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**Competing interests statement**

The authors declare that they have no competing financial interests.

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**A Jurassic mammal from South America**

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The Jurassic period is an important stage in early mammalian evolution, as it saw the first diversification of this group, leading to the stem lineages of monotremes and modern therian mammals<sup>1</sup>. However, the fossil record of Jurassic mammals is extremely poor, particularly in the southern continents. Jurassic mammals from Gondwanaland are so far only known from Tanzania<sup>2,3</sup> and Madagascar<sup>4</sup>, and from trackway evidence from Argentina<sup>5</sup>. Here we report a Jurassic mammal represented by a dentary, which is the first, to our knowledge, from South America. The tiny fossil from the Middle to Late Jurassic of Patagonia is a representative of the recently termed Australosphenida, a group of mammals from Gondwanaland that evolved tribosphenic molars convergently to the Northern Hemisphere Tribosphenida, and probably gave rise to the monotremes<sup>1</sup>. Together with other mammalian evidence from the Southern Hemisphere<sup>2–4,6–8</sup>, the discovery of this new mammal indicates that the Australosphenida had diversified and were widespread in Gondwanaland well

before the end of the Jurassic, and that mammalian faunas from the Southern Hemisphere already showed a marked distinction from their northern counterparts by the Middle to Late Jurassic. Mammalia Linnaeus, 1758 (sensu McKenna and Bell 1997, ref. 9) Holotheria Wible *et al.*, 1995 (ref. 10) (sensu McKenna and Bell 1997, ref. 9)

Australosphenida Luo *et al.*, 2001 (ref. 1)

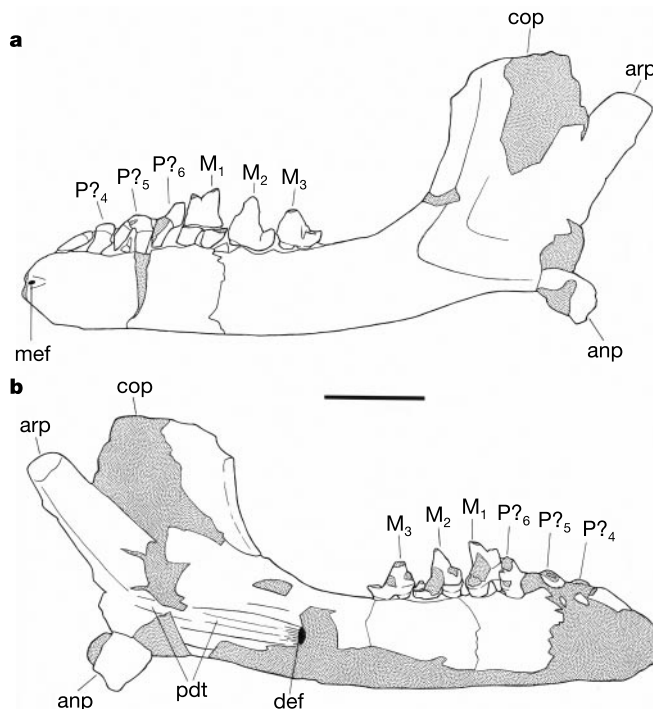
*Asfaltomylos patagonicus* gen. et sp. nov.

**Etymology.** Genus name referring to the Cañadón Asfalto Formation and mylos (Greek), mill, after the grinding function of the well developed talonid; the species name, *patagonicus*, is termed after the origin, from Patagonia.

**Holotype.** Museo Paleontológico Egidio Feruglio (Trelew) collection (MPEF-PV) 1671. Left mandible with roots and crown fragments of the last three premolars and M<sub>1</sub>–M<sub>3</sub> (Figs 1 and 2).

**Horizon and locality.** The specimen comes from the Queso Rallado locality, approximately 4 km west-northwest of the village of Cerro Condor, Chubut, Argentina. The material is derived from a silicified mudstone within a series of lacustrine mudstones and limestones. The sequence can be assigned to the Cañadón Asfalto Formation. The Cañadón Asfalto Formation, which is in the vicinity of Cerro Condor, has repeatedly been dated as Callovian–Oxfordian (latest Middle to earliest Late Jurassic)<sup>11,12</sup>.

**Diagnosis.** *Asfaltomylos* is a small holotherian mammal with fully basined talonids, with hypoconid and hypoconulid at the molars (broken on M<sub>1</sub>). Trigonids are lingually open, the trigonid angle of M<sub>1</sub> is about 130° (obtuse), and for M<sub>2</sub> and M<sub>3</sub> it is about 80° (acute). All preserved teeth are double-rooted, M<sub>1</sub>–M<sub>3</sub> with faint lingual cingulid at the base of the paraconid. There is no distal metacristid present on the talonids. The tooth formula of the mandible is: ?I, ?C, 3+P, 3M. The dentary is slender with a gently rising coronoid process. The angular process is posteroventrally positioned and the dental foramen is placed far towards the anterior (below the origin



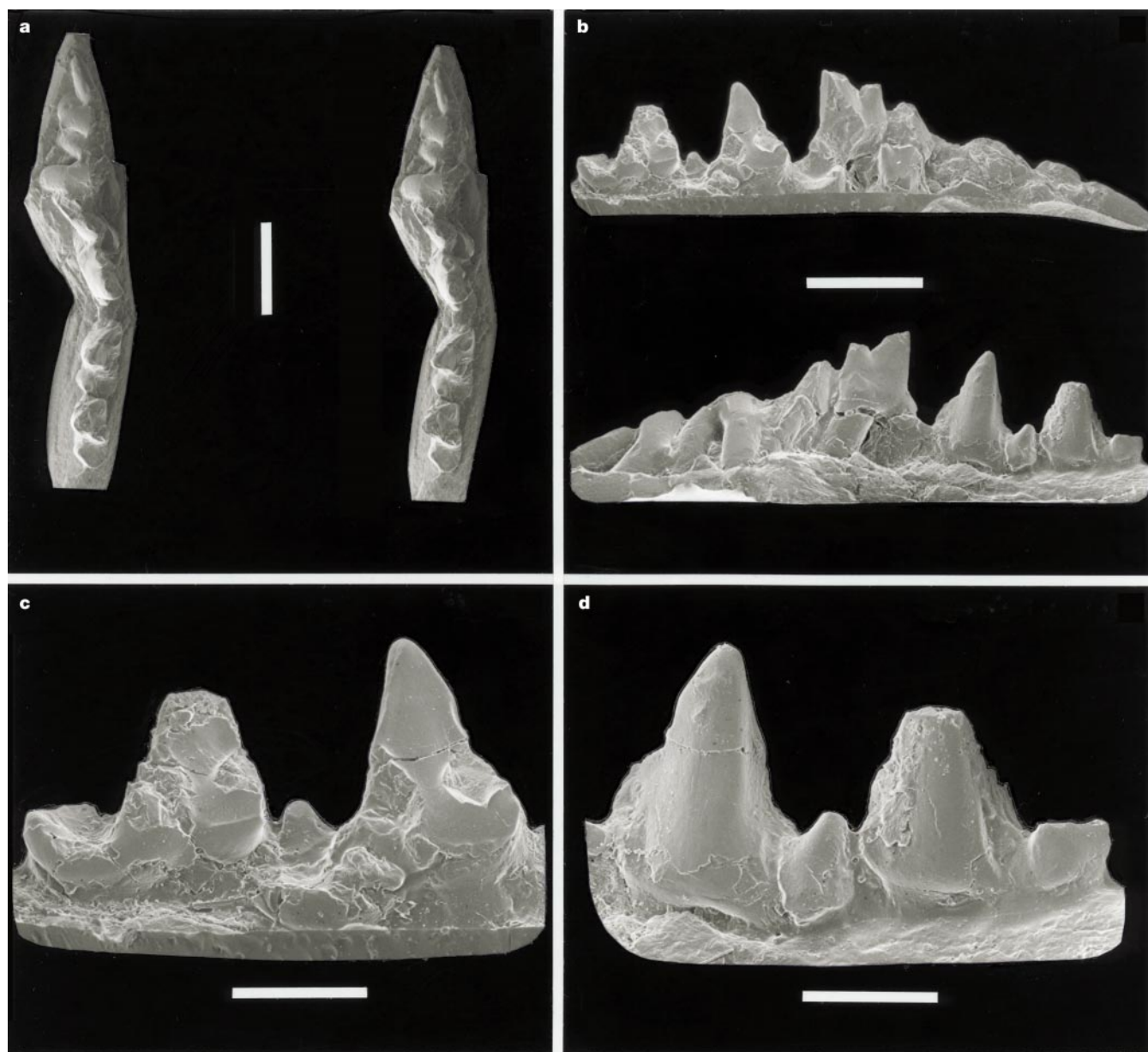
**Figure 1** Camera lucida drawings of the left mandible of *Asfaltomylos patagonicus* (holotype). **a**, **b**, Labial (**a**) and lingual (**b**) view. Damaged areas are shaded. Scale bar, 2 mm. A small mental foramen is situated at the broken anterior end of the mandible. The numeration of the premolars follows comparisons with *Bishops*<sup>8</sup>. anp, angular process; arp, articular process; cop, coronoid process; def, dental foramen; M, molar; mef, mental foramen; P, premolar; pdt, post-dentary trough.

of the coronoid process). There is no developed pterygoid fossa. A shallow post-dentary trough is present, subdivided by longitudinal striations. Meckel's groove is not detectable.

*Asfaltomylos* differs from *Peramus* and other pre-tribosphenic holotherians through the presence of a broad, fully basined talonid with wear on the hypoconid and hypoconulid, lack of a distal metacristid, an anterior position of the dental foramen, presence of a post-dentary trough, and lack of pterygoid fossa. Differs from Theria, and *Holoclemensia* and *Pappotherium* by the presence of a lingually open trigonid. Important characters shared with australosphenidans are the presence of a lingual cingulid at the base of the paraconid, and talonids, which have a greater width than length. Differs from *Ambondro*, from the Middle Jurassic of Madagascar, by the lack of a distal metacristid and a weaker lingual cingulid, which does not wrap around the mesial side. The Early Cretaceous australosphenidan *Ausktribosphenos*, from Australia, is characterized by a number of distinctive autapomorphic features, such as

additional cristids on the metaconid and talonid<sup>13</sup>, which are not present in *Asfaltomylos*. Differs from the Early Cretaceous *Bishops*<sup>8</sup> through the lack of additional cristids in the talonid, a weaker lingual cingulid, and a more slender protoconid.

*Asfaltomylos* is the first Jurassic mammal from South America and the fifth Mesozoic representative of the recently termed Australosphenida<sup>1,14</sup>. Similar to *Ambondro* from the Middle Jurassic (Bathonian) of Madagascar<sup>4</sup>, it exhibits broad, fully rimmed, basined talonids on the molars (only the base of the talonid is preserved on M<sub>1</sub>). On M<sub>2</sub> of *Asfaltomylos*, the talonid represents the broadest part of the tooth. A labially inflated, large hypoconid with pointed tip is present; it bears a lingually oriented wear facet. On M<sub>3</sub>, hypoconid and hypoconulid are well developed and are connected by the talonid rim. On the lingual side, a part of the talonid rim is missing; just distally of the broken area the rim of the talonid rises, which possibly indicates the presence of a small entoconid. A large wear facet connecting hypoconid and hypoconulid is clearly visible.



**Figure 2** Dentition of the holotype of *Asfaltomylos patagonicus*. **a**, Occlusal view (stereopair); **b**, lingual (upper) and labial view (lower); **c**, detail of M<sub>2</sub> and M<sub>3</sub> in oblique lingual view; **d**, detail of M<sub>2</sub> and M<sub>3</sub> in oblique labial view. Scale bars: **a**, **b**, 1 mm;

**c**, **d**, 0.5 mm. M<sub>1</sub> has an obtuse angular trigonid; M<sub>2</sub> and M<sub>3</sub> have acute angular trigonids and fully basined talonids, which have a greater width than length. There is a faint lingual cingulid at the base of the paraconids of M<sub>1</sub> to M<sub>3</sub>.

From this wear facet the presence of a functional protocone on the upper molar is inferred, making *Asfaltomylos* a fully tribosphenic mammal. High-resolution X-ray analysis did not reveal any trace of an unerupted tooth germ in the wide space behind M<sub>3</sub>.

Other important similarities to *Ambondro* include the basis of the paraconid being higher than that of the metaconid, and the talonid having a greater width than length. These characters constitute differences compared with the situation found in the Laurasian tribosphenic mammals, the boreosphenidans<sup>1</sup>; together with the presence of a medial cingulid in the molars, they represent synapomorphies of the Australosphenida<sup>1,14</sup>, thus supporting this concept and the placement of *Asfaltomylos* within this group.

The slender dentary of *Asfaltomylos* is broken anteriorly of P?4 and is crushed in the premolar region. On the partially broken lingual side, no Meckel's groove is visible (present in *Ausktribosphenos* from Australia<sup>7,13</sup>). The subdivision of the post-dentary trough indicates the presence of distinct post-dentary bones<sup>15</sup>. This is a very primitive character<sup>16</sup> that supports a basal phylogenetic position for australosphenidans<sup>1,14,17</sup> within holotherians, despite their highly derived molar morphology. The angular process is well developed. As preserved, it is pointing ventrally

owing to compression, and the original orientation was most probably pointing posteriorly, as in other australosphenidans<sup>14</sup>. The articular process rises steeply and points posterodorsally. Below the origin of the coronoid process, opens the large dental foramen, which is at a very anterior position compared with *Peramus* and tribosphenic Zatheria<sup>18,19</sup>.

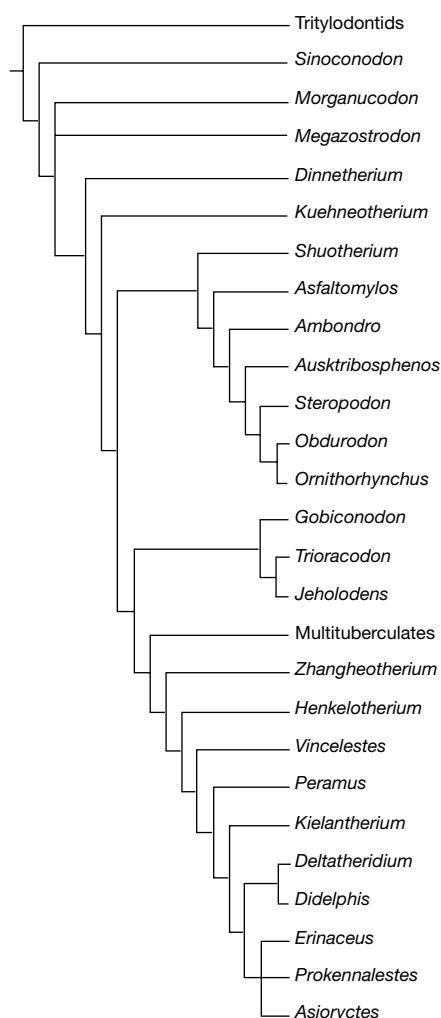
**Discussion.** *Asfaltomylos* extends the fossil record of Jurassic mammals to South America, and corroborates the existence of a Middle Jurassic (or even earlier) radiation of tribosphenic holotherians on Gondwanaland. The development of tribosphenic molars on the southern continents predates that on Laurasia by about 25 Myr.

To test the phylogenetic position of *Asfaltomylos* within mammals, character codings for this taxon were added to the three data matrices published in the Supplementary Information of ref. 1 (see Supplementary Information). When we included *Asfaltomylos* in the phylogenetic analysis of ref. 1, it appeared as the most basal member of Australosphenida (Fig. 3).

The Australosphenida group to date is based on only a few taxa, and its history is still largely unknown. The oldest known representative is *Ambondro* from the Bathonian of Madagascar<sup>4</sup>. Only three other Mesozoic members of this clade are currently known, *Ausktribosphenos*, *Bishops* and *Steropodon*, all from the Early Cretaceous of Australia<sup>6-8,14</sup>. The addition of *Asfaltomylos* to the analysis resolves the polytomy within Australosphenida found by ref. 1, and thus demonstrates that *Ambondro* and *Ausktribosphenos* represent successively closer outgroups to Monotremata, which include *Steropodon*. This pattern is in general accordance with the stratigraphic occurrence of these taxa.

Together with the occurrence of *Ambondro* in the Bathonian of Madagascar, the discovery of *Asfaltomylos patagonicus* in the Middle to Late Jurassic of southern South America indicates that the Australosphenida had already diversified and spread over much of Gondwanaland by the Middle Jurassic. Of note, no australosphenidan mammal has been reported from the Cretaceous period of South America, although a variety of mammalian taxa are known from that time. The South American mammalian fauna during the Cretaceous was dominated by Dryolestida, with a few 'triconodonts', gondwanatherians, and a questionable docodont<sup>20-23</sup>, which may indicate that the Australosphenida had already largely been replaced on this continent by that time. Together with the gondwanatherians—which are known from the Cretaceous of Madagascar (*Lavanify*<sup>20</sup>), India (undetermined taxon) and southern South America (*Ferugliotherium*, *Gondwanatherium*, *Sudamerica*<sup>20,24</sup>)—the surviving Australosphenida from the Cretaceous of Australia (*Ausktribosphenida*<sup>7,8</sup>, *Steropodon*<sup>6</sup>) and the Palaeocene epoch of South America (*Monotrematum*<sup>25,26</sup>) might represent relics of a Jurassic radiation of purely Gondwanan mammals. More fossil evidence, particularly from the Cretaceous of Africa and the Late Jurassic to Early Cretaceous of South America, is needed to test this hypothesis.

A second aspect worth noting is the already marked differentiation between the mammalian faunas of the Southern and Northern Hemispheres towards the end of the Jurassic. The late Middle to Late Jurassic mammalian faunas of Laurasia are dominated by multituberculates, symmetrodonts, docodonts, dryolestids, and stem-lineage representatives of modern therian mammals, such as peramurids<sup>27-30</sup>. In contrast, the sparse fossil evidence from the Southern Hemisphere indicates a mammalian fauna consisting of endemic and highly derived groups, the Australosphenida, and very probably the Gondwanatheria<sup>20</sup>, in addition to relics of an archaic group, the Haramiyida<sup>3</sup>, which is unknown from rocks younger than the Early Jurassic in the Northern Hemisphere. However, other taxa are still found on both landmasses, such as triconodonts, dryolestids, and peramurids<sup>2</sup>, indicating that some faunal interchange might still have occurred towards the end of the Jurassic. Commonly, the great success of eutherian (and to some extent metatherian) mammals is attributed to the evolution of tribo-



**Figure 3** Phylogenetic position of *Asfaltomylos*. Inclusion of *Asfaltomylos* in a phylogenetic analysis of the main taxa of Mesozoic and several younger mammals (based on 125 characters from the whole skeleton using PAUP 3.1.1, with the heuristic branch-and-bound search, set at random with 100 replicas; see ref. 1 and Supplementary Information) markedly reduced the number of equally parsimonious trees and resolved the polytomy of *Ambondro*, *Steropodon* and *Ausktribosphenos*. *Asfaltomylos* appears as the most basal member of Australosphenida.



sphenic molars, which allowed a much more effective processing of food and energy exploitation. However, this was only the case in Boreosphenida (tribosphenic mammals from the Northern Hemisphere), whereas the Australosphenida apparently decreased in diversity since the Late Jurassic, and finally evolved completely reduced dentition, as seen in extant Australian monotremes (egg-laying mammals). □

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**Bacterial growth and primary production along a north–south transect of the Atlantic Ocean**

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The oceanic carbon cycle is mainly determined by the combined activities of bacteria and phytoplankton<sup>1,2</sup>, but the interdependence of climate, the carbon cycle and the microbes is not well understood. To elucidate this interdependence, we performed high-frequency sampling of sea water along a north–south transect of the Atlantic Ocean. Here we report that the interaction of bacteria and phytoplankton is closely related to the meridional profile of water temperature, a variable directly dependent on climate. Water temperature was positively correlated with the ratio of bacterial production to primary production, and, more strongly, with the ratio of bacterial carbon demand to primary production. In warm latitudes (25° N to 30° S), we observed alternating patches of predominantly heterotrophic and autotrophic community metabolism. The calculated regression lines (for data north and south of the Equator) between temperature and the ratio of bacterial production to primary production give a maximum value for this ratio of 40% in the oligotrophic equatorial regions. Taking into account a bacterial growth efficiency<sup>3,4</sup> of 30%, the resulting area of net heterotrophy (where the bacterial carbon demand for growth plus respiration exceeds phytoplankton carbon fixation<sup>4–6</sup>) expands from 8° N (27 °C) to 20° S (23 °C). This suggests an output of CO<sub>2</sub> from parts of the ocean to the atmosphere<sup>6,7</sup>.

We report here large-scale distributions of microbial variables as determined from the north–south Atlantic transect of the JGOFS (Joint Global Ocean Flux Study) *Polarstern* expedition ANT X (53° N to 65° S) during November 1991 to January 1992 (Fig. 1). High-frequency water sampling was performed continuously at intervals of 4–8 h, corresponding to 50–100 nautical miles, and summing up to 170 samples along the transect. Water samples were taken at 11 m depth from the moving ship.

The measured chlorophyll distribution along the transect corresponded well to the time-integrated pattern of chlorophyll recorded by the CZCS (coastal zone colour scanner) satellite (Fig. 1a). The meridional profiles of chlorophyll and bacterial production (in terms of tritiated leucine incorporation (TL<sub>i</sub>; Fig. 1b) were similar. In detail, however, chlorophyll concentrations showed a wider overall range than bacterial production, and bacterial production in relation to chlorophyll was high—particularly in the oligotrophic tropical regions<sup>8</sup> (Fig. 1a and b). Owing to seasonal and regional (extremely high microbial values on the Patagonian shelf) effects, higher mean values and ranges of microbial variables were measured in the south than in the north (Table 1).

In contrast to the individual variables, the ratio (expressed in per cent) of bacterial production (TL<sub>i</sub>) to primary production was highly correlated with temperature in the North as well as in the South Atlantic (Table 2). The ratio between bacterial production and primary production changed significantly from about 2–10% in the cold and temperate climate zones to 40% in the tropics (Fig. 2). This indicates a large-scale temperature-dependent shift from net-autotrophic to increasingly heterotrophic conditions in the surface of the Atlantic. The strongly scattered individual data points around the regression lines suggest an alternating predominance of autotrophic and heterotrophic regimes in patches along the transect (Fig. 2). The estimates derived from tritiated thymidine