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A NEW SAUROPOD DINOSAUR (TITANOSAURIA) FROM THE LATE CRETACEOUS OF BRAZIL

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Abstract A new titanosaur, *Gondwanatitan faustoi* n. gen., n. sp., is described and compared with other members of that sauropod clade. The specimen consists of an incomplete skeleton (MN 4111–V) that comes from the Álvares Machado region (State of São Paulo, Brazil) and was found in the continental deposits of the Late Cretaceous Bauru Group. This new taxon has the following autapomorphies: distal articular surfaces of proximal and mid caudals "heart-shaped"; deltopectoral crest of humerus very well developed and curved medially, tibia with anterior part of the proximal articulation projecting dorsally and cnemial crest only slightly curved laterally. Although its phylogenetical position is not clear, this new taxon is not closely related to members of the Saltasaurinae and can also be distinguished from more basal titanosaurs like *Andesaurus* and *Malawisaurus*. It shares at least one unique character with *Aeolosaurus*, a strongly anteriorly directed neural spine of the anterior and anterior midcaudals, but more material of both taxa is needed to confirm a close relationship.

Resumo Um novo titanossauro, *Gondwanatitan faustoi* n. gen., n. sp., é descrito e comparado com outros membros deste clado de saurópodes. O espécime é formado por um esqueleto incompleto (MN 4111–V) proveniente do Município de Álvares Machado (Estado de São Paulo, Brasil), tendo sido encontrado nos depósitos continentais do Grupo Bauru (Cretáceo Superior). Este novo táxon possui as seguintes autapomorfias: articulação distal das vértebras caudais proximais e medianas em forma de "coração", crista deltopeitoral do úmero bem desenvolvida e curvada para a região interna, tíbia com parte anterior da articulação proximal projetada dorsalmente e com crista cnemial apenas levemente curvada lateralmente. Apesar da posição filogenética deste novo táxon ainda não estar bem definida, o mesmo náo está proximamente relacionado com os Saltasaurinae e pode ser separado de titanossauros basais como *Andesaurus e Malawisaurus* . Esta espécie compartilha pelo menos uma característica única com *Aeolosaurus* (espinho neural das vértebras anteriores e ântero-medianas fortemente dirigido para a região anterior), mas materiais complementares são necessários para que esta relação filogenética possa ser confirmada.

Introduction

In 1983 Mr. Yoshitoshi Myzobuchi discovered some fossil bones on his farm situated in the region of Álvares Machado in the State of São Paulo (Fig. 1). Dr. Fausto Luiz de Souza Cunha, at that time vertebrate paleontologist of the Museu Nacional/Universidade Federal do Rio de Janeiro (MN), was notified of this find and identified the material as belonging to a titanosaurid dinosaur. Recognizing the importance of this specimen, Dr. Fausto and his crew spent the next three field seasons at the "Myzobuchi Site" (1984–1986) collecting this and some other fossil vertebrate remains, which are now housed at the Museu Nacional (Rio de Janeiro). Despite a small note (Cunha and Suarez, 1985) and a paper describing some geological aspects of the site (Cunha *et al.*, 1987), this specimen (MN 4111–V) remained unstudied.

In September 1997, preparation of this dinosaur was restarted, revealing that it belongs indeed to a titanosaur sauropod new to science, here named *Gondwanatitan faustoi* n. gen., n. sp. The description and comparison of this material, which constitutes the most complete sauropod found in Brazil so far, is presented here. *Gondwanatitan faustoi* has been compared with the following titanosaurs: *Aeolosaurus rionegrinus* Powell 1986; *Aeolosaurus sp.* Salgado and Coria (1993); *Alamosaurus sanjuanensis* Gilmore 1922; *Andesaurus delgadoi* Calvo and Bonaparte 1991; *Antarctosaurus wichmannianus* Huene (1929); *Argentinosaurus huinculensis* Bonaparte and Coria 1993; *Argyrosaurus superbus* Lydekker 1893; *Epachthosaurus sciuttoi* Powell 1990; *Malawisaurus dixeyi* (Haughton 1928); *Neuquensaurus australis* (Huene 1929); *Opisthocoelicaudia skarzynskii* Borsuk-Bialynicka 1977; *Pellegrinisaurus powelli* Salgado 1996; *Saltasaurus loricatus* Bonaparte and Powell 1980; *Titanosaurus araukanikus* (Huene

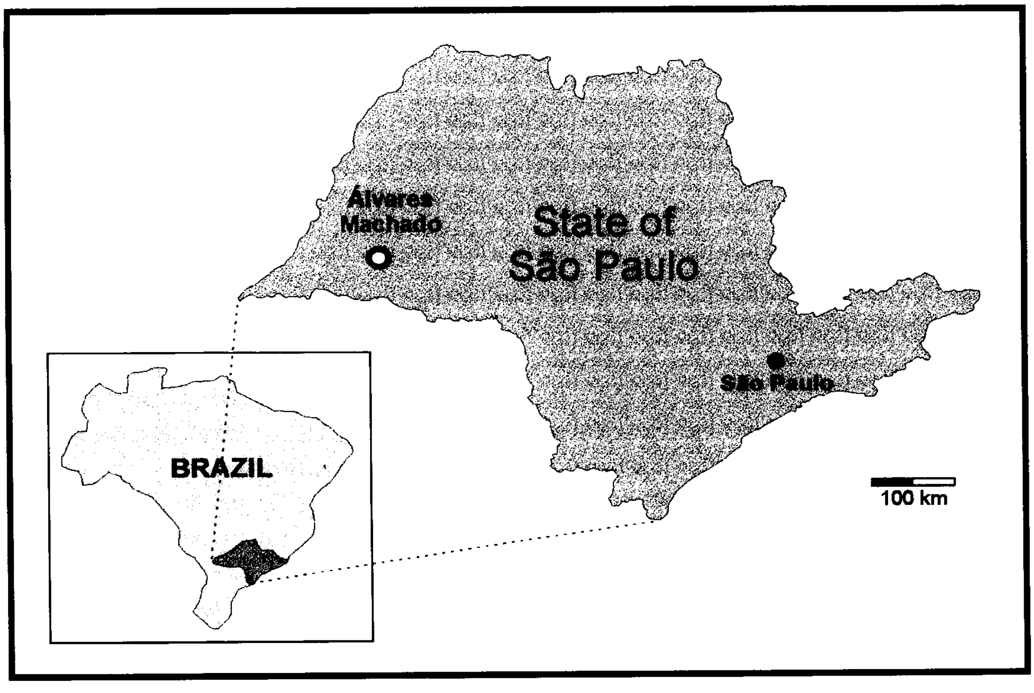

Fig. 1. Locality map showing Alvarez Machado, São Paulo, where *Gondwanatitan faustoi*, n. gen., nov. sp. was found.

1929); *Titanosaurus colberti* Jain and Bandyopadhyay 1997; and the vertebral series found in Peirópolis (series B = MCT 1488–R; series C = MCT 1490–R). The data from the mentioned titanosaur taxa was obtained from the original description and complemented with other papers including Powell (1992), Jacobs *et al.* (1993), Bonaparte (1996), Salgado *et al.* (1997), and Tomida (1998: illustrations of *Argentinosaurus*).

The Bauru Group

Composed predominantly of fluvial (locally eolian) sandstones, siltstones, and mudstones, the Bauru Group represents the most significant Cretaceous sedimentary occurrence in Brazil. Outcrops of this unit extend for about 370,000 km^2, reaching six Brazilian states (São Paulo, Minas Gerais, Mato Grosso, Mato Grosso do Sul, Goiás, and Paraná), and can also be found in Paraguay, Uruguay, and Argentina (Petri and Fúlfaro, 1983; Fernandes and Coimbra, 1996). The first nominal reference to those strata was presented by Campos (1905) that introduced the term "grés de Bauru". Some years later, based on titanosaurid sauropod remains, Huene (1927; 1929) proposed a Cretaceous age for those sedimentary rocks. Since that time, those strata were studied in detail and, depending on the author, vary in the stratigraphic hierarchy from series to member (Petri and Fúlfaro, 1983).

The most accepted subdivision of those continental layers was proposed by Soares *et al.*, (1980), that elevated the Bauru Formation to the category of group and subdivided those strata into four formations: Caiuá, Santo Anastácio, Adamantina, and Marília. Later, Souza (1984) added the Uberaba Formation, that outcrops only in the State of Minas Gerais and is interdigitated with the Adamantina Formation. More recently, based on tectonic and sedimentological studies, Fernandes and Coimbra (1996) separated the sedimentary rocks above the Serra Geral basaltic intrusion of the Paraná Basin as a different tectonic feature, the Bauru Basin. Those authors recognized two chronocorrelative groups: Caiuá Group, composed of the formations Rio Paraná, Goio Erê, and Santo Anastácio; and Bauru Group, with the formations Adamantina, Uberaba, Marília, and some alkaline volcanic rocks ("Taiúva analcimite"). The latter interdigitates with the Adamantina Formation and has only been observed in subsurface.

Fernandes and Coimbra (1996) suggested that these continental deposits were formed between the Santonian and the Maastrichtian. This dating is based mainly on the fossil vertebrates found in the Adamantina and Marília formations (regarded as Senonian by Huene), absolute ages determined on the mineral analcimite, and lithostratigraphic similarities between the Caiuá and Bauru groups (Fernandes and Coimbra, 1996). For a review of the paleontological content of the Adamantina and Marília formations see Bertini *et al.*, (1993).

Geological Setting and Associated Remains

The type material of *Gondwanatitan faustoi* was found in the region of Álvares Machado, in the State of São Paulo. It comes from a mudstone layer that is part of a fining upward fluvial sequence (Fig. 2). The latter is truncated by cross-laminated sandstones overlain by a conglomeratic layer that has yielded isolated remains of turtles and crocodilians. Based on the geologic map of São Paulo, the strata of the Bauru Group that crop out in the area of Presidente Prudente belong to the Adamantina Formation (*e.g.* Fernandes and Coimbra, 1996).

Turtle remains consist of two partial skeletons with almost complete carapaces and several isolated bones and carapace plates. Preliminary studies of these specimens suggest that they belong to a new taxon related to some Eurafrican forms (Kischlat, 1996). The crocodilian remains consist of several teeth that are not diagnostic of any particular group.

During the preparation of the titanosaur material, some smaller non-dinosaurian vertebrae were found. They consist of two sacrals and some dorsal vertebrae, all from one individual, which are still being prepared. Based on preliminary comparisons, these vertebrae appear to be crocodilian.

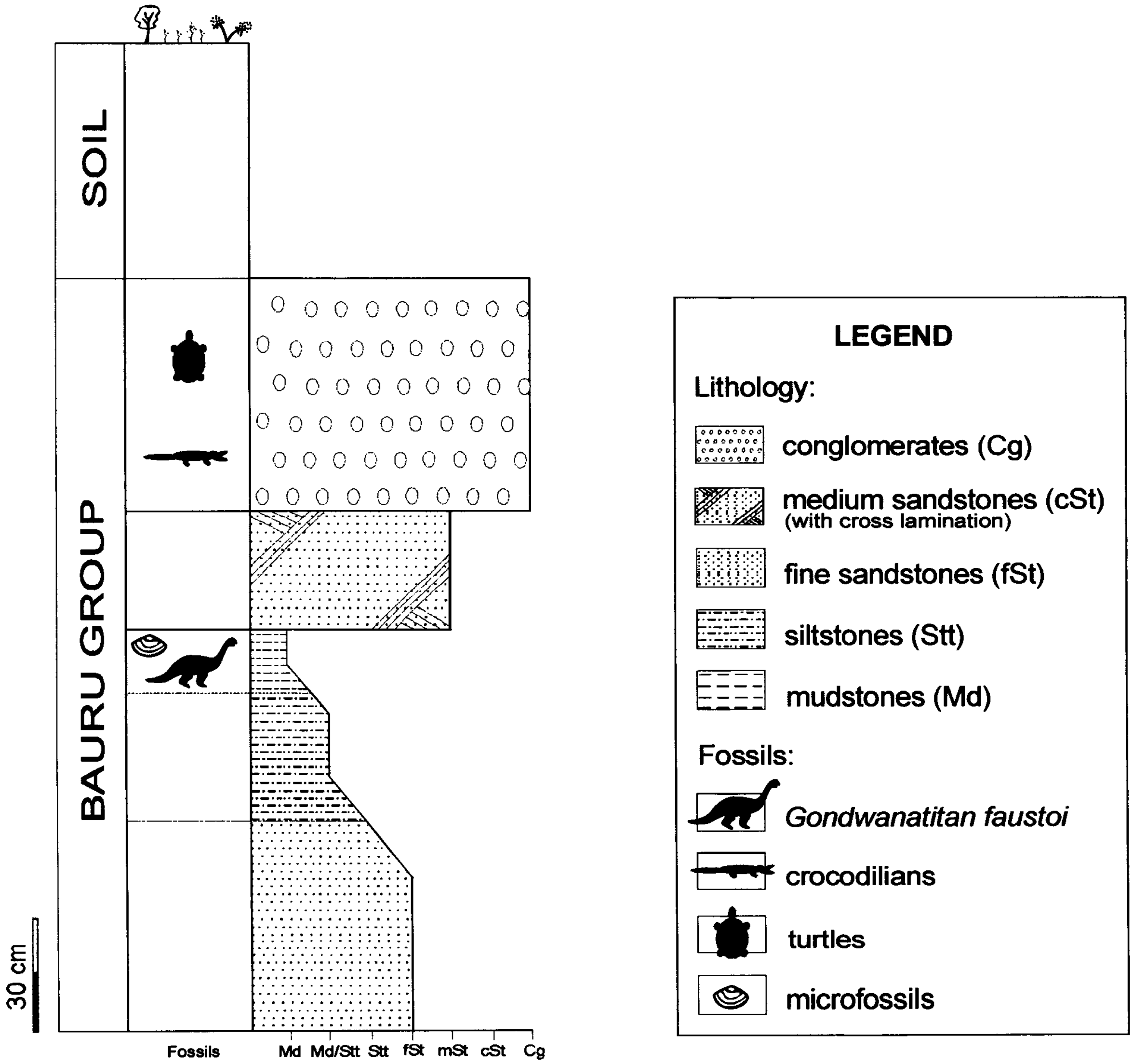

Fig. 2. Stratigraphical column of the site "Myzobuchi" in Alvares Machado, São Paulo.

Systematic Paleontology

Saurischia Seeley, 1888
Sauropodomorpha Huene, 1932
Sauropoda Marsh, 1878
Titanosauria Bonaparte and Coria, 1993

Gondwanatitan gen. nov.

Type-species: *Gondwanatitan faustoi* n. sp., type by monotypy.

Etymology: The generic name is formed by "Gondwana", the continental mass that once united all southern continents (and India), and "Titan", which relates to a group of Greek divinities.

Diagnosis: Titanosaur with the distal articulation surface of proximal and mid caudals "heart-shaped"; deltopectoral crest of humerus very well developed and curved medially; tibia with anterior part of the proximal articulation projecting dorsally; and cnemial crest only slightly curved laterally.

Gondwanatitan faustoi sp. nov.

Holotype: incomplete skeleton (Fig. 3), composed of two partial cervicals, seven dorsals, six sacrals, twenty-four caudals (some articulated), and four unidentified vertebrae; proximal part of left scapula, left ilium (incomplete), middle portion of both pubis, both ischia (incomplete), both humeri, both tibiae, several remains of ribs, and several unidentified fragments. All bones were found at the same outcrop and are regarded as belonging to a single individual. The material (MN 4111-V) is housed at the Paleovertebrate Section of the Geology and Paleontology Department (DGP), Museu Nacional/UFRJ. Reconstructed drawing based on the holotype is given in figure 4.

Etymology: The species is named in in honor of Dr. Fausto L. de Souza Cunha, former curator at the Museu Nacional/UFRJ, who collected and recognized the importance of this specimen.

Type locality: "Sítio Myzobuchi" is located near the city of Álvares Machado in the São Paulo State.

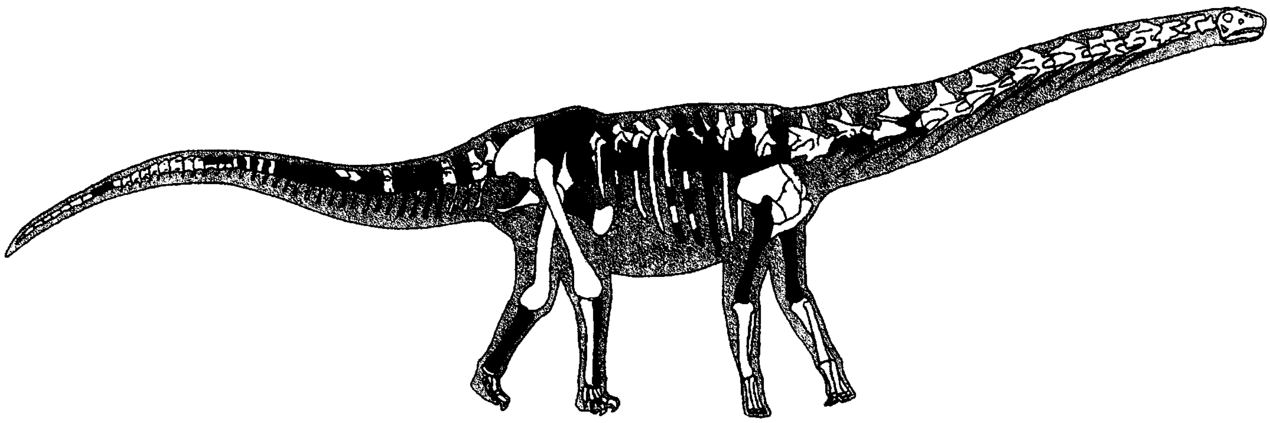

Fig. 3. Sketch of a titanosaur skeleton indicating the preserved parts of *Gondwanatitan faustoi* n. gen., n. sp.

Fig. 4. Reconstruction of *Gondwanatitan faustoi* n. gen., n. sp.

Geological setting of Type locality: A mudstone layer, truncated by a cross laminated sandstone, overlain by a conglomerate, all part of the Bauru Group (Cunha *et al.*, 1987).

Diagnosis: Same as for the genus.

Description and Comparisons

Generalities

The preservation of the material of *Gondwanatitan faustoi* is variable. Some bones are complete and well preserved (*e.g.*, humeri, tibiae, caudal vertebrae). Others, however, were exposed on the surface or damaged by the roots of the vegetation where the bones were found (*e.g.*, pelvis, dorsal vertebrae). From the available remains, it is clear that much more of the specimen was preserved, but was in such poor condition that it could not be collected (Ramsés Capilla, personal comm. 1997). According to Cunha *et al.,* (1987), most elements were not articulated but all were associated and confined to a small area. All bones were overlain by a dark and hard layer of manganese oxide, which could be removed, despite the fragility of some elements (*e.g.*, pelvis, scapula). Some postmortem compression affected the shape of several bones, especially the dorsal vertebrae and the sacrum. Based on the length of the cervical, dorsal and caudal vertebrae of other titanosaurs, the total length of this individual at time of death was between 6 to 7 meters, making it a relatively small-sized member of this sauropod group.

The laminae of the vertebrae, particularly the dorsals, have different nomenclature depending on the authors (*e.g.*, Salgado *et al.*, 1997; Jain and Bandyopadhyay, 1997). Here we adopted the terminology used by Salgado *et al.,* (1997).

Axial Skeleton

The remains of two incomplete cervicals, seven dorsals, six sacrals, twenty-four caudals,

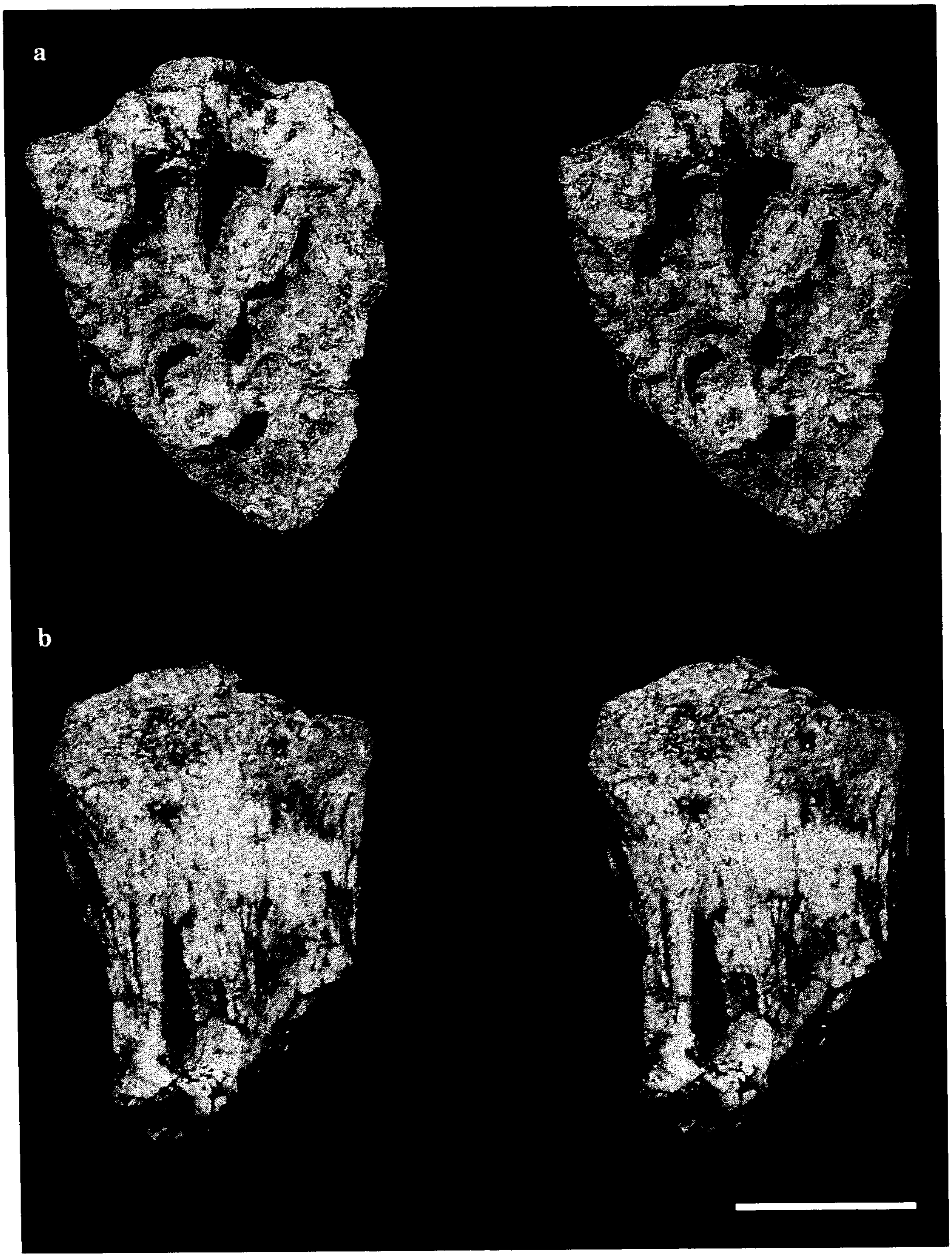

Fig. 5. Anterior part of cervical vertebra of *Gondwanatitan faustoi* n. gen., n. sp., (a), stereophotographs of dorsal view; (b), stereophotographs of ventral view. Note the "chambers" inside the centrum (a) and the two ventral depressions, separated by a bony ridge (b). Scale bar 50 mm.

and four unidentified vertebrae were found (Figs. 5, 6). Since the vertebral column of *Gondwanatitan faustoi* is not complete, the tentative position of each element is based on the partial articulated series of two titanosaurid specimens known from the region of Peirópolis (State of Minas Gerais), known as the "series B and C" (Powell, 1987).

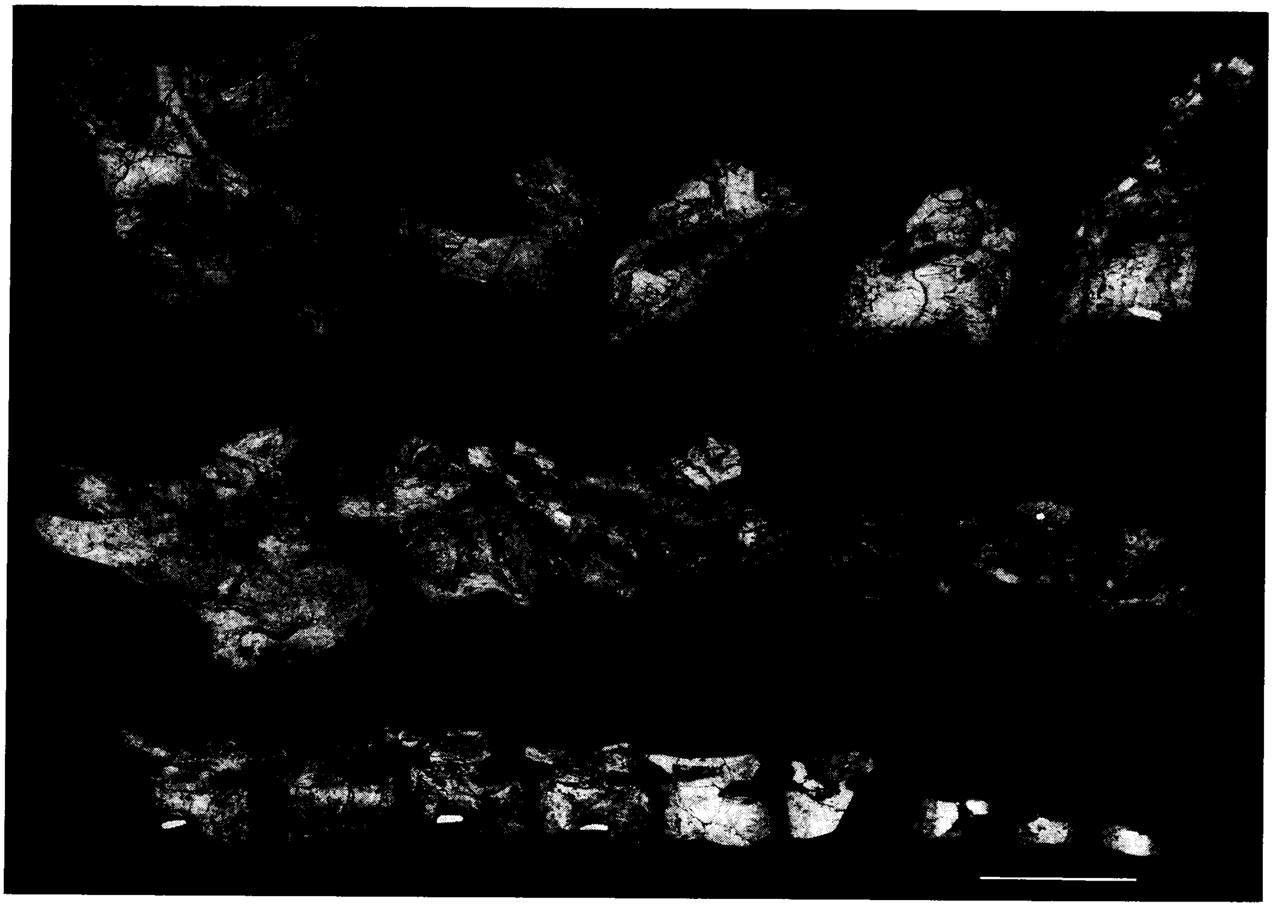

Fig. 6. Vertebrae of *Gondwanatitan faustoi* n. gen., n. sp. in left lateral view; dorsals 6 to 10 (upper row) and selected vertebra of the caudal series (middle and lower rows). Scale bar 100 mm.

Cervical Vertebrae (Fig. 5). The only parts of the cervical series identified in the type material of *Gondwanatitan faustoi* are an incomplete centrum and a very incomplete partial vertebra, one of which shows evidence of one cervical rib. The lateral sides of the centrum are concave and do not show any evidence of a pleurocoel. The ventral part has two concavities, which are separated by a bony ridge. In dorsal view, this vertebra is very lightly built, with several small chambers present in the internal part of the centrum. The cervical rib of the second specimen is a long, thin, and anteroposteriorly oriented structure.

Due to the fragmentary nature of the cervical remains of *Gondwanatitan*, comparisons with other titanosaur taxa are very limited and do not provide any taxonomically useful information.

Dorsal Vertebrae (Figs. 6, 7). Although there is no detailed information about the original position of how the several elements of *Gondwanatitan faustoi* were found in the field, it seems that from the eight identified dorsal vertebrae, the last six were articulated and represent a continuous sequence. Based on more complete dorsal series (particularly MCT 1488–R from Peirópolis, Minas Gerais), the dorsal elements represented appear to be 1, 3, 5–10. There are other remains that possibly belong to both missing vertebrae, but their fragmentary nature does not allow any further reconstruction. Although the degree of

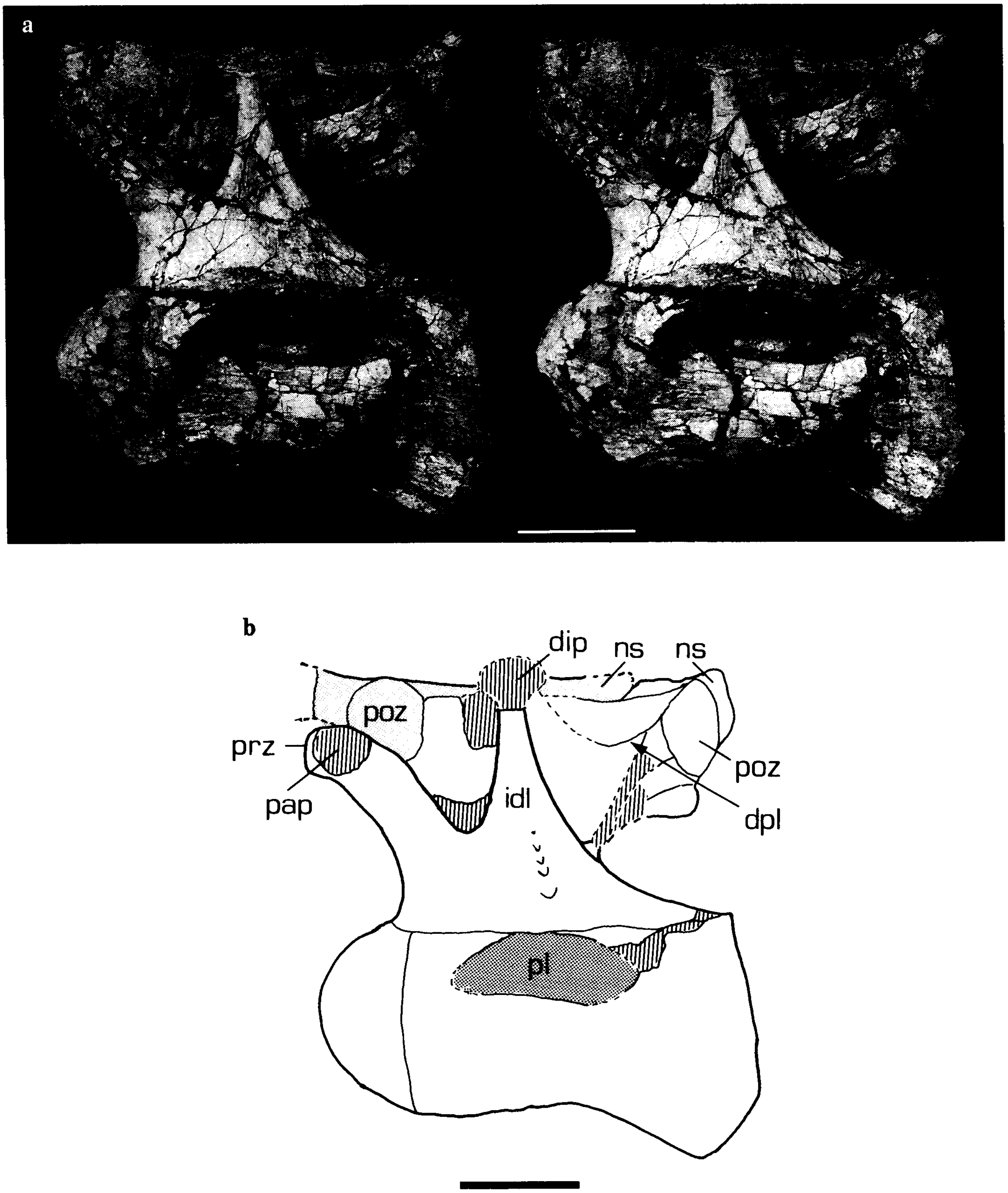

Fig. 7. Left lateral view of the sixth dorsal vertebrae of *Gondwanatitan faustoi* n. gen., n. sp.; (a), stereoview; (b), sketch indicating the main structures. Note that the neural spine, including the postzygapophyses of the 5th dorsal is partially articulated with this vertebra. Abbreviations: dep–depression; dip–diapophysis; dpl–diapo-postzygapophyseal lamina; idl–infradiapophyseal lamina; ns–neural spine; pap–parapophysis; pl–pleurocoel; poz–postzygapophysis; prz–prezygapophysis. Straight lines represent broken areas, slightly darker pointed indicates the 5th dorsal, dark points indicate the pleurocoel. Scale bar 50 mm.

preservation varies, where observable the dorsals are strongly opisthocoelous and have a well developed lateral pleurocoel just below the neural arches (Fig. 7). The pleurocoel is elongated and deep, occupying between 40 to 60% of the centrum length. The size of the centrum varies, being relatively longer in the middle dorsals. The anterior surfaces are hemispherical and convex while the posterior surfaces are larger and concave. No hyposphene-hypantrum is present in the preserved elements.

In only a few dorsal vertebrae (1st [not figured], 6th, and 10th) the neural spine, neural arches, and transverse processes are partially preserved (Fig. 6). The first dorsal has an undivided massive neural spine that is oriented dorsally and shows the presence of a postspinal laminae. In the 5th and 6th (middorsals), the neural spine forms a long, low, and posteriorly oriented structure that extends to the middle part of the proceeding vertebrae (Fig. 7). In the last dorsal (10th), the neural spine is higher and less inclined posteriorly (compare first and last dorsal vertebrae of Fig. 6). In the sole middorsal where the anterior part of the neural spine is preserved, a medial prespinal lamina is present, which forks into two rami before reaching the basal part of the neural spine. No dorsals of *Gondwanatitan faustoi* are sufficiently preserved so as to allow the identification of an accessory spino-diapophyseal laminae.

The neural arches have a broad lateral base, which occupies more than 50% of the centrum length. Near the contact with the centrum, above the pleurocoel, the bone is expanded forming a ridge-like structure that possibly indicates the contact surface between centrum and neural arch. The transverse process is distally relatively thin, but proximally forms a broad base, that shows a small depression (Fig. 7). The infradiapophyseal lamina extends from the diapophysis (not preserved) downwards reaching the centrum. The presence of diapo-postzygapophyseal lamina, although not complete in the preserved dorsals, can also be verified in two vertebrae (6th and 10th).

The zygapophyses are only observed in a few dorsals (Fig. 6). The prezygapophyses are comparatively short, face lateroventrally, with large suboval articulation surfaces that are higher than long. The parapophysis, only observable in the 6th dorsal, is preserved very close and lateral to the prezygaphophysis. If *Gondwanatitan faustoi* also has an centro-parapophyseal laminae, however, it could not be verified in the available material. The postzygapophyses are short, face ventrolaterally, with the articulation surfaces having a sub-horizontal position. In the 1st dorsal the postzygapophyses are very well developed, with the articulation surfaces large and facing ventrally.

Overall, the dorsal vertebrae of *Gondwanatitan faustoi* differ from most titanosaur taxa in being proportionally longer (similar to *Saltasaurus*), having larger pleurocoels (similar to *Epachthosaurus*), and by having the neural spines relatively more inclined. *Gondwanatitan faustoi* further differs from *Andesaurus* and *Epachthosaurus* by the lack of hyposphene-hypantrum, and from MCT 1488-R and *Opisthocoelicaudia* by having a diapopostzygapophyseal lamina (absent in those two taxa). Furthermore, *Opisthocoelicaudia* shows the neural spine bifurcated into two “low metapophyses”(Borsuk-Bialynicka, 1977), a feature not observed in any other titanosaur. The dorsals of *Pellegrinisaurus powelli,* known only from very few incomplete remains, have the centra twice as wide as high (Salgado, 1996), similar to *Opisthocoelicaudia* (see Borsuk-Bialynicka, 1977, Fig. 2), but differing from

Fig. 8. Sacral vertebrae of *Gondwanatitan faustoi* n. gen., n. sp. in ventral view. Scale bar 100 mm.

Gondwanatitan faustoi.

Despite the limited information available about the dorsal vertebrae of *Malawisaurus dixeyi*, homologous elements in this taxon show wider and more robust transverse processes than in *G. faustoi* (Jacobs *et al.*, 1993; Tomida, 1998: p. 61). Compared to the preserved dorsals of *Argentinosaurus huinculensis*, *G. faustoi* has a greater size variation within the series.

Ribs. Several remains of thoracic ribs were recovered. They are rather long and massive structures. There is some evidence of the presence of a pneumatic opening on the posterior surface near the proximal articulation to the dorsal vertebrae.

Sacrum (Fig. 8). The sacrum is composed of six vertebrae whose centra are well preserved. Most of the upper moiety, however, which includes the neural arch and the neural spine is partially eroded and poorly preserved. The 2nd to the 5th sacral are strongly fused to each other while the 1st and 6th are not. The centrum of the first and last sacral is shorter but more massive than the remaining ones. The first sacral is opisthocoelic, with the anterior articulation surface showing a well developed convexity and the posterior surface apparently less concave than the dorsals. The last sacral is procoelic, with the anterior articulation slightly concave and the posterior articulation convex. No pleurocoels were observed.

In ventral view, all preserved sacral ribs tend to be robust, and directed laterally. The sacral ribs of the second sacral (and possibly the first one) are slightly inclined posteriorly, while in the last sacral they are slightly inclined anteriorly. The proximal and distal ends are expanded anteroposteriorly. Although the distal ends are not completely preserved, they might have all been connected and at least partially fused with the ilium.

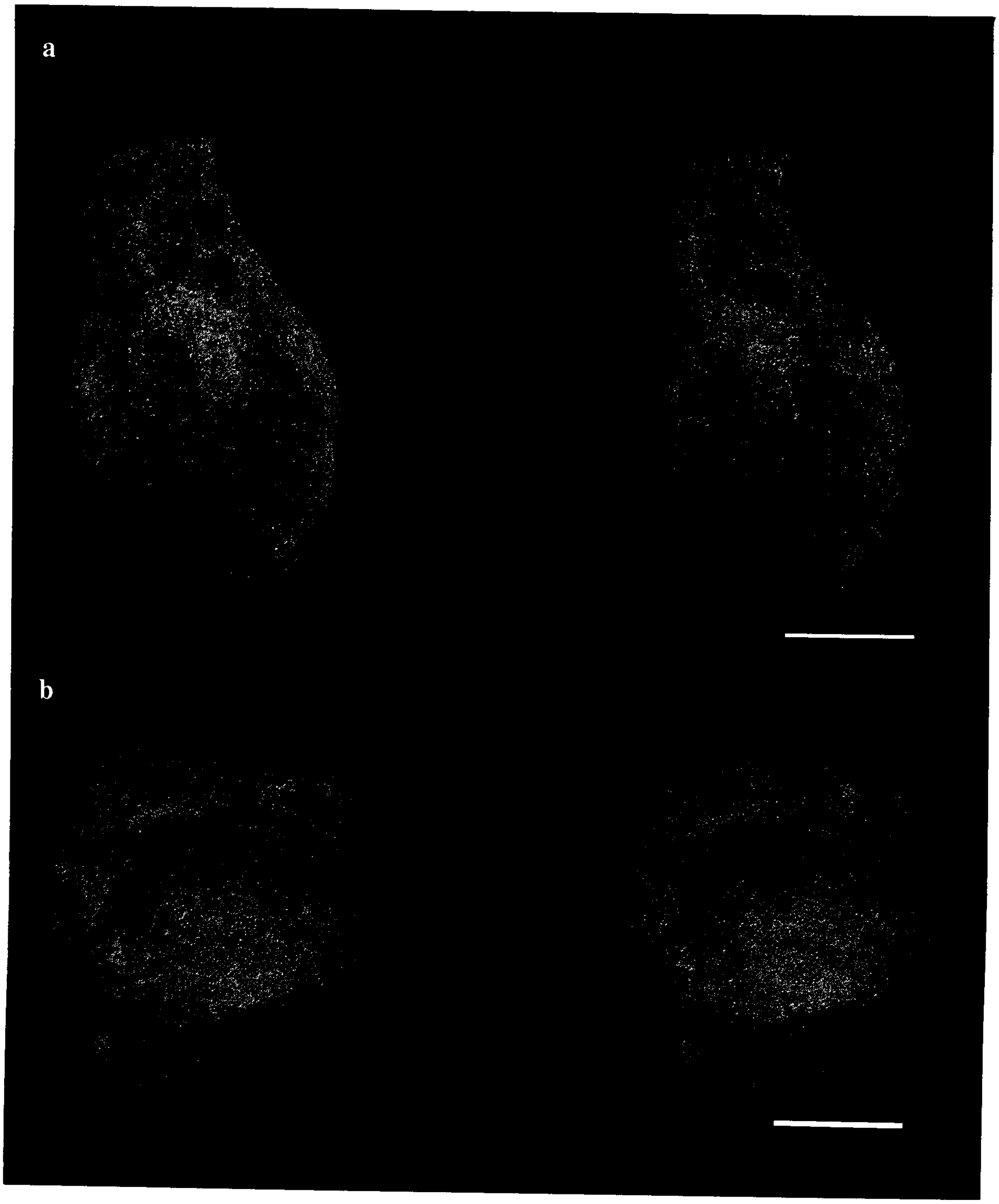

Fig. 9. Stereophotographs of the first caudal (centrum) of *Gondwanatitan faustoi* n. gen., n. sp.; (a), left lateral view; (b) anterior view. Scale bar 50 mm.

Despite the bad condition of the neural arches and spines of the sacrals, it is clear that they show several openings and laminae, displaying a complex structure. Overall they are lightly built, similar to the dorsals and unlike the more massive caudals.

Due to the poor preservation of the sacrals in *Gondwanatitan faustoi* and most other

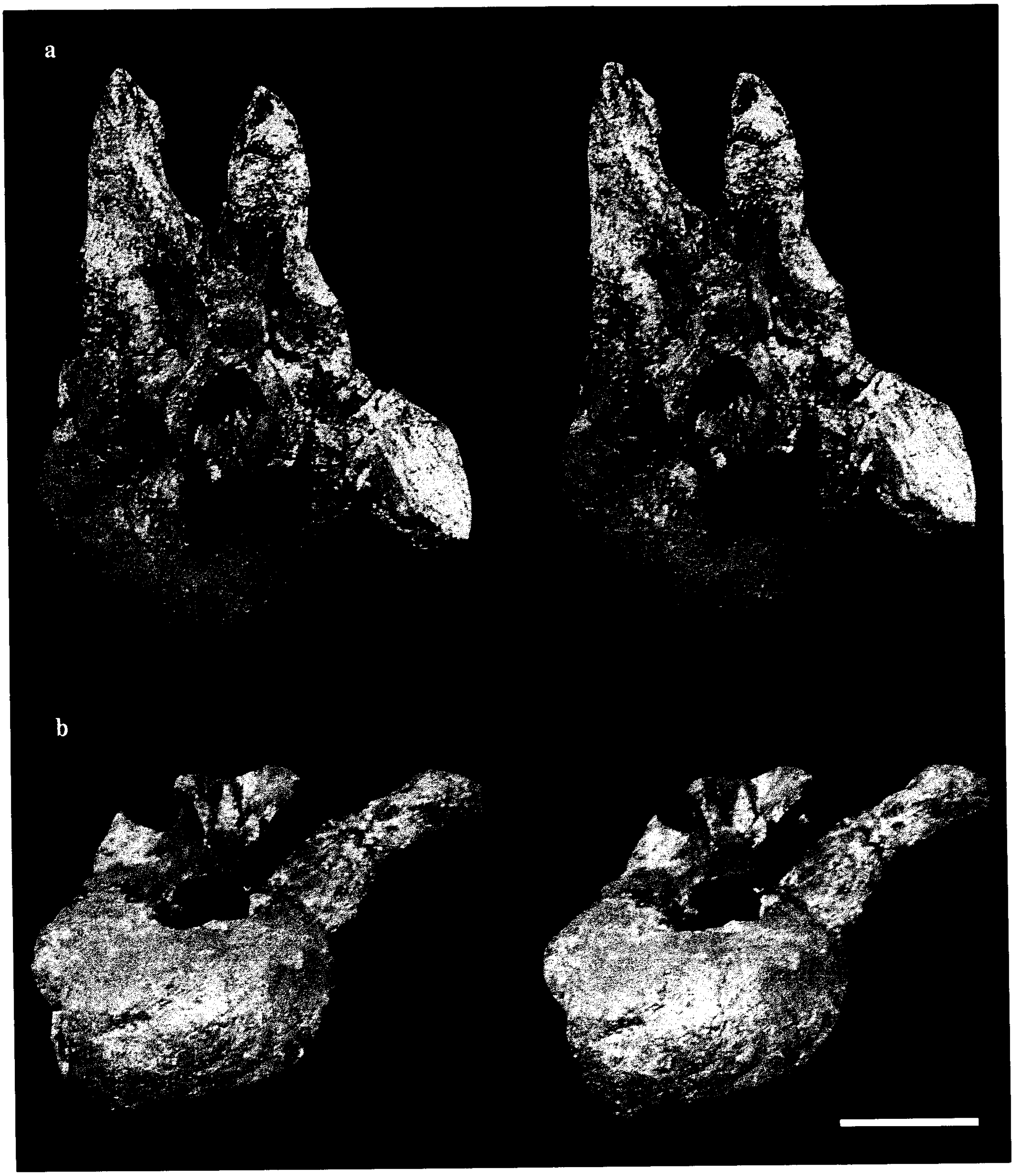

Fig. 10. Stereophotographs of the third caudal of *Gondwanatitan faustoi* n. gen., n. sp.; (a), dorsal view; (b) posterior view. Scale bar 50 mm.

titanosaurs, the comparisons are limited. The number of sacrals (six) is the same as in *Epachthosaurus*, *Malawisaurus* (see Gomani, 1998), *Argentinosaurus*, *Opisthocoelicaudia*, *Saltasaurus* and *Neuquensaurus*. All preserved titanosaurid pelves known from the Bauru Group, particularly from the localities near Peirópolis, have six sacral vertebrae too (Powell, 1987; Kellner and Campos, 1997), which could be a widespread feature among titanosaurids (condition of *e.g.*, *Andesaurus*, *Aeolosaurus* and the non-titanosaurid, but closely related, *Chubutisaurus* is unknown). The condition of the last sacral, having a convex posterior articulation surface distinguishes *Gondwanatitan faustoi* from Opisthocoelicaudia, *Aeolosaurus*, *Pellegrinisaurus*, *Alamosaurus* and *Neuquensaurus.* The sacral ribs of *Gondwanatitan faustoi* are, in ventral view, more elongated than those in *Titanosaurus colberti*.

Caudal Vertebrae (Figs. 6, 9–16). The remains of twenty four caudals were found, but based on more complete specimens (*e.g. Saltasaurus*) the number must have been considerably greater. Anterior, medial, and posterior caudals are represented, several articulated, allowing a fairly accurate reconstruction of the tail of this titanosaur. Since not all elements were found articulated, the position of some is based on the comparisons of more complete articulated series, particularly MCT 1490–R.

All caudal vertebrae are strongly procoelic, notably the anterior and middle ones. The largest and widest caudal centrum found is also the shortest of all anterior ones and therefore interpreted as the first caudal (Fig. 9). On the lateral faces of this element, particularly on the left side, there is a small rounded depression that does not form a pleurocoel. The next largest caudal (here interpreted as the 3rd) has a longer centrum than the previous one and also shows lateral elongated depressions that lack pleurocoels (Figs. 10, 11). In lateral view, the ventral margin is straight. A depression is developed in the middle part of the ventral surface in all caudals back to the 11th. The centrum is dorsoventrally depressed, having an oval anterior and posterior outline, being almost twice as wide as high. Facets for the haemal arches are only very incipient. The prezygapophyses are long (almost 40% of maximum horizontally projected length of vertebra), directed

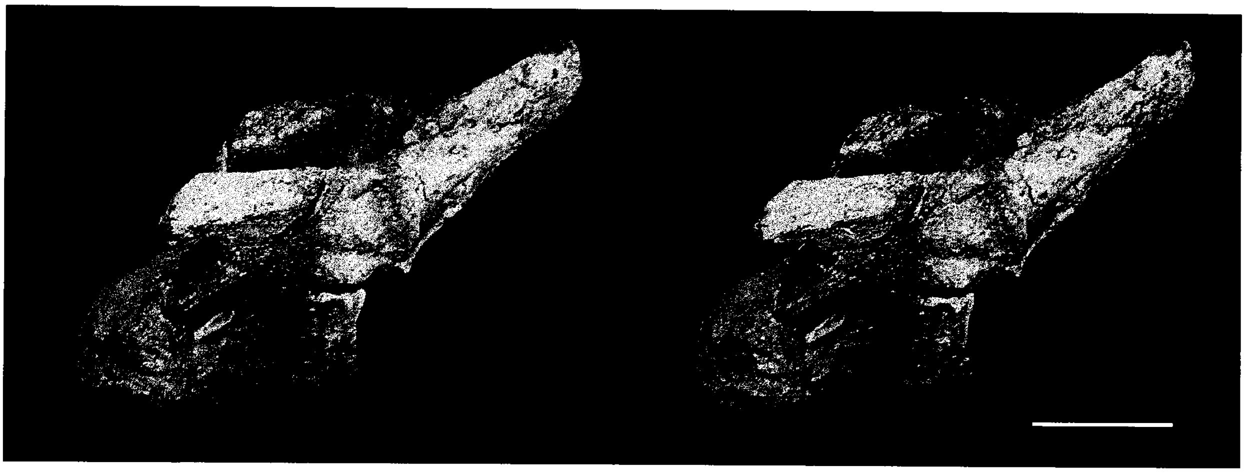

Fig. 11. Stereophotographs of the third caudal of *Gondwanatitan faustoi* n. gen., n. sp., in right lateral view. Scale bar 50 mm.

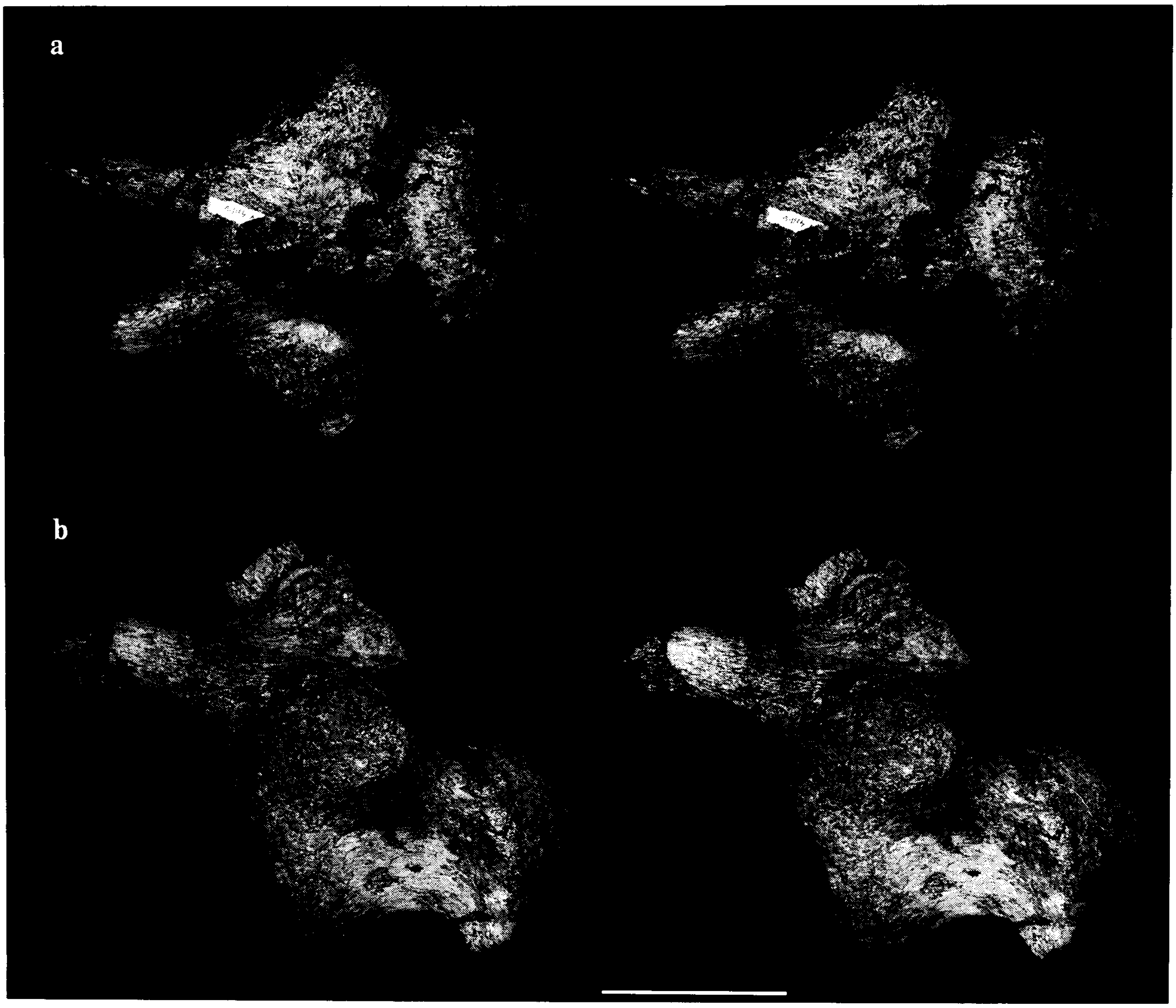

Fig. 12. Stereophotographs of the fifth caudal of *Gondwanatitan faustoi* n. gen., n. sp.; (a), dorsal view; (b) left lateral view. Scale bar 50 mm.

dorsoanteriorly in an angle of about 30°, and clearly reach the middle part of the 2nd caudal (not preserved). On the ventral part of the prezygapophyses there is a well developed bony ridge that terminates in a protuberance directly in front of the anterolateral corner of the centrum, whose function is unknown. Also connected to this protuberance is a second ridge, which is dorsoventrally directed and not as well developed as the first one. The articular surfaces of the prezygapophyses are elongated anteroposteriorly. The transverse processes are "hook-shape", arched posteriorly and slightly ventrally, and have a broad anteroposteriorly elongated base.

The centrum of the remaining anterior caudals increase in elongation up to the 14th caudal, from which it starts to reduce again until the end of the tail. The lateral surface of the centrum of the anterior and midcaudals is concave and inclined towards the midline. Also the ventrolateral margin of the centrum of those vertebrae is concave (Fig. 12-b), differing in this respect from the 1st and 3rd caudals. In the middle part of the ventral

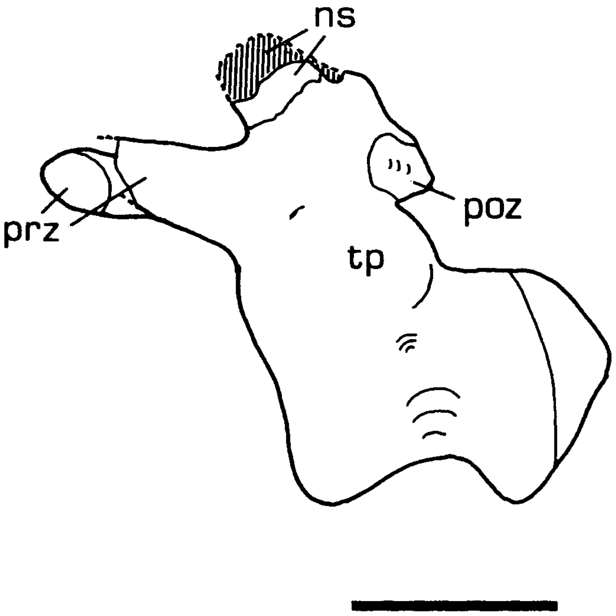

Fig. 13. Left lateral view of the fifth caudal vertebrae of *Gondwanatitan faustoi* n. gen., n. sp.; sketch indicating the main structures. Note that the tip of the neural spine and the left prezygapophysis are broken. Abbreviations: ns–neural spine; poz–postzygapophysis; prz–prezygapophysis; tp–transverse process. Straight lines represent broken areas. Scale bar 50 mm.

surface there is also a well pronounced concavity (Fig. 14-a). On the posteroventral surface, two processes that receive the chevrons are also well developed (Figs. 14-b).

Beginning at least with the 5th caudal, the centrum (in posterior view) has a "heart-shaped" outline, differing from any described titanosaur. Towards the end of the tail, beginning with the 13th caudal, the centrum gets gradually deeper, and possesses a more rounded ventral surface and straighter lateral margins, thus assuming a more quadrangular outline. None of the preserved caudals shows any evidence of pleurocoels.

The neural arch of all the caudal vertebrae is lower than those in the dorsal vertebrae, and is located on the proximal half of the centrum, being inclined anteriorly. Size tends to decrease in the posterior elements of the tail. The transverse processes on the 5th caudal are short but very massive, built on a hemispherical base that gets smaller and less pronounced posteriorly. At the 9th caudal, the transverse process is limited to a lateral anteroposteriorly directed ridge positioned on the base of the neural arch, that tends to disappear towards the posterior end of the tail.

No complete neural spine of any anterior or midcaudals is preserved, but judging from the basal part, such a structure was inclined and directed anteriorly. Towards the end of the tail, the neural spines gradually decrease in size and change their direction around the 9th caudal, getting progressively more inclined towards the posterior region, almost reaching the posterior margin of the centrum. In a fragmentary anterior caudal vertebra (pre-caudal 7), formed by an incomplete neural arch with both postzygapophyses, there is evidence of an incipient postspinal lamina. The dorsal margin of the neural spine of the posterior caudals curves upwards posteriorly (Fig. 6).

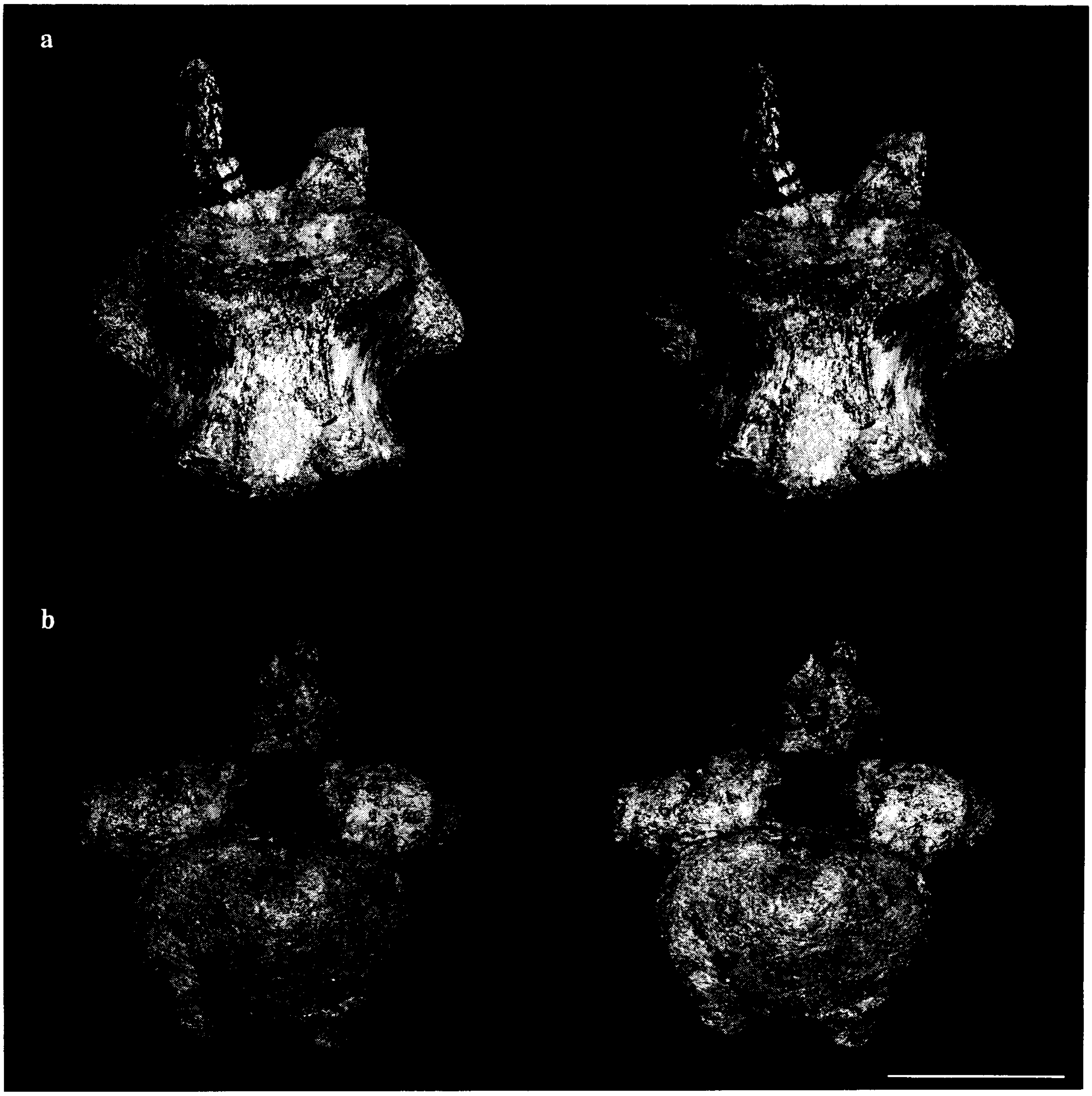

Fig. 14. Stereophotographs of the fifth caudal of *Gondwanatitan faustoi* n. gen., n. sp.; (a), ventral view; (b) posterior view. Scale bar 50 mm.

The prezygapophyses of the 5th caudal becomes less inclined, being sub-horizontal from caudal 7 posteriorly. In all those elements, the prezygapophyses extend well beyond the anterior margin of the centra, but at least from caudal 8 (the prezygapophyses of caudal 9 are incomplete) do not reach the middle part of the preceding vertebra. The articulation surfaces of the prezygapophyses face dorsomedially and in most elements are not well defined. The postzygapophyses are very short and located on the base of the neural spine. On the anterior and midcaudals, the articulation surfaces of the postzygapophyses are comparatively large and form a pronounced concavity, which extends ventrally forming a "half-cylinder" that partially encloses the prezygapophyses of the following vertebra. In

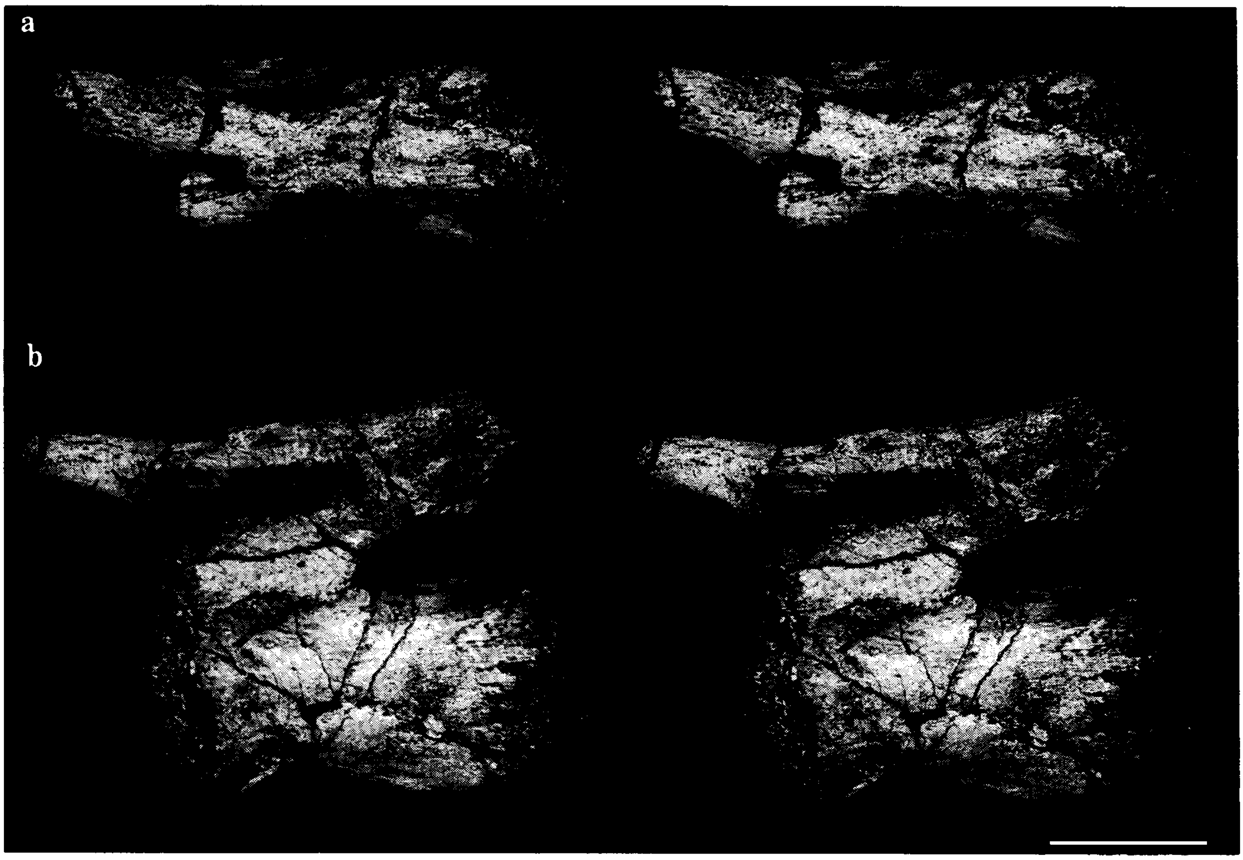

Fig. 15. Stereophotographs of the posterior caudal of *Gondwanatitan faustoi* n. gen., n. sp.; (a), dorsal view; (b) left lateral view. Scale bar 50 mm.

posterior view, the base of the postzygapophyses are joined together by a bony bridge roofing the neural canal (Fig. 14-b), which is also present in the 3rd caudal. Towards the end of the tail the postzygapophyses get gradually less pronounced, tending to disappear altogether in the posterior caudals. The neural canal is rounded and well marked in all elements.

The comparisons of the caudal vertebrae of *Gondwanatitan faustoi* and other titanosaur taxa provides several interesting bits of information. The main feature that differentiates *Gondwanatitan faustoi* from all other described titanosaurids is the "heart-shaped" posterior articulation surfaces of the anterior and midcaudal centra, here regarded as an autapomorphy of this new taxon. The caudal interpreted as the first is procoelic (also supported by the convex condition of the posterior articulation of the last sacral), distinguishing *Gondwanatitan faustoi* from *Aeolosaurus*, *Pellegrinisaurus*, *Alamosaurus* and *Neuquensaurus*, all having the first caudal biconvex (Salgado *et al.*, 1997). The strongly procoelic condition of the anterior and midcaudals further separates *Gondwanatitan faustoi* from *Andesaurus* (only slightly procoelic) and *Opisthocoelicaudia* (opisthocoelic). The procoelic condition of the posterior caudals also distinguishes the new taxon from *Malawisaurus*, that has amphicoelous posterior caudals. The middle and posterior caudals of *Alamosaurus*, *Saltasaurus* and *Neuquensaurus* differ from those of *Gondwanatitan faustoi* by

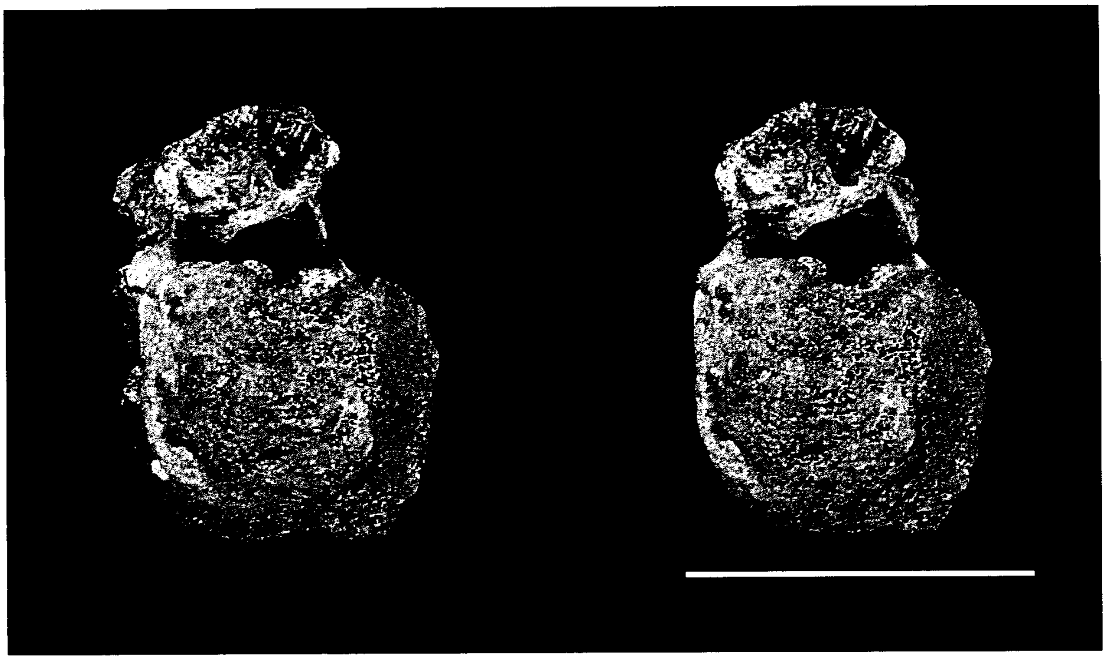

Fig. 16. Stereophotographs of the posterior caudal of *Gondwanatitan faustoi* n. gen., n. sp.; in posterior view. Scale bar 50 mm.

having the centrum dorsoventrally depressed with convex lateral faces. *Gondwanatitan faustoi* can be further distinguished from *Saltasaurus* and *Neuquensaurus* by having the lateral facets of the anterior caudals concave, and from *Saltasaurus*, *Neuquensaurus* and *Titanosaurus colberti* (and perhaps *Titanosaurus araukanikus*) by the position of the anterodorsal margin of the neural spine, which in the new taxon is placed anteriorly relative to the postzygapophyses. *Gondwanatitan faustoi* also has a prominent lateral ridge on the basal part of the neural arch in the midcaudals, which according to Salgado *et al.* (1997) is absent in *Andesaurus*, *Malawisaurus*, *Opisthocoelicaudia* and *Aeolosaurus*.

Gondwanatitan faustoi further differs from *Pellegrinisaurus powelli* that has small pleurocoels in the caudals 2 to 4, the neural spine of the anterior and midcaudals is directed dorsally or posteriorly (and not anteriorly), and the haemal facets on the vertebral centra are reduced. Other differences are found in the posterior caudals, which in *Pellegrinisaurus* have a rounded (not quadrangular) outline of the centrum in posterior view and the dorsal margin of the neural spine inclined posteroventrally (not posterodorsally).

In addition to the differences between *Gondwanatitan faustoi* and Saltasaurinae (*Saltasaurus* +*Neuquensaurus*) already mentioned, the caudals of the former are less elongated, bear longer prezygapophyses, lack pleurocoels (positioned posteroventrally to the transverse processes), and have the neural spine of the anterior elements directed forward. The ventral surface of the anterior and middle caudals of *Saltasaurus* show a comparatively deeper concavity, which in some elements is divided by a bony ridge. Overall the caudals of the Saltasaurinae are more lightly built than in *Gondwanatitan faustoi*, with cancellous bone structures extending back to the caudal vertebrae (more developed in *Saltasaurus* than in

Neuquensaurus).

The inclination and proportional size of the neural spine further distinguish *Gondwanatitan faustoi* from the titanosaurid vertebral series of Peirópolis (MCT 1488–R and MCT 1490–R), *Titanosaurus indicus* (see Jain and Bandyopadhyay, 1997: Fig. 26a–c), and *Titanosaurus colberti*.

No comparisons can be made with some titanosaurs such as *Argentinosaurus*, *Epachthosaurus* and *Antarctosaurus*, where the caudal vertebrae are either unknown or undescribed. The vertebrae attributed to *Argyrosaurus*, whose assignment is questioned by Powell (1986), are higher overall and lack the "heart-shaped" outline in the anterior elements (see Huene, 1929: Plate 39), while the vertebrae attributed to *Titanosaurus araukanikus* (see Huene, 1929: Plate 22) are too fragmentary to allow more detailed comparisons.

The greatest similarities of the caudal sequence of *Gondwanatitan faustoi* are with *Aeolosaurus rionegrinus* and *Aeolosaurus* sp. Among the features shared by those taxa and *G. faustoi* is the anterior directed neural spine of the anterior elements, which constitutes a potential synapomorphy. Other features shared by *Aeolosaurus* and *Gondwanatitan* are the strongly curved ventral margin of the centrum starting around caudal 4 until caudal 10, and the "half-cylinder-shaped" articulation surface of the postzygapophyses. The main distinguishing feature that can be regarded as autapomorphic of *Aeolosaurus*, is the large articulation of the prezygapophyses (Powell, 1986; Salgado and Coria, 1993). As mentioned before, *Gondwanatitan faustoi* also differs from *Aeolosaurus* in the "heart-shaped" posterior articulation surface of the former and the distinctive condition of the first caudal, which according to Salgado *et al.* (1997) is biconvex in the latter. Powell (1986) reported a depression similar to a pleurocoel in the supposed 3rd caudal vertebra of *Aeolosaurus rionegrinus*; *Gondwanatitan faustoi* has a similar depression, but no proper pleurocoel is developed.

Chevrons. The evidence of at least four chevrons of *Gondwanatitan faustoi* were found, all very incomplete, which possibly belong to the middle caudals. These tend to be strongly built and elongated, with the haemal arches fork-like and not completely surrounding the haemal canal. The distal portion is laterally flattened and directed posteriorly.

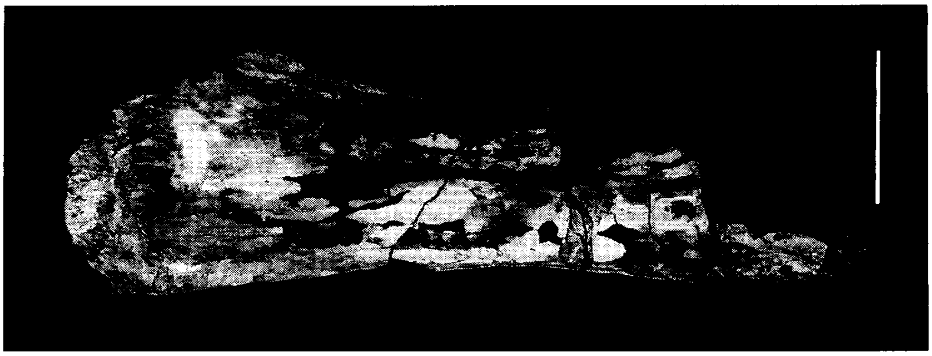

Fig. 17. Left scapula of *Gondwanatitan faustoi* n. gen., n. sp. in medial view. Scale bar 100 mm.

Pectoral Girdle

Scapula (Fig. 17). The proximal part of the left scapula is the only preserved element of the pectoral girdle known in *Gondwanatitan faustoi* (Fig. 3). It is a mediolaterally compressed bone, with an expanded proximal end. The preserved part of this bone indicates that it is curved inwards, particularly the distal region, where the bone tends to be very thick. Medially, an elongated concavity can be observed near the dorsal margin. On the proximal expanded part, which is the thinnest preserved region of the scapula, there is a rugose area, which is interpreted as muscle scars.

Compared to those of other titanosaurids, the scapula of *Gondwanatitan faustoi* is similar to that of *Titanosaurus araukanikus* in having the proximal part curved but differs from *Saltasaurus*, *Neuquensaurus australis*, *Titanosaurus colberti*, which have the proximal border almost straight. *G. faustoi* also differs from *Antarctosaurus wichmannianus*, which has a comparatively straighter dorsal margin. The scapula of *Opisthocoelicaudia* is more curved inwards than in *Gondwanatitan faustoi*. Whether a dorsal prominence on the inner face of the scapula is present, as in *Aeolosaurus*, *Saltasaurus* and *Neuquensaurus*, is unknown, since this region in *Gondwanatitan* is not preserved.

Pelvic Girdle

The pelvis of *Gondwanatitan faustoi* is fairly complete despite its limited preservation.

Fig. 18. Left ilium of *Gondwanatitan faustoi* n. gen., n. sp. in ventral view. Note that a partial sacral rib is connected opposite to the acetabulum. Scale bar 100 mm.

The pelvic elements are represented by the preacetabular region of the left and a fragment of the right ilium, the middle portions of both pubes, the right and the distal half of the left ischium.

Ilium (Fig. 18). This bone suffered from dorsoventral compression, which modified its original shape. Nevertheless, the preacetabular region is blade-like, laterally expanded and has smooth dorsal and ventral surfaces. On the ventral face, anterior to the acetabulum and close to the lateral margin, a low bony ridge that curves medially can be observed in both ilia. Anterior to this ridge there is a shallow depressed area (left ilia).

Although it is fairly incomplete, this region of the ilium is outwardly projected to a certain degree (where known, a feature widespread within titanosaurs). The lateral margin is formed by comparatively thick bone that thins towards the midline. The ischiadic and pubic articulations are not well preserved, but the pubic peduncle is apparently more developed than the ischiadic articulation.

The acetabulum forms an anteroposteriorly elongated embayment in the posteroventral part of the iliac blade. The articulation surface is rugose and changes from very concave anteriorly to less concave towards the posterior end.

Overall, the preserved part of the ilium of *Gondwanatitan faustoi* is similar to that in other titanosaurs. In the case of *Saltasaurus* and *Neuquensaurus*, however, the preacetabular region of this bone projects more outwardly. Whether the posterior process of the ilium is short, as in *Saltasaurus*, *Neuquensaurus* and *Alamosaurus* (Salgado *et al.*, 1997), is unknown because of the poor preservation of this area. It also lacks the marked depression found on the ventral surface of the preacetabular portion of the ilium found in *Titanosaurus colberti.*

Ischium (Fig. 19). The right ischium is almost complete, lacking only the region of contact with the pubis and part of the acetabular margin. Although the exact extent of this contact is unknown, based on the preserved medial part of this element, it was likely to have been long, compared to *Aeolosaurus.* This bone is a posteroventrally oriented structure with a thick dorsolateral margin and arched dorsoventrally. Towards the midline it has a blade-like flange which medioventrally contacts the opposite ischium. The most distal part is slightly expanded mediolaterally.

The iliac peduncle is short and flattened, with the longer axis directed at an angle relative to the midline. On the lateral margin, posterior to the acetabulum, a tuberosity is observed (Fig. 19-b). Proximally, there is a depression on the dorsomedial surface of this bone.

The ischium of *Gondwanatitan faustoi* differs from *Andesaurus*, *Malawisaurus*, *Titanosaurus colberti* and *Saltasaurus* in having a lateral tuberosity and the iliac peduncle less expanded. A similar tuberosity is present in *Opisthocoelicaudia*, which, however, shows a small degree of ventromedial expansion of the ischiadic plate. Based on the reconstruction presented by Salgado and Coria (1993), *Aeolosaurus* also has a less expanded medial ischiadic plate. The pelvic elements of *Antarctosaurus wichmannianus* are too poorly preserved to be compared with *Gondwanatitan faustoi.*

Pubis (not figured). Only the central region of both pubes are preserved. Overall, they are much stronger and more robust relative to the ischia. On the lateroventral part there is strong and blunt bony ridge that disappears distally.

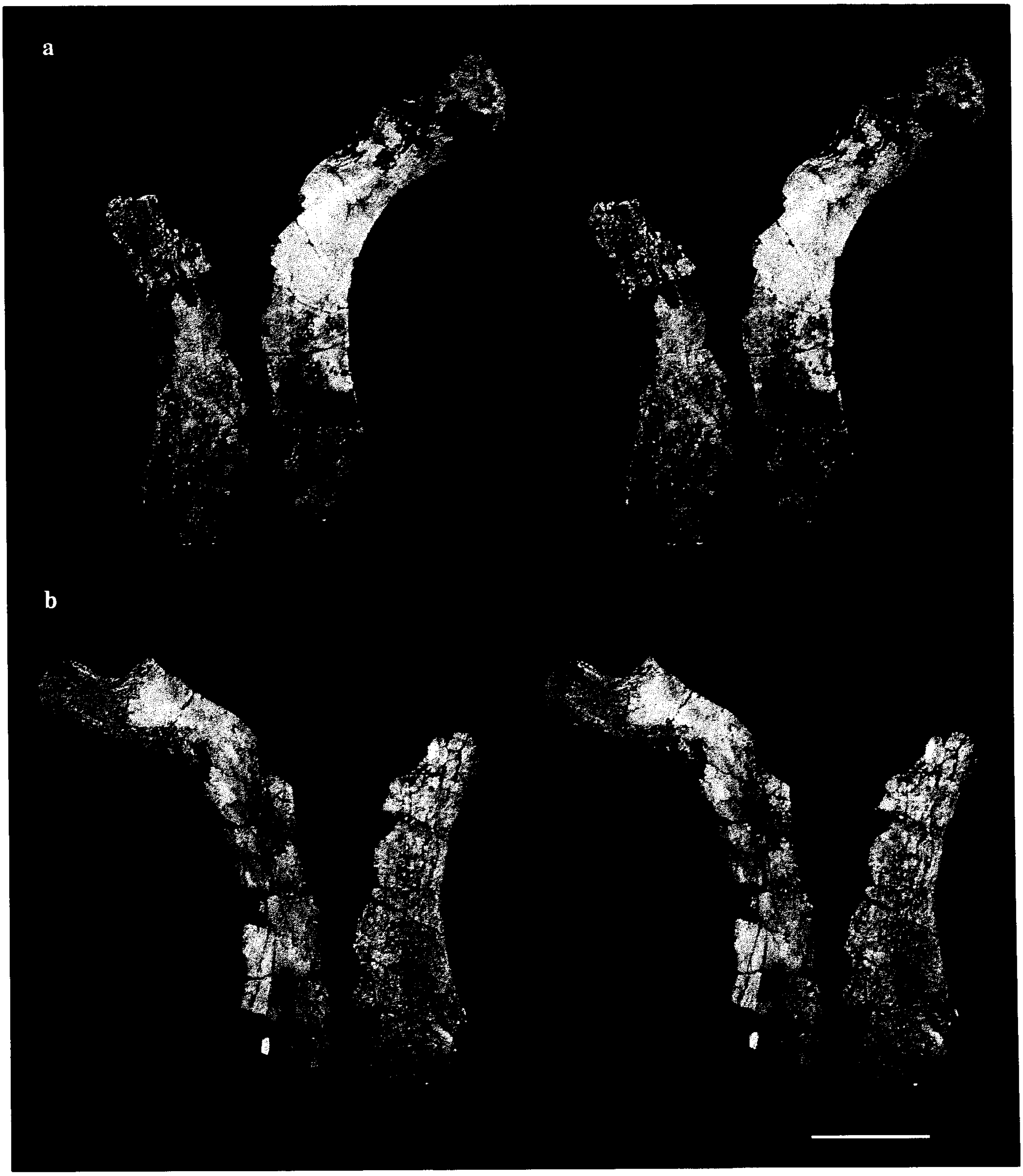

Fig. 19. Stereophotographs of the ischia of *Gondwanatitan faustoi* n. gen., n. sp.; (a), dorsomedial view; (b), ventrolateral view. Scale bar 100 mm.

Due to the incompleteness of the pubes of *Gondwanatitan faustoi*, very few comparisons are possible. A lateroventral ridge is also found in *Aeolosaurus* (Salgado and Coria, 1993: Plate 1, Fig. I) and in *Saltasaurus* and might be widely distributed among titanosaurs.

Limbs

The forelimb of *Gondwanatitan faustoi* is only represented by the humeri and the hindlimb by both tibiae. Except for the most distal part of the left humerus and part of the distal end of the right tibia, all four elements are comparatively well preserved and complete. All underwent some dorsoventral compaction, particularly the right humerus, which has affected their natural shape.

Humerus (Fig. 20). The humerus of *Gondwanatitan faustoi* is a slender bone, with a constricted shaft and expanded articulations. This bone is slightly twisted and has the proximal articulation wider than the distal one. The deltopectoral crest is very well developed, extending for almost 45% of the humerus length. It has a broad base and is

Fig. 20. Stereophotographs of the right humerus of *Gondwanatitan faustoi* n. gen., n. sp. in anterior view. Note the developed deltopectoral crest. Scale bar 100 mm.

strongly curved towards the midline. The anterior surface of the proximal part of the humerus is depressed between the deltopectoral crest and the medial margin. Below the humerus head and closer to the medial margin, a tubercle that extends in a low ridge (possible for muscle attachment) can be observed. On the posterior surface, close to the lateral margin, the bone surface is rugose.

The distal end has two well marked depressions, one anterior and a second posterior, the latter being the more pronounced. The distal condyles are well developed anteriorly, with the medial one projecting more than the lateral. A well developed bony ridge can be observed on the posterolateral margin near the lateral condyle. The humerus/tibia ratio is 1.38.

Due to its slenderness, the humerus of *Gondwanatitan faustoi* is similar to *Titanosaurus colberti* (the humerus figured by Jain and Bandyopadhyay, 1997: Fig. 20, is a right, not a left one) and *Antarctosaurus wichmannianus*. *G. faustoi* differs from those taxa mainly in having the deltopectoral crest very well developed and curved medially. *G. faustoi* further differs from. *T. colberti* in having the deltopectoral crest extended further down the shaft and in having the proximal end broader than the distal one.

There is no complete humerus of *Andesaurus* available, but based on the reconstruction presented by Calvo and Bonaparte (1991), this bone is the most slender humerus among all

Fig. 21. Stereophotographs of the left tibia of *Gondwanatitan faustoi* n. gen., n. sp. in lateral view. Scale bar 100 mm.

titanosaurs and, therefore, differs from the condition found in *Gondwanatitan faustoi.*

Compared to the titanosaur taxa with a more heavy build and shorter humeri such as *Opisthocoelicaudia*, *Argyrosaurus*, *Neuquensaurus* and *Saltasaurus*, *Gondwanatitan faustoi* differs in having a deltopectoral crest which does not extend half the humeral length. Except for *Opisthocoelicaudia*, *G. faustoi* differs from the mentioned taxa in having a more developed and medially curved deltopectoral crest.

Tibia (Figs. 21–23). The tibia of *Gondwanatitan faustoi* is an elongated bone with the expanded ends, the proximal more so than the distal. The shaft is constricted in the middle, expanding anteroposteriorly at the proximal end and transversely at the distal end, resulting in the articulations being at an angle to each other. The proximal articulation is compressed laterally, partially possibly due to post-mortem compression. The most anterior tip of the proximal articulation is the highest point of the tibia in lateral view (Fig. 21). Ventral to this dorsal projection, a well developed cnemial crest is present that is separated from the shaft by a deep longitudinal concavity. The cnemial crest is directed anteriorly and is only slightly curved laterally (Fig. 22). On the most distal part of the crest the bone surface is rugose with ridges and grooves that served for muscle attachment.

The distal articulation is less flattened with the longer axis inclined mediolaterally (Fig. 23). This results in the distal articulation being more transversely expanded than

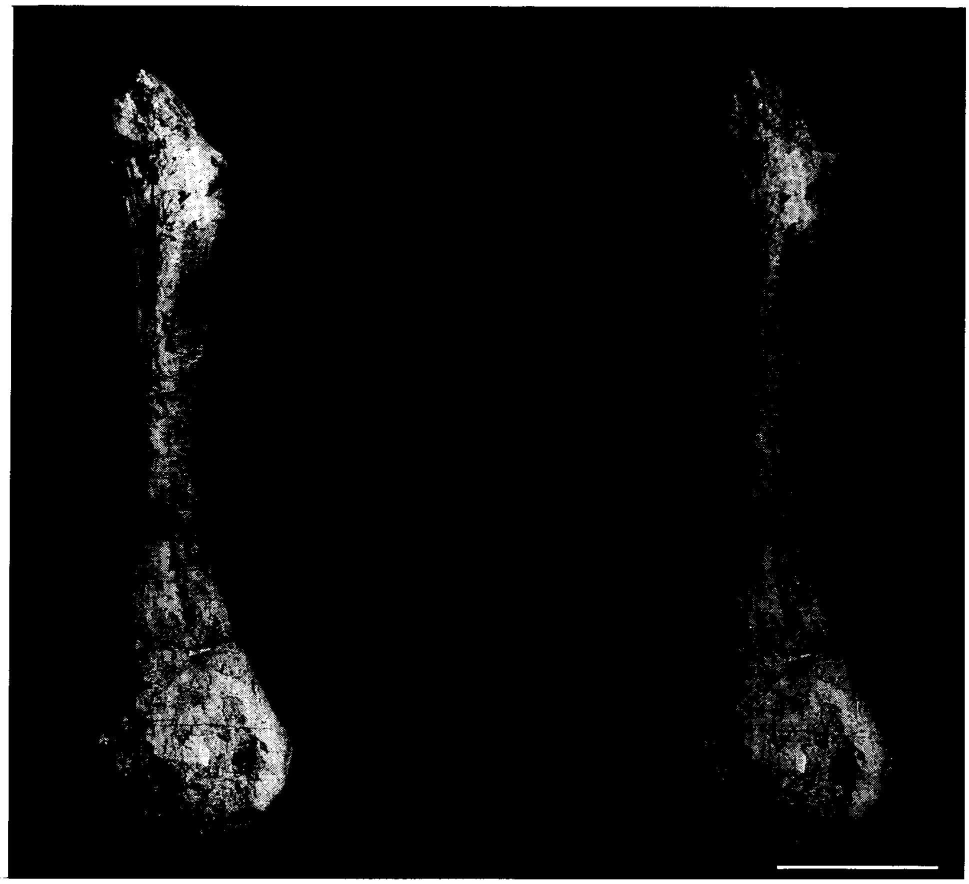

Fig. 22. Stereophotographs of the left tibia of *Gondwanatitan faustoi* n. gen., n. sp. in anterior view. Scale bar 100 mm.

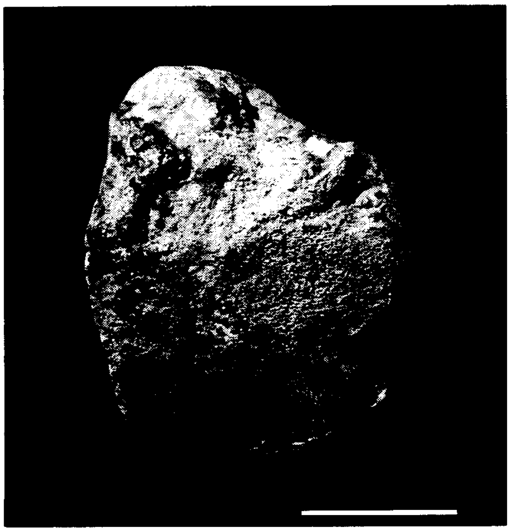

Fig. 23. Left tibia of *Gondwanatitan faustoi* n. gen., n. sp. in distal view. Scale bar 50 mm.

anteroposteriorly, a feature widespread among titanosaurs (Salgado *et al.*, 1997).

Compared to other titanosaurs, the tibia of *Gondwanatitan faustoi* differs by having the anterior end of the proximal articulation dorsally projected and by having the cnemial crest only slightly curved laterally. Furthermore, the proximal articulation of this bone seems to be flatter than in any known titanosaurid, but to what degree this is a natural feature or due to post-mortem compression cannot be established.

Overall, the tibia of this new taxon is elongated as much as in *Titanosaurus araukanikus* and *Antarctosaurus wichmannianus*, and differs in this respect from *Opisthocoelicaudia* and *Saltasaurus*. Compared with *Gondwanatitan faustoi*, *Opisthocoelicaudia* and *Saltasaurus* also have the cnemial crest more developed and the distal end more expanded, while the tibia of *Antarctosaurus wichmannianus* has a straighter shaft and the proximal articulation stronger and heavier built.

Discussion

The studies of sauropods are hampered by the fact that only a few reasonably complete specimens have so far been found. This is particularly true for titanosaurids (= Titanosauria *sensu* Bonaparte and Coria, 1993), where most taxa are based on limited parts of the skeleton, essentially dorsal and caudal vertebrae, occasionally found associated with a few other bones (*e.g.*, *Aeolosaurus*, *Argentinosaurus*, *Epachthosaurus*). The skeleton from very few species can be regarded as well known. Among the few that are, some are based on several individuals (*e.g.* *Saltasaurus loricatus*, *Malawisaurus dixeyi*), while others come from more than one locality (*e.g.*, *Neuquensaurus*). Furthermore, there is an excessive number of taxa known from extremely poor and incomplete material, whose assignment is, at best, very doubtful (*e.g.*,*Titanosaurus? manus* Lydekker, 1893; "*Antarctosaurus brasiliensis*" Arid and Vizotto, 1971). As a result, most of the diagnostic characters given for titanosaurid taxa are based on morphological variations observed in the vertebral column, which in most cases is very incomplete. In a recent phylogenetic analysis of titanosaurids presented by Salgado *et al.* (1997) over half of the characters are based on vertebral features, none of which is known in all analyzed taxa. About 25% of the data is missing in this analysis and the most underrepresented are the titanosaurid taxa (*e.g.*, *Argentinosaurus*, *Alamosaurus*).

Unfortunately, *Gondwanatitan faustoi* is no exception and like most titanosaurid taxa, is known only from dorsal, caudal, and sacral vertebrae, that were found associated with a limited number of other bones (humerus, tibia, and part of the pelvis). Therefore, it cannot be overemphasized that several features present in *G. faustoi*, notably in the neural arches of the dorsal vertebrae, were only observed in the few elements (sometimes incomplete) that are preserved. As a result, like in the majority of titanosaurid taxa, very little is known about the variation of those morphological features within the vertebral column.

So far, very few dinosaurs have been described from Brazil (Campos and Kellner, 1991; Kellner, 1998). The only other sauropod named from this country is "*Antarctosaurus brasiliensis*", which is based on three fragmented remains found during the construction work of a road (Arid and Vizotto, 1971): the distal half of a femur, the proximal part of a humerus, and one incomplete dorsal vertebrae. It is not sure that this material belongs to the same individual. Furthermore, none of those bones are preserved enough to be diagnostic at the specific level. The only titanosaurid feature of this material is the "eye-shaped" pleurocoel of the dorsal vertebra. Therefore, despite admitting the titanosaurid nature of this material (at least the dorsal vertebra), we here consider "*Antarctosaurus brasiliensis*" as Titanosauria indet and are unable to provide a diagnosis that could distinguish this taxon from all the others. Nevertheless, it should be noted that the deltopectoral crest of the humerus attributed to this taxon is comparatively small, similar to several other titanosaur taxa but different from the larger and curved condition of this structure observed in *Gondwanatitan faustoi.*

In order to place *Gondwanatitan faustoi* within titanosaurs we used the data published by Salgado *et al.* (1997). Of the five synapomorphies of Titanosauria recognized by those authors, only three can be shown to exist on the type-material of *G. faustoi*: the dorsal vertebrae have elongated ("eye-shaped") pleurocoels, the posterior dorsals have widened, slightly forked infradiapophyseal laminae, and the anterior caudal vertebrae are procoelic. The remaining two characters (pubis longer than ischium and the presence of centroparapophyseal lamina) could not be discussed since those elements are not well enough preserved in the sole specimen known of *G. faustoi.* When *G. faustoi* is included in the analysis performed by Salgado *et al.* (1997) all nodes above their node 10 combine, with the exception of the Saltasaurinae (*Saltasaurus* + *Neuquensaurus*).

Although a review of titanosaur phylogeny is beyond the scope of this paper, we performed a robustness analysis of the data set presented by those authors, which is known as the Bremer or branch support analysis (for alternative terms see Bremer, 1994). This technique of evaluating phylogenetic results consists of examining strict consensus trees of subsequent less parsimonious sets of trees. The branch support is quantified by the number of extra steps needed to lose a branch in those near-most-parsimonious trees (Bremer, 1988).

Running the data matrix published by Salgado *et al.* (1997) through PAUP 3.1.1 (instead of Hennig 86), maintaining all assumptions of the original work (*e.g.*, ordering characters 2, 14, 16, and 23), and keeping all trees one step longer than the most parsimonious trees, we obtained 33 trees with 55 steps. The strict consensus tree of those collapsed all nodes within Titanosauria, indicating that they all (including Saltasaurinae) have a branch support of 1.

These results indicate that the phylogenetic hypotheses of ingroup relationships among titanosaurs is still very weakly supported (in most cases by only one character) and at least partially explains the result obtained by the inclusion of *Gondwanatitan faustoi* in the analysis.

Regarding the phylogenetic position of *Gondwanatitan faustoi* , it appears not to be a member of the Saltasaurinae, which have depressed anterior caudal centra with convex lateral faces and the anterodorsal edge of the neural spine placed posteriorly relatively to the anterior part of the postzygapophyses (Powell, 1986; Salgado *et al.,* 1997). *G. faustoi* also lacks the dorsoventrally convex lateral faces of the mid- and posterior caudals that unites *Alamosaurus* with the Saltasaurinae. Rather it has a well developed ridge on the base of the neural arch in the midcaudal series that according to Salgado *et al.* (1997), is shared by those taxa. It should be noted, however, that this last feature is also observed in other titanosaurs such as the series of Peirópolis (caudals attributed to DGM series B = MCT 1488–R [but see Campos and Kellner, this volume]; DGM series C = MCT 1490–R) and in *Epachthosaurus* (Martínez in Salgado *et al.*, 1997: 35).

Gondwanatitan faustoi can be separated from *Malawisaurus* and *Andesaurus*, both regarded as basal titanosaurs, in that it has procoelous posterior caudals. The strongly procoelous condition of the anterior and midcaudals (also present in *Malawisaurus* and in advanced titanosaurs) is another feature separating this taxon from *Andesaurus.*

The relationships of *Gondwanatitan faustoi* with the remaining titanosaurs is unclear. It should be noted, however, that this new taxon shares at least one unique feature with *Aeolosaurus*: strongly anteriorly directed neural spines on the anterior caudals and anterior midcaudals. Whether those taxa, indeed, form a monophyletic group can only be determined with more complete material of both. Nevertheless, it should be noted that, other than belonging to the titanosaurid clade (a group of dinosaurs traditionally considered Gondwanan), no particular feature of *G. faustoi* was observed so far that suggests any close relation with African forms, contrary to the similarities shared by some other fossil archosaurs found in Cretaceous strata of several basins situated in the northeastern part of Brazil (Kellner, 1994).

Conclusion

Gondwanatitan faustoi constitutes a new titanosaurid taxa from Brazil. Among its autapomorphic features is the "heart-shaped" distal articulation of the anterior caudal vertebrae where this character is well developed, and changes to a more quadrangular shape towards the end of the tail. This new taxon also has the deltopectoral crest of the humerus well developed and medially curved, and the tibia with anterior part of the proximal articulation very high and cnemial crest only slightly curved laterally.

Due to the limited information available for most titanosaurid taxa, the phylogenetic position of *Gondwanatitan faustoi* is still uncertain. With the present state of knowledge, this taxon can be well separated from the Saltasaurinae (*Saltasaurus* + *Neuquensaurus*) and from the more basal titanosaurs like *Andesaurus* and *Malawisaurus.* It is apparently more closely related to *Aeolosaurus* based on the configuration of the anterior caudal and midcaudal vertebrae.

In the lack of osteological material of ornithischian dinosaurs (Kellner, 1996) and the wide distribution of titanosaurids in Brazil, it appears that sauropods constituted the major herbivore component in the vertebrate fauna during the Cretaceous in this part of Gondwana.

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