914), and is now best known from the excellent reproduction in the monograph of Osborn & Mook (1921, plate LXXXII). In the light of subsequent work, Ryder's reconstruction can be seen to be replete with mistakes: the head is a complete fiction, the neck is too short, the vertebrae in the region of the pectoral girdle are coalesced like the sacrum, there are far too many dorsal vertebrae, the tail is clearly modelled on those of aquatic animals, being dorsoventrally tall for much of its length but not in the proximal region, and the manus does not at all resemble the correct arrangement in sauropods, with the distinctive vertical arcade of near-parallel metacarpals. Nevertheless, Ryder's work remains admirable in some respects: the animal depicted is immediately recognizable as a sauropod, having the distinctive long neck and erect posture, and the dorsal vertebrae are recognizable as those of *Camarasaurus*.

It was not until a year after Ryder's reconstruction that the group Sauropoda got its name – at the fourth attempt. Owen (1859*b*, pp. 164–165) had previously proposed the name Opisthocoelia for the group consisting of *Cetiosaurus* and *Streptospondylus* Meyer 1832, and as the first suprageneric taxon containing a genus now recognized as a sauropod, this name has some claim to priority. A second candidate name for this group, Ceteosauria [sic], was raised by Seeley (1874, p. 690) in a paper describing the partial dorsal neural arch of a stegosaur, which he misinterpreted as part of the braincase of a sauropod, but this name has been mostly overlooked. Marsh (1877*b*, p. 514) ignored both of these prior names and, instead, referred his genera *Atlantosaurus* and *Apatosaurus* to the new family Atlantosauridae, diagnosed by pneumatic vertebra and the absence of the third trochanter on the femur. Finally, the very next year, Marsh (1878*b*, p. 412) subsumed this family within yet another new taxon, Sauropoda:

> A well marked group of gigantic Dinosaurs ... has been characterized by the writer as a distinct family, Atlantosauridae, but they differ so widely from typical Dinosauria, that they belong rather in a suborder, which may be called Sauropoda, from the general character of the feet.

The name is a strange one, as the feet of sauropods do not resemble those of lizards, but it was quickly adopted. Marsh's diagnosis consisted of 10 characters and, while most of these are now known to be plesiomorphies characterizing a larger clade, two or three remain diagnostic. Marsh's name did not immediately win unanimous acceptance: Osborn (1898, p. 227) used the name Cetiosauria, listing 12 included genera that encompass diplodocoids, camarasaurs and titanosaurs; Riggs (1903*b*, pp. 166–169) discussed the names Opisthocoelia, Cetiosauria and Sauropoda in detail, concluding that 'the three terms are essentially co-ordinate and co-extensive. "Opisthocoelia" has priority, and is entitled to preference'; and Matthew (1915) also preferred the name Opisthocoelia. However, Hatcher (1903*b*, pp. 47–48) considered the name Cetiosauria 'of subordinal rank only' (i.e. less inclusive than Sauropoda), and also rejected Owen's Opisthocoelia on the grounds that 'it was

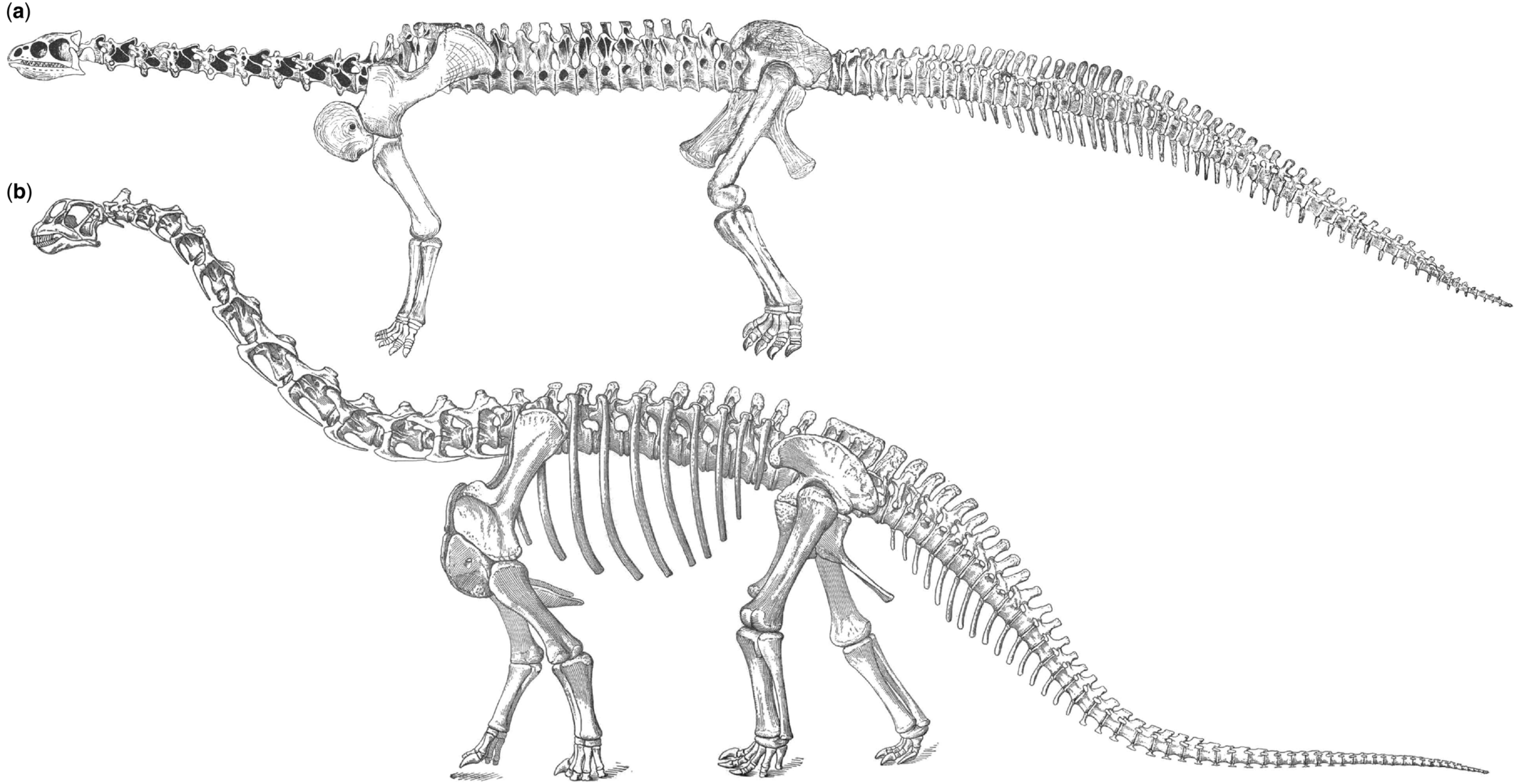

Fig. 3. Early reconstructions of *Camarasaurus*. Top: Ryder's 1877 reconstruction, the first ever made of any sauropod, modified from Osborn & Mook (1921, plate LXXXII). Bottom: Osborn & Mook's own reconstruction. modified from Osborn & Mook (1921, plate LXXXIV).

initially proposed as a suborder of the Crocodilia' and that Owen 'did not adequately define his proposed suborder and did not recognize its real relationships as being with the Dinosauria rather than the Crocodilia'. Instead, Hatcher (p. 48) concluded that 'Sauropoda, proposed and defined by Marsh . . . should be accepted as the first adequately defined name for this group of dinosaurs', and this usage has since been followed almost unanimously.

Diplodocus Marsh 1878*a* was described in the same year as the name Sauropoda was first used, and *Brontosaurus* a year later. Both would become the subjects of important developments: *Brontosaurus* as the first sauropod to be satisfactorily reconstructed and *Diplodocus* as the first sauropod for which a complete skull was described (Marsh 1884). Both would also become among the most iconic of sauropods owing to the discovery of complete or near-complete skeletons and the erection of famous mounts in museums around the world. Marsh (1883) reconstructed *Brontosaurus* far more accurately than Ryder had been able to do with *Camarasaurus* 6 years earlier, correctly depicting the anterior dorsals as not coalesced, reducing the trunk to 10 dorsal vertebrae, greatly increasing the height of the sacral neural spines, showing the tail as decreasing evenly in height along its length and wrapping the coracoids around the anterior part of the trunk (Fig. 4a). Marsh also gave a reasonably accurate estimate of the mass of *Brontosaurus* as 'more than twenty tons' (Marsh 1883, p. 82). Some important mistakes were made, though: most importantly, the wrong skull was used, based on that of a camarasaur (YPM 1911) rather than that of a diplodocid; only 11 cervical vertebrae were included, rather than 15; the forelimbs were posed in a strongly flexed posture, with the humeri at 25° and 55° from the vertical; and the manus was reconstructed as plantigrade, like the pes, rather than with a vertical arcade of metacarpals. Marsh's errors in the forelimb and manus resulted in the shoulder girdle, and hence the cervicodorsal transition, being much too low, and therefore in the neck leaving the shoulders anteroventrally so that even pronounced extension of the neck resulted only in the head being at the same height as the scapula. Eight years later, Marsh (1891) provided a revised reconstruction of *Brontosaurus* (Fig. 4b), but while this correctly increased the number of cervicals, it also incorrectly increased the dorsal count from 10 to 14, and failed to correct the skull even though the new reconstruction's skull was based on a different specimen, YPM 1986 (now USNM 5730), now thought to belong to *Brachiosaurus* Riggs 1903*a* (Carpenter & Tidwell 1998). Osborn (1899, p. 213) criticized Marsh's reconstructions for making the mid-dorsal vertebrae the highest point of the axial column rather than the sacrum, thereby relegating the tail to being 'an appendage of the body instead of an important locomotor organ of the body', and provided his own reconstruction of the posterior dorsals, sacrum and tail of *Diplodocus* (Osborn 1899, fig. 1), the only parts of that animal then available to him. (The articulation of the sauropod manus would not be properly understood until 21 years later, when Osborn (1904, p. 181) began a paper with the refreshingly honest statement, 'my previous figures and descriptions of the manus are all incorrect', and figured a correctly articulated manus.)

Having already named the first Gondwanan sauropod, the globe-trotting Englishman Richard Lydekker (1893) also named the first sauropods from South America, which has subsequently become a very important region for sauropods: two new species of his genus *Titanosaurus*, *T. australis* and *T. nanus*, and two new genera, *Argyrosaurus* and *Microcoelus*. Of these taxa, only *Argyrosaurus* remains valid, with *T. australis* having been referred to the new titanosaurian genus *Neuquensaurus* Powell 1992, and *Microcoelus* and *T. nanus* being nomina dubia (Powell 2003, p. 44; Wilson & Upchurch 2003, p. 140). Huene (1929*a*, fig. 10) would go on to provide the first reconstruction of a titanosaur; and, in the same year, Huene (1929*b*, p. 497) was also to provide what was probably the first life restoration of a titanosaur. This figure is remarkable not so much for the rather poorly proportioned main individual as for the sketch of two more individuals fighting in the background, one of them rearing on its hind legs.

Stage 3: interpretation and controversy (1897–1944)

By the end of the nineteenth century sauropod osteology was sufficiently well understood that it had become possible to make palaeobiological inferences. Three controversies have dominated discussions of sauropod palaeobiology ever since: habitat, athleticism and neck posture. Although early illustrations of sauropods used a variety of neck postures, the subject was not explicitly discussed until relatively recently, beginning with the work of Martin (1987). By contrast, arguments about habitat and athleticism date right back to Phillips's comments in his 1871 book.

Ballou (1897) included, as one of his six figures, the first published life restoration of a sauropod, executed by Knight under the direction of Cope (Fig. 5a). This illustration, subsequently republished by Osborn & Mook (1921, fig. 127), depicted four *Amphicoelias* individuals in a lake, two of them entirely submerged and two with only their heads

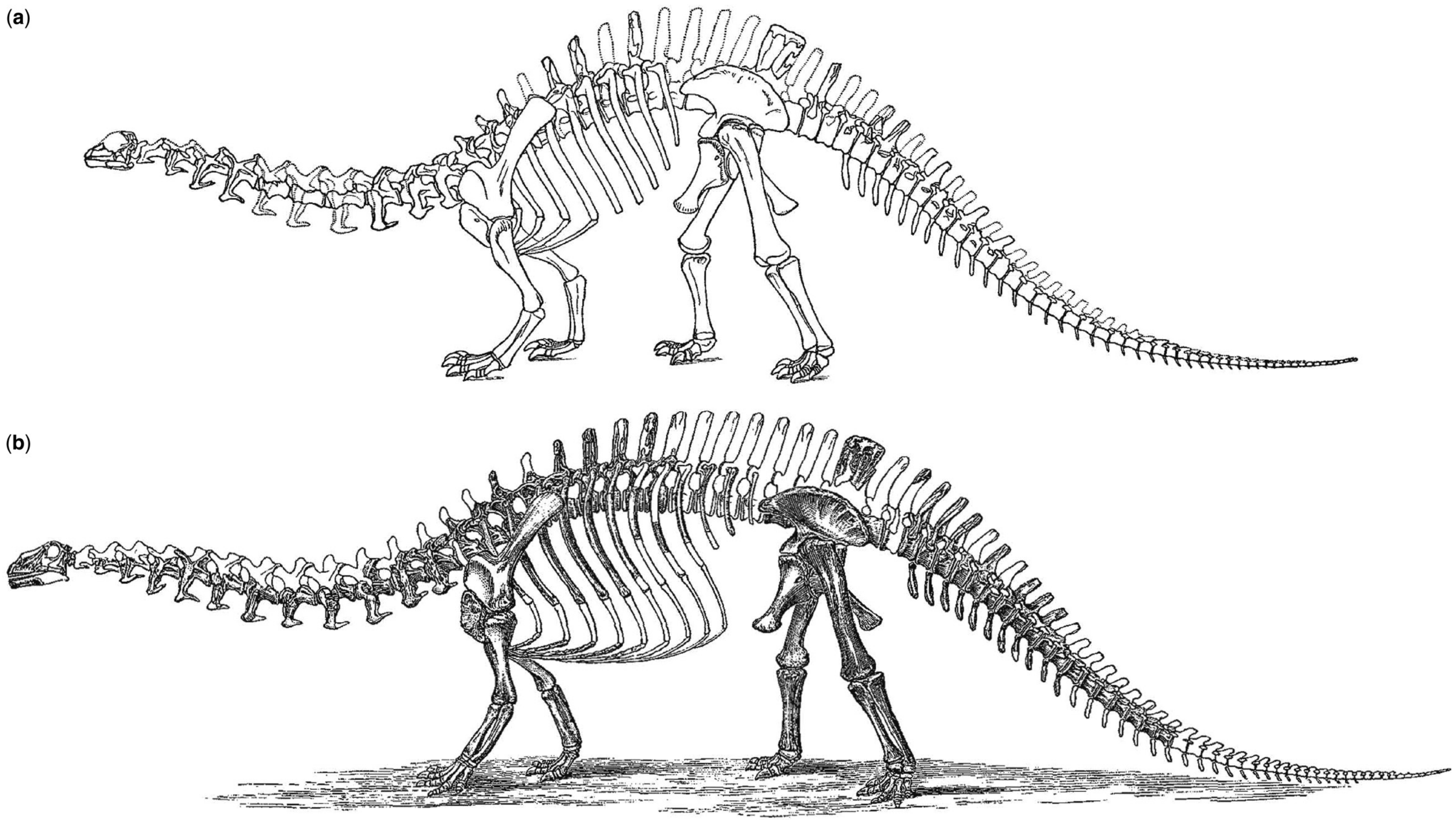

Fig. 4. Marsh's reconstructions of '*Brontosaurus*' (now *Apatosaurus*). Top: first reconstruction, modified from Marsh (1883, plate I). Bottom: second reconstruction, modified from Marsh (1891, plate XVI).

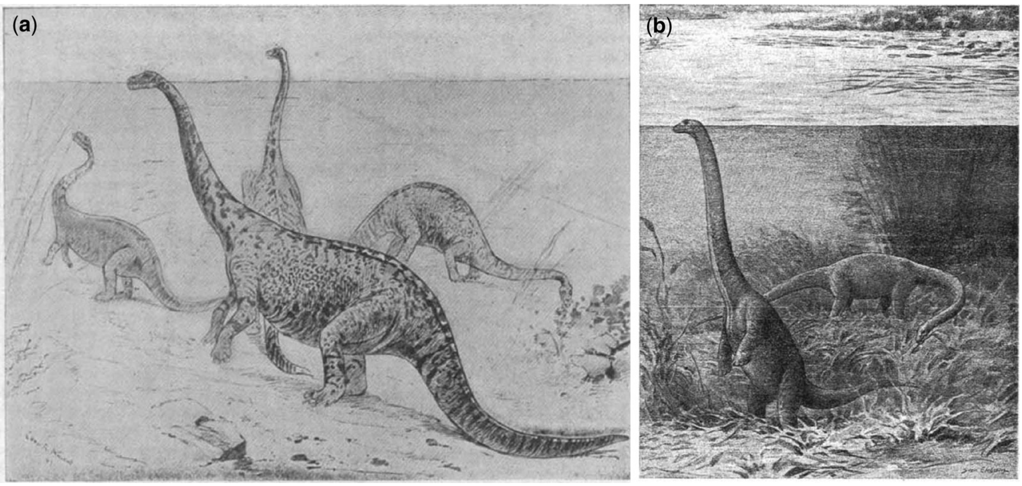

Fig. 5. Snorkelling sauropods. Left: the first-ever life restoration of a sauropod, Knight's drawing of *Amphicoelias*, published by Ballou (1897), modified from Osborn & Mook (1921, fig. 127). Right: a similar scene with '*Helopus*' (now *Euhelopus*), modified from Wiman (1929, fig. 5).

above the water. The skins were shown with a bold mottled pattern like that of some lizards, which would not be seen again in a sauropod restoration for the best part of a century.

Later the same year came what may still be the most immediately recognizable of all sauropod depictions: Charles Knight's 1897 painting of *Brontosaurus* (Fig. 6a), executed under the direction of Osborn and reproduced by Matthew (1905, fig. 4). The centrepiece of Knight's painting was an amphibious *Brontosaurus* in right anterolateral aspect, its legs, tail and most of its torso submerged, with its back projecting above the surface of the water and its neck nearly vertical. In the background, a *Diplodocus* grazed on the lake shore, shown in lateral view. Both animals were a uniform dull grey. Knight was unwittingly setting the template for how sauropods would be depicted for the next three quarters of a century, not least in the Jurassic part of Zallinger's mural (see later). In Knight's world, sauropods were clumsy, lumbering behemoths, barely able to support their weight out of water: even the terrestrial *Diplodocus*, lighter than its swamp-bound cousin, looks ponderous and inert. A dramatically different opinion, at least as regards *Diplodocus*, was offered by Osborn (1899,

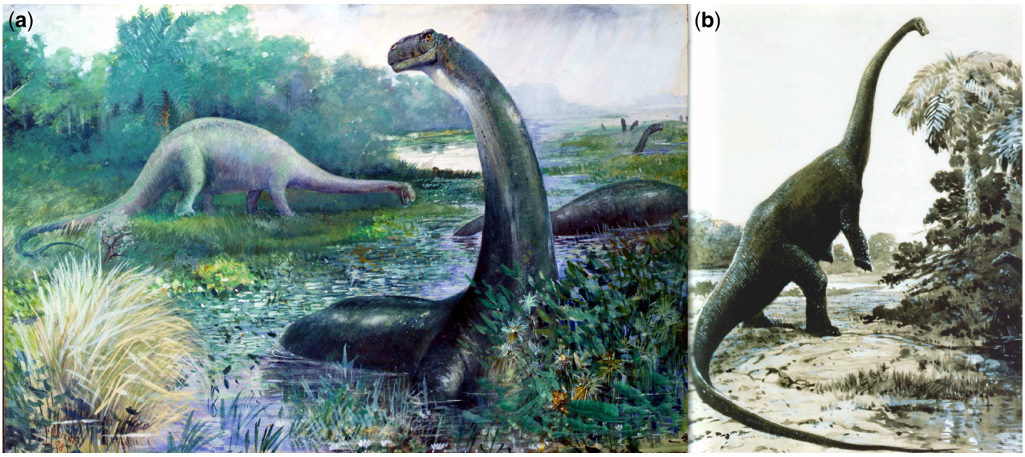

Fig. 6. Two classic sauropod paintings by Knight. Left: swamp-bound '*Brontosaurus*' (now *Apatosaurus*), painted in 1897, with static terrestrial *Diplodocus* in background. Right: athletic *Diplodocus*, painted in 1907.

pp. 213–214), who considered sauropods much more athletic and not restricted to an aquatic lifestyle – although still at least partially aquatic by habit:

> The animal was capable not only of powerful but of very rapid movements. In contrast with *Brontosaurus* it was essentially long and light-limbed and agile. Its tail was a means of defence upon land and a means of rapid escape by water from its numerous carnivorous foes.

Osborn also asserted that *Diplodocus* was capable of rearing to feed:

> the tail . . . functioned as a lever to balance the weight of the dorsals, anterior limbs, neck, and head, and to raise the entire forward portion of the body upwards. This power was certainly exerted while the animal was in the water, and possibly also while upon land. Thus the quadrupedal Dinosaurs occasionally assumed the position characteristic of the bipedal Dinosaurs – namely, a tripodal position, the body supported upon the hind feet and the tail.
>
> (p. 213)

Ironically, it was the same artist, Knight, who was to depict this more nimble *Diplodocus*, in his painting of 1907 (Fig. 6b), created as a cover image for *Scientific American* to celebrate the American Museum of Natural History's donation of one of its *Diplodocus* skeletons to the Senckenberg Museum in Frankfurt, Germany. In this painting, the animal is depicted with its torso raised about 60° from the horizontal, its forefeet raised to knee height and its neck high in the air – well above the foliage that it seems to be trying to eat, in fact. Even this athletic *Diplodocus*, however, is accompanied by the traditional aquatic counterpart, whose head and neck are visible peering into the frame from the body of water on the right of the picture.

One of the most important sauropod workers of the early twentieth century was Elmer S. Riggs of the Field Columbian Museum (now the Field Museum of Natural History, Chicago). Riggs (1903*a*) named and briefly described *Brachiosaurus*, which had been found by the expedition that he led to Grand Junction, Colorado in 1900. It was at that time the largest known dinosaur. In the same year as the description of *Brachiosaurus*, Riggs published an important monograph on *Apatosaurus* that argued that Marsh's genus *Brontosaurus* was synonymous with his own earlier *Apatosaurus*, and that the difference in the number of sacral vertebrae between the two genera was an ontogenetic character, the latter having been described from a juvenile specimen in which not all the sacral vertebrae had fused by the time of death (Riggs 1903*b*). Although Riggs's argument has since proven conclusive for most palaeontologists, so that the older name *Apatosaurus* takes priority over its junior synonym, the more euphonious and resonant name *Brontosaurus* continued to be used in scientific publication for some time after Riggs's work, and remains popular with the public even today (e.g. Chapman & Cleese 1989). The next year, Riggs (1904) published a full monographic description of *Brachiosaurus*, erecting the family Brachiosauridae to contain this genus and *Haplocanthosaurus* Hatcher 1903*a*. This work was also important for its forceful argument in favour of a terrestrial lifestyle for sauropods:

> There is no evidence among [sauropods] of that shortening or angulation of limb, or the broadening of foot, which is common to amphibious animals. Nor is there anything in the structure of the opisthocoelians [i.e. sauropods] which is not found in some terrestrial forms. The straight hind leg occurs in quadrupeds only among those forms which inhabit the uplands . . . The short, stout metapodials and blunted phalanges . . . would be as ill adapted for propulsion in water or upon marsh lands as are those of the elephant . . . In short, if the foot structure of these animals indicates anything, it indicates specialization for terrestrial locomotion.
>
> (pp. 244–245)

Riggs also argued that, while *Apatosaurus* and *Diplodocus* were capable of rearing on their hind limbs, *Brachiosaurus* would have found this much more difficult – a finding consonant with current thinking.

February 1905 saw the unveiling of the mounted skeleton of *Brontosaurus* at the American Museum of Natural History, its posture based on the results of dissections of alligators and other reptiles to elucidate the functioning of the joints (Matthew 1905). This mount, the first of a sauropod, consisted primarily of the remains of a single individual, AMNH 460, with some elements from AMNH 222, AMNH 339 and AMNH 592, and the remainder cast or modelled in plaster. Most important among these constructed elements was the *Camarasaurus*-like skull, modelled after the reconstructions of Marsh (1883, 1891) discussed above. Osborn's thoughts on *Brontosaurus* have not aged well: he estimated the mass of the mounted specimen as 'not less than ninety tons' (p. 64) and its age as 'some eight millions of years' (p. 66), and followed Owen and Cope in considering sauropods as 'spending their lives entirely in shallow water, partly immersed, wading about on the bottom or, perhaps, occasionally swimming, but unable to emerge entirely upon dry land' (p. 67), 'Hence we can best regard the *Brontosaurus* as a great, slow-moving animal-automaton' (p. 69). Based on the mounted skeleton, Knight modelled a 1:16 scale life restoration of *Brontosaurus*, illustrated by Matthew (1905, fig. 3), and, at Osborn's request, Gregory (1905) used this model to calculate the mass of *Brontosaurus* more rigorously, using the volume of water displaced by the model. Gregory's estimate of 38 tons was the first scientifically calculated mass estimate for a sauropod. While much better than Osborn's, the estimate is still rather high: this is partly because it was based on the assumption that *Brontosaurus* was 10% more dense than water – an assumption now known to be incorrect because of the increased understanding of the pneumatic cavities in the skeleton and soft tissue. Gregory's volume estimate was 31.13 m^3, which, using a density of 0.8 kg L^{-1} (Wedel 2005, p. 220), would yield a mass of 24 900 kg, corresponding well to more recent estimates such as 26 000 kg (Anderson *et al.* 1985) and 23 000 kg (Paul 1988*a*) for comparable specimens.

The AMNH *Brontosaurus* mount was followed only 3 months later by the second mounted sauropod, that of *Diplodocus carnegii* Hatcher 1901. The type and cotype specimen of this species (CM 84 and CM 94, respectively) had been discovered at Sheep Creek, Albany County, Wyoming, and collected by J.L. Wortman and O.A. Peterson in expeditions funded by Andrew Carnegie. Hatcher's (1901) description was based on both of these specimens, and included a skeletal reconstruction (Hatcher 1901, plate XIII) based primarily on these two individuals, but with the missing forelimbs provided by an AMNH specimen that subsequently proved to be from *Camarasaurus*. A cast of the combined skeleton was prepared under the direction of first Hatcher and then, after his death, Holland. At the request of King Edward VII, this was sent to the British Museum (Natural History) (BMNH) in London in January 1905, assembled there in April and unveiled on 12 May (Holland 1905, pp. 443–446). Further casts of the same material were subsequently sent to museums in Berlin, Paris, Vienna, Madrid, St Petersburg, Bologna, La Plata, Mexico City and Munich, and the original material mounted at the Carnegie Museum in 1907 (McIntosh 1981, p. 20); making this, perhaps, the single most viewed skeleton of any animal in the world.

The availability of the skeleton of *Diplodocus carnegii* provoked much speculation about its lifestyle. Hay (1908) proposed that it sprawled like a crocodile: 'The mammal-like pose attributed to the Sauropoda is one that is not required by their anatomy and one that is improbable' (p. 677); 'The weight of *Diplodocus* and *Brontosaurus* furnishes a strong argument against their having had a mammal-like carriage' (pp. 679–680); '*Diplodocus* ... could creep about on land, with perhaps laborious effort' (p. 681). Tornier (1909) also rejected Hatcher's mammal-like erect-legged posture for *Diplodocus*, despite its pedigree going all the way back to Phillips, in favour of an interpretation in which *Diplodocus* sprawled like a lizard. Tornier (1909, plate II) provided a bizarre skeletal reconstruction of *Diplodocus* (Fig. 7) in which the scapulae were vertical and articulated with the last cervical rather than the first few dorsals, the glenoid faced directly to the posterior with no ventral component, the radius and ulna formed an acute angle with the humerus, the tibia and fibula formed an acute angle with the femur, and the neck was so flexible that the fifth most proximal cervical was vertical, C6–C10 were inclined

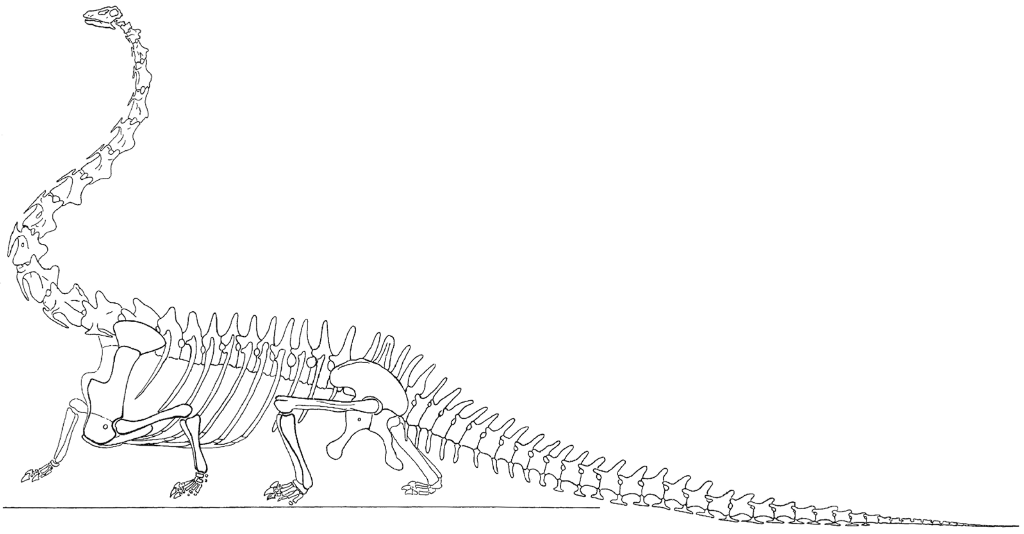

Fig. 7. Tornier's sprawling, disarticulated reconstruction of *Diplodocus*, modified from Tornier (1909, plate II).

backwards, and the skull was held directly dorsal to the shoulder. Hay (1910) reaffirmed and amplified his position, concluding his paper with a drawing by Mary Mason, executed under his instruction, that depicted four *Diplodocus* individuals. In the foreground, two individuals sprawl on dry land, one of them trailing its right leg painfully behind it. Further back, a nearly submerged individual swims towards them; further back still, a fourth lies absolutely flat on a distant shore, its neck, torso and tail all lying on the ground.

The unconventional posture suggested independently by Hay and Tornier was rebutted by Holland (1910), whose paper combined solid anatomical analysis with devastating sarcasm and rhetoric to convincingly demonstrate that the sprawling posture was impossible for *Diplodocus*, and other sauropods, to adopt:

> It was a bold step for [Tornier] immediately to transfer the creature from the order Dinosauria, and evidently with the skeleton of a *Varanus* and a *Chameleon* before him, to proceed with the help of a pencil, the powerful tool of the closet-naturalist, to reconstruct the skeleton upon the study of which two generations of American paleontologists have expended considerable time and labor, and squeeze the animal into the form which his brilliantly illuminated imagination suggested.
>
> (p. 262)

Holland demonstrated that Tornier's posture requires the greater trochanter of the femur to articulate with the ischiadic peduncle of the ilium, 'thus locking the femur into a position utterly precluding all motion whatsoever' and that it disarticulates the knee, leaving the distal articular surface of the femur unused, and the tibia and fibula articulating with the posterior edges of the condyles. He commented on Tornier's skeletal reconstruction that 'As a contribution to the literature of caricature the success achieved is remarkable' (p. 264). Holland (1910, fig. 9) showed that, were the Tornierian posture actually achieved, the chest and belly of *Diplodocus* would be much lower than its feet, so that it would have required deep grooves in the ground to walk along. Although Hay (1911) attempted to counter Holland's arguments, the debate was effectively over. Whatever doubt may have remained was dispelled by the description of a complete and articulated juvenile *Camarasaurus* by Gilmore (1925), which clearly showed that the posture advocated by Holland was correct, and by the fossilized sauropod trackways later described by Bird (1939, 1941, 1944).

The years 1909–1912 saw what was, perhaps, the most ambitious palaeontological undertaking in history: the German expeditions to collect fossils from the Tendaguru region of German East Africa (now Tanzania), under the leadership of Werner Janensch and, subsequently, Hans Reck (Maier 2003). The scale of the undertaking was immense: the Germans recruited 170 native labourers for the 1909 season, rising to 400 and then 500 in subsequent years. In total, 235 tonnes of fossils were shipped back to Germany, having been carried from Tendaguru to the port of Lindi in 5400 4-day-long marches. Much of this material remains unprepared nearly a century later, but the prepared specimens include some of the most spectacular sauropod material in the world, including the *Brachiosaurus brancai* specimen HMN SII (officially MB.R.2181), which is the largest known reasonably complete skeleton of any terrestrial animal. Other new sauropods recognized from the Tendaguru fossils include *Dicraeosaurus* Janensch 1914, *Tornieria* Sternfeld 1911, *Janenschia* Wild 1991, *Tendaguria* Bonaparte *et al.* 2000 and *Australodocus* Remes 2007 – all but the first of which were previously subsumed under the name *Gigantosaurus* Fraas 1908, which was abandoned when found to be a synonym of the nomen dubium *Gigantosaurus* Seeley 1869. The Tendaguru sauropods have a complex nomenclatural history that is only now being resolved (e.g. Remes 2006; Taylor 2009). These sauropods represent several groups: Brachiosauridae (*B. brancai*), Dicraeosauridae (*Dicraeosaurus*), Diplodocinae (*Tornieria* and *Australodocus*) and probably Titanosauria (*Janenschia* and *Tendaguria*, although the former may instead represent a camarasaurid or an apatosaurine, and the latter is enigmatic, known only from a few presacral vertebrae that do not closely resemble those of any other known sauropod). Together with the theropods, ornithopods and stegosaurs of Tendaguru, these taxa constitute one of the richest known dinosaur faunas – all the more amazing in light of the difficult working conditions in which the fossils were excavated and the scarcity of materials, such as plaster for jacketing. Janensch devoted much of his career to an exhaustive series of detailed monographs on the sauropods of Tendaguru (Janensch 1922, 1929*a*, 1935–1936, 1947, 1950*a*, 1961), so that his work on these sauropods spanned more than half a century. Between 1919 and 1930, the British Museum (Natural History) mounted a series of under-resourced expeditions to Tendaguru, but the results were disappointing, with only one good specimen recovered and even that not properly described. A very brief preliminary report was provided by the expedition leader, Migeod (1931), but a full description and analysis of this specimen is only now under way (Taylor 2005), with preliminary results suggesting that Migeod's specimen may represent yet another new taxon.

Matthew (1915) wrote the first book about dinosaurs for non-specialists, which included (fig. 24) the first attempt to reconstruct the skeleton of *Brachiosaurus*, based on both the American *B. altithorax* and the German *B. brancai* material. Given that it was executed only 1 year after Janensch's (1914) initial, brief report of the German brachiosaur material, this reconstruction is impressively accurate: it is instantly recognizable as *Brachiosaurus*, and has all the proportions essentially correct. Unfortunately, sauropods otherwise receive short shrift in Matthew's book, the relevant chapter of which consists primarily of a reprint of his own (1905) account of the mounting of the AMNH *Brontosaurus*, and includes a reproduction of Knight's 1897 *Brontosaurus* painting. The book undoubtedly helped to establish swamp-bound sauropods as conventional wisdom, despite the earlier opposite conclusions of Phillips (1871), Osborn (1899), Riggs (1904) and others. This perception, once established, would prove difficult to shake off.

The 1920s opened with the publication of the sauropod monograph that stands alone: the detailed redescription of *Camarasaurus* by Osborn & Mook (1921). In 141 pages, 127 stunningly detailed figures and 25 large plates, and working from excellent and abundant material, Osborn & Mook did in detail the work that Cope had rushed through so inadequately 40 years earlier (Fig. 3b). So exhaustive was their work that, nearly 90 years on, it remains the most comprehensive guide not only to *Camarasaurus* but to sauropod anatomy in general. The monograph also redescribed *Amphicoelias*, resolved some synonymies and other nomenclatural issues, and reproduced important earlier figures, including the pioneering 1877 *Camarasaurus* reconstruction of Ryder. While palaeobiological hypotheses have come and gone, and as papers that were once highly regarded are now seen as hopelessly wrong, Osborn & Mook's careful and comprehensive descriptive work remains as relevant as ever. Four years later, Gilmore (1925) described the marvellously preserved juvenile *Camarasaurus* CM 11338 in great detail, and was able to correct the vertebral formula and other minor errors of Osborn & Mook. Gilmore presented a skeletal reconstruction in his plate XVII, which was the first reconstruction of a sauropod based on the remains of a single individual. Also significant in the 1920s was the description of *Helopus* Wiman (1929), the first of many Chinese sauropods. Like Gilmore, Wiman was fortunate enough to work from material so complete that it would have been the envy of earlier workers such as Owen and Seeley: the skull, axial and appendicular elements are all figured in multiple views. Like *Amphicoelias* before it, *Helopus* was conceived as a snorkeler (Fig. 5b). (The name *Helopus* was preoccupied, and so this genus is now known as *Euhelopus* Romer 1956.)

Around 1930, during an economic slump in Germany precipitated in part by the Wall Street Crash, plans were made to mount the skeleton of the *Brachiosaurus brancai* type specimen HMN SII at the Humboldt Museum in Berlin (Maier 2003, pp. 260–268). Original plans to mount cast and replica bones were superseded by the yet more ambitious goal of using original bones (from SII and referred specimens) for all but the skull, the fragile presacral vertebrae and a few other minor bones. The Herculean effort took 7 years to complete, and the mounted skeleton was unveiled, to a backdrop of swastika banners, in August 1937 – the year after the Berlin Olympics and just 2 years before the start of World War II. The war would interrupt further work on the Tendaguru material so that it would be a further 13 years before a paper describing the skeletal mount could be published (Janensch 1950*b*).

Bird (1939, 1941, 1944) was the first to describe sauropod tracks from several sites, including Glen Rose and Davenport Ranch, both in Texas. Bird (1944, p. 65) noted that, at the Davenport Ranch site, all 23 individual trackways were headed in the same direction, and concluded 'this suggests that they passed in a single herd, an important conclusion, borne out by the consistency of the preserved tracks'. Equally significantly, despite assuming that the tracks were made on a stream bed, Bird (1944, p. 65) noted that:

> if the the smallest animals in the herd were wading, as the depth of their tracks indicates, then, by comparison, the larger creatures were progressing well out of water. The question 'Could *Brontosaurus* walk on land?' can be answered in all probability in the affirmative.

This evidence of a terrestrial lifestyle continued to be widely overlooked, however, as in Zdeněk Burian's widely reproduced 1941 painting of three snorkelling *Brachiosaurus* individuals – a painting that seems directly descended from Knight's 1897 *Amphicoelias* drawing. In the foreground and the background two of the animals are standing on the bottom of a lake, with only their heads and the anterior part of their necks protruding above water; between them, the third has lowered its neck to eat vegetation growing on the lake bed, and is entirely submerged. This kind of lifestyle was later proved impossible by Kermack (1951), who pointed out that snorkelling cannot be achieved by means of a long neck as water pressure would make it impossible to ventilate lungs below a certain depth.

Stage 4: the dark ages (1945–1967)

Understandably, little effort was put into palaeontology during World War II (1939–1945); more surprisingly, the study of dinosaurs, including sauropods, did not resume after the war, because dinosaurs were perceived as an evolutionary dead end, and mammal palaeontology was perceived as more interesting and important (Bakker 1975, p. 58). Despite the huge popular appeal of Rudolf F. Zallinger's gigantic *Age of Reptiles* mural at the Yale Peabody Museum, completed in 1947 and reproduced in *Life Magazine*'s 1952 series *The World We Live In*, it can only have helped reinforce the popular perception of dinosaurs in general, and sauropods in particular, as sluggish and unathletic. The Jurassic part of the mural, which contains its sauropods, owes a massive debt to Knight's 1897 *Brontosaurus* painting, both compositionally and in terms of the palaeobiology that it represents. Like Knight's image, Zallinger's has as its principal subject an amphibious *Brontosaurus*, in right anterolateral aspect, submerged to the shoulders in a lake and with its neck raised to a near-vertical posture. Also, like Knight's painting, the mural depicts a *Diplodocus* in the background, on land, in lateral view and with a horizontal neck. As with Knight, both sauropods are an undistinguished grey colour. Half a century of palaeobiological work had resulted in absolutely no visible progress in how sauropods were perceived. That Zallinger had a tendency to repeat himself as well as to recycle others' compositions was demonstrated by his 1966 painting of *Brachiosaurus*, published in Watson (1966, pp. 20–21). Once more, the principal subject was depicted in right anterolateral view, up to its shoulders in water, with a steeply inclined neck, in dull grey, and with a second sauropod (this time, another *Brachiosaurus* individual) shown in the background, standing on the shore of the lake. In both the Zallinger paintings, a small, red rhamphorynchoid pterosaur flies with the tip of its left wing in front of the principal subject's neck. Outdated ideas were further propagated by a stream of children's books, such as *The How and Why Wonder Book of Dinosaurs* (Geis 1960) with its grotesquely fat sauropods in poses recycled from the work of Knight.

Apart from work mentioned earlier (e.g. Janensch's monographs on the Tendaguru sauropods and Bird's work on tracks), little significant research was published on sauropods during this period. One exception was the recognition of the first rebbachisaurid, *Rebbachisaurus* Lavocat 1954, from Morocco, although this specimen has never been properly described; another was the description of *Mamenchisaurus* Young 1954, from China, although the extreme neck elongation in this genus would not be recognized until the subsequent description of the referred species *Mamenchisaurus hochuanensis* Young & Zhao 1972.

Of more general interest was the work of Colbert (1962) on dinosaur masses, the first systematic attempt to estimate and compare the masses of different dinosaurs. Colbert used a variation on the method of Gregory (1905), measuring the volumes of scale models by the amount of sand displaced, and multiplying up by the scale to determine the volume of the modelled animal and then by an estimated density of 0.9 kg l^{-1} to determine its mass. Colbert (1962, p. 10) obtained values of 27.87 and 32.42 tonnes for *Brontosaurus* (using two different models, of which he favoured the heavier), 10.56 tonnes for *Diplodocus*, and 78.26 tonnes for *Brachiosaurus* – the latter figure being widely quoted in popular books. Since Colbert's efforts, several further surveys have been made of the masses of various dinosaurs, among which those of Alexander (1985, 1989) and Anderson *et al.* (1985) are of particular interest – the former based on the volumes of models, and the latter based on regression equations that relate limb-bone measurements to mass in extant animals and which extrapolates them to yield the masses of sauropods whose limb bones are known. Mass estimation has progressed significantly in recent years, especially with the growing understanding of how important pneumaticity was for weight reduction. Table 2 presents a summary of the history of mass estimates for *Brachiosaurus brancai*, a much studied taxon owing to its large size and the existence of an excellent near-complete skeleton. Several trends are evident: first, the improvement in methods, from simple *gestalt* estimates via volume measurements of physical models to computer models; second, a tendency to assume lower densities in recent years; and third, generally decreasing estimates of volume owing to the use of more scientifically rigorous models than the grossly obese models available to the earlier studies. The net result of the last two of these is that modern estimates tend to be much lower than older ones, especially if the aberrant result of Gunga *et al.* (1995) is ignored because of its use of circular rather than elliptical conic sections in its model. This trend towards lower mass estimates also applies to other sauropods, although it is more difficult to quantify in the case of, for example, *Apatosaurus* owing to different authors' use of different specimens.

Stage 5: the modern renaissance (1968–present)

Having fallen into dormancy, dinosaur palaeontology reawakened dramatically as the 1960s closed. The beginnings of the 'dinosaur renaissance' (Bakker 1975) are usually attributed to the description of the bird-like theropod *Deinonychus* Ostrom 1969*a* and its full osteology (Ostrom 1969*b*), which pointed out many aspects of its anatomy indicative of an active lifestyle. However, the first shoots of revival had appeared a year earlier, in

Table 2. *Changing mass estimates for* Brachiosaurus brancai

Author and date	Method	Volume (l)	Density (kg/l)	Mass (kg)
Janensch (1938)	Not specified	–	–	'40 t'
Colbert (1962)	Displacement of sand	86 953	0.9	78 258
Russell *et al.* (1980)	Limb-bone allometry	–	–	13 618*
Anderson *et al.* (1985)	Limb-bone allometry	–	–	29 000
Paul (1988*a*)	Displacement of water	36 585	0.861†	31 500
Alexander (1989)‡	Weighing in air and water	46 600	1.0	46 600
Gunga *et al.* (1995)	Computer model	74 420	1.0	74 420
Christiansen (1997)	Weighing in air and water	41 556	0.9	37 400
Henderson (2004)	Computer model	32 398	0.796	25 789
Henderson (2006)	Computer model	–	–	25 922
Gunga *et al.* (2008)	Computer model	47 600	0.8	38 000
Taylor (2009)	Graphic double integration	29 171	0.8	23 337

*Russell *et al.* give the mass as '14.9 t', which has usually been interpreted as representing metric tonnes, for example, 14 900 kg. However, they cite 'the generally accepted figure of 85 tons' (p. 170), which can only be a reference to Colbert (1962). Colbert stated a mass of 85.63 US tons as well as the metric version, so we must assume that Russell et al. were using US tons throughout.

†Paul used a density of 0.9 kg L^{-1} for most of the model and 0.6 kg L^{-1} for the neck, which was measured separately and found to constitute 13% of the total volume, yielding an aggregate density of $(0.9 \times 87\%) + (0.6 \times 13\%) = 0.861$ kg L^{-1}.

‡Alexander did not state which *Brachiosaurus* species his estimate was for, only that it was based on the BMNH model. This model is simply stamped '*Brachiosaurus*'.

Bakker's article 'The Superiority of Dinosaurs', in the magazine of the Yale Peabody Museum (Bakker 1968). Bakker (1968, pp. 14–20) discussed sauropods specifically and at length, advocating a vigorous, endothermic, terrestrial lifestyle on the basis of limb articulations, torso shape, neck length and palaeoenvironmental evidence, and included a revolutionary life restoration (Bakker 1968, fig. 4) showing two individuals of *Barosaurus* Marsh 1890, heads held high and alert, striding briskly across dry land. It is difficult, 40 years on, to appreciate how radical this image seemed at the time: the visual impact of *Jurassic Park*, *Walking With Dinosaurs* and the new generation of palaeoartists has brought such images so firmly into the mainstream that Bakker's drawing no longer surprises. But against the then ubiquitous backdrop of swamp-bound, sluggish sauropods exemplified by the art of Knight, Zallinger and Burian, it was a remarkable departure. As indicated by the title of a subsequent paper (Bakker 1980) and a popular book (Bakker 1986), Bakker was preaching 'dinosaur heresies', and old views were not quick to change – for example, Weaver (1983) argued that *Brachiosaurus* would be physically unable to gather food quickly enough to support the metabolic demands of endothermy, although this study was flawed by its assumption that the head of *Brachiosaurus* was only the size of that of a giraffe; and Dodson (1990) continued to advocate ectothermy for sauropods, with correspondingly long lifespans of multiple centuries.

The first shots had been fired in the battle to bring sauropods out of the swamps, and Coombs (1975) provided many compelling arguments for sauropod terrestriality. In a careful study that found that some anatomical evidence was equivocal, Coombs found that the tall and relatively narrow sauropod torso both resembles that of terrestrial rather than amphibious extant species, and is mechanically optimized for load-bearing. Using this and several other lines of evidence (e.g. lack of secondary palate, weight reduction through pneumaticity, straight-limbed posture, compact feet and the terrestrial sediments in which sauropod remains occur), he concluded that sauropods were primarily terrestrial, although they probably spent some time in water – as do elephants.

McIntosh & Berman (1975) reconsidered the problem of the skull of *Apatosaurus*, which had long been thought, following the reconstructions of Marsh (1883, 1891), to resemble the robust skull of *Camarasaurus*. On reviewing the historical evidence concerning the large *Diplodocus*-like skull CM 11162, they concurred with the earlier suggestion of Holland (1915) that it belonged to *Apatosaurus*. This conclusion has now been widely accepted, although in Holland's time it had been rejected due to the disagreement of Osborn. It is widely believed that the use of the name *Apatosaurus* for the animal previously known as *Brontosaurus* is related to the recognition of the correct skull, but in fact no such connection exists.

Jensen (1985) formally described and named three new giant sauropods, although he had been referring to them informally in print since the late 1970s: *Supersaurus* Jensen 1985, *Dystylosaurus* Jensen 1985 and *Ultrasaurus* Jensen 1985. These attracted much media attention because of the enormous sizes attributed to them: in particular, *Ultrasaurus*, considered a brachiosaurid on the basis of a referred scapulocoracoid, was estimated to weigh as much as 180 tonnes (McGowan 1991, p. 118) – a ludicrously inflated estimate that was based on Colbert's (1962) 78 tonne estimate for *Brachiosaurus*, scaled for an animal 32% larger in linear dimension. Unfortunately, spectacular though they are, Jensen's finds have not proven to be all that he claimed. First, it became apparent that *Ultrasaurus* Jensen 1985 was a junior homonym of *Ultrasaurus* Kim 1983, and so it was given the rather inelegant replacement name *Ultrasauros* Olshevsky 1991. Next, Curtice *et al.* (1996) showed that the dorsal vertebra that was the holotype of *Ultrasauros* belonged to the same individual as the *Supersaurus* holotype, so that *Ultrasauros* was synonymized with *Supersaurus*. This meant that the brachiosaurid scapulocoracoid that had been considered to belong to *Ultrasauros* could not belong to the same animal as the diplodocid *Ultrasauros* = *Supersaurus*. Curtice *et al.* (1996) also showed that this scapulocoracoid was not larger than the largest Tendaguru brachiosaur specimens. Finally, Curtice & Stadtman (2001) showed that the *Dystylosaurus* holotype and only specimen, a dorsal vertebra, also belonged to the same individual as the *Supersaurus* holotype, so that this name became another junior synonym. In short, all of Jensen's three giant sauropods proved to be a single sauropod, with only the referred scapulocoracoid belonging to a different taxon. Nevertheless, *Supersaurus* remains a gigantic animal; its neck is longer than any other for which there is osteological evidence, probably about 15 m in length.

With the debate about sauropod terrestriality having been effectively settled by the mid-1980s, neck posture and flexibility became the next point of contention. From the early days of sauropod palaeontology, it had been assumed that the long necks of sauropods were flexible: for example, 'The slender skull ... was supported by a very long and flexible neck which permitted of an almost unlimited variety of movements throughout a considerable arc' (Hatcher 1901, p. 57). Skeletal reconstructions had shown necks held in a variety of postures. Horizontal and near-horizontal postures had been illustrated by, among others, Ryder for his 1877 *Camarasaurus*, Marsh (1883, 1891) for *Brontosaurus* (= *Apatosaurus*), Hatcher (1901, plate XIII) for *Diplodocus* and Gilmore (1936, plate XXXIV) for *Apatosaurus*. Upward-inclined and near-vertical necks had been depicted by Osborn & Mook (1921, plate LXXXIV) for *Camarasaurus*, Wiman (1929, fig. 3) for *Helopus* (= *Euhelopus*), Janensch (1950*b*, plate VIII) for *Brachiosaurus brancai* and Bakker (1968, fig. 4) for *Barosaurus*. However, as it was generally assumed that sauropod necks were very flexible, it is not clear how much importance these authors attached to the illustrated postures: they probably considered each illustrated posture to be just one of many that were habitually adopted. In contradiction to this, Martin (1987), having investigated the range of motion between adjacent cervical vertebrae during the mounting of the Rutland specimen of *Cetiosaurus* at the Leicester City Museum, concluded that the neck would have been much less flexible than previously assumed – only just able to lower the head to the ground and only able to lift the head about 1 m above shoulder height. Martin also found horizontal flexibility to be limited to only a 4.5 m arc. These findings were later corroborated by the work of Stevens & Parrish (1999) on DinoMorph. a computer program for modelling such articulations digitally. Stevens & Parrish (1999, p. 799) found that both *Apatosaurus louisae* CM 3018 and *Diplodocus carnegii* CM 84 were limited in their ability to raise their heads, but that their osteology did not prevent them from lowering their heads well below ground level – an adaptation that they interpreted as facilitating browsing on aquatic plants from the shore. This interpretation has been opposed by, among others, Paul (1998), who disputed the morphological evidence; Upchurch (2000), who pointed out that the *Apatosaurus* reconstruction was based on badly damaged vertebrae; Christian & Heinrich (1998) and Christian & Dzemski (2007), who argued from the pattern of stresses in the intervertebral joints that *Brachiosaurus brancai* held its neck erect; and Taylor *et al.* (2009), who argued from the behaviour of extant tetrapods that sauropods held their necks raised rather than in neutral pose. The issue is not yet settled.

The release of the film *Jurassic Park* in 1993 marked a turning point in public perception of dinosaurs, and particularly sauropods. Until then, the dinosaur renaissance of Bakker, Ostrom and others, while challenging the traditional views of palaeontologists, had had little impact on non-specialists. The terrestrial and athletic *Brachiosaurus* that is the first dinosaur clearly seen in the film brought this revolution to a far wider audience. Similarly, the depiction of sauropods in the BBC's 1999 documentary series *Walking with Dinosaurs* helped to publicize new ideas, including both the relatively inflexible and horizontal necks advocated by Stevens & Parrish, and rearing in order to feed and to mate. Subsequent films, including the *Jurassic Park* sequels, and TV programmes, including *When Dinosaurs Roamed America*, have continued to present a view of sauropods that is largely in keeping with current thought.

The evolutionary relationships of sauropods were very poorly understood up until the mid-1990s, and their classification had not progressed beyond the establishment of a handful of families – Diplodocidae, Brachiosauridae, Titanosauridae, Cetiosauridae – whose content was unstable, and whose interrelationships were obscure and, indeed, largely unexplored. For example, the evolutionary diagram of Bonaparte (1986) consisted only of a Prosauropoda block leading to a central block representing Cetiosauridae, and with branches leading from it to further undifferentiated and unrelated blocks for Brachiosauridae, Camarasauridae, Diplodocidae and Dicraeosauridae. Against this backdrop, Russell & Zheng (1993) performed the first phylogenetic analysis on sauropods as part of their paper describing the new species *Mamenchisaurus sinocanadorum* (Russell & Zheng 1993). Their analysis consisted of only 21 characters applied to nine taxa, and produced a tree that, in light of more recent work, appears wrong in placing the basal eusauropods *Mamenchisaurus*, *Omeisaurus* Young 1939 and *Shunosaurus* Dong *et al.* 1983 as closely related to the diplodocoids *Dicraeosaurus* and *Apatosaurus*. However, their analysis was quickly followed by others using more characters and taxa, notably those of Upchurch (1995), using 174 characters and 27 taxa; Upchurch (1998), using 205 characters and 26 taxa; Wilson & Sereno (1998), using 109 characters and 10 taxa; Wilson (2002), using 234 characters and 29 taxa; and Upchurch *et al.* (2004), using 309 characters and 47 taxa. The results of Wilson's and Upchurch's independent series of analyses are largely in agreement, with only the position of *Euhelopus* and the nemegtosaurids differing greatly between them. A subsequent collaboration between the authors of these studies (Wilson & Upchurch 2009) has established a consensus phylogeny, in which a sequence of basal sauropods leads to the great clade Neosauropoda, which comprises Diplodocoidea (Diplodocidae, Dicraeosauridae and Rebbachisauridae) and Macronaria (Camarasauridae, Brachiosauridae and Titanosauria). Although some work remains to be done, this basic structure now seems quite well established.

The advent of rigorous phylogenetic methods has dramatically affected the field of sauropod palaeontology by placing classification on a sound theoretical basis and making it possible to trace the evolution of particular features. Before the pioneering studies of the early and mid-1990s, much sauropod work was undertaken by non-specialists, and ideas about the group's classification were arbitrary and often contradictory. Since then, the establishment of a consensus on sauropod phylogeny has made it possible for the first time to carry out meaningful work on palaeobiogeography, diversity and palaeoecology, and these opportunities have attracted a crop of specialist workers who continue to expand the boundaries of sauropod science.

Until relatively recently, discussions on of the feeding strategy of sauropods have been speculative and dominated by then-prevailing ideas about sauropod habitats – hence, the claim of Hatcher (1901, p. 60) and many others that sauropods subsisted on 'tender, succulent aquatic or semi-aquatic plants'. This began to change in 1994, with the publication of two papers in the same volume (Barrett & Upchurch 1994; Calvo 1994) on feeding mechanisms. These papers established the modern approach by forsaking analogies with extant megaherbivores, instead relying on the direct evidence of functional anatomy, tooth wear and stomach contents when available. These and subsequent studies have yielded a consensus view that sauropods used minimal oral processing, although various groups seem to have differed in details of feeding strategy.

Chiappe *et al.* (1998) reported the first known sauropod embryos, those of titanosaurs, from the Auca Mahuevo site of Patagonia. The site covers more than 1 km^2 and has furnished many hundreds of specimens – for example, 200 whole eggs in a single 25 m^2 area (Chiappe *et al.* 2000). The preservation of the embryos is also excellent, including skin as well as bone, and articulated near-complete skulls (Chiappe *et al.* 2001), the first known from any titanosaur.

Curry (1999) applied the techniques of bone histology to sauropod remains for the first time, yielding insights into the growth history of *Apatosaurus*. By sampling bones from juvenile, sub-adult and adult specimens, she determined that growth was rapid and not seasonal, and that near-adult size was attained in about 10 years. Sander (2000) analysed the microstructure of a wide selection of bones from four different Tendaguru sauropods, and was able to demonstrate that the bones of different taxa can be differentiated on histological features alone. He also found two distinct types of histology in the bones of '*Barosaurus*' *africanus* Fraas 1908 (probably *Tornieria* sensu Remes 2006), which he tentatively interpreted as representing sexual dimorphism.

The recognition and description of new sauropod taxa has continued and accelerated in recent years, with significant new genera including *Rapetosaurus* Curry Rogers & Forster 2001, from Madagascar, a titanosaur much more complete than any known up until that time. The association of its skull with an unquestionably titanosaurian postcranial skeleton finally established the nature of titanosaur skulls, and resolved the phylogenetic position of nemegtosaurids as titanosaurs closely related to *Rapetosaurus*.

Today and tomorrow

As with other dinosaurs (Taylor 2006), the rate at which new sauropods are being recognized, described and named is far greater now than at any previous time. Of the 137 valid sauropod genera known at the end of 2006, more than half had been named in the previous 13 years, and all six of the most fruitful years have fallen since 1999. Figure 8 shows the rate of accumulation of valid sauropod genera, broken down by clade and in total. The general trend is towards exponential growth – not a trend that can be maintained indefinitely, but one that shows no signs of slowing yet. While brachiosaurid and diplodocid genera began to accumulate early in the history of sauropod palaeontology, it is only relatively recently that recognized titanosaur diversity has begun to climb, primarily due to the growth of work in South America. Titanosauria now represents one third of valid sauropod genera, whereas of the 20 valid sauropod genera that had been named by 1921 only a single titanosaur genus had been named that is still considered valid today, *Argyrosaurus*. (*Titanosaurus* and *Microcoelus* had also been named, but are no longer considered valid.)

Not only is sauropod diversity rising steeply, so is sauropod disparity – that is, the degree of morphological variation between different sauropods. The sauropod body plan has traditionally been described as conservative, but this prejudice is breaking down in light of the many bizarre forms

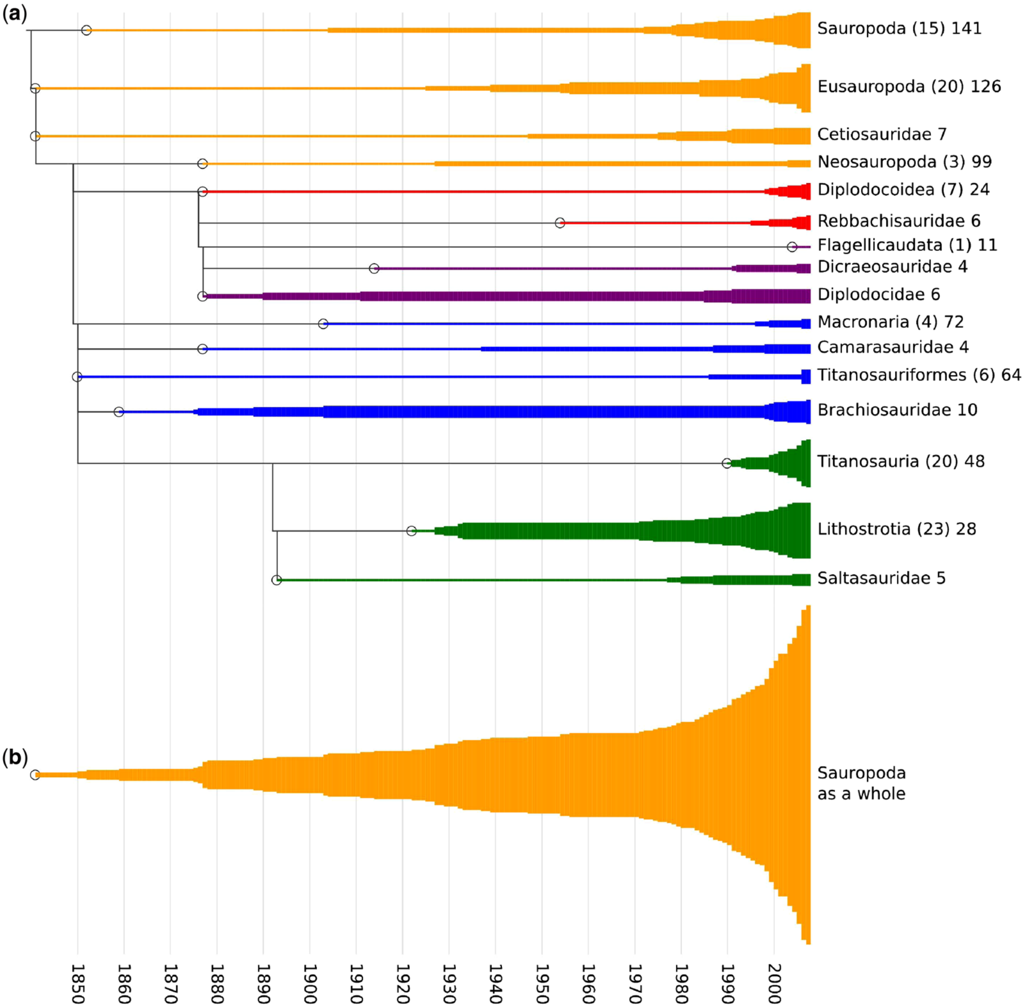

Fig. 8. Growing recognition of sauropod diversity through history. Only genera now considered valid are included. (**a**) Broken down by clade. The vertical thickness of the lines is proportional to the number of genera; the earliest valid genus in each clade is marked by a circle. Terminal clades have simple counts; for non-terminal clades, parentheses enclose the number of basal genera, that is, not members of depicted subclades, and are followed by total counts that include those of all subclades. (**b**) Total recognized diversity.

that have been described in recent years. These include the following.

- *Amargasaurus* Salgado & Bonaparte 1991 is an Argentinian dicraeosaurid with enormously elongated forked neural spines on the cervical and dorsal vertebrae. These spines may have appeared in life as individual spikes or may have supported long, tall, parallel sails.
- *Nigersaurus* Sereno *et al.* 1999 is an African rebbachisaurid whose well-preserved skull has a distinctive dentary with a completely straight, transversely oriented tooth row, extending further laterally than the posterior part of the skull does. The skull is also extraordinarily lightly built, even by sauropod standards (Sereno *et al.* 2007, fig. 1E).
- *Agustinia* Bonaparte 1999 is an armoured sauropod from Argentina, with spiked dorsal osteoderms that would have made the animal somewhat resemble *Stegosaurus*. Bonaparte found *Agustinia* so distinctive that he raised the new monogeneric family Agustiniidae to contain it, although it is probably a titanosaur.
- *Tendaguria*, from the Tendaguru Formation of Tanzania, is represented by only two dorsal vertebrae, one of which was figured by Janensch (1929*b*, fig. 11) as '*Gigantosaurus*' *robustus* Fraas 1908. They are unique in having neural spines so low as to be all but absent, so that they are much broader than they are tall. Bonaparte *et al.* (2000, p. 47) considered these vertebrae sufficiently distinct to merit another monogeneric family, Tendaguriidae, perhaps related to Camarasauridae.
- *Brachytrachelopan* Rauhut *et al.* 2005 is an Argentinian dicraeosaurid unique among known sauropods in having a proportionally short neck, so that in profile it more closely resembles an ornithopod than a classic sauropod.
- Conversely, *Erketu* Ksepka & Norell 2006 seems likely to have had the proportionally longest neck of any known sauropod, as the anterior cervical vertebrae from which it is principally known are more elongate even than the mid-cervicals of *Sauroposeidon* Wedel *et al.* 2000.
- *Europasaurus* Mateus, Laven and Knötschke in Sander *et al.* 2006 is a German titanosauriform somewhat resembling *Brachiosaurus*, except in its diminutive size: it is the smallest of all known sauropods, with adults measuring up to 6.2 m and weighing, perhaps, 500 kg – about the mass of a cow.
- At the other end of the size scale, *Futalognkosaurus* Calvo *et al.* 2007 joins its fellow Argentinian titanosaurs *Argentinosaurus* Bonaparte & Coria 1993 and *Puertasaurus* Novas *et al.* 2005 as one of the largest known sauropods. All three of these animals would have massed in the region of 50–100 tonnes.
- *Xenoposeidon* Taylor & Naish 2007, a British neosauropod, is known from a single partial dorsal vertebra, but has several features unique among all sauropods (e.g. neural arch is taller than centrum, covers dorsal surface of centrum, slopes forward by 35° and has featureless areas of unlaminated flat bone on its lateral surfaces). *Xenoposeidon* may represent a major new group of sauropods, of which further specimens are greatly to be desired.

The study of sauropods has come a long way since Owen named the tooth of *Cardiodon* 169 years ago, and the future looks very bright: with new sauropods being named at an ever-increasing rate, new techniques being applied to their study and old specimens being re-evaluated in the light of new knowledge, our understanding of sauropod morphology, ecology and phylogeny seems set to grow in richness and scope for the foreseeable future. At the same time, a great deal of work remains to be done. New specimens are being found and excavated more quickly than they can be described, and many sauropods named in recent years still await the monograph to follow up an often inadequate preliminary description. Also, many historical genera are long overdue for revision: for example, no modern analysis exists of the various species of *Diplodocus* or *Camarasaurus*. Much is being done, and much must be done in the future. Although they have been dead for 65 Ma, history continues to roll relentlessly on for sauropods.

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