

New data on the palaeontology and sedimentology of the Lower Jurassic Lisbon Formation (Karoo Supergroup), Ellisras Basin, South Africa

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With 7 figures

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Abstract: Published records on the palaeontology of the Lower Jurassic Lisbon Formation in the Ellisras Basin (a South African continuation of the Botswana Kalahari Karoo Basin) are virtually non-existent. Here we review the geology of this extremely poorly exposed unit, and describe a newly discovered ichnofossil and fossil vertebrate association, consisting of constructed structures resembling termitaria as well as of basal sauropodomorph remains. Our paleontological and sedimentological analyses permit a direct bio- and lithostratigraphic correlation of the Lisbon Formation at farm Lisbon with the upper part of the Elliot Formation in the main Karoo Basin as well as other Lower Jurassic continental red bed successions throughout southern Africa. We tentatively suggest that the formation (especially its upper part) was deposited in a dryland setting with well-drained soils that at least episodically supported some flora and a fauna probably dominated by basal sauropodomorphs.

Key words: Dinosauria, Early Jurassic, Karoo, Lisbon Formation, South Africa.

1. Introduction

Vertebrate and trace fossils were discovered in the upper part of the Lisbon Formation (GPS 23°27'42.19"S; 27°18'14.25"E) in the north-western part of South Africa (Figs. 1-2), in an area that is characterized by extremely rare and poor natural exposures. To date, these are the only Mesozoic vertebrate fossils described in any detail from the entire region, thus here we present a short description of the geological context and palaeontology of the finds. The fossils need to be collected, prepared and preserved. They are situated in an environmentally vulnerable position, right on the eastern banks of the Limpopo River, on farm Lisbon 19LQ, approximately on a proposed

route for a major transfrontier power line corridor by Eskom (South African electricity public utility).

2. Geological background

The Ellisras Basin (also referred to as the Waterberg Coalfield), a southeastward continuation of the Botswana Kalahari Karoo Basin (SMITH 1984; MACRAE 1988) (Fig. 1) is filled by the Late Carboniferous – Early Jurassic Karoo Supergroup which in here attains a maximum thickness of over 600 m and is subdivided into formations with local names (Fig. 2) (SIEPKER 1986; BRANDL 1996; FAURE et al. 1997). The basin fill rests unconformably on Archaean rocks of the



Fig. 1. Map of the southern Africa showing the distribution of the Karoo-age deposits and the location of the study site in the Ellisras Basin (map modified after JOHNSON et al. 1996).

Limpopo Belt in the north, and is downfaulted against the Proterozoic Waterberg Group in the south (BRANDL 1996; REID et al. 1997). This east-west elongated basinal structure is dissected by numerous smaller and bounded by larger normal and strike-slip faults. Some of the faults (e.g., Mhalapshwe, Zoetfontein, Daarby) are of regional importance and mostly run ENE-WSW, parallel to the structural fabric of the Limpopo Belt (COX et al. 1965; GREEN et al. 1980; REID et al. 1997). Evidence suggests syn-Karoo extensional tectonic activity along these faults, and it is based on the irregular thickness distribution of the Karoo formations within the basin, which is highlighted by the fact that the lower part of the succession is complete only within some of the downfaulted areas of the south-easterly and easterly portions of the basin (GREEN et al. 1980). The virtually non-existent outcrops of the region are only weakly complemented by coal exploration borehole data (mostly available at the South African Council for Geoscience) which mainly detail the lower, coal-bearing Permian part of the Karoo succession.

3. Sedimentology

The focus of this study, the fossil-bearing strata of the Lisbon Formation, ranges in thickness from ~72 m to 153 m (borehole MQ1- 23°27'S, 27°50'E), and has an average thickness of ~100 m. The thickness is fairly constant through the basin with the exception of two zones of slightly larger thicknesses in the NE and SW (Fig. 3). In boreholes, the formation seems to be present throughout the area, but there is only one exposure on farm Lisbon 19 LQ, on the eastern bank of the Limpopo River, close to its upper boundary (BRANDL 1996; EMB & AB, pers. obs.). The Formation which is considered to be a correlative of the Upper Triassic-Lower Jurassic Elliot Formation in the main Karoo Basin (JOHNSON et al. 1996) (Fig. 2B), has conformable lower and upper boundaries, and it is underlain by the Greenwich Formation and overlain by the Clarens Formation. The underlying Greenwich Formation is erosively based and composed of medium- to coarse-grained purplish red, whitish or greenish, feldspathic, locally slightly micaceous,

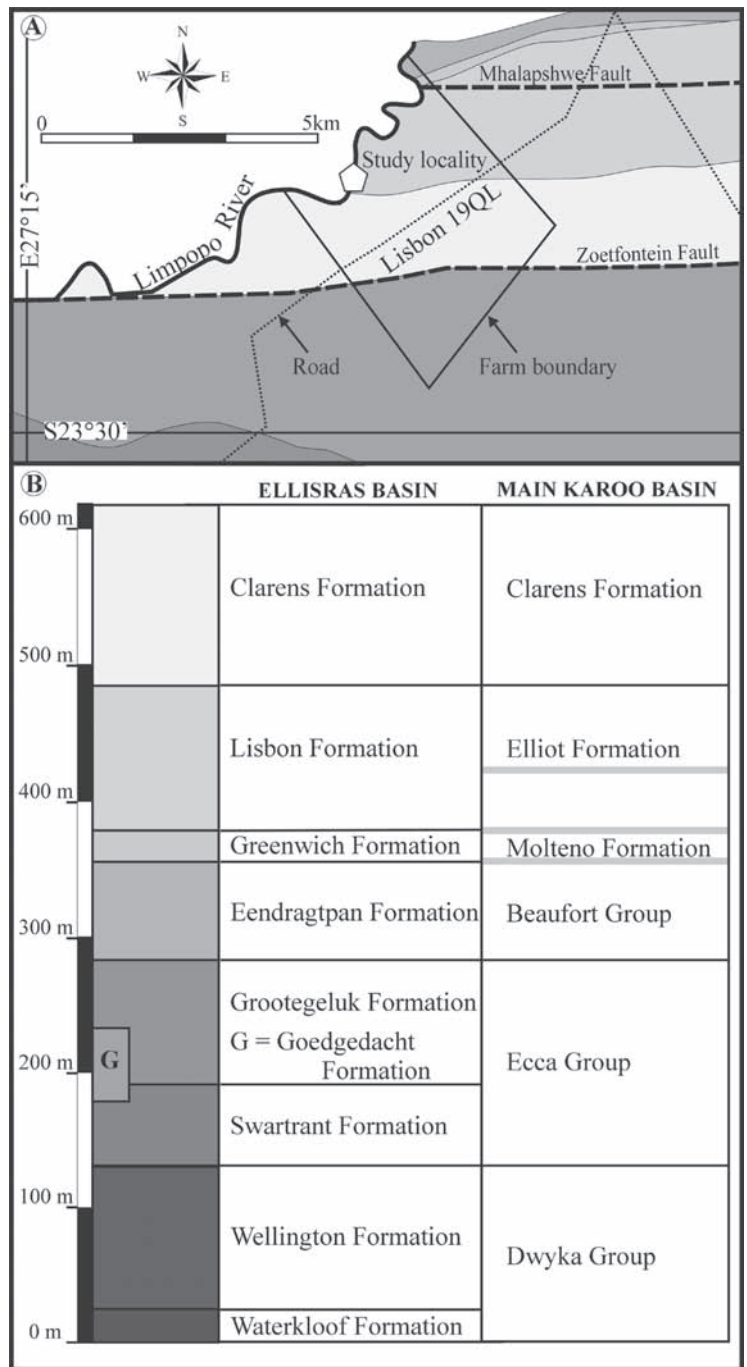


Fig. 2. A. Geological map of the farm Lisbon and its vicinity in the Ellisras Basin (South Africa) (modified after BRANDL 1996). See Fig. 1 for regional context, and 2b for legend. **B.** Stratigraphic correlation showing the subdivision and correspondence of the sedimentary units of the Late Carboniferous – Early Jurassic Karoo Super-group units in the Ellisras and main Karoo Basins (after JOHNSON et al. 1996; FAURE et al. 1997). Grey indicate stratigraphic gaps in the ‘Stormberg Group’ (for details see CATUNEANU et al. 1998; BORDY et al. 2004a). The Wellington Formation was shown palynologically to contain the Carboniferous-Permian boundary (MACRAE 1988). Based on lithological and stratigraphic arguments, DE JAGER (1983) suggested that the upper, coal-bearing part of the Grootegeluk Formation is equivalent to the Late Permian lower Beaufort Group. The Karoo lavas that cap the succession show comparable ages (Early Jurassic: 179 ± 5 Ma) to the Karoo continental flood basalts in the main Karoo Basin (REID et al. 1997).

cross-bedded sandstone and grit with local thin conglomerate lenses and mudstone intercalations. The conglomerates consists mainly of rounded, 1 to 2 cm quartz pebbles (max. 4.5 cm in borehole 125-23° 33'7"S, 27°35'20"E), and very rare grey clay fragments. This 2 to 48 m thick, Molteno-equivalent unit contains mainly 1 to 10 m thick upward-fining sand-

stone units, and a few upward-coarsening units too (DE JAGER 1983; BRANDL 1996). The unit was most likely deposited in a high energy fluvial system that drained from north and east (BRANDL 1996). The overlying Clarens Formation is a fine-grained, white to light pink coloured sandstone succession that is generally massive, well-sorted and rarely cross-bed-

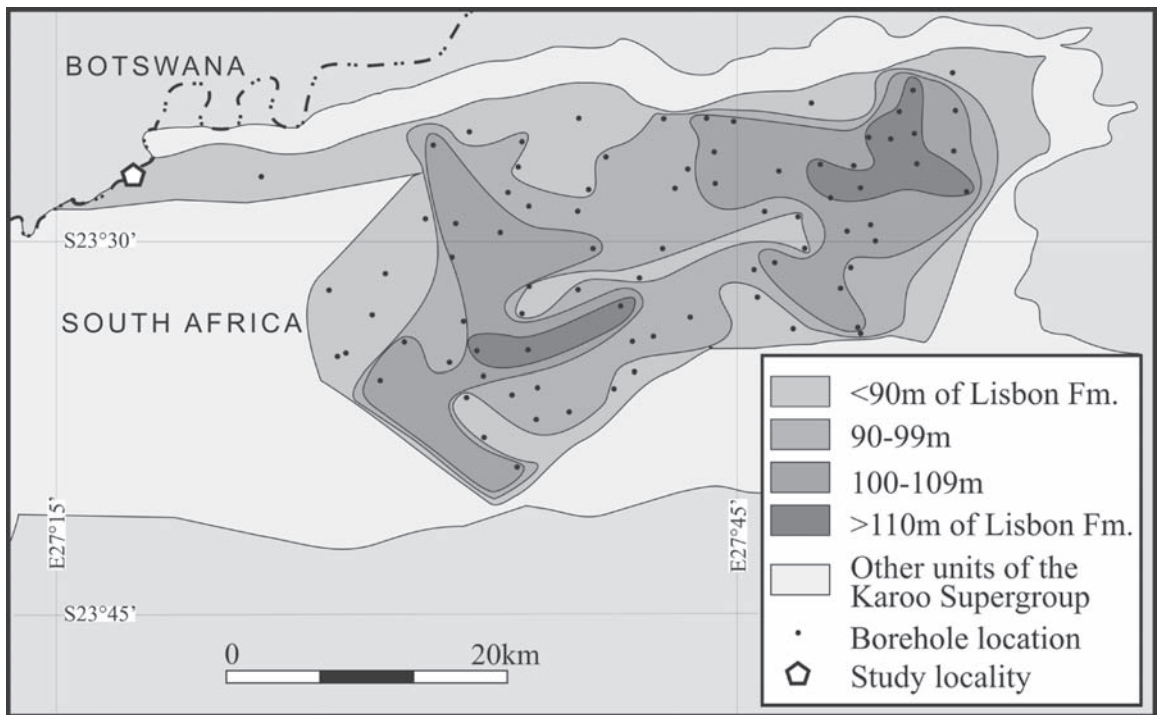


Fig. 3. Thickness map of the Late Triassic-Early Jurassic Lisbon Formation in the Ellisras Basin (South Africa). Thickness figures based on coal exploration borehole descriptions which are stored at Council for Geoscience (Pretoria).

ded with well-rounded quartz grains showing a high degree of sphericity, a few pebbly horizons and rare root imprints (BRANDL 1996). This maximum 130 m thick unit was probably deposited in an aeolian system dominated by a palaeowind regime that blew from WSW to ENE and was characterized by small ephemeral streams feeding occasionally vegetated, inland sabkhas (BRANDL 1996).

The Lisbon Formation is dominated by red, maroon, purple, rare pale grey massive mudstones with pink to dark red siltstone as well as some mostly red or maroon, massive silty sandstone and fine- to coarse-grained sandstone with pebble washes (BRANDL 1996; EMB & AB pers. obs.) (Fig. 4). The upward-fining sandstone-siltstone-mudstone successions are 5 to 10 m thick and have sharp bases (BRANDL 1996). Petrographic studies indicate that the majority of the sandstones are quartz arenites containing >95% monocrystalline, non-undulatory quartz; <5% feldspar and <5% lithic fragments, which are predominantly locally sourced angular mudstone, siltstone and sandstone fragments. Micaceous are extremely rare. Some sandstones show bimodal grain sizes distribution with fine sand (0.16-0.2 mm) making up ~60%, and

medium sand (0.4-0.5 mm) ~40% of the sample. The larger grains are much better rounded and show good grain size and roundness sorting. Overall the sandstones are immature to submature as they contain ~5-10% clay matrix, are poorly-sorted and have not well-rounded grains. The sandstones may contain soft sediment deformations (boreholes NY1-23°26'S, 27°33'E; FF1-23°31'23"S, 27°49'33"E; MQ1-23°27'S, 27°50'E), and bioturbation features (borehole ZB1-23°26'6"S, 27°47'52"E). The red, locally colour mottled massive mudstones contain well-developed calcareous rootlets, root traces (Fig. 5), *in situ* calcareous concretions, and at one locality (borehole SF1-23°23'50.5"S, 27°50'51.6"E), a 5 cm thick layer of evaporites. The calcareous concretions also form the pebble washes (Fig. 6) at the base of the upward fining units, and consist of a medium- to coarse grained sandy matrix and reworked pedogenic carbonate nodules ranging in size from <0.5 to ~3 cm in diameter (average 1 cm). The carbonate nodule conglomerates, which are clast-supported, massive and range in thickness from 0.1 to 1.5 m (e.g., borehole CD/C1-23°31'43"S, 27°38'26"E), locally may contain reworked fragments of vertebrate fossils (Fig. 7C)

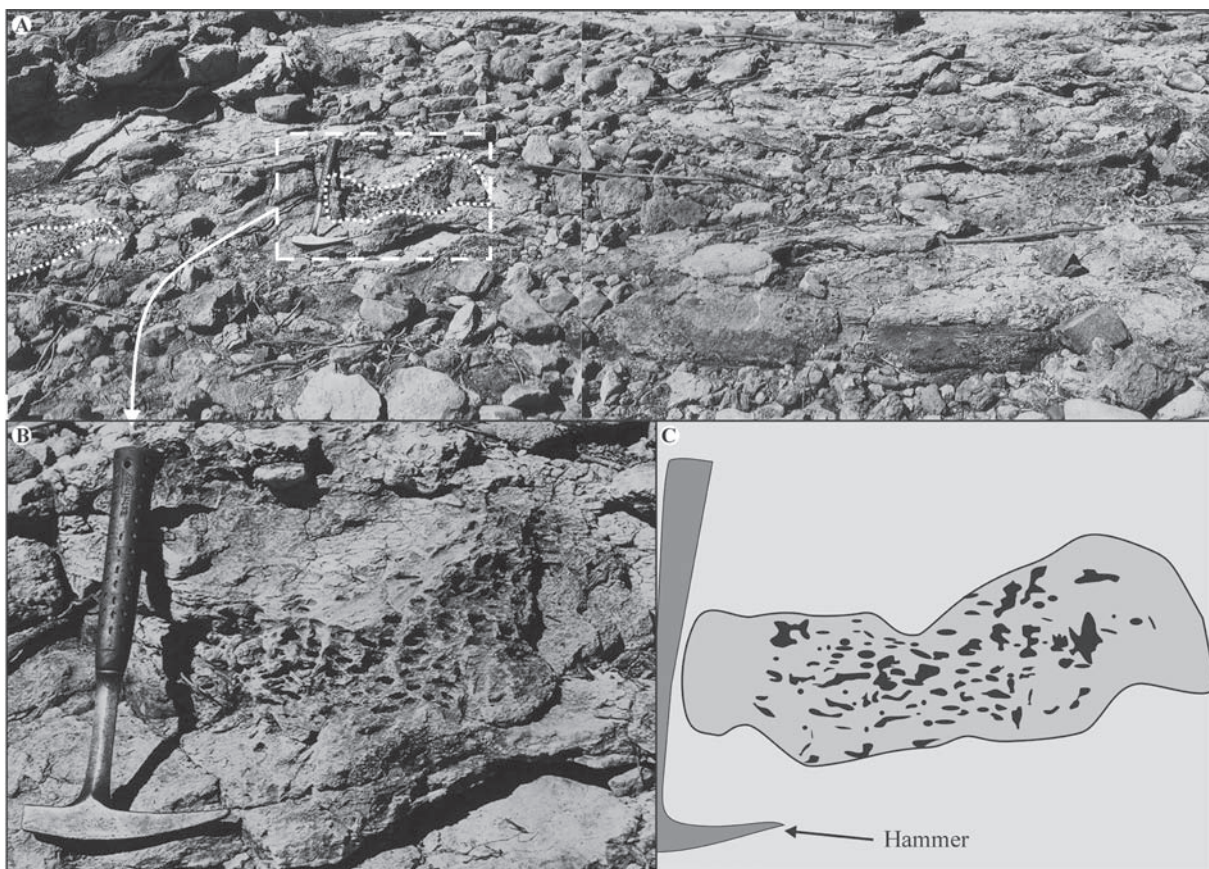


Fig. 4. Massive, medium grained-sandstones of the Lisbon Formation containing vertebrate and ichnofossils. The position of the hollow, spongy-texture trace fossils is outlined. See insert for close up and text for details. Hammer for scale ~30 cm.

and clay pellets as well. Locally, clay pellet conglomerates may be up to 1 m thick (borehole 140-23°32'S, 27°47'27"E).

The Lisbon Formation shows striking lithological and stratigraphic similarities to the upper Elliot Formation in the main Karoo Basin (BORDY et al. 2004a) as well as to the red bed succession (i.e., Bosbokpoort Formation and Red Rocks Member of the Clarens Formation of South Africa; Mpandi Formation in Zimbabwe) of the neighbouring Tuli Basin (Fig. 1) (BORDY & CATUNEANU 2001; ROGERS et al. 2004). The lithological correspondence is due to the similar facies architectures including dominance of red beds; similar mean grain sizes and sedimentary structures; abundance of *in situ* pedogenic nodules; bone-bearing, pedogenic nodule conglomerates, etc. The stratigraphic similarity is due to the identical stratigraphic position of the studied unit and its correlatives

within the Karoo Supergroup (i.e., all sandwiched between the equivalents of the coarse-grained, conglomeratic sandstones of the Molteno Formation and fine- to medium-grained, dune cross-bedded Clarens Formation).

The limited sedimentological data collected in the field, and gathered from brief borehole core descriptions (Council for Geoscience) and published literature suggest that the Lisbon Formation in the Ellisras Basin was probably deposited either (1) in a low energy fluvial system that was characterized by vast floodplains that were the common sites of sediment accumulation rather than the relatively higher energy fluvial channels; or (2) relatively higher energy river systems with smaller floodplains where mud was not only settling out from suspension, but was transported as sand- and silt sized aggregates in the bed load of the channels (cf. WRIGHT & MARRIOTT 2007).

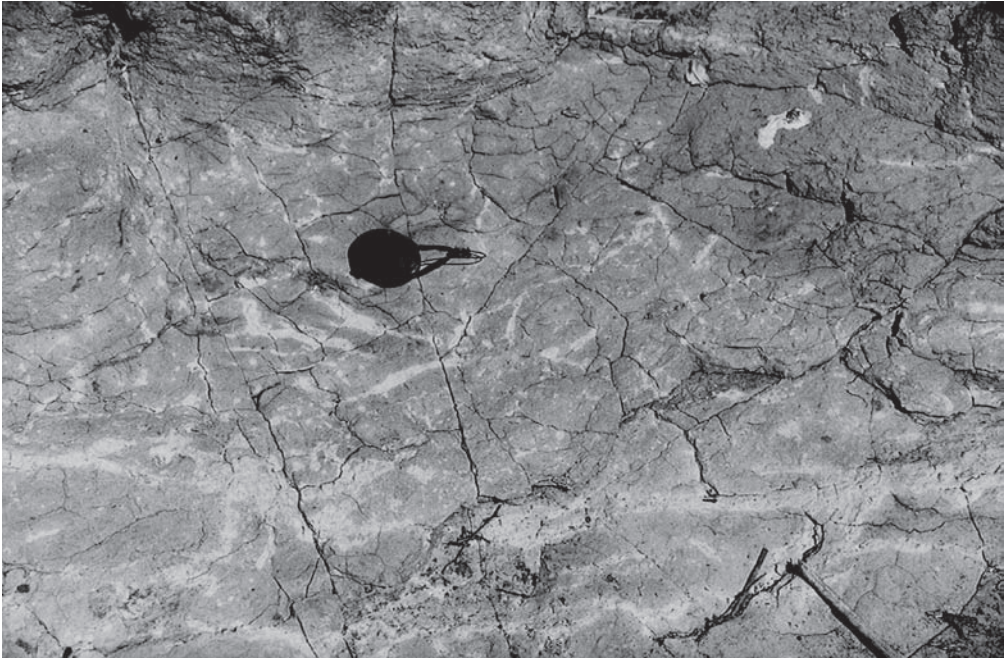


Fig. 5. Well-developed calcareous rootlet and root traces in colour mottled, mostly red massive silty mudstones of the Lisbon Formation. Lens cap for scale ~5.8 cm.

In the latter scenario, progressive burial would result in the compaction of the sand- to silt-grade mud aggregates into chiefly massive mudstones. Unfortunately, there is not sufficient evidence to date to determine whether the massive mudstones of the Lisbon Formation are suspension load sediments on floodplains or reworked clay aggregates that accumulated as bed load sediments in channels.

The calcareous root traces and the *in situ* pedogenic nodules suggest that vegetation may have flourished at least episodically or more permanently locally, along river banks. Calcareous root traces, *in situ* as well as reworked pedogenic nodules develop under any climatic regime where a net moisture deficit is maintained, but such conditions are most common under dryland climates where long dry seasons alternate with moister periods of shorter duration and the mean annual precipitation is <760 mm (ROYER 1999). Thus, the presence of such structures may imply well-drained soils in a somewhat dry milieu, with a strongly seasonal moisture regime. The locally preserved evaporite layer further supports the episodically extremely dry conditions. As attested by the reworked pedogenic nodules, the floodplains were often stripped off their soils and pedogenic nodules,

most probably during the wetter seasons or periods. Furthermore, this facies also suggests that the succession represents a dryland succession with a complex history of sedimentation and reworking (i.e., products of long periods of little or no sedimentation alternating with deposits of brief erosion and subsequent rapid sedimentation) (cf. WRIGHT & MARRIOTT 2007). Similar environmental interpretation was also possible for the above mentioned lithostratigraphic correlatives of the Lisbon Formation (BORDY & CATUNEANU 2001; BORDY et al. 2004a; ROGERS et al. 2004).

4. Palaeontology

Trace fossils previously reported from red massive mudstones in the Lisbon Formation were identified as *Skolithos* sp. and *Cruziana* sp. by BRANDL (1996). In addition to these ichnofossils, two occurrences of a new form of trace fossil were discovered during the recent study on farm Lisbon (Fig. 4). The trace fossils are preserved between poorly exposed layers of massive, medium-grained sandstone, and display a hollow, spongy-texture confined to elongated forms that are 15-20 cm high and 30-45 cm long. The structures consist of well-cemented, medium-grained



Fig. 6. Calcareous, pedogenic nodule conglomerates in the Lisbon Formation. They are clast-supported, massive, and contain reworked fragments of vertebrate fossils. Hammer for scale ~30 cm.

sandstone riddled by dense, empty, gently curving, vertically slightly flattened tubes that are 1 to 1.3 cm in diameter and show no tapering along their length. The thickness of the walls between the tubes is 3 to 5 mm. Owing to the poor quality outcrop, it is impossible to appraise whether or not these two trace fossil occurrences were physically connected at the time of their formation, however it was possible to ascertain that the hollow features are not the replica of weathered out clay pebbles, but true hollow tubes that penetrate deep into the host sandstone in a contorted manner.

Although the trace-makers of the newly described ichnofossils are very difficult to identify, due to the striking similarities to the internal structure of modern termite nests, we speculate that these trace fossils may be structures constructed by Early Jurassic termites or termite-like social insects. Similar trace fossils have been previously reported from the Elliot Formation in the main Karoo Basin by SMITH & KITCHING (1997) as well as from the Clarens Formation of the neighbouring Tuli Basin, Tshipise Basin and the main Karoo Basin by BORDY et al. (2004b; in press).

In addition to these trace fossils, bones were also found at this site both in massive, medium-grained

sandstones (Fig. 7A, B) and calcareous nodule conglomerates (Fig. 7C). Long bones and vertebrae are recognized in the assemblage in Fig. 7A. Two nearly articulated vertebrae are especially interesting. The centra are very elongate (more than four times longer than high), not pleurocoelous, and they have roughly planar or concave articular surfaces. The neural spines are moderately developed. On the whole, they are more reminiscent of the cervical vertebrae of some sauropodomorphs such as *Massospondylus* (COOPER 1981: fig. 5) than those of any other potential taxon. Indeed, elongate cervical vertebrae have been considered a synapomorphy of Sauropodomorpha (e.g., GAUTHIER 1986; UPCHURCH 1997; RAUHUT 2003). In fact, somewhat elongate cervical vertebrae are found in a number of non-sauropodomorph saurischian dinosaurs (e.g., in the theropod *Liliensternus*; VON HUENE 1934: pl. 14, figs. 2-4; FK pers. obs.), but especially low and long cervical centra did be present in the most primitive sauropodomorphs (e.g., *Panphagia*; MARTINEZ & ALCOBER 2009: fig. 7B). In any case, the non-opisthocoely of the cervical vertebrae suggests that they pertain to a taxon more primitive than *Isanosaurus* (BUFFETAUT et al. 2000).

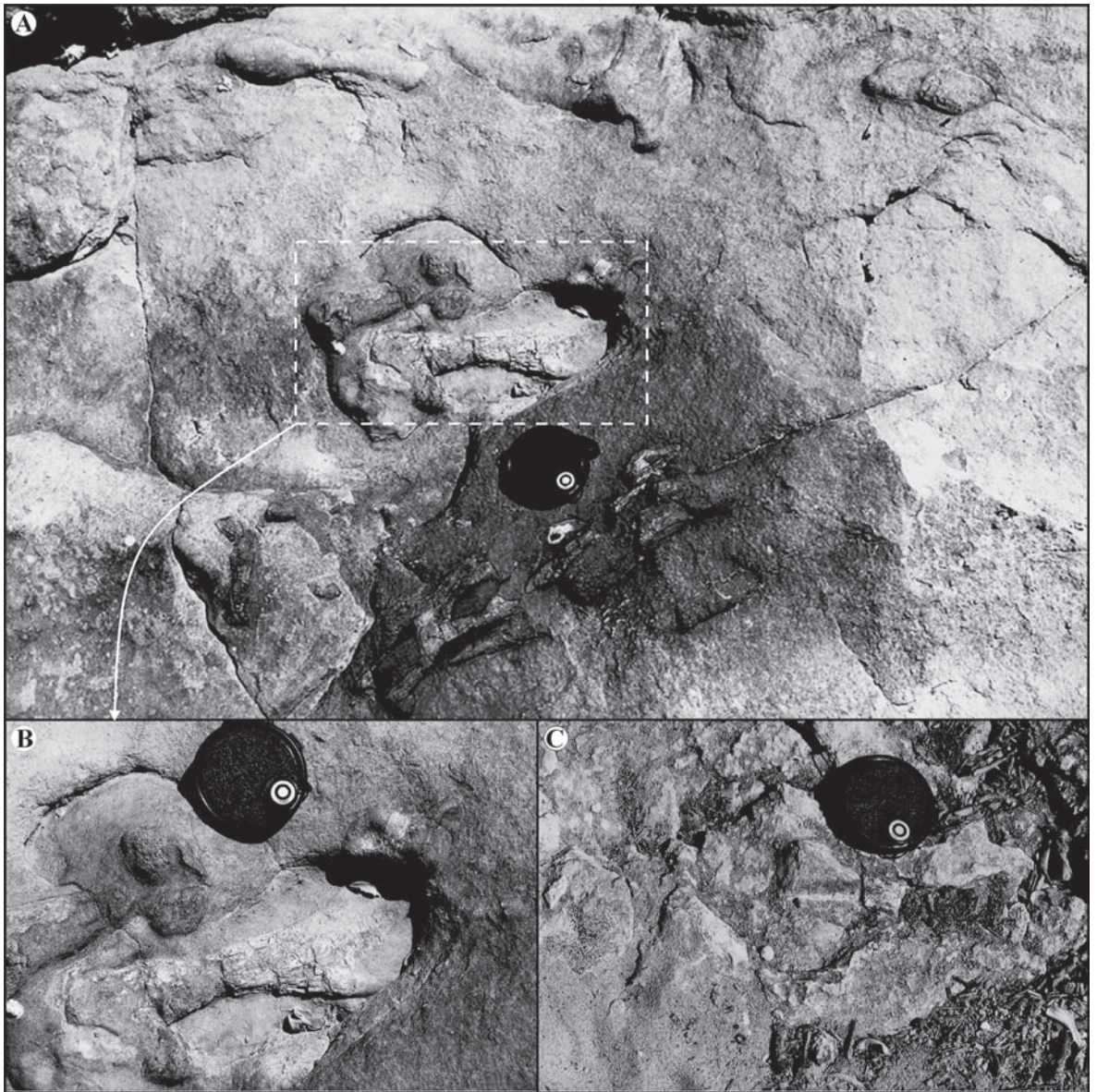


Fig. 7. Vertebrate fossils (basal Sauropodomorpha indet.) *in situ* in the Lower Jurassic part of the Lisbon Formation, on the eastern bank of the Limpopo River (GPS 23°27'42.19"S; 27°18'14.25"E) on farm Lisbon 19QL. See text for further details. Fossils in (A) and (B) are hosted in massive, medium grained sandstones, whereas those in (C) are contained in pedogenic nodule conglomerates. Lens cap for scale ~5.8 cm.

Fig. 7B is a close-up view of an element from the assemblage seen in Fig. 7A. It is a long bone with expanded extremities (one being more widened than the other). As the specimen is largely embedded in the matrix and partly masked by another bone (metacarpal?), its anatomical identification is difficult. Nevertheless the complete lack of long, more or less isodiametric diaphysis suggests that it is more pro-

bably a humerus than any other long bone. A massive phalanx lies near the largest extremity of this bone; it looks similar to the first phalanx of manual digit I in *Massospondylus* (COOPER 1981: figs. 42 d-f, 45). Though the exact degree of twisting between the proximal and distal articular axes is uncertain in this specimen, it is relevant to note that a great torsion of the pollex phalanx is a potential synapomorphy of

Prosauropoda according to UPCHURCH et al. (2007) and is fundamentally present in taxa more derived than *Efraasia*, but more primitive than *Antetonitrus* according to the phylogenetic analysis of YATES (2007).

On Fig. 7C a fragmentary humerus can be identified. It includes about the distal half of the bone, from the midshaft to the ulnar and radial condyles. Fortunately, the matrix keeps an impression of the missing proximal half of the bone. This allows estimating the original length of the bones as about 179 mm. Although no morphological character permits a precise systematic allocation, the outline of the bone matches that of the humerus of *Massospondylus* (COOPER 1981: figs. 26-27). In addition, its length falls within the size range of the humeral specimens of this taxon considered by COOPER (1981: table 2) and it is very close to the midpoint between the maximum and minimum values (184 mm).

Inasmuch as no vertebrate remains were described so far from the Lisbon Formation, the discovery of a probable medium-sized basal sauropodomorph at farm Lisbon is of importance. Admittedly, the discovery of a few bones of a large taxon from the Ellisras Basin was alluded to by some authors (HAUGHTON 1924: 454-455; DU TOIT 1954: 316). This material, which was never described, is stored under the specimen number SAM-PK-5757 at the Iziko South African Museum (Cape Town) as “anchisaurid” (S. KAAL, pers. comm. 2009) and an old label with the batch of bones indicates “*Plateosaurus*?”. It is very poor, but it comprises a phalanx whose morphology is indeed fully consistent with that of a basal sauropodomorph. This bone is not very large (nearly 5 cm long), but still it is larger than the first manual phalanx in an average *Massospondylus* (EB & FK, pers. obs.). The exact stratigraphic position of these fossils is unknown, but it is possibly also the upper part of the Lisbon Formation at farm Lisbon, considering that at present there is a single outcrop of the Lisbon Formation in the entire Ellisras Basin and the physiography of the study area (i.e., low weathering rates under a semi-arid climate) is probably insufficient to effectively eradicate a site over a century.

Sauropodomorphs are the most common vertebrates of the coeval Lower Jurassic upper Elliot Formation in the main Karoo Basin (KNOLL 2005). In the transfontier Tuli Basin, several localities in the upper levels of the Lower Jurassic red bed succession have also yielded basal sauropodomorph specimens both in Zimbabwe and South Africa (BORDY 2000 and

references therein; ROGERS et al. 2004 and references therein). Besides, sites in the Mid-Zambezi Basin (extension of the Kalahari Karoo Basin) and Mana Pools-Cabora Bassa basins (Zimbabwe), which are probably very close in stratigraphic position to the succession on the farm Lisbon, have produced remains of basal sauropodomorph (RAATH et al. 1970; COOPER 1981 and references therein). In Namibia, no dinosaur has been found so far in the uppermost Upper Omingonde Formation (equivalent to the upper Elliot Formation), but the unique dinosaur recovered from the overlying, slightly younger Etjo Formation is a partial skeleton of *Massospondylus* from the Waterberg Basin (HOLZFÖRSTER 2002).

5. Conclusion

In spite of the extremely limited field exposures, the above-conducted sedimentological and paleontological analyses indicate that at least the upper part of the Lisbon Formation in the Ellisras Basin (a south-eastern continuation of the Botswana Kalahari Karoo Basin) is a litho- and biostratigraphic correlative of the upper part of the Elliot Formation in the main Karoo Basin as well as other Lower Jurassic continental “red bed” successions throughout southern Africa. Similar to these units, the formation was deposited in a dryland setting with well-drained soils that were at least episodically capable to support some flora and a fauna probably dominated by basal sauropodomorphs.

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References

- BORDY, E. M. (2000): Sedimentology of the Karoo Supergroup in the Tuli Basin, Limpopo River area, South Africa. – Unpublished Ph.D. Thesis, Rhodes University, South Africa. – 266 pp.
- BORDY, E. M., BUMBY, A., CATUNEANU, O. & ERIKSSON, P. G. (2004b): Advanced Early Jurassic termite (Insecta: Isoptera) nests: evidence from the Clarens Formation in the Tuli Basin, southern Africa. – *Palaios*, **19**: 68-78.
- (2009): Possible trace fossils of putative termite origin in the Lower Jurassic (Karoo Supergroup) of South Africa and Lesotho. – *South African Journal of Science*, **105**: 356-362.
- BORDY, E. M. & CATUNEANU, O. (2001): Sedimentology of the upper Karoo fluvial strata in the Tuli Basin, South Africa. – *Journal of African Earth Sciences*, **33**: 605-629.
- BORDY, E. M., HANCOX, P. J. & RUBIDGE, B. S. (2004a): Fluvial style variations in the Late Triassic–Early Jurassic Elliot Formation, main Karoo Basin, South Africa. – *Journal of African Earth Sciences*, **38**: 383-400.
- BRANDL, G. (1996): The geology of the Ellisras area. – Explanation of the Sheet 2326, Geological Survey of South Africa. – 49 pp.
- BUFFETAUT, E., SUTEETHORN, V., CUNY, G., TONG, H., LE LOEUF, J., KHANSUBHA, S. & JONGAUTCHARIYAKUL, S. (2000): The earliest known sauropod dinosaur. – *Nature*, **407**: 72-74.
- CATUNEANU, O., HANCOX, P. J. & RUBIDGE, B. S. (1998): Reciprocal flexural behaviour and contrasting stratigraphies: a new basin development model for the Karoo retroarc foreland system, South Africa. – *Basin Research*, **10**: 417-439.
- COOPER, M. R. (1981): The prosauropod dinosaur *Massospondylus carinatus* OWEN from Zimbabwe: its biology, mode of life and phylogenetic significance. – Occasional Papers of the National Museums and Monuments, Rhodesia, (B), **6**: 689-840.
- COX, K. G., JOHNSON, R. L., MONKMAN, L. J., STILLMAN, C. J., VAIL, J. R. & WOOD, D. N. (1965): The geology of Nuanetsi Igneous Province. – *Philosophical Transactions of the Royal Society, (A)*, **257**: 71-218.
- DE JAGER, F. S. J. (1983): The Geology of the Springbok Flats, Waterberg, Soutpansberg and Limpopo Coal Fields (with an addendum on the geology of the Komati-poort coal field). – Unpublished Report 1983-0120, 11 pp.; Pretoria (South African Geological Survey).
- DU TOIT, A. L. (1954): The Geology of South Africa (3rd ed.) – 611 pp.; Edinburgh (Oliver & Boyd).
- FAURE, K., ARMSTRONG, R. A., HARRIS, C. & WILLIS, J. P. (1996): Provenance of mudstones in the Karoo Supergroup of the Ellisras Basin, South Africa: geochemical evidences. – *Journal of African Earth Sciences*, **23**: 189-204.
- GAUTHIER, J. A. (1986): Saurischian monophyly and the origin of birds. – *Memoirs of the California Academy of Sciences*, **8**: 1-55.
- GREEN, D., CROCKETT, R. N. & JONES, M. T. (1980): Tectonic control of Karoo sedimentation in mid-eastern Botswana. – *Transactions of the Geological Society of South Africa*, **83**: 213-219.
- HAUGHTON, S. H. (1924): The fauna and stratigraphy of the Stormberg Series. – *Annals of the South African Museum*, **12**: 323-497.
- HOLZFÖRSTER, F. (2002): Sedimentology, stratigraphy and synsedimentary tectonics of the Karoo Supergroup in the Huab and Waterberg-Erongo areas, N-Namibia. – *Beringeria*, **30**: 3-144.
- HUENE, F. v. (1934): Ein neuer Coelurosaurier in der thüringischen Trias. – *Paläontologische Zeitschrift*, **16**: 145-170.
- JOHNSON, M. R., VAN VUUREN, C. J., HEGENBERGER, W. F., KEY, R. & SHOKO, U. (1996): Stratigraphy of the Karoo Supergroup in southern Africa: an overview. – *Journal of African Earth Sciences*, **23**: 3-15.
- KNOLL, F. (2005): The tetrapod fauna of the Upper Elliot and Clarens formations in the main Karoo Basin (South Africa & Lesotho). – *Bulletin de la Société Géologique de France*, **176**: 81-91.
- MACRAE, C. S. (1988): Palynostratigraphic correlation between the lower Karoo sequence of the Waterberg and Pafuri Coal-bearing Basins & the Hammanskraal plant macrofossil locality, Republic of South Africa. – *Geological Survey of South Africa Memoirs*, **75**: 1-217.
- MARTINEZ, R. N. & ALCOBER, O. A. (2009): A basal sauropodomorph (Dinosauria: Saurischia) from the Ischigualasto Formation (Triassic, Carnian) and the early evolution of Sauropodomorpha. – *PLoS One*, **4**: e4397.
- RAATH, M. A., SMITH, C. C. & BOND, G. (1970): A new Upper Karoo dinosaur fossil locality on the Lower Angwa River, Sipolilo District, Rhodesia. – *Arnoldia*, **4**: 1-10.
- RAUHUT, O. W. M. (2003): The interrelationships and evolution of basal theropod dinosaurs. – *Special Papers in Palaeontology*, **69**: 1-213.
- REID, D. L., REX, D. C. & BRANDL, G. (1997): Karoo basalts in the Ellisras Sub-basin, Northern Province. – *South African Journal of Geology*, **100**: 151-156.
- ROGERS, R. R., ROGERS, K. C., MUNYIKWA, D., TERRY, R. C. & SINGER, B. S. (2004): Sedimentology and Taphonomy of the Upper Karoo-equivalent Mpandi Formation in the Tuli Basin of Zimbabwe, with a new ⁴⁰Ar/³⁹Ar age for the Tuli basalts. – *Journal of African Earth Sciences*, **40**: 147-161.
- ROYER, D. (1999): Depth to pedogenic carbonate horizon as a paleoprecipitation indicator? – *Geology*, **27**: 1123-1126.
- SIEPKER, E. H. (1986): Genetiese stratigrafie en sedimentologie van die Opeenvolging Karoo in die westelike and noordelike deel van die Waterbergsteenkoolveld. – Unpublished M.Sc. thesis, Rand Afrikaans University, Johannesburg. – 177 pp.
- SMITH, R. A. (1984): The lithostratigraphy of the Karoo Supergroup in Botswana. – *Botswana Geological Survey Department Bulletin*, **26**: 184-205.

- SMITH, R. M. H. & KITCHING, J. (1997): Sedimentology and vertebrate taphonomy of the *Tritylodon* Acme Zone: a reworked palaeosol in the Lower Jurassic Elliot Formation, Karoo Supergroup, South Africa. – *Palaeogeography, Palaeoclimatology, Palaeoecology*, **131**: 29-50.
- UPCHURCH, P. (1997): Sauropodomorpha. – In: CURRIE, P. J. & PADIAN, K. (Eds.): *Encyclopedia of Dinosaurs*, 658-660; New York (Academic Press).
- UPCHURCH, P., BARRETT, P. M. & GALTON, P. M. (2007): A phylogenetic analysis of basal sauropodomorph relationships: implications for the origin of sauropod dinosaurs. – *Special Papers in Palaeontology*, **77**: 57-90.
- WRIGHT, V. P. & MARRIOTT, S. B. (2007): The dangers of taking mud for granted: Lessons from Lower Old Red Sandstone dryland river systems of South Wales. – *Sedimentary Geology*, **195**: 91-100.
- YATES, A. M. (2007): The first complete skull of the Triassic dinosaur *Melanorosaurus* HAUGHTON (Sauropodomorpha:Anchisauria). – *Special Papers in Palaeontology*, **77**: 9-55.
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