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A new species of *Panochthus* (Xenarthra, Glyptodontidae) from the late Pleistocene of Argentina

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ABSTRACT

In the late Pleistocene, *Panochthus* was the most diverse genus of glyptodontids with five species: *P. jaguaribensis*, endemic to the intertropical region of Brazil, *P. hipsilis* from Bolivia, *P. greslebini* from Brazil and Argentina, *P. tuberculatus* from Uruguay and Argentina and *P. frenzelianus,* probably from the Pampean region, Argentina. In this paper we describe the robust caudal tube of a new species, *Panochthus florensis* n. sp., that inhabited the center of the Pampean region of Argentina at the end of the Pleistocene. The reduction in the number of central figures, a single apical figure, the absence of an apexian figure, and the lack of figures between the first pair of dorsal figures allow a rapid differentiation from the already known species. The striking diversity of *Panochthus* contrasting with that of other late Pleistocene glyptodontids, lead us to propose hypotheses for explaining this fact.

Author statement

All authors contributed equally.

1. Introduction

Panochthus is one of the main genera of Glyptodontidae; giant and armored xenarthra that inhabited South America during the Pleistocene. The genus is widely distributed in Brazil, Uruguay, Bolivia, and Argentina where it is recorded in the Chaco-Pampean, Mesopotamian, Sub-Andean, and Patagonian regions (Zamorano et al., 2014a). Recently, this genus has also been recorded from Perú (Zamorano and Almonte, 2018), further expanding the known distribution.

The known diversity of *Panochthus* is strikingly high and the taxonomic history began with the description of *Glyptodon tuberculatus* Owen, 1845 based on fragments of the carapace. Later, was fully described by Burmeister in a series of papers (Burmeister, 1864, 1866, 1874) and this author finally considered placing it in a different genus, as *Panochthus tuberculatus* (Owen, 1845) Ameghino (1889) established two species: *Panochthus frenzelianus* and *Panochthus voghti*. The geographical provenance of *P. frenzelianus* is uncertain and the material referred to as holotype has been the subject of controversies recently discussed by Fernicola et al. (2014), while *P. voghti* has been considered *nomen nudum* by Zamorano et al. (2014a).

Panochthus intermedius Lydekker, 1895 has the oldest records of the genus (early-medium Pleistocene) (Zamorano et al., 2014b) and the species was founded on the basis of an almost complete dorsal carapace found in the port of Buenos Aires. Castellanos (1933) established other species, *Panochthus subintermedius*, but without characterizing it correctly at that time, although later (Castellanos, 1937) he validated the species based on large fragments of carapace and a caudal tube, extracted from Palermo, Buenos Aires (Zamorano, 2012). This same author (Castellanos, 1942) established other three species: *Panochthus rusconii*, *Panochthus oliveiraroxoi*, and *Panochthus greslebini* with descriptions based on photographic observations of the specimens (Zamorano et al., 2015). Then, Moreira (1965) established a further species, *Panochthus jaguaribensis* based on a caudal tube and a fragment of the caudal ring. The material was collected from the State of Ceará, Brazil and corresponds to the Pleistocene. After a review of the material and comparison with another specimen collected in Taperoá, Paraíba State, Brazil, Moreira (1971) established the genus *Parapanochthus* including *P. jaguaribensis*. Bergqvist (1993) reviewed the material studied by Moreira but did not find enough differences to justify the genus *Parapanochthus*, so that it was considered a synonym of

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Panochthus (Zamorano et al., 2014a).

In 1954, the species *Panochthus rochai* was established by Paula Couto based on a distal fragment of the caudal tube (Paula Couto, 1954). However, Moreira (1971) and Porpino and Bergqvist (2002) considered *P. oliveiraroxoi* and *P. rochai* synonymous of *P. greslebini*. *Panochthus hipsilis* Zurita et al. (2017) from Bolivia is hitherto the most recently established species; regarding its caudal tube, it is characterized by an ornamentation with depressed small and poorly developed lateral figures.

In summary, seven Pleistocene species of *Panochthus* are currently considered valid: *P. tuberculatus*, *P. frenzelianus*, *P. intermedius*, *P. subintermedius*, *P. greslebini*, *P. jaguaribensis,* and *P. hipsilis*, while *Panochthus lundii* (Burmeister, 1874), *Panochthus morenoi* (Ameghino, 1881), *P. voghti* and *P. rusconii* would be synonyms of *P. tuberculatus* (Zamorano et al., 2014a).

In this context, during the summer of 2009 a great drought affected the Salado River in the center-east of province of Buenos Aires, near Las Flores city (Fig. 1) and the material presented here was found by the biochemist Hector Crispiani and the team from the Museo de Las Flores. A detailed anatomical description shows that, in the late Pleistocene, a new species of *Panochthus* lived in Buenos Aires, Argentina.

2. Material and methods

The anatomical terminology of the caudal tube follows the proposals of Porpino et al. (2014) and Castellanos (1927), with modifications. We denominate 'central figures' all those depressed, circular or elliptical figures, generally twice the size of the small polygonal figures that form the bottom lattice and are in the central region of the caudal tube from dorsal and ventral view.

Panochthus frenzelianus (Ameghino, 1889) has not been included in the present study because the caudal tube AMNH FM 11249 exposed in the American Museum of Natural History would not be part of the holotype and cannot be with certainty assigned to the species in question (Fernicola et al., 2014). However, this caudal tube should be studied since it presents a combination of characteristics that differentiate it from the species treated here: 1) the presence of a deep apexian figure as in *P. greslebini*, 2) two small figures on each side between the apical figures and the apexian figure, and 3) two apical figures as in *P. tuberculatus*.

Institutional Abbreviations— **DGM**: Divisão de Geología e Mineralogia, Rio de Janeiro, Brasil; **MACN-Pv**: Sección Paleontología de Vertebrados, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Ciudad Autónoma de Buenos Aires, Argentina; **MLF**: Museo de Ciencias Naturales 'Florentino Ameghino', Las Flores, Buenos Aires, Argentina; **MHNS**: Museo de Historia Natural de Sucre, Bolivia; **MLP**: División Paleontología de Vertebrados, Facultad de Ciencias Naturales y Museo de La Plata, Universidad Nacional de La Plata, La Plata, Buenos Aires, Argentina; **MNRJ**, Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brasil; **MMH-QUQ**, Colección Quequén Salado del Museo Municipal de Ciencias Naturales "Vicente Di Martino", Monte Hermoso, Buenos Aires, Argentina; **MRCA**: Museo Regional Cara cará Añá, Carcarañá, Santa Fe, Argentina.

Revised Materials: *Panochthus florensis*: MLF 642; *Panochthus greslebini*: DGM1-M, MNRJ 2760/IV, MMH-QUQ 09-03-01; *Panochthus jaguaribensis*: MNRJ 2759/IV; *Panochthus hipsilis*: MHNS 8; *P. subintermedius*: MACN-Pv 5130; *Panochthus tuberculatus*: MACN-Pv 1745, MLF 400, MRCA 008.

2.1. Systematic paleontology

Superorder XENARTHRA Cope, 1889.
Order CINGULATA Illiger, 1811.
Suborder GLYPTODONTIA Ameghino, 1889.
Superfamily GLYPTODONTOIDEA Gray, 1869.
Family GLYPTODONTIDAE Gray, 1869.
Genus *PANOCHTHUS* Burmeister, 1866.
Type Species: *Glyptodon tuberculatus* Owen, 1845

2.1.1. *Panochthus florensis n. sp.*

Holotype. MLF 642, a caudal tube, almost complete, without the proximal end.

Etymology. Its name derives from the type locality, Las Flores.

Type locality. Las Flores, Buenos Aires, Argentina (Fig. 1).

Stratigraphic origin. Lujan Formation, late Pleistocene.

Diagnosis. Main dorsal figures (d1) almost in contact in their distal portion, with no central main figure between d1 (Fig. 3). A single apical figure, sharp point without apexian figure. Ventrally, rhomboidal apical figure, first major ventral figures (v1) in contact with each other, absence of central figures between v1 and the marginal ventral figures (VM).

Description and remarks. The material consists of a 91 cm long

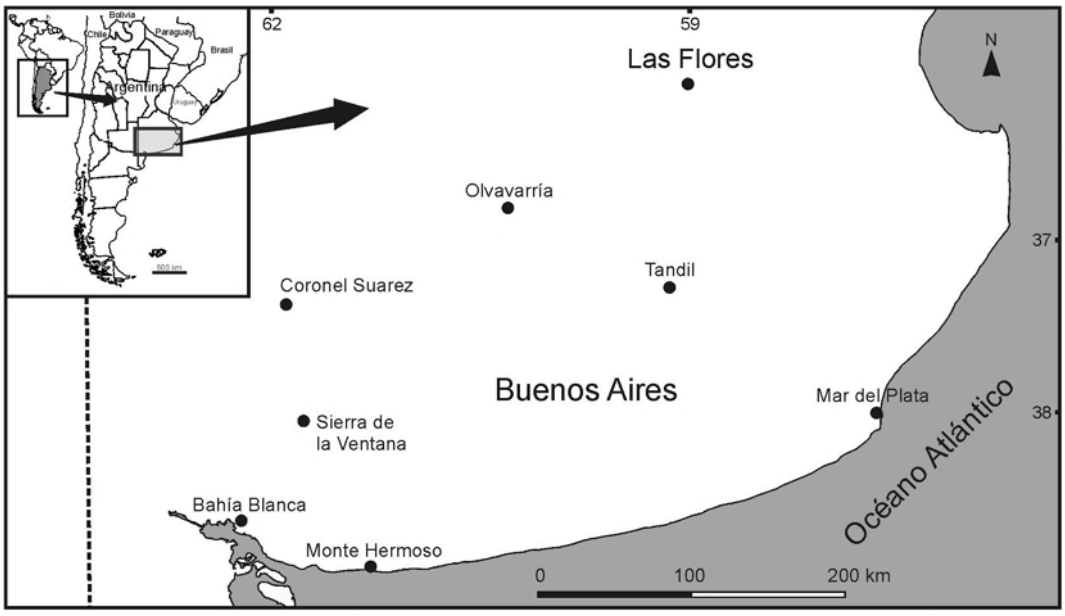

Fig. 1. Map showing the type locality, Las Flores, located in the center-east of Buenos Aires.

caudal tube, compressed dorsoventrally and with subcircular section towards the distal end (Fig. 2A). This characteristic differentiates it from *P. jaguaribensis*, a species that has a caudal tube with a more cylindrical cross section in the middle region. A laterally more robust caudal tube and large figures differentiate it from *P. subintermedius* and *P. hipsilis*.

In dorsal view, the first main dorsal figures (d1) are elliptical, depressed and are almost in contact in the most distal portion since there is no deep figure (Fig. 3, cf-d1) in the middle of them like that seen in the other species of the late Pleistocene such as *P. greslebini*, *P. jaguaribensis*, *P. tuberculatus*. In a distal position with respect to the two d1s is found a single circular figure (apf), half the size of the previous ones. This characteristic is shared only with *P. greslebini* and *P. subintermedius* while *P. jaguaribensis* has 3 circular figures (two more proximal and one distal to the previous ones) and *P. tuberculatus* has two figures of unequal size and in some specimens one extra figure in distal position with respect to those of unequal sizes (Cruz et al., 2011). Finally, the lack of an apexian figure in MLF 462 establishes a strong difference with *P. greslebini* (Fig. 3) that will be discussed later. Three marginal figures (dmf) are located on each side between d1 and d2, and some central figures separate them.

Ventrally, the apical figure is small and has a rhomboidal shape. The first main ventral figures (v1s) are uneven in size. As in the dorsal view, there is an absence of intermediate figures between the v1s, which cover practically the entire width of the ventral side in that section of the caudal tube.

The v1s directly contact marginal ventral figures (MV) while in *P. greslebini*, *P. jaguaribensis* and *P. tuberculatus* a main central figure (mcf) is among them (Fig. 3). On each side, three marginal ventral figures extend between v1 and v2 while the most distal MVs contact each other directly, without the presence of central figures (cf). Both, the main ventral figures and the marginal ventral figures have a rough surface with a slight elevation approximately in the center of the figure. The three MV figures on each side are located on the edge of L1.

In lateral view three pairs of figures (L1-L3) are presented, these are located between the terminal figures (t) and the figures of the annular round. The L1-pair have a deep depression marked at the edges and a marked roughness that decreases towards L3. Similarly, the elevation that they have in the center of the concavity loses height from L1 to L3.

Proximately, a group of figures form a ring that is located immediately in the position before figure L3, unlike *P. greslebini*, which has the

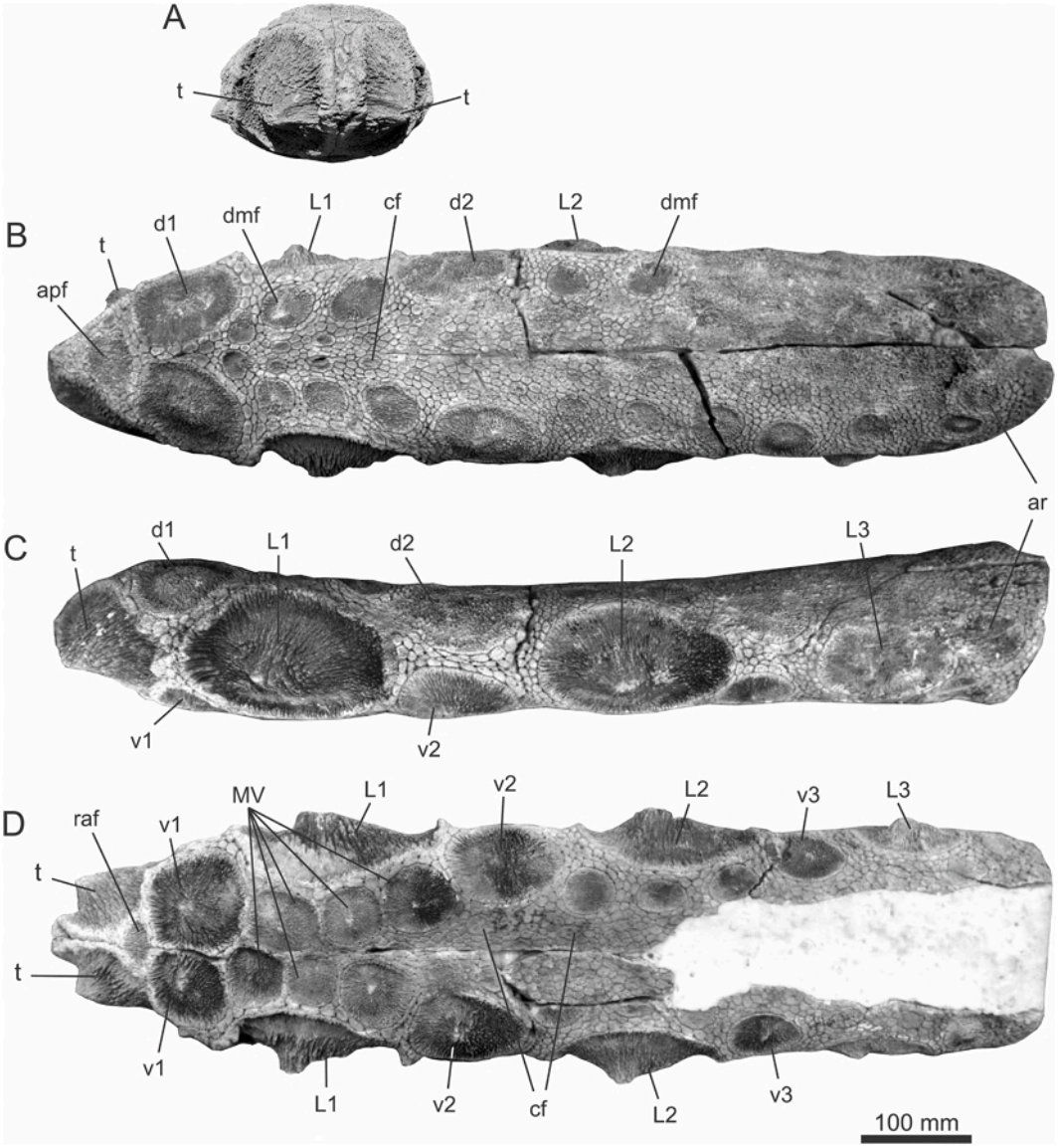

Fig. 2. *Panochthus florensis* n. sp. Caudal tube MLF 462 (holotype): A, distal view; B, dorsal view; C, lateral view; D, ventral view. Abbreviations: apf, apical figure; ar, annular row; raf, rhomboidal apical figure; cf, central figure; d1- d3, main dorsal figure; dv1 - dv3, main ventral figure; L1–L3, lateral figures; dmf, dorsal marginal figures; MV, marginal ventral figure; t, terminal figure; v1 - v3, main ventral figure.

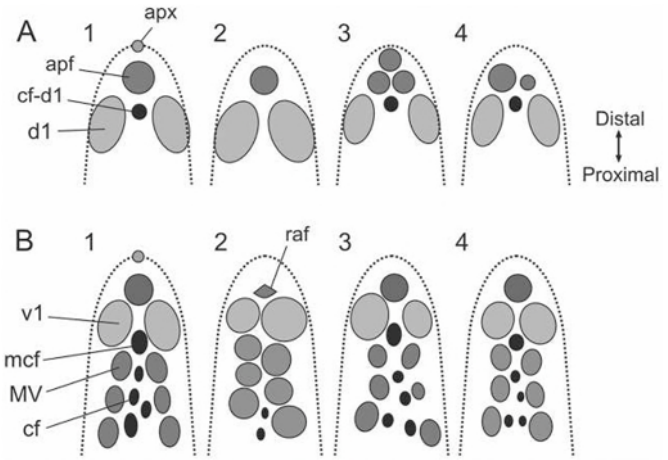

Fig. 3. Diagrams showing the distribution of figures on the tips of the caudal tubes of late Pleistocene *Panochthus*. A, dorsal view; B, ventral view. 1, *P. greslebini* DNPM 1-M; 2, *P. florensis* n. sp. MLF 642; 3, *P. jaguaribensis* MNRJ 2759/IV; 4, *P. tuberculatus* MLF 400. Lateral figures (L), not shown. Abbreviations: apf, apical figure; apx, apexian figure; cf, central figure; mcf, main central figure; cf-d1, central main figure between d1 figures; d1, main dorsal figure; MV, marginal ventral figures; raf, rhomboidal apical figure; v1, first main ventral figure.

ring separated from the lateral figure.

3. Discussion

Species of the genus *Panochthus* present differences in the organization of the figures of the caudal tube and these differences have been given great relevance from a taxonomic point of view. On the other hand, species such as *P. intermedius* and *P. hipsilis* have a different appearance from the other species, as they have softer and smaller marks.

Some types of figures show great stability in number and position, therefore changes in those are interpreted as a change at the species level, while others may be more variable in position and number. In particular, the most variable figures are the central ones and to a lesser extent, the proximal marginal figures. The figures whose changes show differences between species are concentrated in the distal portion of the caudal tube, and they are the apical figures, main dorsal figures, ventral figures, apical figure and to a lesser extent marginal figures of the distal portion. The flattened dorsoventrally in the middle portion shape is the most common shape of the caudal tube of *Panochthus*. In this sense, the caudal tube of *P. florensis* has the flattened shape and is very robust and broad. *Panochthus florensis* presents a unique combination of characteristics summarized in Table 1.

The absence of a deep, circular, and larger figure (cf-d1) than the central figures (cf) separating the first dorsal figures (d1) is a diagnostic characteristic of the new species. The presence of this "separating" figure is a plesiomorphic character that can be observed in late Pleistocene species, predominantly in a distal position between d1. The absence of this central figures (cf-d1) in this position is an autapomorphy of *P. florensis* (Fig. 3). Its loss could be related to the dorsalization and increase in size of the corneal structures located on the d1 figures such as can be observed in *P. florensis*. Its loss is also accompanied by the disappearance of a spacer figure in the same position on the ventral side with similar consequences for the structures inserted into the main ventral figures.

A single apexian figure positioned in the tip of the caudal tube is an easily observable character in *P. greslebini* and it is a diagnostic characteristic of this species as it was reported by Porpino et al. (2014). In the south of the Buenos Aires Province, in a geographical area close to the town of Las Flores, the southernmost finding of the *P. greslebini* species

Table 1
Main differences in caudal tubes figures of *Panochthus*.

Taxon	apx	cd-d1	N° apf	mcf
Panochthus florensis n. sp.	–	–	1	–
Panochthus greslebini	+	+	1	+
Panochthus jaguaribensis	–	+	2	+
Panochthus tuberculatus	–	+	2	+

Abbreviations: apx, apexian figure; cd-d1, presence of a central figures between d1 figures; N° apf, number of apical figure; mcf, presence of main central figure (s).

was reported (Zamorano et al., 2015); the specimen has all the attributes corresponding to the species as the distinctive apexian figure. This figure is observed from a distal view and is displaced towards the dorsal side, established on a wide surface in the middle of the terminal figures (Porpino et al., 2014: Fig. 3F; Zamorano et al., 2015: Fig. 3). In *P. florensis* the presence of this apexian figure is not observed and it stands out, at the same time that the separation between the terminal figures is very narrow, reaching only a third of the separation between the terminal figures of *P. greslebini*. Consequently, the distal region is somewhat sharp and reminiscent of the condition observed in *P. subintermedius*.

Panochthus florensis has three lateral figures that decrease in size and depth towards the proximal end. Such polarity in the development of the figures can be seen in *P. tuberculatus*, *P. jaguaribensis* and *P. greslebini*, although the specimen of the latter species found in Argentina has lateral figures of similar size. Regarding the total number of lateral figures *P. jaguaribensis* (MNRJ 2759/1V) has four, *P. tuberculatus* (MRCA 008) has five and *P. subintermedius* (MACN-Pv 5130) has a different number of lateral figures, three on one side and four on the other, so this character exhibits some variability.

In late Pleistocene four species distributed in the Pampean region are counted: *P. frenzelianus*, *P. tuberculatus*, *P. greslebini* and *P. florensis*. To this set must be added the exclusive Brazilian species *P. jaguaribensis* and the Bolivian species *P. hipsilis*. These species denote the remarkable diversity reached by the genus at the late Pleistocene, contrasting with that of other genera of large glyptodonts such as *Glyptodon*, with only one species known in Pampean region (*Glyptodon reticulatus* Owen, 1845), or *Doedicurus,* which is represented by *Doedicurus clavicaudatus* (Owen, 1847). This pattern may not have a direct correlation with the concept of biological species; some listed species could correspond to the same biological species, since the observed differences could be merely the product of intraspecific variation. In this case we could still propose a greater genetic diversity of *Panochthus* that would be evidenced in the display of numerous ornamental patterns of the caudal tube and other skeletal parts of the animal not addressed here. The answers could be rooted in the evolutionary origin and divergence of the lineages that would allow accumulating more variability due to changes in the DNA of those species with ancestors with the longest evolutionary time elapsed. Furthermore, evolutionary constraints could have operated in the lineages that gave rise to *Doedicurus* and *Glyptodon*, limiting the variability within these genera/lineages. On the other hand, an alternative such as the polyembryony process that currently occurs in armadillos of the genus *Dasypus* (Fernandez, 1915; Prodöhl et al., 1996) could explain, at least in part, the morphological patterns so conserved over time in *Glyptodon* and *Doedicurus*. Polyembryony reduces the combination and spread of new gene variants (alleles) in each generation in the population. Genetic novelties would not only spread more slowly over time but could also be limited in their geographical distribution. This latter being the case, a distancing or flexibilization of the phenomenon of polyembryony in *Panochthus* could have allowed a faster distribution of new alleles in the populations, a greater morphological variability and evolution in contrast to that of other glyptodonts.

4. Conclusions

Panochthus florensis n. sp. is clearly differentiable from the remaining known species of *Panochthus*, expanding the knowledge about the diversity of the genus. This work highlights the outstanding diversity of *Panochthus* that contrasts with that of other glyptodonts, however different reproductive phenomena such as polyembryony among glyptodonts could explain differences in diversity observed among the Pleistocene genera. The anatomical information compiled in this work provides clues for further analysis of specimens scattered in regional museums hitherto assigned to *Panochthus* sp. which have the potential to generate new hypotheses about the evolution, diversity and distribution of species at the end of the Pleistocene.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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