THE COELOPHYSOID *LOPHOSTROPHEUS AIRELENSIS*, GEN. NOV.: A REVIEW OF THE SYSTEMATICS OF *"LILIENSTERNUS" AIRELENSIS* FROM THE TRIASSIC-JURASSIC OUTCROPS OF NORMANDY (FRANCE)

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ABSTRACT—In the early 1990s a theropod dinosaur found close to the Triassic-Jurassic boundary of France was assigned to a second species of the genus *Liliensternus*: *L. airelensis* (Moon Airel Formation). This contribution reveals that common features that purportedly unite *"L."* *airelensis* with *L. liliensterni* are more widely distributed among coelophysoids and basal dinosaurs than it was thought. A cladistic analysis reveals that *"L."* *airelensis* is more closely related to the Coelophysidae than to *L. liliensterni*. A feature that supports this systematic arrangement includes a supraacetabular crest forming a well-developed ridge continuous with the lateral margin of the brevis fossa, with non-distinct notch between both structures. The new genus *Lophostropheus*, gen. nov., is therefore erected to include the species *L. airelensis*. Thus, the new combination *Lophostropheus airelensis* is proposed.

INTRODUCTION

In 1966, Larsonneur and Lapparent described the remains of a theropod dinosaur from the Moon-Airel Formation (uppermost Rhaetian-lowermost Hettangian; Normandy, France), assigning the material to *Halticosaurus* sp. This interpretation was maintained, until Cuny and Galton (1993) re-assigned the Airel theropod to the genus *Liliensternus* Welles, 1984 and erected the new species *L. airelensis*. The original species, *L. liliesnterni*, is based on two partial subadult skeletons of similar size (with very fragmentary cranial remains and almost complete postcranial elements), which come from the Knollenmergel (Thüringen; Norian) of Germany (Rauhut and Hungerbüler, 2000). The assignation of the Airel theropod to *Liliensternus* was widely followed by subsequent researchers (e.g., Rauhut, 2003; Carrano and Sampson, 2004), albeit Rauhut and Hungerbühler (2000) suggested that features such as the presence of two pair of pleurocoels in the cervical vertebrae of *L. airelensis* (and only one pair in *L. liliensterni*) makes questionable the referral of the Airel theropod to the genus *Liliensternus*.

The present re-examination of available morphological data of the Airel theropod reveals that supposed common features shared by the French taxon and *L. liliensterni* are actually more widely distributed among other coelophysoids and basal dinosaurs. Furthermore, comparisons carried out here show that the Airel theropod exhibits features also present in coelophysids, but not in *L. liliensterni*. In fact, our cladistic analysis shows that the Airel theropod is more closely related to Coelophysidae (i.e., *Coelophysis* + *"Syntarsus"*; sensu Holtz, 1994) than to *L. liliensterni*. In this phylogenetic context, a closer relationship of *"L."* *airelensis* to *L. liliensterni* than to other coelophysoids is dismissed, and a new genus is erected for the Airel theropod.

Another interesting point concerning the Airel theropod relates to the age of the outcrops from which the material was exhumed. Cuny and Galton (1993) pointed out that palynological studies revealed that the Moon Airel Formation lacks both characteristic Rhaetian and Hettangian microfossils, a transition zone that palynologists call "uppermost Rhaetian." In this regard, the Moon Airel Formation correspond to an outcrop that closely approaches the Triassic-Jurassic boundary. The end-Triassic is identified as one of the five major global mass extinction events of the Phanerozoic (Raup and Sepkoski, 1982), and the Airel theropod comes from close to this stage. The occurrence of this French coelophysoid and other late Triassic and early Jurassic dinosauriforms (e.g., herrerasaurians, coelophysoids, prosauropods) allow identification of a decline of the dinosaurian taxa in the fossil record near the Triassic-Jurassic boundary, when it is compared with the proportionally high Carnian-Norian and Early Jurassic dinosaurian records.

Institutional Abbreviations—CM, Carnegie Museum, Pittsburgh, Pennsylvania.

Systematic Nomenclature—We follow the definition of Neotheropoda (Sereno, 1998) as a node-based clade that includes *Coelophysis bauri*, Neornithes, and all the descendants of their common ancestor. Within Neotheropoda, we accept Rauhut's (2003) phylogenetic hypothesis that the Coelophysoidea are the sister-group of all other known neotheropods (i.e., Ceratosauria (all theropods closer to *Ceratosaurus nasicornis* than to birds; Rowe, 1989; see Rauhut, 2003) + Tetanurae, rather than to coelophysoid theropods) (phylogenetic arrangement supported in the present phylogenetic analysis). Thus, regarding Coelophysoidea systematics we follow the definition proposed by Sereno (1998) and Padian and colleagues (1999) as a stem-based node that encloses all theropods closer to *Coelophysis bauri* than to *Ceratosaurus nasicornis*. Coelophysidae comprises *Coelophysis*, *"Syntarsus,"* and all the descendants of their most recent common ancestor (Holtz, 1994). Bristowe and Raath (2004) indicate that *"Syntarsus" rhodesiensis* is not generically separable from *Coelophysis bauri*; thus they refer *"Syntarsus" rhodesiensis* to the genus *Coelophysis*. In fact, the present phy-

logenetic analysis depicted that *"Syntarsus" rhodesiensis* is more closely related to *Coelophysis bauri* than to *"Syntarsus kayentakatae,"* as was also indicated by Tykoski (2005). The genus *"Syntarsus"* is here used only to refer to the species *"Syntarsus" kayentakatae.* The term Averostra was coined by Paul (2002:25) to "include ceratosaurs, megalosaurs, and abelisaurs." In this regard, these groups include both Ceratosauria + Tetanurae (sensu Rauhut, 2003:node 11). Averostra defined here as a node-based clade (following Paul's original arrangement) that includes *Ceratosaurus nasicornis*, *Allosaurus fragilis*, and all the descendants of their common ancestor. In this regard, Averostra is used here to refer to the Ceratosauria + Tetanurae clade.

MORPHOLOGICAL RE-DESCRIPTION OF THE AIREL THEROPOD AND COMPARISONS WITH OTHER THEROPODS

Since the species *"L." airelensis* was coined by Cuny and Galton (1993), new contributions have substantially improved our knowledge of the Coelophysoidea (e.g., Carpenter, 1997; Tykoski, 1998; Carrano and Sampson, 2004). In spite of the detailed description and comparisons provided by Cuny and Galton (1993), we carry out a re-comparison of the Airel theropod material with other coelophysoids. This comparison will be focused on derived features of the Coelophysoidea, to elucidate some aspects of the relationships of the Airel theropod within the clade.

Tooth—The density of serrations onto each edge of the tooth of the Airel theropod (20 per 5 mm onto its rostral edge and 16 per 5 mm onto its caudal edge; Cuny and Galton, 1993), resembles more the pattern exhibited in *Dilophosaurus* (20–14 per 5 mm; Welles, 1984) than that of other theropods in which the density of the serrations is considerably higher (e.g., *Gojirasaurus*, *C. bauri*, *Herrerasaurus*; Carpenter, 1997) or lower (e.g., *Ceratosaurus*; Carpenter, 1997). The chisel-shaped morphology of the serrations of the French coelophysoid is in accordance with that of other basal theropods (e.g., *C. bauri*, Abelisauroidea; Carpenter, 1997; Coria and Arcucci, 2004). This condition differs in the coelophysoid *Gojirasaurus*, where Carpenter (1997) emphasized the peculiar and diagnostic morphology of the serrations of this taxon, characterized by the orientation of the serrations toward the tip of the tooth.

Cervical Vertebrae—The preserved cervical series of the Airel theropod presents the typical coelophysoid condition with low and craniocaudally elongated vertebrae (Fig. 1A). In fact, the length of cervical centrum of the vertebrae of the Airel theropod represents three times the height of its cranial articular facet. Following previous authors (Sereno, 1999; Tykoski and Rowe, 2004), this character represents a derived feature only shared by *L. liliensterni*, *Coelophysis*, and *"Syntarsus"* (Sereno et al., 2004:character 78) (Figs. 1B–D). In contrast, in *Dilophosaurus*, this ratio does not reach the rate observed in the previously mentioned taxa; on the other hand, this index approaches that of *Herrerasaurus* and ceratosaurians. Recent cladistic reinterpretations of basal Dinosauria (e.g., Yates, 2003; Langer, 2004) show Theropoda more closely related to Sauropodomorpha, rather than to Herrerasauridae and *Eoraptor*. These four taxa form a stem-based Saurischia, whereas Theropoda and Sauropodomorpha form a node-based Eusaurischia (sensu Langer, 2004). In this phylogenetic context, the presence of elongated cervical vertebrae in Prosauropoda (Fig. 1E), that closely resembles the ratios described for coelophysoids, indicates that the feature in Coelophysoidea could constitute a plesiomorphy, probably apomorphy of Eusaurischia.

Among basal theropods, elongated cervical vertebrae are also exhibited in the basal abelisauroid *Elaphrosaurus* (Carrano et al., 2002). However, this trait is likely to represent a convergence with coelophysoids, because the basalmost non-abelisauroid
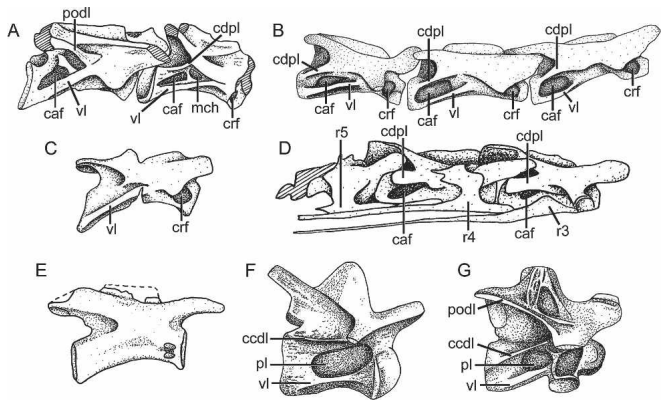

FIGURE 1. Cervical vertebrae of several saurischians. **A**, cervicals 3 and 4 of *Lophostropheus airelensis*, **B**, mid-caudal cervicals of *Coelophysis bauri*, **C**, cranial cervical of *Liliensternus liliensterni*, **D**, cervicals 3, 4, and partial 5 of *"Syntarsus" kayentakatae*, **E**, cervical 4 of *Riojasaurus*, **F**, cervical of *Kotasaurus yamanpalliensis*, and **G**, cervical 7 of *Jobaria tiguidensis*. **Abbreviations**: **caf**, caudal fossa, **ccdl**, caudal centrodiapophyseal lamina, **cdpl**, centrodiapophyseal lamina, **crf**, cranial fossa, **mch**, medial chonos, **r 3–5**, ribs 3–5, **podl**, postzygodiapophyseal lamina, **vl**, ventral lamina. Not to scale. (**A** modified from Cuny and Galton, 1993; **C** modified from von Huene, 1934; **D** modified from Tykoski, 1998; **E** modified from Bonaparte, 1999; **F** modified from Yadagiri, 2001; **G** modified from Sereno et al., 1999).

ceratosaur *Ceratosaurus* presents craniocaudally short cranial cervical vertebrae.

Regarding the cervical centrum pneumatization, previous authors have claimed that an apneumatic centrum represents an ancestral condition for Dinosauria (Britt, 1993) (Fig. 1E). Among basal neotheropod dinosaurs (i.e., Coelophysoidea, Ceratosauria), two pairs of openings are present in the postaxial cervical centrum (Fig. 1A, B, D). In Coelophysoidea, these openings are represented by blind fossae (Rowe, 1989; Rauhut, 2003; Tykoski, 2005). This condition is also present in the Airel theropod. *L. liliensterni* differs from other coelophysoids, including the Airel theropod, in the absence of the caudal fossa, only exhibiting a cranial rounded fossa (Fig. 1C). Furthermore, in ceratosaurians two pairs of pneumatic openings were retained, but these pneumatizations pierced into the centrum, resulting in pneumatic camerae within the centra (Britt, 1993). In tetanuran theropods, the caudal pleurocoel seems to have been lost, and only one pair of foramina is present in the centrum of basal tetanurans (e.g., *Allosaurus*, *Torvosaurus*; Madsen, 1976; Britt, 1991). In sum, within the Coelophysoidea, *L. liliensterni* differs from the pattern exhibited by the Airel theropod and coelophysids (Rauhut, 2003).

Additionally, caudal blind excavations seem to be also present in *Elaphrosaurus* (Janensch, 1925:plate 2), resembling the pattern exhibited by the Airel theropod and coelophysids. This may indicate that a combination of features (e.g., craniocaudally elongated cervical vertebrae, blind caudal excavation) were convergently acquired by *Elaphrosaurus* to develop a "coelophysoid-like" neck morphology.

The presence of a pair of laminae in the cervical vertebrae of the Airel theropod and its condition in other coelophysoid taxa will be discussed subsequently (see character 1). Nevertheless, its presence is only shared by coelophysoids among Theropoda.

Dorsal Vertebrae—Only a half centrum attached to the last dorsal vertebra are available among the dorsal series of *"L." airelensis* (Cuny and Galton, 1993). The last dorsal vertebra of the Airel theropod has a moderately long centrum, being 1.3 times longer than the height of the cranial articular facet. This ratio resembles the condition exhibited by other

FIGURE 2. Articulated pelvic girdle region and hindlimb elements of *Coelophysis bauri* in left lateral view. Lower reference in centimeters. Note the enclosed pubic obturator foramen, the probably almost complete pubo-ischiadic plate, and the continuous supraacetabular crest with the lateroventral margin of the postacetabular process of the ilium. **Abbreviations**: **cv**, caudal vertebrae, **dv**, dorsal vertebrae, **fe**, femur, **fi**, fibula, **il**, ilion, **is**, ischion, **of**, obturator foramen, **pu**, pubis, **sac**, supraacetabular crest, **ti**, tibia.

basal neotheropods, including *L. liliensterni*, *Dilophosaurus, and Ceratosaurus*. The elongation of the caudal dorsal vertebra is more pronounced in the coelophysids *C. rhodesiensis* (Raath, 1977:fig 9c; Rauhut, 2003:fig 27b) and *C. bauri* (CM C-3-82) (Fig. 2), where the centrum is strongly elongated and also proportionally low, exhibiting a centrum length 2.5 times the height of the cranial articular surface (Figs. 3B, C). Above the level of centrum mid-height, onto its lateral surface, a large, oval, and shallow fossa exists (Cuny and Galton, 1993). A similar depression is also exhibited by the basal saurischian *Herrerasaurus* (Rauhut, 2003:fig. 27a) (Fig. 3A), but this feature does not occur in *Dilophosaurus*, *C. rhodesiensis*, and *L. liliesnterni*. Although the neural arch of the last dorsal vertebrae is badly crushed and distorted (Cuny and Galton, 1993), the hyposphene is well preserved. The hyposphene of the Airel theropod is well extended dorsoventrally in comparison with the central length, a condition that clearly contrast with the low hyposphene present in other saurischians, such as *Herrerasaurus* (Novas, 1993), *C. rhodesiensis* (Raath, 1977), *L. liliensterni* (von Huene, 1934), and *Dilophosaurus* (Welles, 1984).

Sacrum—Cuny and Galton (1993) interpreted the sacrum of the Airel theropod as composed by four sacral vertebrae. The centrum morphology of the dorsosacral vertebra (first sacral) resembles that of *Dilophosaurus*, with a depressed area on the proximal sector of the centrum. In the Airel theropod the presence of a medial and lateral chonoses has been described for the first sacral vertebra (Cuny and Galton, 1993). Britt (1993) reported the lack of pneumatic features in the sacral vertebrae of *C. bauri* and *Dilophosaurus*. On the other hand, Welles (1984) described the presence of a large foramen at the base of the neural arch of the sacrals one and two, interpreting the feature as the exit of the sacral nerve. The opening present in the Airel theropod is similar in morphology and position (proximal and caudal to the mid-length of the centrum) to that reported by Welles for *Dilophosaurus*, indicating that the foramen of the Airel theropod could also indicate the exit of the sacral nerve, rather than the presence of a pneumatization on the sacral vertebrae. The contact area of the sacral ribs with the iliac blade are positioned at level with the proximal margin of the sacral centra

in the Airel theropod, a condition that resembles that of other neotheropod dinosaurs, such as *L. liliensterni* (von Huene, 1934), *Coelophysis*, *Dilophosaurus* (Welles, 1984), and *Allosaurus* (Madsen, 1976). Nevertheless this condition contrast with that of the basal dinosauriform *Silesaurus* (Dzik, 2003) and the basal prosauropod *Thecodontosaurus* (Benton et al., 2000), where the attachment zone of the sacral ribs are leveled with the ventral margin of the sacral centra. Thus, the presence of dorsally positioned attachment between sacral ribs and iliac blade seems to constitute a neotheropodan attribute.

The sacral two (third sacral) is badly crushed. The overall morphology of the caudosacral one (fourth sacral) of the Airel theropod is in accordance with that of *Dilophosaurus* and other basal neotheropods, mainly in the dorsally oriented transverse process.

Caudal Vertebrae—Several caudal vertebrae are available among the type material of the Airel theropod. The third caudal vertebra was described by Cuny and Galton (1993), but not illustrated, neither was it by Larsonneur and Lapparent (1966); so this bone is here figured for the first time (Fig. 4). The overall morphology of the first and third caudal vertebrae resembles those of *Dilophosaurus*, *L. lilienterni*, *C. bauri*, and *C. rhodesiensis*. An interesting feature of these cranial caudal vertebrae is the incipient concave cranial margins of the centra. Other coelophysoids (e.g., *L. liliensterni*, *C. rhodesiensis*, *C. bauri*; von Huene, 1934; Raath, 1977; Colbert, 1989), as well as most basal dinosauriforms (e.g., *Thecodontosaurus*, *Silesaurus*; Benton et al., 2000; Dzik, 2003), exhibit rather planar articular surfaces. On the other hand, *Herrerasaurus* (Novas, 1993:fig. 4a) and *Dilophosaurus* (Welles, 1984:fig. 21b) present a slight concavity on the cranial articular surface of the third caudal; whereas more derived theropods seems to apomorphically share a marked concave cranial articular surface in the cranial caudal vertebrae (e.g., *Allosaurus*,
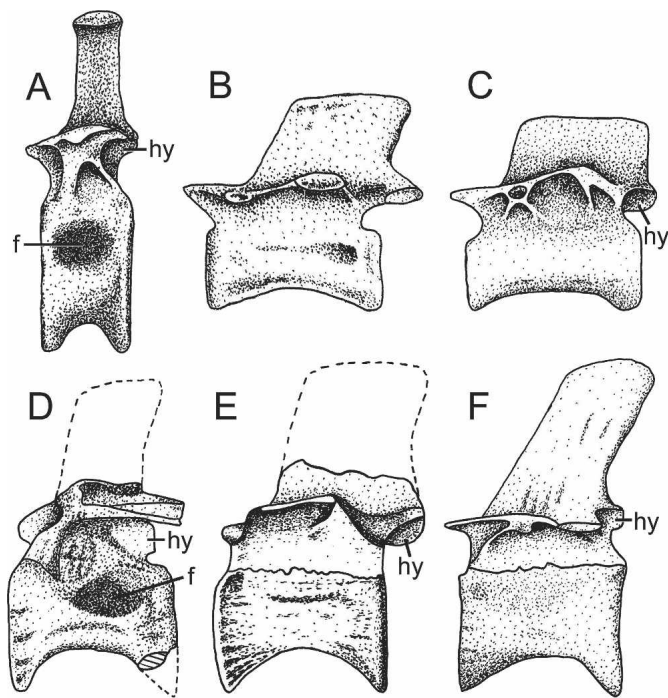

FIGURE 3. Caudal dorsal vertebrae of several saurischians in lateral view. **A**, *Herrerasaurus ischigualastensis*, **B**, *Coelophysis bauri*, **C**, *Coelophysis rhodesiensis*, **D**, *Lophostropheus airelensis*, **E**, *Liliensternus liliensterni*, and **F**, *Dilophosaurus wetherilli*. **Abbreviations**: **f**, fossa, **hy**, hyposphene. Not to scale. (**A** modified from Rauhut, 2003; **B** modified from Colbert, 1989; **C** modified from Rauhut, 2003; **D** modified from Cuny and Galton, 1993; **E** modified from von Huene, 1934; **F** modified from Welles, 1984).
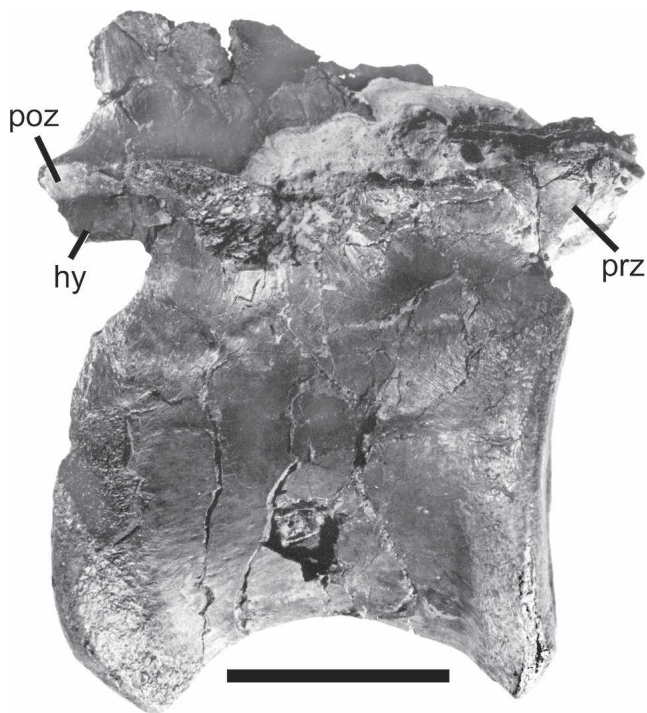
FIGURE 4.   Third caudal vertebra of *Lophostropheus airelensis* in right lateral view. **Abbreviations**: **hy**, hyposphene, **poz**, postzygapophysis, **prz**, prezygapophysis. Scale bar equals 3 cm.

Carnotaurus, *Torvosaurus*, *Sinraptor*, *Ceratosaurus*; Madsen, 1976; Bonaparte et al., 1990; Britt, 1991; Currie and Zhao, 1993; Madsen and Welles, 2000). This latter attribute of averostran theropods resembles that of the Airel theropod. Both preserved cranial caudal vertebrae exhibit a ventral groove, feature typical of the Neotheropoda.

Cuny and Galton (1993) previously pointed out the constant length of each posterior caudal axial element, all about 70 mm (± 5 mm). This trait is only shared by *Dilophosaurus* among basal Theropoda (Cuny and Galton, 1993). The posterior caudal vertebrae of the Airel theropod are considerably elongated. In fact, the centrum length fairly excess three times the height of the cranial articular surface. This condition is also present in Coelophysoidea (Rauhut, 2003). However, the elongation of these posterior vertebrae is not as developed as in Coelophysidae (e.g., *C. bauri*; CM C-3-82), where the length of the centrum exceeds five times its height.

Ilium—The presence of a vertical ridge on the iliac blade of the Airel theropod seems to be an autapomorphy that distinguishes this taxon from other coelophysoids and non-tetanuran dinosaurs (Fig. 5). Following the interpretation carried out by Carrano and Hutchinson (2002), this vertical ridge may have separated the zone of origin of the M. iliofemoralis externus and M. iliofibularis. Rowe and Gauthier (1990) established as a diagnostic feature of Coelophysidae the presence of a distinct caudal rim on the ilium for the M. iliofemoralis fossa. The caudal rim present in *C. bauri* and *C. rhodesiensis* (Rowe and Gauthier, 1990) represents the fossa for the origin of the M. iliofibularis (sensu Carrano and Hutchinson, 2002) (Figs. 5D, E), rather than the origin of the M. iliofemoralis externus.

Resembling the plesiomorphic condition of Herrerasauridae and more basal dinosauriforms (e.g., *Marasuchus*, *Silesaurus*), most coelophysoids (e.g., *C. bauri*, *C. rhodesiensis*, *Liliensternus*, *Dilophosaurus*; Tykoski, 2005) retained a ventral margin of the preacetabular process not ventrocranially protracted (Figs. 5A–

E). In contrast, in *Sarcosaurus*, ceratosaurians (e.g., *Ceratosaurus*, *Carnotaurus*), and tetanurans (e.g., *Allosaurus*) the preacetabular process nearly reaches the pubic peduncle (Figs. 5F–J). However, the latter trait could be subdivided in two different conditions. On the one hand, in *Sarcosaurus woodi* the preacetabular process nearly reaches the pubic peduncle, but as a consequence of the cranioventral orientation of the process, it results in a strongly convex dorsal margin of the iliac blade. On the other hand, contrasting with *Sarcosaurus*, in abelisauroids (e.g., *Carnotaurus*) and tetanurans (e.g., *Allosaurus*) the preacetabular process also approaches the pubic peduncle but as a result of the presence of a ventral hook (Rauhut, 2003) (i.e., an expansion of the cranioventral part of the preacetabular process that not implies its cranioventral orientation).

The supraacetabular crest is well-developed above the entire length of the acetabulum in the Airel theropod (Fig. 5C). Furthermore, as in most neotheropods, this crest forms a rather continuous lamina with the lateral margin of the brevis shelf. This morphology differs from that of basal Dinosauriformes (e.g., *Silesaurus*, Herrerasauridae, *Guaibasaurus*), where the supraacetabular crest is well separated from the lateral margin of the brevis shelf (Fig. 5A). However, the Airel theropod and coelophysids (e.g., *C. rhodesiensis*, some specimens of *C. bauri* at least; Raath, 1977; CM C-3-82) present a supraacetabular crest continuous with the lateral margin of the brevis fossa, forming a well-developed ridge, with non-distinct separation between both structures (Figs. 5C–E). This trait differs from that of *L. liliensterni*, *Dilophosaurus*, and other neotheropods (Figs. 5B, G, I, J), but it seems to have been convergently developed by the Ceratosauria (e.g., *Ceratosaurus*; Gilmore, 1920).

Another common feature shared by the Coelophysoidea is the presence of a pronounced kink in the pubic peduncle resulting in two distinct articular facets, with the cranial part facing almost
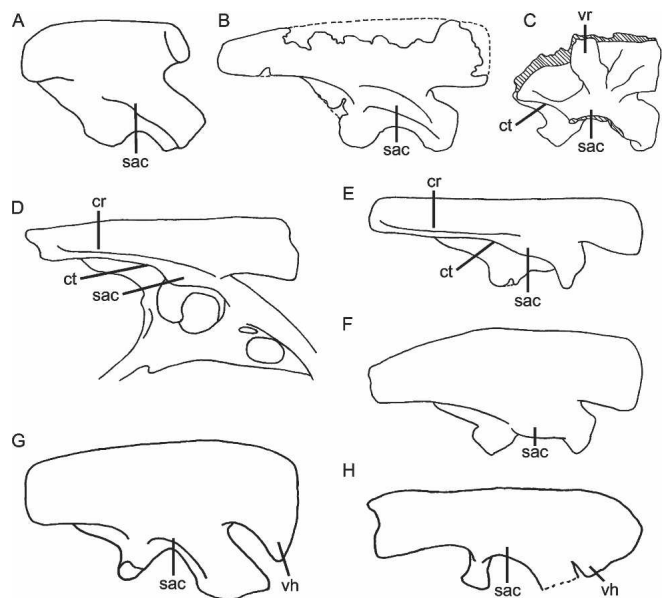

FIGURE 5.   Right ilia of several saurischians in lateral view. **A**, *Herrerasaurus ischigualastensis*, **B**, *Liliensternus liliensterni*, **C**, *Lophostropheus airelensis*, **D**, *Coelophysis rhodesiensis*, **E**, *Coelophysis bauri*, **F**, *Dilophosaurus wetherilli*, **G**, *Allosaurus fragilis*, and **H**, *Carnotaurus sastrei*. **Abbreviations**: **cr**, caudal rim for origin of M. iliofibularis, **ct**, continuity between supraacetabular crest and lateral margin of brevis fossa, **sac**, supraacetabular crest, **vh**, ventral hook, **vr**, vertical ridge. Not to scale. (**A** modified from Novas, 1993; **C** modified from Cuny and Galton, 1993; **D** modified from Raath, 1977; **F** modified from Bonaparte et al., 1990; **G** modified from Madsen 1976; **H** modified from Tykoski, 2005).

entirely cranially (Rauhut, 2003) (Figs. 5B–E, G). The Airel theropod clearly presents the apomorphic state of this feature. A caudally well-developed medial blade of the postacetabular process of ilium is caudally protracted from the base of the pubic peduncle, resembling the condition of *Liliensternus*, *C. bauri*, *C. rhodesiensis* (Raath, 1977), and other basal theropods.

Furthermore, comparisons between the ilia of *"L." airelensis* and *Dilophosaurus* indicates that the Airel theropod was a medium-sized theropod (5.5–6 m), slightly smaller than the type specimen of *D. wetherilli* (Welles, 1984). In this regard, *"L." airelensis* fits in the size range reported for basal coelophysoids (i.e., *Liliensternus*, *Gojirasaurus*, *Zupaysaurus*, *Dilophosaurus*, *Sarcosaurus*), contrasting with the smaller-sized coelophysids (i.e., *Coelophysis*, *"Syntarsus"*).

Pubis—The proximal end of both pubes are available, but badly crushed (Cuny and Galton, 1993). The proximocranial coner of both pubes are preserved, resulting in the presence of partial pubo-ischiadic plates. The morphology of this structure resembles that of *C. rhodesiensis* (Fig. 5D) and *C. bauri* (Fig. 2; CM C-3-82). A shallow depression is present just cranial to the enclosed obturator foramen, probably indicating the origin for the M. ambiens (Hutchinson, 2001). Nevertheless, because of its fragmentary nature, this bone is considered to be phylogenetically uninformative within the Coelophysoidea (see discussion of character 5).

REAPPRAISAL OF THE DIAGNOSTIC CHARACTERS OF *"L." AIRELENSIS*

Cuny and Galton (1993) based the assignation of the Airel theropod to the genus *Liliensternus* on 5 diagnostic features, and proposed an emended diagnosis for the genus based on six characters (although one cranial trait was not preserved in *"Liliensternus" airelensis*). These characters are discussed below:

(1) Cranial Cervical Vertebrae Elongated With Two Lateral Buttresses From the Base of the Diapophyses—As described by Cuny and Galton (1993), the cranial cervical vertebrae of the Airel theropod exhibit a pair of laminae (buttresses; sensu Cuny and Galton, 1993) extending from the base of the diapophyses (Fig. 1A). In fact, the fourth cervical vertebra of *"L." airelensis* exhibits a dorsocaudally oriented dorsal lamina, reaching the postzygapophysis; moreover, a ventrocaudally directed ventral lamina extends below the caudal fossa, and reaches the caudoventral corner of the cervical centra (Cuny and Galton, 1993). On the other hand, in the third cervical vertebra meanwhile the ventral lamina is morphologically similar, the slanting dorsal lamina of the fourth vertebra is absent. In the third cervical a caudally oriented lamina is present, running above the caudal fossa and reaching the caudodorsal corner of the vertebral centrum.

Cuny and Galton (1993) indicated that the morphological pattern of these laminae on the cranial cervical vertebrae (only present in the C4) was a character diagnostic of *Liliensternus*. However, the validity of this feature as only shared by *L. liliensterni* and the Airel theropod was recently questioned by Carrano and Sampson (2004), who argued that this ridge is also present in other coelophysoid taxa, but faintly developed. In fact, in the North American taxa *C. bauri* (CM C-3-82; Fig. 1B) and the Shake-N-Bake coelophysoid (Tykoski, 2005: fig. 40d) the ventral border of the caudal fossa is represented by a rod-like longitudinal structure, extending from below the diapophysis. This structure clearly corresponds to the ventral lamina of *L. liliensterni* (Fig. 1C) and the Airel theropod. As in the Airel theropod, a dorsal lamina is also present in *C. bauri* (CM C-3-82; Fig. 1B) and *"Syntarsus" kayentakatae* (Tykoski, 1998) (Fig. 1D). However, the overall morphology of these structures only matches the kind of dorsal lamina found in the C3 of the Airel theropod. In fact, the dorsal laminae of *C. bauri* and *"S." kay-*

entakatae are not slanting and does not reach the postzygapophysis, but rather the dorsocaudal corner of the centrum.

Rauhut (2003) recently revised the character here discussed and retained a modified version of the original feature of Cuny and Galton (1993), to support the sister-taxon relationship between *L. liliensterni* and the Airel theropod. Rauhut (2003) described as a synapomorphy of the genus *Liliensternus* the presence of a broad ridge extending from the diapophyses to the ventral rim of the caudal end of the cervical centrum (Rauhut, 2003:character 98, fig. 24B). This character only alludes to the ventral lamina, but excludes the dorsal one. The discussion carried out above shows that the ventral lamina is widely present among coelophysoids, and does not constitute a feature only shared by *L. liliensterni* and the Airel theropod. On the other hand, the "dorsal buttresses" of the Airel theropod exhibit, at least, two kinds of different morphologies among cranial cervical vertebrae. The dorsal lamina of C3 resembles that of *C. bauri* and *"S"*. *kayentakatae*, whereas the dorsal lamina of C4 approaches the dorsal lamina figured by von Huene (1934) for the C3 of *L. liliensterni*. All in all, the presence of two lateral laminae in cranial cervical vertebrae is a feature widely distributed among the Coelophysoidea.

Beyond the discussion about the distribution of this axial feature among the Coelophysoidea, it is also interesting to note that two of the multiple laminae present in the axial skeleton of sauropods (e.g., *Jobaria*, *Kotasaurus*, *Diplodocus*; Sereno et al., 1999; Yadagiri, 2001; Wilson, 2002) resembles coelophysoid dorsal laminae (Figs. 1F, G). In fact, the postzygodiapophyseal lamina of sauropods clearly approaches the "dorsal lamina" of *L. liliensterni* and the Airel theropod, starting from the diapophyses and extending dorsocaudally in order to reach the postzygapophysis. In the same way, the "dorsal lamina" of *"S." kayentakatae* and *C. bauri* resembles the caudal centrodiapophyseal lamina of sauropods, starting also from the diapophysis and extending caudally to the dorsocaudal corner of the centrum. However, the "dorsal lamina" of the C4 of *"L." airelensis* differs from that of *C. bauri* and *"S." kayentakatae*. To mark this morphological dichotomy, the "dorsal lamina" of the C4 of *"L." airelensis* is here named postzygodiapophyseal lamina, whereas the "dorsal laminae" of *C. bauri*, *"S." kayentakatae*, and C3 of *"L." airelensis* are named centrodiapophyseal lamina (following the sauropod nomenclature, sensu Wilson, 2002).

(2) Four Unfused Sacral Vertebrae—The fusion or not of the sacral vertebrae is a condition that depends on the ontogenetic development of the animal. The presence of four sacral vertebrae previously described for *L. liliensterni* (Welles, 1984) and *"L." airelensis* (Cuny and Galton, 1993), was also reported for *Dilophosaurus* (Welles, 1984). Recently, the presence of four sacral vertebrae was questioned by Carrano and Sampson (2004). These authors pointed out that issues on the preservation and miscounting of vertebrae by Welles (1984) may obscure the real sacral count of *Dilophosaurus* and *L. liliensterni*. In fact, recently Tykoski (2005) reported that scars on ilia of new specimens of *Dilophosaurus* indicate that the ilium of this taxon was contacted by five sacral vertebrae, resembling the typical neotheropodan condition. Carrano and Sampson (2004) suggested that the proposed last dorsal vertebra of *"L." airelensis* may represent the dorsosacral 2, resulting in a sacrum composed of five sacral vertebrae, resembling the pattern exhibited by other theropods. In this regard, the presence of four sacral vertebrae in both *"L." airelensis* and *L. liliensterni* cannot be positively demonstrated.

(3) Sacral Ribs Fused Together to Form an Arch—Cuny and Galton (1993) described that the sacral ribs of *L. liliensterni* and *"L." airelensis* are fused together, forming an arch. However, this trait may depend on the degree of fusion of the sacrum during the ontogenetic development of the individual. In the basal Di-

nosauriformes *Silesaurus* the sacral ribs of both sacral vertebrae are fused together forming an arch (Dzik, 2003:fig. 10). Among sauropodomorphs, in some taxa the sacral ribs are also fused forming an arch (e.g., *Apatosaurus*, *Thecodontosaurus*; Ostrom and McIntosh, 1966:pl. 27; Benton et al., 2000:fig. 8). In *C. bauri* (Colbert, 1989:fig. 56) and *C. rhodesiensis* (Raath, 1977) the sacral ribs are also fused together, resulting in an arch-like structure in the North American taxon, whereas in *C. rhodesiensis* the co-ossification of the transverse processes result in a sheet-like structure in dorsal view. Fusion between the sacral ribs was also reported for *Dilophosaurus* (Tykoski, 2005). In addition, the basal ceratosaurian *Ceratosaurus nasicornis* presents fused sacral ribs (Gilmore, 1920:pl. 21), also forming an arch, resembling the condition exhibited by *L. liliensterni* and *"L." airelensis*.

(4) Ischial Peduncle of the Ilium Caudoventrally Directed—In most basal Dinosauria (e.g., *Plateosaurus*, *Herrerasaurus*, *Guaibasaurus*, *Thecodontosaurus*; von Huene, 1926; Novas, 1993; Bonaparte et al., 1999; Benton et al., 2000), including *C. rhodesiensis* and *C. bauri* as well as the more derived ceratosaurians and tetanurans, the ischial peduncle of the ilium is almost ventrally oriented (Fig. 5). On the other hand, as was claimed by Cuny and Galton (1993), in *Liliensternus liliensterni* and the Airel theropod the ischial peduncle is caudoventrally oriented (Figs. 5B, C). However, the pelvic condition exhibited by *L. liliensterni* and the Airel theropod not substantially differs from that of *Dilophosaurus* when the ilium is seen in lateral view (Figs. 5F). In *Dilophosaurus* the ischial peduncle of the ilium is also caudoventrally directed (Welles, 1984; Tykoski, 2005), indicating that this feature is more widely distributed among coelophysoids that it was thought.

(5) Single Opening in the Pubic Plate (i.e., obturator foramen)—This feature represent a plesiomorphic character for Neotheropoda, because it is present in basal Dinosauriformes (e.g., *Silesaurus*; Dzik, 2003), "Prosauropoda" (e.g., *Plateosaurus*; von Huene, 1926), and Herrerasauridae (Novas, 1993). Among neotheropods, the presence of a single pubic opening (i.e., obturator foramen) is also exhibited by ceratosaurians (except *Ceratosaurus*, Rowe and Gauthier, 1990) and basal tetanurans (e.g., *Piatnytzkysaurus*; Bonaparte, 1986). Contrasting with Colbert's interpretation, (1989:figs. 73, 77a, 78) *C. bauri* exhibits an enclosed pubic obturator foramen (Fig. 2; CM C-3-82), resembling the condition of *C. rhodesiensis* (Raath, 1977), *Segisaurus* (Camp, 1936), and the Airel theropod (Cuny and Galton, 1993).

The characters purportedly only shared by *L. liliensterni* and *"L." airelensis* are in fact more widely distributed among theropods (e.g., *C. rhodesiensis*, *C. bauri*, *Ceratosaurus*) and basal dinosaurs (e.g., *Herrerasaurus*, *Plateosaurus*). In this regard, the close relationships between both species of the genus *Liliensternus* have been weakened.

CLADISTIC ANALYSIS

Methods

A data matrix made of 145 characters (Appendix 1, 2) and 13 supposed theropodan (sensu Sereno et al., 1993; Rauhut, 2003) taxa was analyzed. Character polarity was determined using the basal dinosaur *Eoraptor lunensis* Sereno et al., 1993 as a default outgroup taxon. *Herrerasaurus ischigualastensis* Reig, 1963 was also included in the matrix as an outgroup taxon, meanwhile *Dilophosaurus wetherilli* Welles, 1954; *Liliensternus liliensterni* Welles, 1984; *Lophostropheus airelensis* (nov gen. et nov. comb. Cuny and Galton, 1993; see below); *Coelophysis bauri* Cope, 1889; *Coelophysis rhodesiensis* Raath, 1969; *"Syntarsus" kayentakatae* Rowe, 1989; *Ceratosaurus nasicornis* Marsh, 1884; *Carnotaurus sastrei* Bonaparte, 1985; *Baryonyx walkeri* Charig and
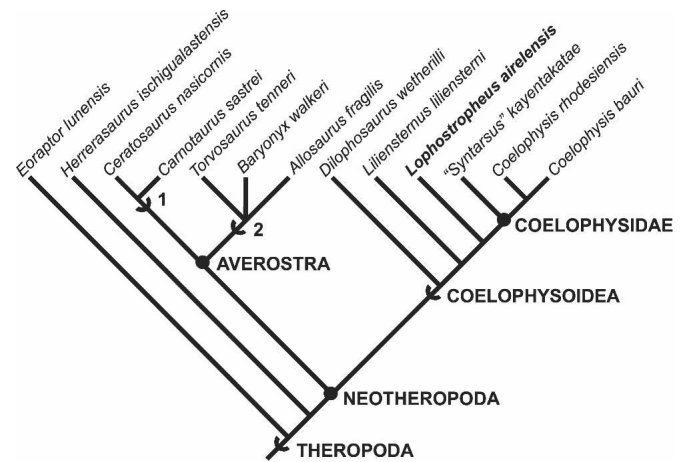

FIGURE 6. Cladogram showing the phylogenetic relationships of *Lophostropheus airelensis* among neotheropod dinosaurs. Strict consensus tree resulting from the analysis of the data matrix composed by cranial and post-cranial characters, length 295 steps, C.I. 0.61 and R.I. 0.74. Stem-based clades are indicated by arches and node-based clades are indicated by circles at the root of the node. **References**: **1**, Ceratosauria, and **2**, Tetanurae.

Milner, 1986; *Torvosaurus tanneri* Galton and Jensen, 1979; and *Allosaurus fragilis* Marsh, 1877 as ingroup taxa. The coelophysoid theropods *Gojirasaurus quayi* and *Zupaysaurus rougieri* (sensu Ezcurra and Novas, 2005, in press; Carrano et al., 2005) were not included in the present analysis due to the fragmentary nature of the postcranial skeleton and the almost non-overlapping elements of their type materials with the Airel theropod. The data matrix was analysed using NONA program (Goloboff, 1993) under 100 replications, with search strategy of multiple tree bisection-reconnection of branch-swapping (multiple TBR + TBR), and unambiguous optimization.

Results

The result of the analysis of the data matrix were three trees composed of 295 steps and 11 nodes, with a consistency index of 0.61 and a retention index of 0.74 (Fig. 6; Appendix 3). The differences between the three different trees are present within the interrelationships among tetanuran taxa. A strict consensus of the three trees depicted a trichotomy within the Tetanurae, the relationships among the clade remaining unresolved.

The present analysis places the Airel theropod into a clade within the Coelophysoidea, composed of the French taxon and Coelophysidae. *Dilophosaurus* and *L. liliensterni* were regarded as sucessive more basal members of Coelophysoidea. In fact, based on the result of the phylogenetic analysis, we can define the following derived features that are shared by the Airel theropod and the Coelophysoidea: (1) transverse processes of the dorsal vertebrae broad, extending to lateral margin of the prezygapophyses (Rowe and Gauthier 1990); (2) caudal dorsal vertebrae centrum length equal or more than 1.33 times the height of the cranial articular surface (Rauhut, 2003; Tykoski, 2005); (3) at least some caudal vertebrae with narrow, sharply defined, longitudinal, ventral groove (Rowe and Gauthier 1990); (4) distal caudal centrum length more than four times centrum height (modified from Sereno, 1999); and (5) articulation facet of pubic penducle of ilium with pronounced kink and cranial part facing almost entirely cranially (Rauhut, 2003). Furthermore, the Airel theropod shares with *L. liliensterni* and more derived mem-

bers of the clade (i.e., *Coelophysis* and "*Syntarsus*"), but not *Dilophosaurus*, the following derived characters: (6) mid-cervical (C3-C6) centrum length more than 3 times the height of the cranial articular surface (Sereno, 1999); (7) postzygodiapophyseal lamina in cervical vertebrae, protracted from the diapophyses and reaches the postzygapophyses; (8) ventral lamina, protracted from the diapophyses to the ventral rim of the caudal end of the vertebral centra in cervical centra (Cuny and Galton, 1993; Rauhut, 2003); and (9) postaxial cervical neural spines extremely low (Russell and Dong 1993).

Moreover, the French coelophysoid shares only with Coelophysidae (excluding *L. liliensterni*) the presence of a (10) supraacetabular crest continuous with the lateral margin of the brevis fossa, forming a well-developed ridge, without a notch between both structures. Additionally, *Liliensternus* seems to contrast with the Airel theropod and Coelophysidae in the lack of a centrodiapophyseal lamina from the diapophyses to the dorsocaudal corner of the centrum in cervical vertebrae and the absence of the caudal pleurocoel in the cranial cervical vertebrae. Furthermore, the Airel theropod (together with *Dilophosaurus* and *Liliensternus*) differs from the Coelophysidae in the absence of mid-cervical (C3–C6) centrum length more than 4 times the height of its cranial articular surface (modified from Sereno, 1999), and the lack of significantly elongated caudal dorsal vertebrae, with centrum length equal or more than two times the height of its cranial articular surface (Rauhut, 2003; Tykoski, 2005). The tree resulting from the present analysis also shows among averostran theropods a monophyletic Ceratosauria (i.e., *Ceratosaurus* + *Carnotaurus* [Abelisauroidea]) + Tetanurae clade.

A bootstrap analysis (1000 replication) was carried out, depicted well-supported Neotheropoda (94%), Averostra (92%), Ceratosauria (92%), and Coelophysoidea (96%) clades. Within the Coelophysoidea, the node that encloses *Liliensternus*, The Airel theropod, and Coelophysidae was also well supported with a bootstrap value of 97%. The Airel theropod + Coelophysidae node exhibits a bootstrap value of 60% and Coelophysidae 66%. The close relationship of *C. rhodesiensis* to *C. bauri* (i.e., *Coelophysis*) than to "*S.*" *kayentakatae* was supported by a bootstrap value of 86%. A node that encloses both *L. liliensterni* and the Airel theropod was depicted in less than 1% of the results of the bootstrap.

A secondary test have been carried out only keeping postcranial features in the data matrix (the first 68 characters of the original matrix were deleted). The result was a single tree with an identical topography to that of the first test regarding the Coelophysoidea. The tree was composed of 146 steps, with a consistency index of 0.67 and a retention index of 0.80. Nevertheless, some changes have occurred among the interrelationships of averostran theropods. The interrelationships among the Tetanurae were resolved, depicting *Baryonyx* as more closely related to *Torvosaurus* than to *Allosaurus* (i.e., Spinosauroidea). These changes are not unexpected because purportedly apomorphic features of Tetanurae ingroups were not used in the data matrix. In this regard, this second cladistic analysis only based on postcranial features strongly supports the original test, exhibiting both higher consistency and retention index than in the first analysis. This increase in the tree indexes is prospectively due to the incomplete nature of the cranial remains of both *L. liliensterni* and the Airel theropod. Thus, the affiliation of the Airel theropod with *L. liliensterni*, rather than to other coelophysids, was weakened. In fact, the French coelophysoid is more closely related to Coelophysidae than to *L. liliensterni*. In this regard, the assignation of the Airel theropod to the genus *Liliensternus* is not supported here. So in this contribution, the new genus *Lophostropheus* is coined to elevate the species *L. airelensis* to the status of genera. This results in the new combination *Lophostropheus airelensis*.

SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen, 1842
SAURISCHIA Seeley, 1887
THEROPODA Marsh, 1881
NEOTHEROPODA Bakker, 1986, sensu Sereno, 1998
COELOPHYSOIDEA Nopcsa, 1928, sensu Holtz, 1994
LOPHOSTROPHEUS, gen. nov.

Etymology—*Lophos*, crest (Greek); *strophe*, vertebrae (Greek). In allusion to the prominent dorsal and ventral laminae present in the postaxial cranial cervical vertebrae.

Holotype—Incomplete skeleton represented by one tooth, five cervicals, two caudal dorsals, four sacrals plus caudal vertebrae, plus part of ilia, ischia, proximal pubes (Cuny and Galton, 1993), and a fragmentary unidentified bone. Material deposited at the University of Caen, without collection number (Cuny and Galton, 1993).

Locality—Moon-Airel Formation (uppermost Rhaetian–Early Hettangian), Airel quarry (Manche), southeast of the Cotentin peninsula, in the Carentan basin, Normandy, France (Cuny and Galton, 1993).

Diagnosis—*Lophostropheus* differs from other basal dinosaurs in the presence of the following autapomorphies: moderately convex cranial articular surface of the cranial postaxial cervical vertebrae (resembling averostran theropods), large and oval lateral fossa onto last dorsal vertebral centrum (convergent in *Herrerasaurus*), dorsoventrally well-extended hyposphene in the last dorsal vertebra, incipient concavity on the cranial articular surface of cranial caudal vertebrae (also present in averostran theropods), constant length of caudal vertebrae along the tail (also in *Dilophosaurus*), and vertical ridge above the acetabular crest on the ilium (convergent in the tetanuran taxa *Piatnitzkysaurus*, Megalosauridae, and Tyrannosauridae; Rauhut, 2003).

LOPHOSTROPHEUS AIRELENSIS
(Cuny and Galton, 1993), comb. nov.

Halticosaurus sp.: Larsonneur and Lapparent, 1966:108; figs. 3–4; pl. 1-2; Lapparent, 1967:8 (cite)
Theropoda indet.: Weishampel, 1990:77 (cite)
Liliensternus airelensis: Cuny and Galton, 1993:261, figs 2–11, 12a, 13a, 14a (new species)

Diagnosis—The same as for the genus.

DISCUSSION

The earliest record of the coelophysoid lineage comes from the uppermost Carnian, as documented by the North American taxon "*Camposaurus*" (Hunt et al., 1998). During the Norian a wide radiation of coelophysoids is well documented around the world, with well known taxa that include *Gojirasaurus* (Carpenter, 1997), *Zupaysaurus* (Carrano and Sampson, 2004; Ezcurra and Novas, 2005), *C. bauri* (Colbert, 1989), *Liliensternus* (von Huene, 1934), and *Procompsognathus* (Fraas, 1913). Furthermore, *Lophostropheus airelensis* comes from a French outcrop in the Moon Airel Formation close in age to the Triassic-Jurassic boundary (TJB). The uppermost Rhaetian is characterized by a worldwide decline of the coelophysoid theropod fossil record, a condition that clearly contrasts with the numerous coelophysoid taxa that constitute part of the Norian tetrapod terrestrial faunas. *Lophostropheus airelensis* is indeed the only well-known theropod found so close to the Triassic/Jurassic boundary.

The available fossil record indicates that the Norian radiation of coelophysoids was approximately concomitant with the diversification of prosauropods (e.g., *Plateosaurus*, *Sellosaurus*, *Melanorosaurus*, *Riojasaurus*, *Coloradisaurus*, *Mussaurus*, *Lessemsaurus*, *Ruehleia*; von Meyer, 1837; von Huene, 1907–8; Haughton, 1924; Bonaparte, 1969; Bonaparte, 1978; Bonaparte and

Vince, 1979; Bonaparte, 1999; Galton, 2001) in the same geographical area. On the other hand, a decline of diversity of those groups is recorded in the Rhaetian sedimentary rocks (see Carrano and Sampson, 2004; Galton and Upchurch, 2004). This sharp decline of both lineages in the Rhaetian fossil record and the later resurgence of the diversity of both prosauropod (e.g., *Massospondylus*, *Anchisaurus*, *"Gyposaurus,"* *Yimenosaurus*, *Melanorosaurus thabanensis*, *Jingshanosaurus*; Owen, 1854; Marsh, 1885; Young, 1941; Bai et al., 1990; Gauffre, 1993; Zhang and Yang, 1995) and early neotheropod taxa, including coelophysoids (e.g., *Podokesaurus*, *Sarcosaurus*, *Segisaurus*, *C. rhodesiensis*, *Dilophosaurus*, *"S." kayentakatae*, Shake-N-Bake taxon; Talbot, 1911; von Huene, 1932; Camp, 1936; Raath, 1969; Welles, 1984; Tykoski, 1998), in the Early Jurassic outcrops (depicting a probable second radiation of dinosaurian taxa) may suggest the presence of a large number of missing data (Lazarus taxa) during the Rhaetian. This gap may be an artifact, a consequence of the relatively short duration of the Rhaetian (~4 MY) (in comparison with the Norian (~ 11 MY)) or/and poor preservation in the formations of this age. However, Benton (1991) pointed out that one should not always assume that a gap in the fossil record is just an artifact. Sedimentary rocks of Rhaetian age are well represented world-wide, mainly in Europe (e.g., Lower Höganäs Formation (Sweden), Rhaetian Beds of Wales, Westbury Formation (England), Grès de I'Infralias (France); sensu Benton, 1994; Weishampel et al., 2004). Norian outcrops are also well represented worldwide, but Rhaetian dinosaur taxa are not as widely represented as in the Norian. Recently, Lucas and Tanner (2005) pointed out that several non-dinosauriform tetrapod family-level lineages common during the Norian are not present in Rhaetian formations (e.g., Proganochelyidae, Kuehneosauridae, Pachystropheidae, Trilophosauridae, Stagonolepididae, Rauisuchidae, Ornithosuchidae, Traversodontidae; sensu Lucas, 1994; Lucas and Tanner, 2005). This decline in Rhaetian biodiversity could be highlighted by the probable disappearance of typical Carnian and Norian dinosauriform lineages such as the non-dinosaurian Dinosauriformes (*Silesaurus* [late Carnian]; *Eucoelophysis* [early Norian], sensu Novas and Ezcurra, 2005; Ezcurra, in review) and the pre-Rhaetian basal saurischians (e.g., herrerasaurians [Carnian-early Norian], *Guaibasaurus* [Norian]; Novas, 1997; Bonaparte et al., 1999) (Novas and Ezcurra, 2005). The recent suggestion of Lucas and Tanner (2005) of pre-Triassic-Jurassic boundary high extinction rates, that would minimize the supposed effects of the end-Triassic mass extinction as a single event at the TJB, seems also to be supported by the dinosauriform fossil record available at the moment. Furthermore, the high extinction rates are also accompanied by considerably low origination rates. In this regard, following Lucas and Tanners hypothesis (2005), the fall of diversity and number of Rhaetian tetrapod taxa may reflect a mass extinction stage (Bakker, 1977), reflecting a biotic stress, leading to low origination rates. Future discoveries of new materials close to the Triassic-Jurassic boundary would get light on that problem, and reveal whether the coelophysoid lineage radiated actually twice during its evolutionary history or whether its decline near the TJB is an artifact.

CONCLUSIONS

The comparisons carried out previously, as well as the cladistic analysis performed, do not support a close relationship between the Airel theropod and *L. liliensterni*. In fact, the tree obtained here depicted a closer relationship of the Airel theropod (*Lophostropheus*) to coelophysids (*Coelophysis* + *"Syntarsus"*) than to *Liliensternus*.

In sum, *Lophostropheus* represents a basal coelophysoid theropod, with morphological novelties on its axial anatomy (e.g., convex cranial articular surface of cranial cervical vertebrae, incipient concavity of cranial articular surface of cranial caudal vertebrae) reminiscent to averostran attributes. This taxon constitutes also one of the unique world-wide dinosaurian taxon documented from an outcrop close to the Triassic-Jurassic boundary, filling a temporal gap in the evolutionary history of the coelophysoid lineage.

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APPENDIX 1.   List and description of characters used in the present phylogenetic analyses. Characters are treated as unordered unless specified otherwise and original citations and subsequent modifications are detailed.

(1) Skull length (premaxilla-quadrate condyle) versus skull height (articular condyle of quadrate to dorsalmost edge of parietal): less than 3 times (0); equal or more than 3 times (1). (Forster, 1999; Sereno, 1999; Tykoski, 2005)

(2) Angle between rostral margin and alveolar margin of premaxilla: equal or more than 70° (0); less than 70° (1); equal or less than 40° (2). (modified from Rauhut, 2003)

(3) Height:length ratio of premaxilla below external naris: 0.5–1.25 (0); < 0.5 (1); > 1.25 (2). (Holtz, 1994, 2000)

(4) Main body of the premaxilla: lacks or shows few neurovascular foramina (0); laterally perforated by a moderate sized pit at the base of the premaxillary nasal process above the level of the second maxillary alveolus (1); laterally perforated by multiple neurovascular foramina (2). (reversed and modified from Tykoski, 1998; Tykoski and Rowe, 2004; ordered)

(5) Premaxilla nasal process: less than or equal to half of the rostrodorsal narial border (0); forms more than half the rostrodorsal narial border (1). (reversed from Holtz, 2000)

(6) Ventral process at the caudal end of premaxillary body: absent (0); present (1). (Rauhut, 2003)

(7) Serrations on premaxillary teeth: not substantially different from other teeth (0); serrations or denticles on premaxillary teeth greatly reduced or absent (1). (Tykoski, 1998)

(8) Premaxilla union to maxilla: firmly attached (0); loosely attached with the capability of passive kinesis, without a terminal rosette on the premaxilla (1). (Tykoski, 1998; Sereno 1999)

(9) Sub-narial foramen: present (0); absent (1). (Gauthier, 1986; Sereno et al., 1993)

(10) Subnarial gap: absent (0); present (1). (Gauthier, 1986)

(11) Constriction between articulated premaxillae and maxillae: absent (0); present (1). (Rauhut, 2003)

(12) Angle between the dorsoventral margin of the maxilla and the alveolar margin: equal or more than 75° (0); less than 75° (1). (Ezcurra and Novas, in press)

(13) Rostral process of maxilla: between 10% and 25% of total maxilla length (0); equal or less than 10% of total maxilla length (1); equal or more than 25% or total maxilla length (2). (Tykoski, 2005)

(14) Ventral border of rostral tip of maxilla: relatively straight, contacts ventral edge of premaxilla, and tooth row continuous (0); ventral border of rostral-most maxilla sharply curves dorsally to meet the maxillary process of the premaxilla (1). (Rowe, 1989; Tykoski, 1998)

(15) Rostromedial process of maxilla: dorsoventrally deep and short to moderate in length, being slightly visible in lateral view (0); rostrocaudally long and dorsoventrally low, being well rostrally extended and far visible in lateral view (1). (Ezcurra and Novas, in press)

(16) Medial surface of rostromedial process of maxilla: smooth (0); bears longitudinal ridges (1). (Sereno et al., 1998)

(17) Antorbital fossa, rostral end, in late ontogeny: caudal to caudal end of external naris (0); ventral to caudal end of external naris (1). (modified from Sereno, 1999)

(18) Rostral margin of maxillary antorbital fossa: rounded or pointed (0); squared (1). (Rauhut, 2003)

(19) Promaxillary foramen: absent (0); present (1). (Carpenter, 1992)

(20) Lateral surface of maxillary antorbital fossa at the base of the ascending process: smooth (0); with deep, large, and subcircular or oval blind pocket/s (1). (modified from Carrano et al., 2002)

(21) Ventral rim of the antorbital fossa: parallel to tooth row (0); ventrally sloped in its caudal part (1). (Sereno, 1986)

(22) Dorsoventrally compressed ridge on lateral surface of maxilla, forming the ventral border of the antorbital fossa: absent (0); present (1). (Rowe and Gauthier, 1990)

(23) Maximum length of internal antorbital fenestra: less than 25% of skull premaxilla-quadrate length (0); 25% or more than maximum skull premaxilla-quadrate length (1). (Rowe, 1989)

(24) Ascending process of the maxilla: confluent with rostral rim of maxillary body and gently sloping caudolaterally (0); offset from the rostral rim of maxillary body, with rostral projection of maxillary body shorter than high (1); offset from rostral rim of maxillary body, with rostral projection of maxillary body as long as high or longer (2). (Sereno et al., 1996; Rauhut, 2003; ordered)

(25) Ascending process of maxilla angulation: between 35° and 50° (0); less than 35° (1); more than 50° (2). (Tykoski, 2005)

(26) Number of maxillary tooth in the adulthood: 18 or less (0); more than 18 (1). (Ezcurra and Novas, in press)

(27) Maxillary tooth row caudal extension: extends caudally to approximately half the length of the orbit (0); completely antorbital, tooth row ends rostral to the vertical strut of the lacrimal (1). (Gauthier, 1986; Rauhut, 2003)

(28) Pronounced lateral rims of the nasals and dorsolateral margins of lacrimal: absent (0); conforming a low and laterally projected pair of crests (1). (modified from Rauhut, 2003)

(29) Nasal fenestrae: absent (0); present (1). (Rowe and Gauthier, 1990)

(30) Lacrimal rostral ramus: subequal or shorter than the ventral ramus in length and width (0); longer than the ventral ramus (1); absent (2). (modified from Sereno et al., 1996)

(31) Lateral lamina of bone in the lacrimal: almost covering most of the bone (0); with no interruption of the lacrimal antorbital fossa and restricted to the caudal margin of the ventral ramus along its dorsoventral extension (1); only interrupting the lacrimal antorbital fossa near the proximal end of the ventral ramus and ventrally restricted to caudal margin of the ventral ramus (2). (Ezcurra and Novas, in press; ordered)

(32) Lacrimal antorbital pneumatic recess (into central body of lacrimal): absent (0); present (1). (Molnar et al., 1990; Novas, 1992)

(33) Lateral ridge longitudinally traversing the rostral and caudal processes of the jugal: absent (0); present (1). (Sereno and Novas, 1993; Tykoski, 1998; Tykoski and Rowe, 2004)

(34) Rostral process of jugal: contributes to the caudoventral margin of the internal antorbital fenestra (0); excluded from the internal antorbital fenestra (1); expressed at the rim of the internal antorbital fenestra and with a distinct process that extends rostrally underneath it (2). (Holtz, 1994; Rauhut, 2003)

(35) Sublacrimal part of jugal: tapering (0); bluntly squared rostrally (1); expanded (2). (modified from Rauhut, 2003; ordered)

(36) Angle between ascending process and caudal process of jugal: right or obtuse (0); acute, with an ascending process strongly dorsocaudally oriented (1). (Ezcurra and Novas, in press)

(37) Orbit length: subequal to or longer than internal antorbital fenestra length (0); shorter than internal antorbital fenestra length (1). (Holtz, 2000)

(38) Frontal process of the postorbital: sharply upturned (0); at about the same level as or slightly higher than the squamosal process, resulting in a T-shaped postorbital (1). (Currie, 1995)

(39) Quadratojugal process of the squamosal: broad, and usually somewhat expanded (0); tapering (1). (reversed from Rauhut, 2003)

(40) Quadrate foramen: developed as a distinct opening between the quadrate and quadratojugal (0); almost entirely enclosed in the quadrate (1); absent (2). (Holtz, 2000; Rauhut, 2003)

(41) Infratemporal fenestra shape: rostrocaudally wide (0); strongly rostrocaudally compressed (1); strongly widen, resulting in its length being 1,5 times the length of the orbit (2). (modified from Rauhut, 2003)

(42) Ventral border of infratemporal fenestra in lateral view: mostly constituted by the jugal or equal participation of both jugal and quadratojugal (0); mostly constituted by the quadratojugal (1). (Ezcurra and Novas, in press)

(43) Prefrontal: widely exposed on the rostrodorsal rim of the orbit in lateral view with a slender ventral process along the mediocaudal rim of the lacrimal (0); reduced, with little participation on the rostrodorsal rim of the orbit in lateral view, being displaced caudally and/or medially, ventral process absent (1). (modified from Rauhut, 2003)

(44) Frontal: elongated triangular (0); square shaped (1). (reversed from Holtz, 1994)

(45) Supratemporal fossa, postorbital participation: present (0); absent (1). (Sereno, 1999)

(46) Ventral process of squamosal: tapering (0); broad, and usually somewhat expanded (1). (Rauhut, 2003)

(47) Squamosal caudal process: short and not well caudally extended (0); strongly caudally extended and longer than the rostral process, sometimes exceeding the caudal level of the quadrate condyle in lateral view (1). (Ezcurra and Novas, in press)

(48) Squamosal-quadratojugal contact: present, but small contact between the bones (0); present, broad contact (1); absent (2). (reversed from Holtz, 1994)

(49) Dorsal ramus of the quadratojugal: longer than the rostral ramus (0); of the same length, or shorter, than the rostral ramus (1). (Sereno, 1986; Langer, 2004)

(50) Caudal curvature of the proximal end of quadrate: absent or slight, proximal half of quadrate almost straight (0); present, with quadrate head caudodorsally oriented (1). (Ezcurra and Novas, in press)

(51) Basisphenoid between basal tubera and basipterygoid processes: approximately as wide as long, or wider (0); significantly elongated, at least 1,5 times longer than wide (1). (Rauhut, 2003)

(52) Lateral surface of basisphenoid: penetrated by a small foramen for passage of internal carotid, below the crista prootica (0); penetrated by a large pneumatic foramen, partially covered by the crista prootica (1). (Tykoski, 1998)

(53) Basisphenoid fontanelle: present (0); absent (1). (Sereno, 1999)

(54) Ectopterygoid: slender, without ventral fossa (0); expanded, with a deep ventral depression medially (1); as above, but with a deep groove excavated into the body of the ectopterygoid from the medial side (2). (Gauthier, 1986; Sereno et al., 1996; Rauhut, 2003)

(55) Exit of nerve V in lateral view: positioned at the level of the caudal half of the basisphenoid (0); positioned at the level of the rostral half of the basisphenoid (1). (Ezcurra and Novas, in press)

(56) Exit of nerves X and XI: laterally through the jugular foramen (0); caudally through a foramen lateral to the exit of the nerve XII and the occipital condyle (1). (Chatterjee, 1993; Rauhut, 2003)

(57) Exit of mid-cerebral vein: included in trigeminal foramen (0); vein exits braincase through a separate foramen rostrodorsal to the trigeminal foramen (1). (Rauhut, 2003)

(58) Mandibular joint: approximately straight below the quadrate head (0); significantly caudal to the quadrate head (1). (Rauhut, 2003)

(59) Ventral rim of the basis of the paroccipital processes: above or level with the dorsal border of the occipital condyle (0); situated at mid-height of occipital condyle or lower (1). (Rauhut, 2003)

(60) Occipital condyle size: subequal or smaller than foramen magnum diameter (0); larger than foramen magnum diameter (1). (Ezcurra and Novas, in press)

(61) Rostral end of dentary dorsoventrally expanded: absent (0); present (1). (Gauthier, 1986)

(62) Mediolateral width of anterior end of dentary: equal to that of caudal part (0); expanded (1). (Carrano et al., 2005)

(63) Caudoventral process of dentary: extends further caudally than caudodorsal process (0); subequal in length to caudodorsal process (1). (Sereno, 1999)

(64) Caudal end of splenial: straight (0); forked (1). (Sereno et al., 1996)

(65) Angular reaches caudal end of mandible, blocking surangular from ventral margin of the jaw in lateral view: absent (0); present (1). (Tykoski, 2005)

(66) Retroarticular process of the mandible: narrow and rod-like (0);

broad with muscle scar (1). (Sereno et al., 1996; Harris, 1998; Rauhut, 2003)

(67) Enlarged fang-like mesial dentary teeth: absent (0); present (1). (Gauthier, 1986)

(68) Dentary tooth count: 18 or less (0); 20–29 (1); more than 29 (2). (modified from Russell and Dong, 1993)

(69) Postaxial centra pneumatization: not pneumatized (0); pneumatized by a single pair of fossae, that does not penetrate into the centra (1); pneumatized by two pair of fossae, that does not penetrate into the centra (2); pneumatized by two pair of foramina, that penetrate into the centra resulting in a pneumatic camerae within it (3); pneumatized by a single pair of foramina, that penetrate into the centra resulting in a pneumatic camerae within it (4). (modified from Gauthier, 1986 and Britt, 1993; ordered)

(70) Axial intercentrum length-axial centrum length ratio: 25–40% (0); 40–70% (1). (Sereno 1999)

(71) Axial neural spine: broad and blade-shaped (0); laterally invaginated and craniocaudally reduced and rod-like (1). (modified from Molnar et al., 1990)

(72) Axial diapophysis: absent (0); present (1). (reversed from Rowe and Gauthier, 1990)

(73) Axial parapophysis: strongly reduced or absent (0); well developed (1). (reversed from Rowe and Gauthier, 1990)

(74) Axial pleurocoels: absent (0); present (1). (note: can substitute "pneumatic foramen" or "fossa" for "pleurocoel" (Tykoski, 1998)) (reversed from Rowe and Gauthier, 1990)

(75) Cranial articular facet of cranial cervical vertebrae: approximately as high as wide or higher (0); significantly wider than high (1). (Gauthier, 1986; Rauhut, 2003)

(76) Cranial face of cervical and cranial dorsals: amphiplatyan or amphicoelous (0); slightly convex (1); strongly convex, having ball-like articulation (2). (Gauthier, 1986; ordered)

(77) Mid-cervical (C3-C6) centrum proportions: equal or less than 3 times the height of the cranial articular surface (0); more than 3 times the height of the cranial articular surface (1); more than 4 times the height of the cranial articular surface (2). (Sereno, 1999; ordered)

(78) Lamina protracted from the diapophyses in cervical vertebrae: absent (0); postzygodiapophyseal lamina, reaches the postzygapophyses (1); centrodiapophyseal lamina, reaches the dorsocaudal corner of the centrum (2).

(79) Ventral lamina, from the diapophyses to the ventral rim of the caudal end of the vertebral centra in cervical centra: absent (0); present (1). (Cuny and Galton, 1993; Rauhut, 2003)

(80) Transverse process shape of caudal cervical and dorsal vertebrae: subrectangular (0); subtriangular (1). (Sereno, 1999)

(81) Cranial cervical epipophyses: low and blunt (0); long, thin and not well developed (1); long and well developed (2); craniocaudally lengthen and extremely developed (3). (Novas, 1992; ordered)

(82) Postaxial cervical neural spines: dorsoventrally tall (0); extremely low (1). (Russell and Dong 1993)

(83) Cranial and mid-dorsal centrum length: subequal to centrum height (0); more than 2 times centrum height (1). (modified from Sereno, 1999)

(84) Transverse processes of the dorsal vertebrae: craniocaudally narrow (0); broad, extending to lateral margin of the prezygapophyses (1). (Rowe and Gauthier, 1990)

(85) Caudal dorsal vertebrae: strongly shortened, centrum length less than 1.33 times the height of the cranial articular surface (0); relatively short, centrum length equal or more than 1.33 times the height of the cranial articular surface (1); significantly elongated, centrum length equal or more than 2 times the height of the cranial articular surface (2). (Rauhut, 2003; Tykoski, 2005; ordered)

(86) Neural spines of caudal dorsals: broadly rectangular and approximately as high as long (0); high rectangular, significantly higher than long (1). (Rauhut, 2003)

(87) Fusion of sacral centra: do not fuse, or they remain distinct from one another (0); extensively fused to one another, obliterating all sutures by adulthood (1). (Tykoski, 1998)

(88) Sacral ribs and ilia: remain separate throughout ontogeny (0); fuse to medial wall of ilia late in ontogeny (1). (Tykoski, 1998)

(89) Sacral transverse processes in the adulthood: slender and well separated (0); very massive and strongly expanded (1); forming a more or less continuous sheet in ventral or dorsal view (2). (Rowe and Gauthier, 1990; reversed from Rauhut, 2003)

(90) Ventral surface of caudal vertebrae: smooth or weakly grooved longitudinally (0); at least some caudal vertebrae with narrow, sharply defined, longitudinal, ventral groove (1). (Rowe and Gauthier, 1990)

(91) Distal caudal centrum length: less than four times centrum height (0); more than four times centrum height (1). (modified from Sereno 1999)

(92) Prezygapophyses of distal caudal vertebrae: not elongated (0); strongly elongated, overhanging at least one-quarter of the length of the preceding centrum (1). (Gauthier, 1986; Rauhut, 2003)

(93) Cervical ribs: stout, and less than three centra long (0); very thin, and extend caudally at least three centra behind their vertebra of origin (1). (Holtz, 1994)

(94) Distal expansion of scapular blade: marked as a fan-shaped expansion (0); narrow with subparallel margins or strap-like (1). (Currie and Zhao, 1993)

(95) Shape of craniodorsal corner of distal scapular blade: rounded (0); acuminate (1). (Carrano et al., 2005)

(96) Spacing between ventral glenoid and caudoventral coracoid process (= sternal process): more than dorsoventral depth of glenoid (0); less than dorsoventral depth of glenoid (1). (Carrano et al., 2005)

(97) Caudoventral process (= sternal process) of the coracoid: rounded and not projected beyond glenoid fossa (0); tapering and projected beyond the caudal margin of the glenoid fossa (1). (Sereno et al., 1996)

(98) Humerus: sigmoid in lateral view (0); straight in lateral view (1). (Holtz, 1994)

(99) Humeral shaft torsion of proximal and distal ends: absent (0); present (1). (Holtz, 2000)

(100) Metacarpal IV: present with phalanges but lacking ungual (0); present but lacking phalanges (1); absent (2). (Gauthier, 1986; Holtz, 2000; ordered)

(101) Pubic plate: solid below obturator foramen (0); perforated by a large circular fenestra below the obturator foramen (1). (Rowe and Gauthier, 1990)

(102) Pelvic girdle: separate elements throughout ontogeny (0); fused together by late ontogeny (1). (Rowe and Gauthier, 1990)

(103) Lateral surface of caudal end of ilium: smooth (0); distinct caudal rim on ilium for M. Iliofibularis (1). (modified from Rowe and Gauthier, 1990)

(104) Dorsal margin of iliac blade: straight (0); strongly convex (1).

(105) Preacetabular process strongly cranioventrally oriented, thus it closely approaches the iliac pubic peduncle at the base of the process: absent (0); present (1).

(106) Pronounced ventral hook on cranial expansion of ilium: absent (0); present (1). (Gauthier, 1986; Rauhut, 2003)

(107) Caudal margin of ilium: squared or rounded off when viewed laterally (0); postacetabular process caudal margin concave in lateral view (1). (Sereno et al., 1994)

(108) Supraacetabular crest and ventrolateral margin of the postacetabular blade continuity: not continuous (0); continuous by a weakly developed ridge (1); continuous by a well developed ridge, with non-distinct notch between both structures (2).

(109) Brevis fossa: narrow and with subparallel margins (0); very strongly caudally expanded (1). (Molnar et al., 1990; Rauhut, 2003)

(110) Ischial obturator notch (or foramen): absent (0); present (1). (Gauthier, 1986; Sereno et al., 1994)

(111) Ischial mid-shaft cross-sectional shape (paired): oval (0); heart-shaped (1); subrectangular (2). (Sereno, 1999)

(112) Ischium length: at least three-quarters the length of pubis (0); ischium two-thirds or less the length of the pubis (1). (Gauthier, 1986)

(113) Distal end of ischium: slightly expanded or not at all (0); craniocaudal expansion of distal tip of ischium forms large ischial boot (1). (Tykoski, 1998)

(114) Articulation facet of pubic penduncle of ilium: facing more ventrally than cranially, and without pronounced kink (0); with pronounced kink and cranial part facing almost entirely cranially (1). (Rauhut, 2003)

(115) Pubic shaft: strongly caudally bowed (0); nearly straight (1). (modified from Sereno, 1999)

(116) Distal expansion of the pubis: non-expanded or slightly expanded

(0); strongly expanded, resulting in a pubic foot (1). (Gauthier, 1986; reversed from Sereno, 1999)
(117) Pubic apron: completely closed (0); with medial opening distally above the pubic foot (1). (Rauhut, 1995; 2003)
(118) Femoral dimorphism: absent (0); present, expressed in muscle scars, attachments, and processes (robust versus gracile morphs) (1). (Rowe and Gauthier, 1990)
(119) Proximal surface of femur: with a transversely extended groove (0); smooth (1). (Ezcurra, in review)
(120) Caudal surface of proximal femur: smooth (0); marked by an obturator ridge in robust individuals (1). (Raath, 1977)
(121) Cranial trochanter: absent or poorly developed (0); spike-like or pyramidal prominence (1); broadened ("wing like") (2). (Rauhut, 2003; ordered)
(122) Placement of the cranial trochanter: at distal end of femoral head (0); more proximally placed, but below the greater trochanter (1). (Gauthier, 1986; Rauhut, 2003)
(123) Tibiofibular crest of distal femur: smoothly continuous with fibular condyle (0); sharply demarcated from fibular condyle by a sulcus or concavity (1). (Rowe, 1989)
(124) Femoral popliteal fossa in adults: smooth (0); transversed by infrapopliteal ridge between tibial condyle and tibiofibular crest (1). (Tykoski, 1998)
(125) Craniomedial crest on distal femur: absent (0); proximal to condyles, blend smoothly together (1); an hypertrophied craniomedial crest on the distal femur separates cranial and medial surfaces of femur (2). (Holtz, 1994)
(126) Cranial surface of distal femur: strongly convex (0); cranial surface planar or slightly concave, showing a poorly developed cranial intercondylar groove (1); strongly concave, showing an incipient and deep cranial intercondylar groove (2). (modified from Rauhut, 2003; ordered)
(127) Ridge on lateral side of tibia for connection with fibula: absent (0); present, extending from the proximal articular surface distally (1); present, clearly separated from proximal articular surface (2). (Gauthier, 1986; Rauhut, 2003; ordered)
(128) Distal tibial lateral malleolus: lobe-shaped (0); polygonal-shaped (1). (Sereno, 1999)
(129) Development of lateral malleolus in distal tibia: partially caudally overlaps the distal end of fibula and calcaneum (0); nearly completely overlaps the distal end of fibula and calcaneum (1). (modified from Sereno et al., 1994)
(130) Distal articular surface of tibia: subrectangular in outline and slightly wider transversely than craniocaudally (0); subrectangular with small lateral process (1); narrow triangular in outline and strongly mediolaterally expanded (2). (Rauhut, 2003; ordered)
(131) Facet for the reception of the ascending process of the astragalus in the distal tibia: craniocaudally as well as transversely well developed (0); subtriangular, not well developed cranially (1); subrectangular, cranially poorly developed (2); nearly absent (3). (Ezcurra and Novas, in press; ordered)
(132) Ridge on medial side of proximal end of fibula, that runs anterodistally from the posteroproximal end: absent (0); present (1). (Rowe and Gauthier, 1990)
(133) Medial surface of proximal fibula: flat or slaghtly concave (0); caudodistally opening sulcus on medial surface of proximal fibula (1). (Rowe and Gauthier, 1990)
(134) Astragalus and calcaneum: remain separate elements throughout ontogeny (0); fused to each other by later stages of ontogeny (1). (Welles and Long, 1974)
(135) Ascending process of astragalus: lower than astragalar body (0); higher than the astragalar body (1). (Welles and Long, 1974)
(136) Astragalar ascending process thickness: wedge-shaped, dorsal margin inserting into tibia (0); low plate, 2–5 times taller than thick craniocaudally at midpoint (1). (Gauthier 1986; modified from Sereno et al., 2004; ordered)
(137) Deep fossa at the base of the ascending process of the astragalus: absent (0); present (1). (Ezcurra and Novas, in press)
(138) Horizontal groove across cranial face of astragalar condyles: absent (0); present (1). (Welles and Long, 1974)
(139) Tibial facet of calcaneum: with no participation of the tibial facet (0); with small participation of the tibial facet on the caudomedial-most corner of the bone (1); with large tibial facet, reaching the lateral margin of the bone (2). (modified from Rauhut, 2003; ordered)

(140) Proximal tarsals: remain separate from tibia throughout ontogeny (0); astragalocalcaneum fuses to distal end of tibia in adults to create a functional tibiotarsus (1). (Rowe and Gauthier, 1990)
(141) Distal tarsal III: remain a separate element throughout life (0); fused to the proximal end of metatarsal III (1). (Rowe and Gauthier, 1990)
(142) Metatarsal I: contacts the ankle joint (0); reduced, elongated splint-like, attached to Mt II and not reaching the ankle joint (1); broadly triangular and attached to the distal part of Mt II (2). (Gauthier, 1986; Rauhut, 2003; ordered)
(143) Metatarsals II and III: separate (0); fusion of proximal ends of metatarsals II and III to each other (1). (Rowe and Gauthier, 1990)
(144) Proximal end of metatarsal III position: does not back to the ventral side of metatarsals II and IV (0); backs metatarsals II and IV ventrally, resulting in a T-shaped proximal profile ("antarctometatarsus") (1). (Carrano et al., 2002; Tykoski, 2005)
(145) Metatarsal V: with rounded distal articular facet (0); strongly reduced and lacking distal articular facet (1); short, without articular surface, transversely flattened and cranially bowed distally (2). (Gauthier, 1986; Rauhut, 2003; ordered)

APPENDIX 2. Characters-states codification used in the first data matrix, under the following distribution (0, plesiomorphic state; 1, 2, 3, etc, apomorphic state; ?, non-preserved, unknown, or indeterminate).

Eoraptor lunensis
01010000010011??01001101000000001010000100000000001???????00??00?00?0000100000000000?000000000??00100000000100?000100??0000?000000?0000000?000000

Herrerasaurus ischigualastensis
102000?00000000?0000000000000000012200000000010010000????100001?1000000110000000000010[01]100??1001000000000000000001000100000000000000000000000000

Allosaurus fragilis
0002000000000000100100001001100210120110100110101100002111111001101004111111200002000010000010100101200000101010000110102100122012201011012002012

Baryonyx walkeri
?212?010000121010?????0?????00211?2??1?0??11????0000?11?1111100??124?1111120000200001000????1?0111??00001010??000001??0?100?220???0?0????2??????

Carnotaurus sastrei
00220000100010??00100001200002000220110220110100[02]11???????1110000010030011111000031000111200??0100110101001112?00?1?1110?02011211??????2????????????

Ceratosaurus nasicornis
00220000000000010011000100000021010011022011010101000000???11100000??03111111[01]0000300101112100?1001100100001?20000100111?0200121100?2111[01]10121??01?

Coelophysis bauri
121101111111111?110111011010110 11?1101?1100101 2011?1????00?101?00?120000000221111112011211 010 1110101110001[12]1011 0100010110[01][01]101101 11111001001 11111

Coelophysis rhodesiensis
1211011111111 1101 101111110101101?1110101100101201111 10000001?100011200000?02??111112011211110101010 111000121021010001011 01?1011011 11100101111111

Dilophosaurus wetherilli
1212111111102111001000100 0[01]?0[01]?002201100000?0102 10000?111001100101020000100000100111?1?111?0001010??0000110 00?010011101010111001101?00100??1002

Liliensternus liliensterni
????????????0??1???1?11?????????? 0?1?000????1???0???1???0??11????111 ????00110110110 11????111?0?1001 ???0?00010?1101100?10100110 1101101100100??? 01?

Lophostropheus airelensis
??
?????2??????11[12]1?11?11????11?????????????00?2?????1?????????
?????????????????????

Syntarsus kayentakatae
12111?111111111011101111010111201110110011101110011111110?100100
?10112?0000?0220111????1??1??10111??0?1??0????0210?000?11101120
1101211100101111111

Torvosaurus tanneri
0102?0?000002001?01000020???00110?2011???????????0???????1??00?
?????4?????12000020001?0?0???1???11?0000010[12]00?000100??????
??201220101101200?01?

APPENDIX 3. Characters supporting each node (ambiguous characters in italic) of the tree result of the analysis of the first data matrix (bootstrap value is indicated after the clade) (Fig. 6A).

—Neotheropoda (94%) (node 2): 19 (1), 31 (12), 37 (1), 48 (1), 69 (2), 81 (1), 121 (1), 125 (1), 127 (1), 130 (1), 131 (1), 133 (1), 142 (1), 145 (1).
   ACCTRAN: 4 (2), 28 (1), *38 (1)*, 60 (1), 75 (1), 87 (1), 89 (2), 102 (1), 107 (1), 115 (0), 117 (1), 126 (1), 134 (1), 140 (1), 144 (1).
   DELTRAN: none.

—Averostra (92%) (node 3): *43 (0)*, 44 (1), 59 (1), 66 (1), 69 (3), 74 (1), 76 *(1)*, 81 (2), 98 (1), 106 (1), 121 (2), *131 (2)*, 136 (1), 138 (1), 139 (2).
   ACCTRAN: *1 (0)*, *31 (2)*, 32 (1), 40 (1), *65 (0)*, 70 (1), 71 (1), 100 (1), 130 (2), 135 (1), 142 (2), *145 (2)*.
   DELTRAN: *4 (2)*, *38 (1)*, *43 (1)*, *58 (1)*, *60 (1)*, *73 (1)*, *75 (1)*, *94 (1)*, *117 (1)*, *126 (1)*, *144 (1)*.

—Ceratosauria (92%) (node 4): *2 (0)*, *3 (2)*, 40 (2), 41 (2), 81 (3), *99 (0)*, *108* (2), 113 (1), *116 (1)*, *124 (1)*, *125 (2)*.
   ACCTRAN: *28 (0)*, 54 (0), *92 (0)*, *132 (1)*.
   DELTRAN: *87 (1)*, *88 (1)*, *89 (2)*, *102 (1)*.

—Tetanurae (79%) (node 5): 69 (4), 76 (2), *89 (0)*, 122 (1), 126 (2), 127 (2).
   ACCTRAN: *13 (2)*, 27 (1), 54 (2), *87 (0)*, *88 (0)*, 100 (2), *102 (0)*, *107 (0)*, 129 (1), *134 (0)*, *140 (0)*.
   DELTRAN: *32 (1)*, *71 (1)*.

—Coelophysoidea (96%) (node 7): *2 (2)*, 6 (1), *7 (1)*, 8 (1), *9 (1)*, 11 (1), 15 (1), 23 (1), *61 (1)*, *67 (1)*, 72 (0), *84 (1)*, 85 (1), *90 (1)*, 91 (1), 114 (1), *118 (1)*, 137 (1).
   ACCTRAN: 5 (1), *10 (1)*, *14 (1)*, 30 (1), 48 (2), *58 (0)*, *62 (1)*, *73 (0)*, 93 (1), *94 (0)*, *101 (0)*, 112 (1), *115 (0)*, *123 (1)*, 141 (1).
   DELTRAN: *1 (1)*, *88 (1)*, *92 (1)*.

—*Liliensternus* + *Lophostropheus* + Coelophysidae (97%) (node 8): *21 (1)*, *22 (1)*, *35 (1)*, 68 (1), 77 (1), 78 (1), 79 (1), *82 (1)*, 96 (1), 111 (1), *124 (1)*, 128 (1).
   ACCTRAN: *4 (1)*, 16 (0), 17 (1), *18 (1)*, 26 (1), *38 (0)*, *41 (1)*, 42 (1), 45 (1), 47 (1), *49 (0)*, 51 (1), 52 (1), 53 (1), 56 (0), 57 (0), *60 (0)*, *75 (0)*, *86 (0)*, 95 (1), *117 (0)*, *126 (0)*.
   DELTRAN: 112 (1), *134 (1)*, *144 (1)*.

—*Lophostropheus* + Coelophysidae (60%) (node 9): *108 (2)*.
   ACCTRAN: *12 (1)*, *33 (1)*, *50 (1)*, *62 (0)*, 78 (2), 80 (1), 83 (1), 103 (1), 109 (1), 111 (2), 120 (1), *132 (1)*, 139 (1), 143 (1).
   DELTRAN: none.

—*Coelophysidae* (66%) (node 10): 77 (2).
   ACCTRAN: 85 (2).
   DELTRAN: *12 (1)*, 16 (0), 17 (1), *18 (1)*, 26 (1), *28 (1)*, 30 (1), *33 (1)*, *41 (1)*, 42 (1), 45 (1), 47 (1), *49 (0)*, *50 (0)*, 51 (1), 52 (1), 53 (1), 56 (0), 78 (2), 80 (1), *87 (1)*, 93 (1), 95 (1), *102 (1)*, *115 (0)*, 120 (1), *123 (1)*, *132 (1)*, *140 (1)*, 141 (1), 143 (1).

—*Coelophysis* (86%) (node 11): *19 (0)*, *20 (1)*, 25 (1), *36 (1)*, 39 (1), *46 (0)*, *63 (1)*, 119 (0).
   ACCTRAN: *5 (0)*, 55 (0), *65 (0)*.
   DELTRAN: *48 (2)*, 83 (1), 85 (2), *86 (0)*, *89 (2)*, *101 (1)*, 103 (1), *107 (1)*, 109 (1).