

***In vitro* digestibility of fern and gymnosperm foliage: implications for sauropod feeding ecology and diet selection**

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Sauropod dinosaurs, the dominant herbivores throughout the Jurassic, challenge general rules of large vertebrate herbivory. With body weights surpassing those of any other megaherbivore, they relied almost exclusively on pre-angiosperm plants such as gymnosperms, ferns and fern allies as food sources, plant groups that are generally believed to be of very low nutritional quality. However, the nutritive value of these taxa is virtually unknown, despite their importance in the reconstruction of the ecology of Mesozoic herbivores. Using a feed evaluation test for extant herbivores, we show that the energy content of horsetails and of certain conifers and ferns is at a level comparable to extant browse. Based on our experimental results, plants such as *Equisetum*, *Araucaria*, *Ginkgo* and *Angiopteris* would have formed a major part of sauropod diets, while cycads, tree ferns and podocarp conifers would have been poor sources of energy. Energy-rich but slow-fermenting *Araucaria*, which was globally distributed in the Jurassic, was probably targeted by giant, high-browsing sauropods with their presumably very long ingesta retention times. Our data make possible a more realistic calculation of the daily food intake of an individual sauropod and improve our understanding of how large herbivorous dinosaurs could have flourished in pre-angiosperm ecosystems.

Keywords: herbivorous dinosaurs; Mesozoic food plants; herbivory; nutrition

1. INTRODUCTION

Many attempts have been made to reconstruct the nutritional ecology of dinosaurian megaherbivores such as the giant sauropod *Brachiosaurus brancai*, but all are hampered by the tremendous body weights (BW) of up to 70 t (Mazzetta *et al.* 2004) in combination with a restriction of potential food plants to pre-angiosperm taxa until the Mid-Cretaceous (Weaver 1983; Farlow 1987). Both factors push sauropods out of the ecological framework that has been established for extant herbivores (Van Soest 1994). In principle, an increase in body size has been considered beneficial with regard to digestive capacity (see Clauss *et al.* 2007 for a review and revision); however, it also implies different constraints such as a very high absolute energy requirement or a low degree of selectivity (Owen-Smith 1988).

The kinds of food plants that were available is another major difference between extant herbivores and sauropods. While it was recently reported that sauropods ingested grass during the Late Cretaceous (Prasad *et al.* 2005), their food plants must have consisted exclusively of ferns, fern allies, such as horsetails, and gymnosperms during most of their existence, namely in the Late Triassic, throughout the Jurassic and into the Early

Cretaceous. Nevertheless, it is commonly believed that all non-angiosperm forages are of exceptionally low nutritional quality (Coe *et al.* 1987; Wing & Tiffney 1987; Van Soest 1994; Taggart & Cross 1997; Midgley *et al.* 2002; Farlow 2007). Furthermore, palaeobotanists have hypothesized that herbivorous dinosaurs preferred soft-tissued plants such as ferns, ginkgoes and the extinct Cheirolepidiaceae over the woodier, spinier and phytochemically less palatable conifers (Coe *et al.* 1987; Tiffney 1997), and others have advocated ferns as the prime sauropod food (Dodson 1990; Taggart & Cross 1997). Krassilov (1981) put forth ferns and horsetails as diplodocid and cycads and conifers as camarasaurid food plants. Based on the reconstructions of the sauropod neck position, Stevens & Parrish (2005) state that only brachiosaurids and camarasaurids would have been able to feed on tall trees, while other taxa should have focused on low-growing ferns and fern allies. By contrast, Fiorillo (1998) dismissed ferns and horsetails as suitable food plants for sauropods due to the lower gross energy content of these plants, while Engelmann *et al.* (2004) accepted ferns and horsetails as the sauropod fodder, despite their presumed low energy content. It should be noted here that this energetic ranking of taxa was based on gross energy measurements by Weaver (1983) on extant relatives of potential sauropod food plants. However, using gross energy measurements as an estimate of the energy available

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Table 1. Nutrient and metabolizable energy (ME) contents of potential dinosaur food plants. (ME for the data of Weaver (1983) was calculated by multiplying gross energy with a factor of 0.5 (digestible energy, according to Weaver 1983), and consequently with a factor of 0.76 to obtain ME (according to Robbins 1993). Gp, gas production; DM, dry matter; NDF, neutral detergent fibre.)

sample type (no. of spp.)	ME (Gp at 72 hours) (MJ kg ⁻¹ DM)	ME (Weaver 1983)	crude protein (% DM)	NDF
grasses (16)	11.3 (9.3–13.6)		15.3	62.8
forbs (11)	10.4 (9.1–11.9)		19.8	37.8
dicot browse (13)	7.5 (5.5–10.0)		20.7	43.2
<i>Ginkgo</i> (1)	8.6	6.7	15.6	27.5
Araucariaceae (5)	9.4 (8.0–11.6)	7.0	4.4	65.2
Podocarpaceae (3)	5.9 (5.0–6.1)		6.6	62.3
various conifers (13)	8.3 (6.3–10.8)	7.0 (6.4–7.5)	10.0	51.3
cycads (7)	6.1 (4.4–7.7)	7.6 (7.1–8.6)	11.4	65.3
various ferns (9)	7.7 (4.7–11.7)	6.6 (5.4–7.4)	11.5	62.8
tree ferns (5)	6.4 (3.6–9.3)	6.9 (6.6–7.2)	11.3	63.6
<i>Equisetum</i> (3)	11.6 (10.8–12.9)	5.3	11.7	48.4

to herbivores, e.g. metabolizable energy (ME), may not yield accurate or even reasonable results for the plant material (GfE 2003). The example of coal explains the concept: coal is high in combustion energy, but its energy is virtually indigestible and hence inaccessible to animals.

Standard feed evaluation techniques, such as *in vitro* fermentation methods, make possible a 'semi-biological' estimation of the energy content of leafy plant tissue available to herbivores (= degradability; Van Soest 1994). The application of this approach to sauropods here was made on the grounds that most authors agree that the basic physiological and anatomical set-up of fibrous plant digestion in herbivorous dinosaurs followed the same general rules as in extant herbivores with a gut fermentation chamber (Farlow 1987; Dunham *et al.* 1989; Marshall & Stevens 2000; Mackie 2002). Specifically, the energy yield from the fibrous plant material is determined by the rate and extent of its digestion and fermentation (plant factors), in combination with the duration of retention in the digestive tract (animal factor; Waldo *et al.* 1972; Van Soest 1994), and not by the biological affinity of the herbivore. The use of a standardized inoculum, namely from a mammalian donor, is acceptable here, as the gut microbe populations of different herbivores are comparable in their biochemical characteristics (Van Soest 1994). In other words, in regard to the metabolic energy yield, it is secondary whether the microbial process occurs in the gut of an herbivorous reptile, bird or mammal.

The aim of our study is to estimate the nutritional quality of the extant relatives of potential sauropod food plants in regard to energy content using modern feed evaluation techniques. Comparison of the experimental data is used here to deduce sauropod food preferences and to shed light on the general nutritional ecology of herbivorous dinosaurs.

2. MATERIAL AND METHODS

Foliage samples of nearest living relatives of major plant groups in the Mesozoic were taken, some of which are identical to their Mesozoic relatives at the genus level. These included *Equisetum*, ferns such as the Dicksoniaceae, Matoniaceae and Osmundaceae, cycads, *Ginkgo* and conifers such as the Araucariaceae, Podocarpaceae and Taxodiaceae.

Angiosperm forage groups (browse, forbs and grasses) were included for reference (Hummel *et al.* 2006), and the results of the living Mesozoic flora were ranked within this framework.

Foliage was collected between May and July 2004 from botanical gardens and parks in Germany. In the laboratory, the samples were dried at 60°C and milled through a 1 mm sieve in preparation for experimental trials using an *in vitro* fermentation method, a modified Hohenheim gas test (Menke *et al.* 1979). The microbes were obtained from the rumen liquid of sheep fed on a standardized diet. The milled plant tissue was weighed in airtight glass syringes and placed in an incubator at 39°C for 72 hours. Gas production (Gp) was recorded after 4, 8, 12, 24, 32, 48, 56 and 72 hours. The gas produced during the fermentation represents a measure of feed degradation and consists of nearly equal parts of the CO₂ evolving from the buffer (bicarbonate) reaction with the volatile fatty acids developing during fermentation and the waste gases of fermentation (Blümmel *et al.* 1999). Nonlinear regression on cumulative Gp curves was run using an exponential model (Blümmel & Ørskov 1993). Dry matter (DM), crude protein (CP; $N \times 6.25$), cell wall (neutral detergent fibre, NDF; ash corrected) and ether extract (EE) contents were quantified as well.

An estimation of the ME content was performed using a standard regression for grasses and forbs (using Gp at 24 hours, CP and EE to predict ME according to Menke & Huss 1987), and by calculating a regression between Gp and ME from this database ($n=40$), which was used to estimate the ME content of the gymnosperm and fern samples based on their Gp during 72 hours ($(ME \text{ (MJ kg}^{-1} \text{ DM)} = 0.1842 \times Gp \text{ (ml per 200 mg DM)} + 1.9649)$; $R^2=0.85$; s.d. of the residuals $Sy.x=0.474$). Values calculated in this way represent ME for ruminants (ME_r); these values can be extrapolated to ME for a hindgut fermenter (the horse, ME_h) using the formula of Jansson (2004): $ME_h = 1.12 \times ME_r - 1.1$. Since ME_r and ME_h differed only slightly from one another, only ME_r values are given in table 1.

3. RESULTS

In general, fern and gymnosperm foliage yielded levels of energy that were only moderately lower than for forbs and grasses. *Ginkgo* and some conifers performed at a level similar to temperate browse. However, another group

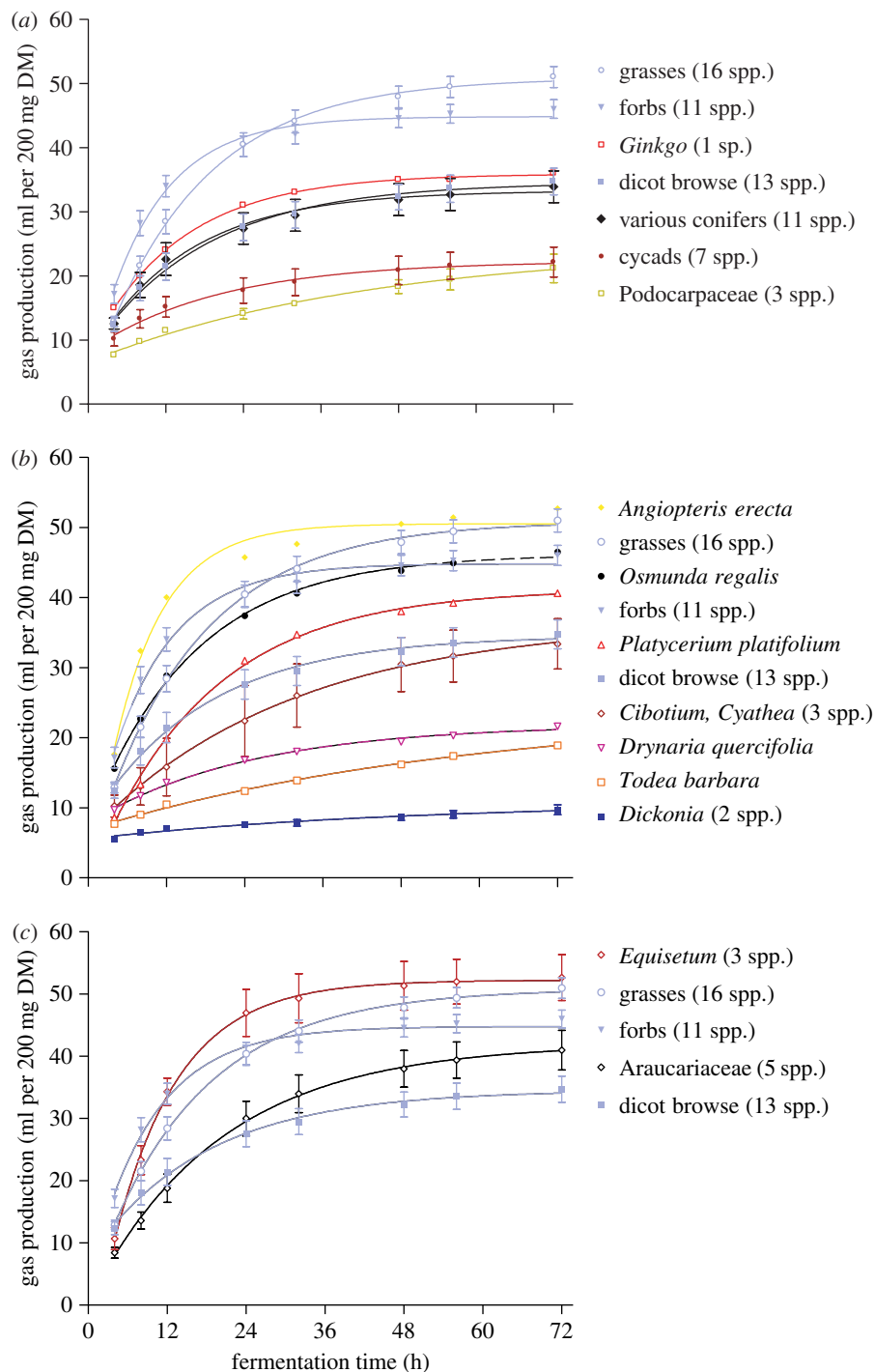


Figure 1. Fermentative behaviour of potential dinosaur food plants compared with that of angiosperms. Gp in the Hohenheim gas test is plotted versus fermentation time. (a) Various gymnosperms compared with angiosperms. Note that *Ginkgo* and some conifers (Cephalotaxaceae, Taxodiaceae, Pinaceae and Taxaceae) performed at the level of angiosperm browse, whereas podocarp conifers and cycads fared poorly. (b) Ferns compared with angiosperms. Note the great variability among ferns, including the very poor performance of the tree fern *Dicksonia*. (c) Araucariaceae and horsetails (*Equisetum* spp.) compared with angiosperms. Note that horsetails even surpass grasses and that araucarias outperform browse after 72 hours (DM, dry matter; means and standard error of the mean (s.e.m.) are indicated).

of conifers with an extensive Mesozoic record, the Podocarpaceae, and the cycads both yielded rather low amounts of energy (figure 1a). The ferns were quite variable; *Angiopteris* or the royal fern *Osmunda* were highly digestible, while others, such as the tree fern *Dicksonia*, were very poor energy sources (figure 1b).

Interestingly, the Araucariaceae showed a pattern reminiscent of grasses by starting out slowly, but in the end attaining higher values than those of browse, *Ginkgo*

or other conifers after 72 hours. *Equisetum*, representing the most basal plant group in the study, yielded the highest fermentative energy output, exceeding even that of grasses, especially in the initial phases of fermentation (figure 1c).

The resulting ME content was high in *Equisetum* ($11.6 \text{ MJ kg}^{-1} \text{ DM}$) and also in Araucariaceae (9.4 MJ per kg DM ; table 1). Crude protein level was found to be high in *Ginkgo* (15.6% DM) and low in Araucariaceae

Table 2. Estimates of daily dry-matter food consumption of a sauropod and an elephant with respect to differing energy densities of fodder and differing energy requirements on the part of the herbivore. (ME, metabolizable energy; DM, dry matter; BW, body weight.)

	energy requirement (kJ ME/kg BW ^{0.75} × d)	food energy (ME) content		
		10 MJ/kg DM	8 MJ/kg DM	6 MJ/kg DM
		estimates of daily dietary intake (DM) (kg)		
30 t sauropod	55	14	17	23
	280	64	80	106
	410	93	117	156
	550	125	157	209
70 t sauropod	55	26	32	43
	280	120	151	201
	410	176	221	294
	550	237	296	394
7 t elephant	550	42	53	70
10 t elephant	550	55	69	92

(4.4% DM). Several of the plants investigated showed high cell wall (NDF) contents of more than 60% DM, while *Ginkgo* was low in NDF (27.5% DM).

4. DISCUSSION

In general, the degradability of the pre-angiosperm plants investigated was surprisingly high in many taxa. This is true despite the use of a non-specific (but therefore standardized) inoculum, the rumen liquid from sheep. Since a comprehensive discussion of this topic is beyond the scope of this paper (but see Hummel *et al.* 2006 for a review), we note that using better adapted inoculum would only increase the degradability values of the pre-angiosperm flora.

From a nutritional point of view, the data predict that herbivorous dinosaurs in a pre-angiosperm world would have preferred *Equisetum* above all other food sources. The crude protein content of 11.7% DM supports the view that *Equisetum* was a staple food resource for smaller herbivores with a greater need for a higher quality diet. *Equisetum* may have also been an important food source for sauropods such as specialized low browsers like dicraeosaurids, as Mesozoic sphenophytes are thought to have produced large amounts of biomass by forming dense thickets in open or disturbed moist habitats, much as they do today (Wing & Sues 1992). Since *Equisetum* has changed very little in its morphology, anatomy or growth habits since the Mesozoic (Gould 1968), it is reasonable to assume that it accumulated silica in its outermost cells then as well. However, Wing & Sues (1992) comment that there is no direct evidence of similar quantities of silica phytoliths in Mesozoic horsetails. While it is generally thought that the large quantity of silica in horsetails has an inhibitory effect on digestion (Van Soest 1994) and wears down the teeth of herbivores excessively (Massey *et al.* 2006), herbivorous taxa that are not dependent on intensive oral processing of their food, such as sauropods (Upchurch & Barrett 2000) and other dinosaur groups such as prosauropods (Crompton & Attridge 1986), stegosaurs (Galton & Upchurch 2004) and ankylosaurs (Coombs 1978), would have accepted horsetails much more readily. Extant species feeding on horsetails are found among the birds (Thomas & Pevett 1982)—herbivores independent of dental food processing. Although not as nutritious as

Equisetum, the ginkgoes, conifers and ferns such as *Angiopteris* would also have fulfilled nutritional needs of smaller herbivorous dinosaurs.

It has long been believed that the long neck of sauropods evolved in connection with high browsing on tall trees, which would include conifers of the Araucariaceae. With increased gut retention times, *Araucaria* foliage would have become especially attractive as an energy-efficient food source. Such long retention times were most probably typical of adult individuals of sauropod species owing to their low mass-specific energy requirements and enormous body size (Farlow 1987; Wings & Sander 2007).

The crude protein content of 4.4% DM in *Araucaria* spp. falls below the requirements of extant large herbivores such as ruminants, and therefore makes the exclusive use of *Araucaria* by young, actively growing animals with higher requirements for this nutrient unlikely. By contrast, it would have been feasible for adult sauropods to have relied on *Araucaria* as a major food source. Moreover, it should be noted that nutritional requirements of herbivores depend and develop in concert with the quality of their food (Grubb 1992; Midgley 2005), and that low dietary protein contents can lead to the evolution of low requirements for this nutrient. For marsupials such as the sugar glider (*Petaurus breviceps*), protein requirements as low as 1.4% DM have been described (Smith & Green 1987).

In megaherbivores like the sauropods, it is most likely that a wide range of food plants was consumed (Owen-Smith 1988), thereby compensating for the low nutrient content in single forages. However, given the global distribution of *Araucaria* in the Mid-Mesozoic and its tall, arborescent, forest-forming habit in conjunction with its high energy yield, it is well probable that *Araucaria* was targeted as commonly available nutritious food source by many high-browsing megaherbivores. The cosmopolitan distribution of *Araucaria* in the Jurassic, for example, extended as far north as present-day northern England (Harris 1979) and as far south as the Antarctic Peninsula (Gee 1989), as well as into the mid-latitudes of various continents (e.g. Mildenhall & Johnston 1971; Sharma & Bohra 1977; Stockey 1978; Aberhan *et al.* 2002). Recently, a large, virtually monospecific compression

flora of *Araucaria* was found in a Late Jurassic bone bed in Wyoming, where it occurs alongside articulated skeletons of a diverse megaherbivore fauna (Ayer 1999), suggesting a close relationship between *Araucaria* and these herbivorous dinosaurs. For low-browsing taxa such as *Dicraeosaurus* and other diplodocids, *Equisetum* may have been a favoured food source. By contrast, cycads and podocarps, despite their abundance in the Jurassic record, are inferred by our data to have been of very low nutritional quality and therefore probably played a lesser role in the diet of herbivorous dinosaurs. It may be possible, using coprolites/fossilized gut contents of Mesozoic herbivores (e.g. Stokes 1964; Chin & Gill 1996; Prasad *et al.* 2005), to test these hypotheses on food choice, although the assignment of these remains to sauropods is difficult to prove.

We note that the hypothesis that particularly low-quality forage in Mesozoic ecosystems led directly to gigantism in dinosaurs (Midgley *et al.* 2002) is not substantiated by our data because the energy yield from many potential sauropod food plants is comparable to that measured in extant browse species. Estimates of the ME content of some samples even reached above 10 MJ ME/kg DM. The assumption of Tiffney (1997) that fern foliage is generally more nutritious than gymnosperm foliage is also not supported. Furthermore, our data also show a considerably higher energy yield for most taxa than indicated by the results of Weaver (1983), which were simply based on a measurement of gross energy and the assumption of constant digestibility. The ranking of potential dinosaur food plants in our study is thus considerably different from that of Weaver (1983), who ranked cycads best and *Equisetum* worst. We emphasize again that measuring the gross energy of plant material provides little information (if any at all) on its ME content (GfE 2003).

If the nutritional quality of some potential dinosaur food plants is higher than expected, then why do few herbivores feed on pteridophytes and gymnosperms today? Possible explanations include (i) increased plant defences in extant compared with the Mesozoic taxa (Tiffney 1997), e.g. due to severe competition with angiosperms in addition to feeding pressure from herbivores, (ii) lower tolerance to indigestible or toxic secondary plant compounds in extant herbivores (although the range of secondary compounds in pteridophytes and gymnosperms is considered to be narrower than in angiosperms; Swain 1978), and (iii) low accessibility of these plant groups to extant herbivores, owing to the low frequency of pteridophytes and gymnosperms in angiosperm-dominated ecosystems.

A major question in any discussion on giant sauropod feeding ecology is the quantities of food that must have been ingested by an individual on a daily basis (Farlow 2007). These values are strongly influenced by the level of metabolism assumed for the animal and the energy yield of the food plants. Table 2 presents our calculations of the daily dietary intake of a sauropod of either average (30 t) or maximal (70 t) BW based on different metabolic rates: 100, 75, 50 and 10% of extant tachymetabolic animals (birds and mammals), the latter percentage being at the level of the metabolic rate of extant true bradymetabolic animals (such as reptiles). Energy requirements for extant tachymetabolic animals were calculated to be 1.75 times the basal metabolic rate, plus a supplement of 15% for free-ranging conditions (Blaxter 1989; Robbins 1993).

These values, in turn, were compared with those of modern tachymetabolic megaherbivore analogues, 7 t elephants (Colbert 1993). As an extreme example for extant elephants, the exceptional 10 t African elephant bull mentioned in Owen-Smith (1988) was also included in the calculations.

Using the unrealistically low metabolic rate of extant reptiles (55 kJ ME/kg BW^{0.75}), the resulting necessary food intake for a sauropod is rather unspectacular, even for a 70 t animal (26–43 kg DM per day). For an average-sized sauropod of 30 t, a metabolism of 50% of today's true tachymetabolic animals (280 kJ ME/kg BW^{0.75}) would result in 64–106 kg DM for an animal per day, while a true tachymetabolic metabolism (550 kJ ME/kg BW^{0.75}) results in the intakes of 125–209 kg DM. When compared with the dietary requirements of elephants, a 70 t sauropod would have had to ingest 4.3 times the amount of dry plant matter necessary for a 10 t elephant and 5.6 times the amount necessary for a 7 t elephant. However, in regard to the actual ingestion of foodstuffs, this might not have posed much of a problem for the sauropods, since adaptations such as the lack of oral food comminution of the plant matter, a wide mouth opening and the lack of cheeks (Paul 1998; Christiansen 1999) would have facilitated a high intake capacity. In regard to preferences for certain food plants based on nutritional quality, a giant sauropod of 70 t with a high energy requirement that fed only on low-energy yielding tree ferns and cycads would have needed to ingest 394 kg of dry plant matter daily. The same giant sauropod would need only approximately 237 kg of dry plant matter if browsing on a mixture of horsetails and araucarias, a total of 40% less. Another important aspect in regard to food preferences is the differing amounts of nutrients in the potential food plants. *Araucaria*, for example, yields high amounts of energy over a long retention time, yet it offers very little in the way of protein, especially when compared with the low energy/high protein content of tree ferns. *Ginkgo* offers both moderate amounts of energy and high amounts of protein, and *Equisetum* supplies both high protein and high energy.

5. CONCLUSIONS

In summary, our study indicates that the energy supply for the large sauropods was not as problematic as commonly thought and helps to explain how a non-angiosperm flora could have nourished a diverse fauna of megaherbivores. It is thus quite plausible that pteridophyte and gymnosperm floras could have even sustained huge dinosaurs. In particular, the pattern of fermentative behaviour in *Araucaria* foliage suggests that these globally widespread, tall, forest-forming trees provided the largest high-browsing sauropods with a widely available and energy-rich source of food.

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