A new large caseid (Synapsida, Caseasauria) from the Permian of Rodez (France), including a reappraisal of “*Casea*” *rutena* Sigogneau-Russell & Russell, 1974

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ABSTRACT

The description of a new large caseid, *Ruthenosaurus russellorum* n. gen., n. sp. from the Early Permian (upper Cisuralian to lower Lopingian) of the Rodez Basin, France, is based on a partial postcranial skeleton that was initially collected at the same time as the holotype of “*Casea*” *rutena* Sigogneau-Russell & Russell, 1974. Despite its distinctly larger size than “*C.*” *rutena*, the holotype of *Ruthenosaurus* n. gen. clearly represents an immature individual, as shown most clearly by the lack of fusion of the neural arches to their respective vertebral centra and incomplete ossification of the ends of the limb elements, including the absence of an ossified olecranon on the ulna. Nonetheless, *Ruthenosaurus* n. gen. is diagnosed by several autapomorphic characters, including dorsal vertebrae with anteriorly tilting neural spines and a diamond-shaped outline in transverse section, a first sacral rib with a dorsoventrally expanded distal head, and a low iliac blade with a poorly developed anterior process. The new taxon is further distinguishable from the only other known French caseid, "*Casea*" *rutena*, by the shape of the distal part of the humerus, including an ectepicondylar notch rather than a fully enclosed foramen, the specific shape of the ulna, and the overall robustness of the specimen. The taxonomic status of "*Casea*" *rutena* is discussed and it is concluded that this species should be moved into a new genus named *Euromycter* n. gen. The occurrence of the large-sized *Ruthenosaurus* n. gen. in France increases our knowledge about the early diversity of this clade in Europe.

KEY WORDS
Synapsida,
Caseasauria,
Caseidae,
Europe,
France,
Permian,
new genera,
new species.

RÉSUMÉ

Un nouveau grand caséidé (Synapsida, Caseasauria) du Permien du bassin de Rodez, France, et réévaluation de "Casea" rutena *Sigogneau-Russell & Russell, 1974.*

La description d'un nouveau grand caséidé, *Ruthenosaurus russellorum* n. gen., n. sp. du Permien (Cisouralien inférieur à Lopingien inférieur) du bassin de Rodez, France, est basée sur un squelette postcrânien partiel initialement collecté en même temps que l'holotype de « *Casea* » *rutena* Sigogneau-Russell & Russell, 1974. Bien que nettement plus grand que « *C.* » *rutena*, l'holotype de *Ruthenosaurus* n. gen. représente clairement un individu immature, comme le montrent l'absence de fusion des arcs neuraux à leur centre vertébral respectif et l'ossification incomplète des bouts des éléments des membres, dont l'absence d'un olécrâne ossifié sur l'ulna. Néanmoins, *Ruthenosaurus* n. gen. est diagnostiqué par plusieurs caractères autapomorphiques comprenant des vertèbres dorsales avec une épine neurale inclinée antérieurement et avec une section transverse en losange, une première côte sacrée avec une tête distale élargie dorsoventralement et une lame iliaque basse avec un processus antérieur mal développé. De plus, le nouveau taxon se distingue du seul autre caséidé français connu, « *Casea* » *rutena*, par la forme de la partie distale de l'humérus (comprenant une encoche ectépicondylaire plutôt qu'un foramen complètement enclos), la forme spécifique de l'ulna et la robustesse générale du spécimen. Le statut taxonomique de « *Casea* » *rutena* est discuté et il en est conclu que cette espèce devrait être placée dans un nouveau genre nommé *Euromycter* n. gen. L'occurrence du grand *Ruthenosaurus* n. gen. en France accroît nos connaissances sur la diversité précoce de ce clade en Europe.

MOTS CLÉS
Synapsida,
Caseasauria,
Caseidae,
Europe,
France,
Permien,
genres nouveaux,
espèce nouvelle.

INTRODUCTION

The origin and initial diversification of Synapsida represents an important stage in the evolution of terrestrial vertebrates. Paleozoic synapsids include not only some of the oldest known amniotes, but also the majority of Late Carboniferous and Permian taxa (Reisz 1986; Kissel & Reisz 2004). The fossil record provides strong evidence that among Paleozoic amniotes, it is this clade that evolved rapidly, and diversified greatly to dominate the terrestrial ecosystems of the Permo-Carboniferous. Previous phylogenetic analyses have shown that synapsids form one of the two branches of the basal amniote dichotomy (Reisz 1997), and this clade has a long evolutionary history, extending from the Paleozoic to the present. Evolutionary events associated with the early history of this clade are therefore critical to our understanding of the initial phases of amniote evolution.

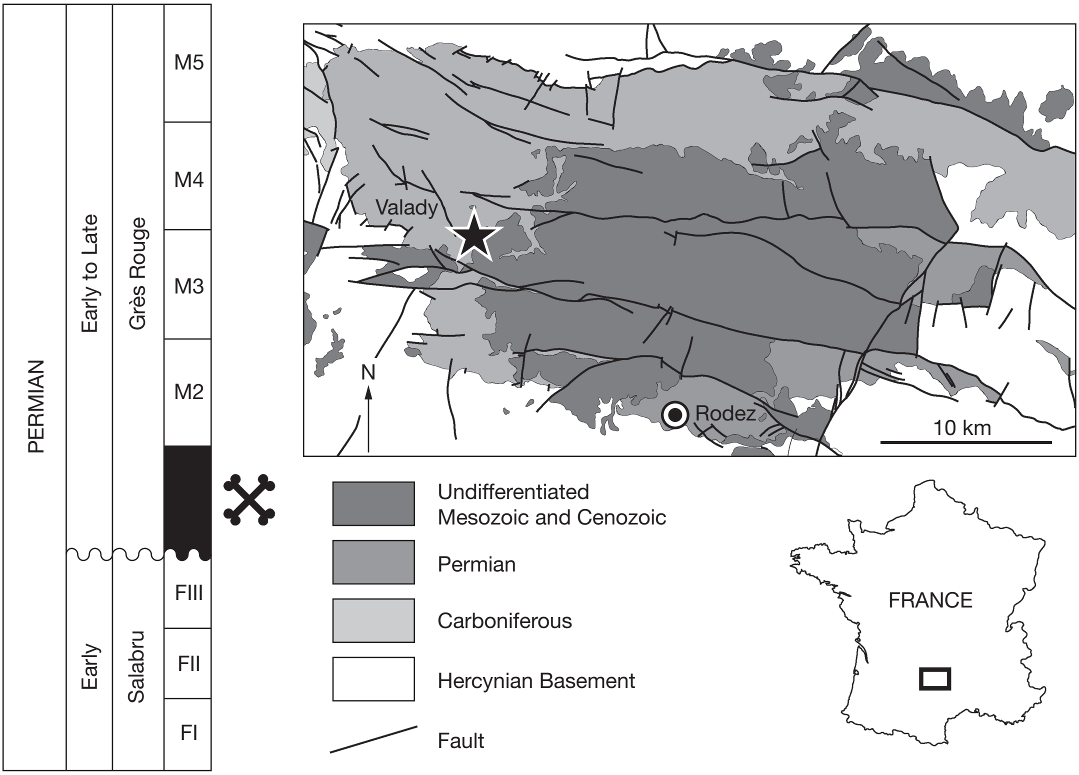

FIG. 1. — Geographical and geological setting of the caseid locality of Saint-Christophe-Vallon, Western Rodez Basin, Southern France (★). Geological map simplified after Burg *et al.* (1988; 1992), Roig *et al.* (2001), and Rousset *et al.* (1989). The crossed bones indicate the stratigraphic position of the caseid specimens described herein. Abbreviations: **M**, megasequence; **FI**-**FIII**, formation.

It is generally recognized that caseasaurs are stem eupelycosaurs, and represent one branch of the basal dichotomy of Synapsida. Reisz (1980, 1986) tentatively divided Caseasauria Williston, 1912, represented entirely by Permian taxa, into Caseidae Williston, 1911 and Eothyrididae Romer & Price, 1940, following Langston (1965). This hypothesized pattern of relationship is supported by more recent phylogenetic analyses (Maddin *et al.* 2008; Reisz *et al.* 2009). Caseidae is comprised of medium to large bodied herbivorous taxa from the upper part of the Lower Permian of North America and Western Europe, but the fossil record of this clade extends into the upper part of the Middle Permian of Northern Russia, making caseids (as well as varanopids) some of the youngest pelycosaur-grade synapsids (Dilkes & Reisz 1996; Reisz & Laurin 2001; Maddin *et al.* 2008). A recent claim of the presence of caseids in the latest Carboniferous of North America (Harris *et al.* 2004) is based on a single tooth, which does not conform to the well-known dental patterns seen in any known caseid. We consider that identification erroneous.

In the summer of 1970, Drs D. Sigogneau-Russell and D. E. Russell discovered the remains of two caseids on the west side of “Le Puech du Cayla” (Cayla Hill, commune of Valady). The two partial skeletons were found less than two kilometers apart horizontally, and 120 m apart vertically. The first specimen is composed of a partial postcranial skeleton (MNHN.F.MCL-1), with the cervical region and cranium completely missing, and presumed to have eroded away. The second specimen (MNHN.F.MCL-2), discovered 120 m lower in the section, is much smaller than the first, and preserves only the anterior part of the skeleton, including the skull, hyoids, cervicals, left forelimb, partial right forelimb, and posterior coracoid. This second specimen formed the basis of a thorough description, and the erection of a new species, "*Casea*" *rutena* Sigogneau-Russell & Russell, 1974 (Sigogneau-Russell & Russell 1974).

The subject of this contribution is the first and larger of the two specimens, which remained largely unprepared until 2003. This skeleton represents the remains of a juvenile individual, even though it is much larger than the fully mature, holotype specimen of "*Casea*" *rutena*. Although the posterior coracoid, humerus, radius, and ulna are the only overlapping skeletal elements between these two caseid skeletons, the anatomical differences discussed below indicate clearly that they represent distinct taxa. Whereas the new material appears to be too fragmentary to test this hypothesis through phylogenetic analysis and therefore too fragmentary to yield a definitive position of MNHN.F.MCL-1 within Caseidae, a new genus and species is erected on the basis of the skeletal autapomorphies listed in the diagnosis, and anatomical features that distinguish these two taxa. Additionally, the assignment of the second, smaller skeleton, MNHN.F.MCL-2 ("*Casea*" *rutena*), to the genus *Casea* Williston, 1910 has recently been questioned (Maddin *et al.* 2008). A discussion and a re-evaluation of the taxonomic status of MNHN.F.MCL-2 are presented. This paper therefore represents a timely revision of current caseid diversity in the increasingly productive Permian deposits of France.

ABBREVIATIONS

CNRS	Centre national de la recherche scientifique;
MGPV	Musée de Géologie Pierre Vetter, Décazeville (France);
MNHN.F	Muséum national d'Histoire naturelle, collection de Paléontologie.

GEOLOGICAL SETTING

Both caseid specimens (MNHN.F.MCL-1 and MNHN.F.MCL-2) were collected in the 1970's by D. Sigogneau-Russell and D. Russell (MNHN) from the base of the Grès Rouge ("Red Sandstone") Group, near the town of Valady, Rodez Basin, southern France (Fig. 1). The Salabru and Grès Rouge groups represent the two main Permian depositional cycles recognized in the north-western part of the Rodez Basin. The latter is subdivided into five hectometric members, M1 to M5, each corresponding to a sedimentary sequence of conglomeratic, sandy, and pelitic clastic deposits, which eroded from the Hercynian Massif (Bourges *et al.* 1987). The specimen MNHN.F.MCL-2 ("*Casea*" *rutena*) comes from the pelitic beds on the top of the first member (M1), whereas MNHN.F.MCL-1, found 120 m above stratigraphically, comes from the upper part of the second member (M2) (Bourges 1987; Gand pers. comm. 2009). Both members were deposited in what is interpreted as a playa-lake environment under a semi-arid, hot climate (Bourges 1987).

Whereas the upper Salabru Group has been dated as Early Cisuralian using fossil tracks and palynology (Gand 1987; Chateauneuf & Gand 1989), the lack of biostratigraphic markers in the Grès Rouge beds renders its age determination difficult. Few associated taxa have been found in these Grès Rouge beds, such as the Permian plant *Peltaspermum martinsii* (Bercovici 2006), the unique tetrapod track *Gilmoreichnus* sp. (Gand pers. comm. 2008), and the invertebrate ichnofossil *Scoyenia* sp. (Steyer pers. comm. 2008), but they are of limited biostratigraphic value. Paleomagnetic data are available for French Permian basins; however, recent workers retained old nomenclatural terms, assigning a "Thuringian" age to the Grès Rouge Group (Diego-Orozco *et al.* 2002), making it difficult to understand its position relative to the surrounding groups that have been dated using ICS terms.

Nevertheless, the Grès Rouge Group is regarded as contemporaneous to the Saxonian Group of Lodève (*sensu* Gand *et al.* 1997), as they correspond to the second depositional cycle of the Permian southern Massif Central basins initiated by a regional rifting episode (Rolando *et al.* 1988). A wealth of paleontological, radiometric and magnetostratigraphic data has been used to assign a date for the Saxonian Group, ranging between the late Sakmarian (= middle of the Early Permian) to early Lopingian (= early Late Permian) (Lopez *et al.* 2008). Therefore, the correlative Grès Rouge Group is here assumed to have the same age (Bourges 1987; Lopez *et al.* 2005, 2008). There is, however, no evidence for a more precise correlation between the M1 or the M2 Member and either of the

FIG. 2. — Photograph of *Ruthenosaurus russellorum* n. gen., n. sp. holotype (MNHN.F.MCL-1) in dorsal view with preserved remains placed in articulation. Scale bar: 10 cm.

Rabejac or the Salagou formations of the Saxonian Group of Lodève.

Globally, the stratigraphic range of Caseidae extends from the lower Kungurian strata of the USA to the Kazanian-Tatarian boundary of western Russia corresponding to a late Middle Permian age (Maddin *et al.* 2008), but caseids may have survived into the Late Permian, as implied by the correlation to the Saxonian Group with a Late Permian (early Lopingian) upper limit to its age range.

Remains of a large caseid have also been recently mentioned in the La Lieude facies of the uppermost Salagou Formation, Lodève Basin (Werneburg *et al.* 2007) and the material is currently being excavated by a French-German team (universities of Dijon, Montpellier; TU Bergakademie Freiberg; CNRS and MNHN; Naturhistorisches Museum Schloss Bertholdsburg, Schleusingen). These beds are assigned to an early Lopingian age (Lopez *et al.* 2008), which is consistent with the time range estimated for the Rodez caseids.

SYSTEMATIC PALEONTOLOGY

SYNAPSIDA Osborn, 1903
CASEASAURIA Williston, 1912
Family Caseidae Williston, 1911

Genus *Ruthenosaurus* n. gen.

Diagnosis. — As for the type and only known species, given below.

Type species. — *Ruthenosaurus russellorum* n. gen., n. sp.

Etymology. — After the name of a Gallic regional tribe, Ruthenie.

Ruthenosaurus russellorum n. sp.
(Figs 2-9)

Holotype. — MNHN.F.MCL-1, a partial postcranial skeleton. Incomplete vertebral column with ribs and vertebrae of 18 presacrals, three sacrals, and 12 anterior caudals. Partial scapulocoracoids: dorsal portion of left scapular blade complete, but not its anterior extent, left coracoid fragment present; posterior edge of right scapular blade, right glenoid region, posterior coracoid nearly complete, fragment of right anterior coracoid, posterior portion of the interclavicle. Right humerus badly crushed and damaged, proximal head incomplete. Left humerus in two pieces, shaft damaged, but both proximal and distal heads well preserved. Complete left ulna, and nearly complete radius. Complete right femur, complete right tibia, and proximal portion of right fibula. Complete right pelvis overlain by vertebral column: right pubis, median one-third of right ischium.

Etymology. — The type species is named in honour of Drs D. Sigogneau-Russell, and D. Russell, the original collectors of the holotype.

Type horizon and age. — Upper part of the red pelitic beds of the M2 Member, Grès Rouge Group of the Rodez Basin, "Saxo-Thuringian", upper Sakmarian to lower Lopingian (Lopez *et al.* 2005, 2008), middle Early to early Late Permian.

Type locality. — 1 km east to the village of Saint-Christophe-Vallon, town of Valady, departement of Aveyron, Southern France.

Diagnosis. — A large caseid with the following autapomorphies: anteriorly tilting neural spines of the dorsal region that are diamond-shaped in outline in transverse section; first sacral rib with robust distal head, twice that of the second sacral rib; short iliac blade with prominent posterior process.

ANATOMICAL DESCRIPTION

The specimen described here represents a partial postcranial, articulated skeleton of a large caseid recognized here as a new genus and species (Fig. 2). Partial remains of the fore and hind limbs accompany a nearly complete axial skeleton. No skull was recovered with this specimen.

Axial skeleton

The preserved remains include 18 presacral, three sacral, and parts of twelve anterior caudal vertebrae (Fig. 2). The total count of the presacrals is partly based on the number of ribs, since the neural arches, and in some cases, the centra have not been preserved, even though the ribs have remained in proper position relative to those ribs that are attached to vertebrae. This suggests that only one or two of the vertebrae are missing in the dorsal region. The preserved vertebrae conform quite closely in anatomy

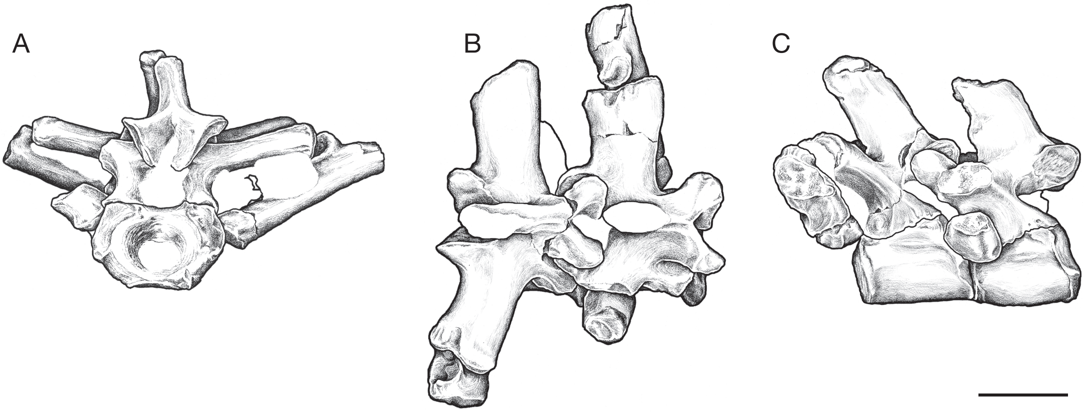

FIG. 3. — Anterior dorsal vertebrae of *Ruthenosaurus russellorum* n. gen., n. sp. (MNHN.F.MCL-1): **A**, posterior view; **B**, dorsal view; **C**, left lateral view (anterior to the left). Scale bar: 3 cm.

to those described for *Cotylorhynchus romeri* Stovall, 1937 (Stovall *et al.* 1966). Details of the vertebral morphology can be discerned only in the anterior half of the dorsal region, the last three lumbars, and sacral region. In these regions, the centra are short and transversely broad, with a flat ventral surface (Fig. 3), and no evidence of any ventral ridge or keel that can be seen in eupelycosaurs, such as varanopids and sphenacodontids (Reisz 1986; Maddin *et al.* 2006; Evans *et al.* 2009). However, in contrast to the condition seen in diadectomorphs and captorhinids, the centra do not have a spool-like appearance. Instead, the ventral surface of the centrum is broad, essentially flattened, and only slightly convex. At the margins of this flattened area, the sides curve upward sharply, and near the sutural area with the neural arches, are slightly pinched medially. The lengths of the centra vary little from the anterior region of the column, being about 3 cm in length on the first vertebra of the series to 3.5 cm in the last lumbar. None of the vertebrae have fully closed neuro-central sutures. The pedicles of the neural arches are clearly separated from the centra in the mid-dorsal region. Even in the lumbar region and on the first sacral, transverse breaks show separate neural arches and centra. The articular surfaces of the centrum are of a typical caseid nature. They are broad, subcircular in outline, expanded laterally at the rim for articulation with the capitulum of the rib, and the adjacent centrum. The body of the centrum is only shallowly amphicoelous, so that the walls of the centrum are thicker than in other early synapsids. Intercentra are absent in the dorsal region, and the shape of the ventral lip indicates that there was no place for them. However, distinct, separate intercentra are preserved in the sacral region.

As in all caseids, the neural arches vary significantly in morphology even throughout the dorsal region of the vertebral column. Those in the anterior dorsal region are more gracile than those in the mid-dorsal and lumbar regions. The transverse processes are well developed in the anterior dorsal vertebrae, extending far laterally and slightly upwards on either side of the midline. As in *Cotylorhynchus romeri* (Stovall *et al.* 1966), each transverse process extends as far laterally from the body of the neural arch as the maximum width of the broad central rim. In dorsal view, the outline of the transverse process can be discerned, where it can be seen to expand gently from the anterior zygapophyses to its slightly swollen and anteriorly tilted articular surface. A slight notch along the lateral edge of the transverse process divides the articular surface into a smaller, nearly circular anterior surface, and an elongate posterior portion. The articular surface of the process is significantly wider than the opposing surface area of the rib tuberculum.

The zygapophyseal surfaces are more strongly tilted in MNHN.F.MCL-1 than in *Cotylorhynchus* Stovall, 1937 or in other caseids (Olson 1968). Thus, the maximum lateral span of the zygapophyseal facets is smaller in MNHN.F.MCL-1 than in other caseids in the anterior part of the vertebral column. The neural spines are also distinct in MNHN.F.MCL-1, and all of the preserved neural spines lean somewhat forward. Thus, the curvature between the posterior edge of the spine and the postzygapophysis is less strongly concave than in other caseids.

The "lumbar" region is defined here as comprised of presacral vertebrae in which the ribs are suturally attached to the centra, and thus not movable. The transverse processes on the "lumbar" vertebrae are very short and stout, and even though the ribs are sutured to them, these sutures are clearly visible (Fig. 4). The neural spines are not blade-like, as in other caseids (e.g., *Cotylorhynchus romeri*) (Stovall *et al.* 1966) but are massive, and diamond-shaped in transverse outline. This is related to the presence of paired massive ridges that extend anterodorsally on the spine from the postzygapophyses to the dorsal tip of the spine. Thus, instead of having an anteroposteriorly elongate dorsal surface, the top of the spine has a diamond-shaped outline.

The sacral vertebrae are the most massively built elements of the vertebral column, with broad, massive but short transverse processes (Fig. 4). The centra have large facets for the massive capitulum. Two intercentra are preserved as distinct elements between the sacral centra, and have the typical crescentic outline. Only the neural arch of the first sacral vertebra is complete, the neural spines of the second and third sacrals vertebrae being broken off near the base. In typical amniote fashion (Reisz 1986), the pre- and postzygapophyses of the first sacral vertebra are dramatically different from each other. The prezygapophyses extend far laterally, slightly beyond the lateral edges of its centrum, as in the "lumbar" vertebrae. This results in large, nearly horizontally arranged zygapophyseal surfaces of articulation. In strong contrast to this condition that characterizes the "lumbar" region of the vertebral column, the postzygapophyses of the first sacral, and those of subsequent sacral and caudal vertebrae, are close to the midline and have relatively small surfaces of articulation that are strongly tilted, usually more than 55° from the horizontal plane. The neural spine of the first sacral vertebra is the tallest in the preserved portion of the vertebral column and is massively built instead of being blade-like in outline. Its anterior edge is narrowed to a slender keel, but the main body of the spine is transversely thick. As in the "lumbar" region, this is caused by a pair of massive ridges that extend from the postzygapophyses to the top of the neural spine. These ridges connect the postzygapophyses to the sides of the spine, creating a strong, buttressed neural spine. However, a modest ridge extends along the posterior median surface of the spine from the point where the two postzygapophyses join at the midline to the unfinished, rugose dorsal surface of the spine, which precludes a diamond-shaped outline as seen in the neural spines of the "lumbar" vertebrae. Although broken, the neural spines of the other sacral vertebrae are also massive, and appear to be similar to those on the first sacral.

Little detailed information is available on the anterior caudal vertebrae. The first caudal vertebra has a massive neural spine, similar to those on the sacrals in being narrow anteriorly, and broad and massive posteriorly. However, it appears to be distinctly reduced in height in comparison to that on the first sacral, and is directed vertically, rather than being tilted anteriorly. The transverse process is only slightly smaller than those on the sacral vertebrae, but the facet for the capitulum is distinctly smaller than those in the sacral region. None of the other caudal neural arches are sufficiently preserved for description. The general morphology of the anterior caudal centra remains similar to those in the dorsal region, and does not show any changes in overall proportions, except for being slightly smaller. The haemal spines have the expected Y-shaped general morphology seen in all early amniotes (Heaton & Reisz 1980) and the typical crescentic saddle across the arms of the chevron formed by the intercentrum. The first preserved haemal spine is at the level of the fifth caudal vertebra, just posterior to the large, plate-like ischium.

The rib-cage of MNHN.F.MCL-1 is well preserved; almost complete even though at least seven pairs of ribs do not have their corresponding verte-

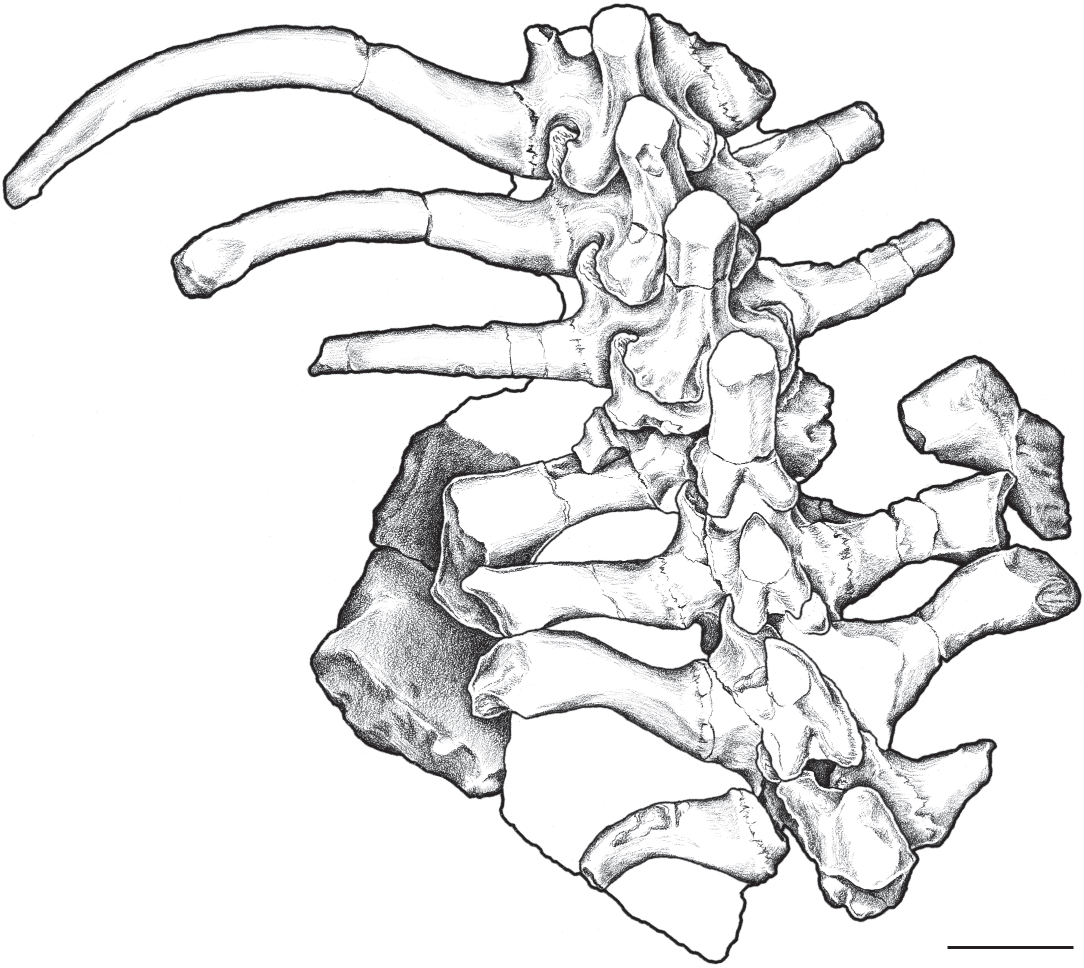

FIG. 4. — "Lumbars" (3), first caudal vertebra and sacral region of the axial skeleton of *Ruthenosaurus russellorum* n. gen., n. sp. (MNHN.F.MCL-1) in dorsal view. Scale bar: 5 cm.

brae preserved. Unfortunately, there are no cervical ribs preserved. As in other caseids (Olson 1968), the ribs are stoutly built, the thick shaft extending outward, and somewhat upward from the capitulum. The articular surface of the capitulum, when exposed in this specimen, is oval in outline with the larger dimension of the oval extending dorsoventrally and occupying the entire head of the rib. The tuberculum is not markedly set off from the rest of the rib in the dorsal region, but becomes more massive and anteroposteriorly broad in the posterior part of the dorsal series, in the "lumbar" region, and especially in the sacrum. The capitulum is largest in the "lumbars" and in the sacrals, and gradually diminishes in width along the anterior caudal series. The surface of articulation of the tuberculum is exposed only in the anterodorsal region, has an elongated oval, slightly twisted surface, that extends anteriorly towards the capitulum, so its shape does not match the anteroposteriorly expanded articular surface of the transverse process. Its shape indicates that respiratory movement may have included a certain amount of anteroposterior movement of the distal portion of the rib, with some sliding and rotation along the transverse process, and perhaps relatively little dorsoventral movement. The relative size of the tuberculum and capitulum can be discerned in some ribs. In the anterior dorsal region, the tuberculum and capitulum are approximately equal in size, and are widely separated by an extended portion of the rib shaft, sometimes up to 4 cm apart. Posteriorward along the dorsal region, the tuberculum and capitulum gradually approach each other, and the tuberculum gradually increases in size, becoming larger than the capitulum. In the "lumbar" region, the articular surfaces of the capitulum and tuberculum are nearly in line with each other, the capitulum lies directly beneath the tuberculum. The tuberculum is nearly three times as wide along its articular surface as the capitulum.

In contrast to the condition suggested for *Cotylorhynchus* (Stovall *et al.* 1966), the shaft of all dorsal ribs is smoothly rounded over most of its length, creating a massive, rounded, and barrel-like trunk. None of the ribs have the distal end preserved, except for the sacrals. Three of the last "lumbar" ribs are nearly completely preserved, and the first one is longer than the comparable rib in *Cotylorhynchus romeri*, but remains shorter than those in the other caseids described by Olson (1968). Since this skeleton (MNHN.F.MCL-1) has not suffered from the level of crushing that characterizes most of the caseids from North America, the real thickness of the ribs can be estimated. Although the distal portion of the dorsal ribs appears normal and undistorted, their transverse width being approximately 1 cm, or about 27% of the length of the centrum, the proximal region and the midshaft of the ribs are much more massively built than in other Permo-Carboniferous amniotes (Reisz 1986). Thus, on an anterior dorsal vertebra where the centrum is 3.5 cm in length, with no space for an intercentrum, the proximal and mid-shaft regions of the corresponding rib are 1.8 and 1.4 cm respectively. In the mid-dorsal region, the same regions are 1.8 and 1.6 cm respectively, and in the posterior dorsal region, just anterior to the "lumbars", the same regions are 2 and 1.7 cm respectively. Three "lumbar" ribs are preserved, and appear to be suturally attached to their respective vertebrae, rather than being fused to them. The "lumbar" rib farthest from the pelvis is strongly curved, matching the curvature of the dorsals, even though it is less than half their length. The penultimate and ultimate presacral ("lumbar") ribs are each progressively shorter and more slender as the pelvis is approached.

There are three massively constructed sacral ribs in MNHN.F.MCL-1 (Fig. 4), as it is typical for caseids with the exception of *Angelosaurus romeri* having four (Olson 1968). They all extend laterally from the sacral neural arches to which they are suturally attached. Although clearly caseid in shape, the sacral ribs are distinct in MNHN.F.MCL-1: they are indeed unusually short and stout, and extend directly laterally, rather than slightly ventrally. Medially, all three sacral ribs are attached to the transverse process with an expanded, large tuberculum, and a smaller capitulum underneath that is attached to the expanded surface of articulation between the centra. An anteroventral depression and a corresponding posteroventral depression on both the rib and vertebra represent the junction between the tuberculum and capitulum on the sacrals, probably for the passage of the intervertebral artery. A similar condition can be seen also on the last three presacral vertebrae. Each sacral rib is narrowed in the mid-shaft region relative to the proximal and distal heads, but overall, the first sacral rib is the most massive, and its neck is similarly slightly thicker than that of all three sacral ribs.

The distal ends of the sacral ribs attach to the iliac blade, the first to the grooved area along the anterior margin of the ilium, the second to a swollen rugose area directly above the acetabulum, and the third sacral rib attaches to another depression next to the second rib. In most caseids, it is the second rib that has the largest distal head because its expanded contact with the ilium extends farther ventrally than the other ribs, to the level of the acetabulum (Olson 1968). Perhaps the most distinctive feature of the sacral ribs of this caseid is the unusually large size of the distal head on the first sacral rib. Not only is its distal head extended slightly farther ventrally along the anterior edge of the ilium, but its surface of articulation with the ilium is also nearly twice as large as that of the second rib. The distal end of the third sacral is expanded only slightly ventrally.

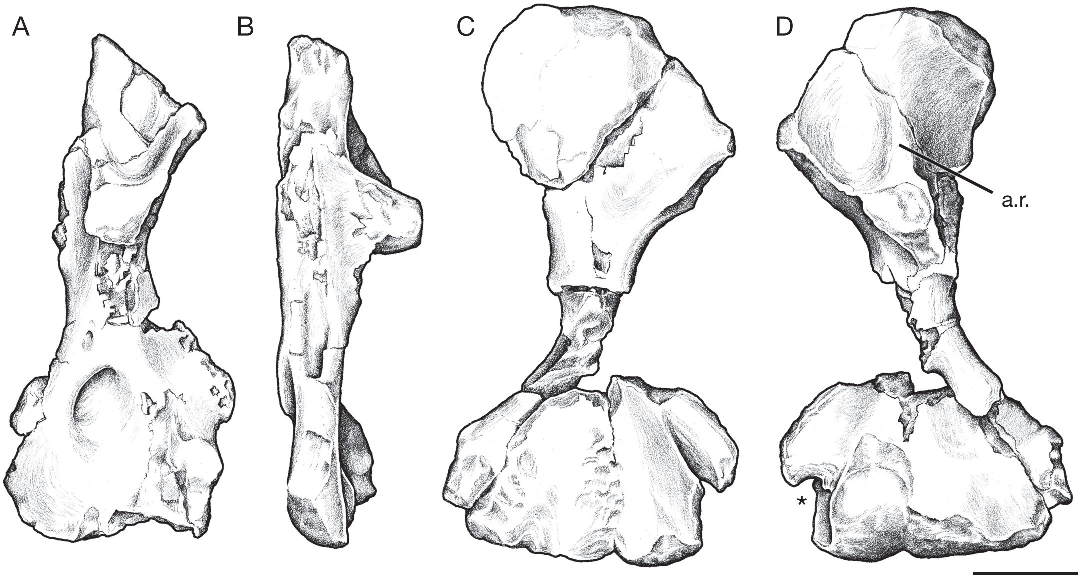

FIG. 5. — Right (**A**, **B**) and left (**C**, **D**) humeri of *Ruthenosaurus russellorum* n. gen., n. sp. (MNHN.F.MCL-1): **A**, ventral view; **B**, anterior view; **C**, dorsal view; **D**, ventral view. Note the low accessory ridge (**a.r.**) on the ventral surface of the proximal head and the deep entepicondylar groove (asterisk). Scale bar: 5 cm.

The caudal ribs are poorly preserved but it is clearly visible that they are strongly recurved. They diminish quickly in size along the anterior caudal region. Nevertheless, the first four caudal ribs are relatively massive, and probably double headed, like the posterior presacrals and sacrals.

Appendicular skeleton

Little information is available on the shoulder girdle as a result of poor preservation. Only the posterior portion (11 cm long) of the interclavicle is preserved, and it is a massive structure with a flat dorsal and gently curving ventral surface. Instead of the shaft being generally blade-like (Reisz 1986), the preserved portion of this interclavicle is rather thick, being approximately 9 mm in thickness along its midline. There is no longitudinal ridge on the ventral surface of the shaft, as seen in eupelycosaurs. Instead, the distal end of the interclavicle of MNHN.F.MCL-1 bears rugose fluting, not seen elsewhere.

Both scapulocoracoids are preserved, but so poorly, that little useful information can be gleaned from them. As in other caseids, the coracoids form a massive, large ventral plate that nearly matches the overall height of the scapulocoracoid. The subglenoid foramen appears to be located within a large circular depression ventral to the glenoid fossa, and slightly posterior to the glenoid buttress. The glenoid has the typical cork-screw shape seen in all early amniotes (Reisz 1997), and extends posteriorly almost to the tip of the posterior coracoid. A distinct triceps process forms the posterodorsal tip of the coracoid. As in most derived caseids, the scapula is not as tall as in *Casea broilii* Williston, 1910, or basal eupelycosaurs, especially when compared to the size of the coracoid plates (Reisz 1986). Nevertheless the posterior edge of the scapula is robust in the supraglenoid region. There is no supraglenoid foramen. A small region of the suture between the coracoid elements is preserved.

Both humeri are preserved, and they are the largest, most massive limb elements of the skeleton (Fig. 5). This is not surprising, since in caseids the humerus is consistently longer than the femur, and both the proximal and distal heads are wider than the corresponding heads of the femur. The right humerus is nearly complete, missing only part of the shaft region. In dorsal view, the proximal head

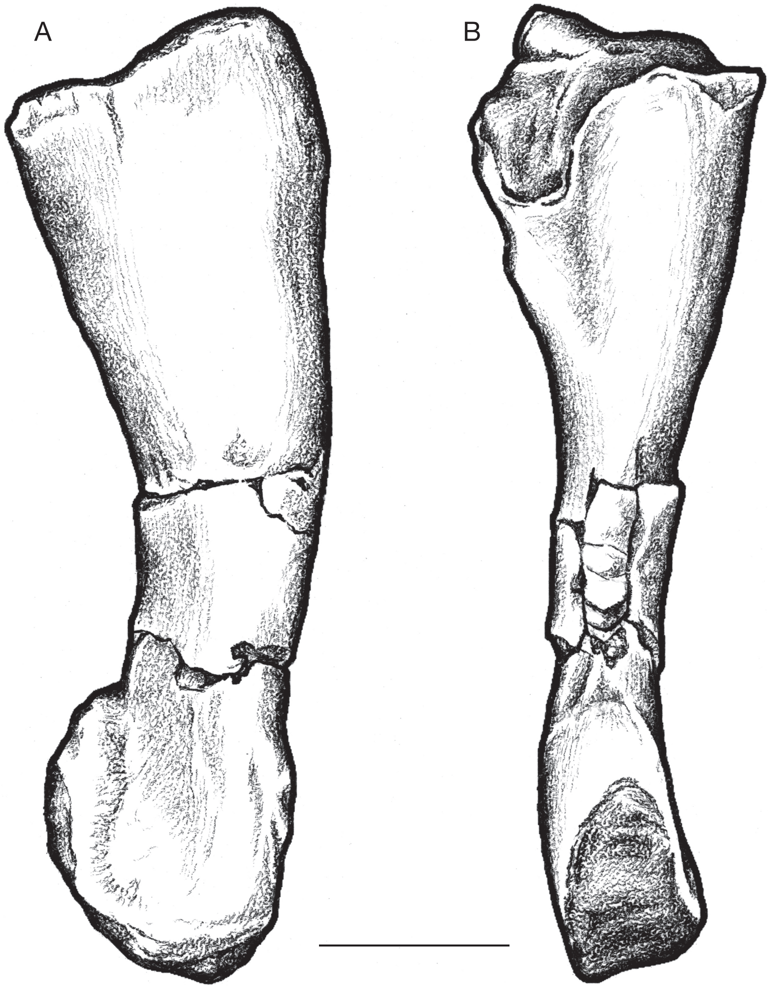

Fig. 6. — Left ulna of *Ruthenosaurus russellorum* n. gen., n. sp. (MNHN.F.MCL-1): **A**, anterior view; **B**, medial view. Scale bar: 5 cm.

is narrower anteroposteriorly than the distal head. A narrow, cylindrical shaft, that may have extended approximately one third of the total length of the humerus, separates the two heads, which are strongly angled from one another.

A low accessory ridge extends from the midline of the proximal head on the ventral surface to the tip of the pectoralis process of the deltopectoral crest (Fig. 5D). This accessory ridge is also seen in varanopid synapsids (Reisz & Laurin 2004; Maddin *et al.* 2006), though in varanopids the ridge creates a gently convex ledge perpendicular to the ventral surface of the proximal head, whereas in those of MNHN.F.MCL-1 and other caseids (Olson 1968), only a shallow depression is present. The distal articular head is anteroposteriorly wide even though the entepicondyle is incomplete posteriorly. A robust supinator process is present on the anterior edge of the humerus and separated from the ectepicondyle by a wide and deep ectepicondylar groove. There is no indication of an entepicondylar foramen in the right humerus, because the region is damaged heavily; however, the foramen is clearly preserved in the left humerus (Fig. 5B).

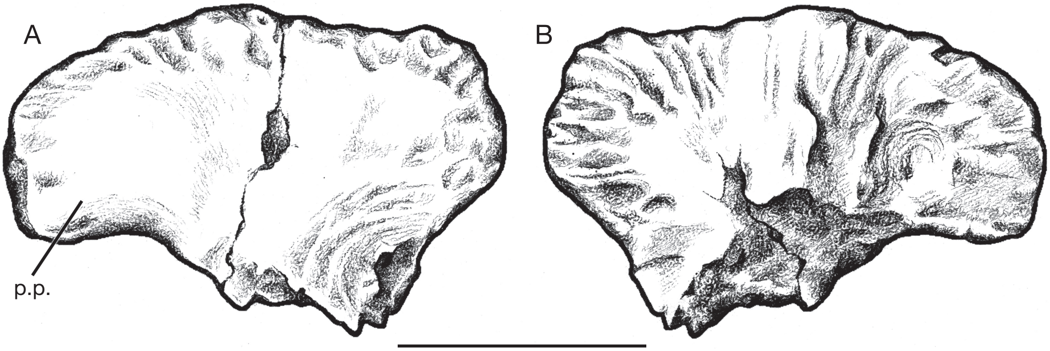

Fig. 7. — Right ilium of *Ruthenosaurus russellorum* n. gen., n. sp. (MNHN.F.MCL-1): **A**, lateral view; **B**, medial view. Note the autapomorphic posterior process (**p.p.**) of the iliac blade. Scale bar: 5 cm.

The left radius is represented by the proximal head and a portion of the shaft. Except for its small size, it bears no notable features. The left ulna is completely preserved, and as in juvenile caseids the olecranon is not ossified (Fig. 6). Nevertheless the proximal head is massively built with a large medial ridge that supports the medial articular surface. The proximal articular surface of the ulna is nearly triangular in outline. The lateral edge of the ulna is strongly rugose along the proximal half of the bone. The distal head of the ulna has an elongate articular surface for the three carpals, and has an unusually long anteriorly facing component, presumably for a large intermedium. A well-developed notch is thus formed by the anteriorly extending articular surface of the enlarged distal head and the anterior edge of the ulnar shaft. This distal morphology is similar to that seen in *Cotylorhynchus romeri* (Stovall *et al.* 1966).

The pelvic girdle is nearly complete, with both ischia and pubes being present beneath the sacral vertebrae and ribs, but only the right ilium is preserved. All elements of the pelvis remain distinct, with a median notch being present ventromedially between the pubes and ischia. The pubis and ischium are broad, plate-like elements, that appear to have faced predominantly ventrally, and would have been only partially visible in lateral view. However, most of the pelvic girdle had to remain unprepared and supported by a plaster jacket for stability, so that little information is available on the anatomy of the distinct elements or the morphology of the acetabulum. Only the dorsally projecting blade of the right ilium was separated and prepared to provide details about the shape of this comparably diagnostic part of the pelvic girdle. Both pubis and ischium are very large and similar in dimension to one another, as in *Casea broilii* and *Cotylorhynchus romeri* (Stovall *et al.* 1966). The pubis bears a distinct obturator foramen.

The ilium is damaged, with its blade having broken off the body, but its overall morphology is well preserved. Well-developed anteroventral and posteroventral ridges of the ilium bracket the dorsal portion of the acetabulum, and meet matching ridges on the pubis and ischium, respectively. Between these ridges, the ilium forms a narrow neck-like portion before expanding dorsally into a relatively large iliac plate-like blade (Fig. 7). However, the size and shape of the blade appear to place this caseid in an "intermediate" position between *Casea broilii* and more derived caseids, such as *Cotylorhynchus romeri* (Stovall *et al.* 1966; Olson 1968). As in *Casea broilii*, the iliac blade has both anterior and posterior processes, instead of extending primarily dorsally above the acetabulum as in most caseids. Thus, the blade is not particularly tall, and has a modest anterior and a larger posterior projection. The anterior projection is less developed than in *Casea broilii* but larger than in other caseids. It is to the medial wall of this anterior process that the enormous head of the first sacral rib attaches, and is accommodated by a match-

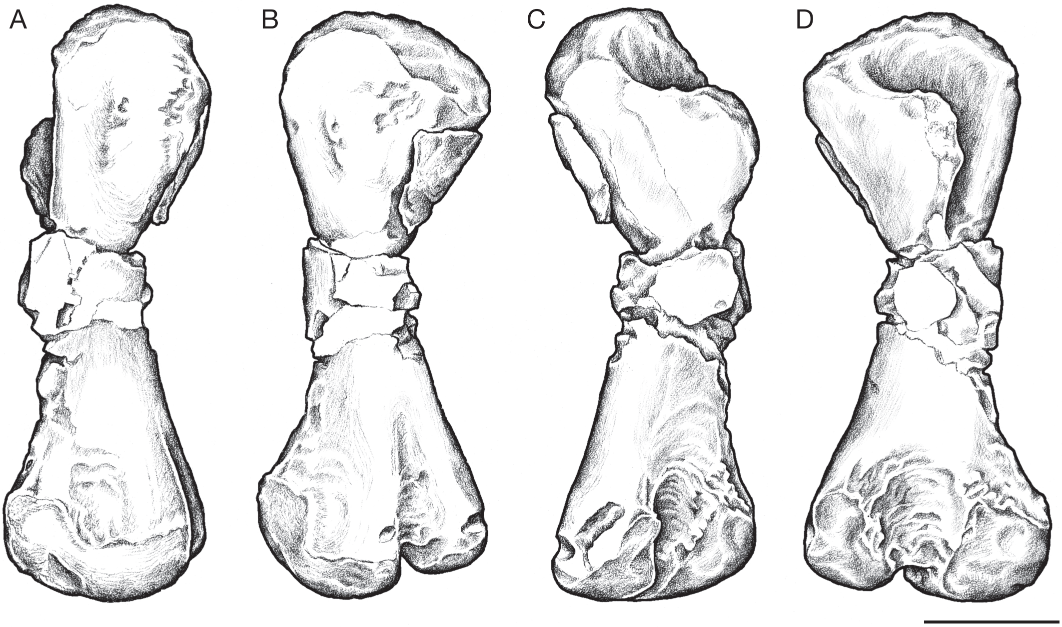

FIG. 8. — Right femur of *Ruthenosaurus russellorum* n. gen., n. sp. (MNHN.F.MCL-1): **A**, posterior view; **B**, dorsal view; **C**, anteroventral view; **D**, ventral view. Scale bar: 5 cm.

ing depression on the medial surface of the blade. The posterior process of the blade is reminiscent of a similar process in sphenacodontids, and is not present in other caseids (Reisz 1986). This process extends directly posteriorly, and extends well beyond the confines of the third sacral rib, whose area of attachment is marked by another distinct depression. Between these two depressions, the medial surface of the iliac blade has a series of vertical ridges that mark the position of the second sacral rib.

A complete right femur is preserved in MNHN.F.MCL-1 (Fig. 8). The proximal and distal heads are much narrower anteroposteriorly than those of the humerus, though the shaft of the femur is significantly more robust. The proximal head is slightly narrower anteroposteriorly than the distal head. The proximal articular surface is smooth and gently convex, and a pronounced internal trochanter projects posteroventrally. The internal trochanter is robust and cups a broad and deep intertrochanter fossa ventrally. There is little indication of a fourth trochanter. The femoral shaft is short and soon after reaching its narrowest point, it begins to widen again distally to accommodate the distal head. The distal head of the femur bears two large and well-defined articular condyles to receive the tibia and fibula. The anterior condyle, which receives the medial proximal head of the tibia, is slightly smaller and terminates short of the posterior condyle. The posterior condyle is larger than the anterior condyle and bears a large articular surface that is not limited to the distal surface, wrapping around onto the ventral surface of the femur to receive the fibula. The two condyles are separated by a deep concave excavation, the popliteal space, on the distal surface.

A complete right tibia is preserved in MNHN.F.MCL-1 (Fig. 9). It is a short, robust element with a strongly flared proximal head. The proximal articular surface is divided into two subcircular regions that accept the anterior and posterior distal condyles of the femur. A deep groove on the dorsal and medial surfaces separates the two proximal articular surfaces. A well-defined cnemial crest divides the lateral surface of the proximal head. Distally, the tibia tapers to a relatively broad shaft before expanding anteroposteriorly into the distal

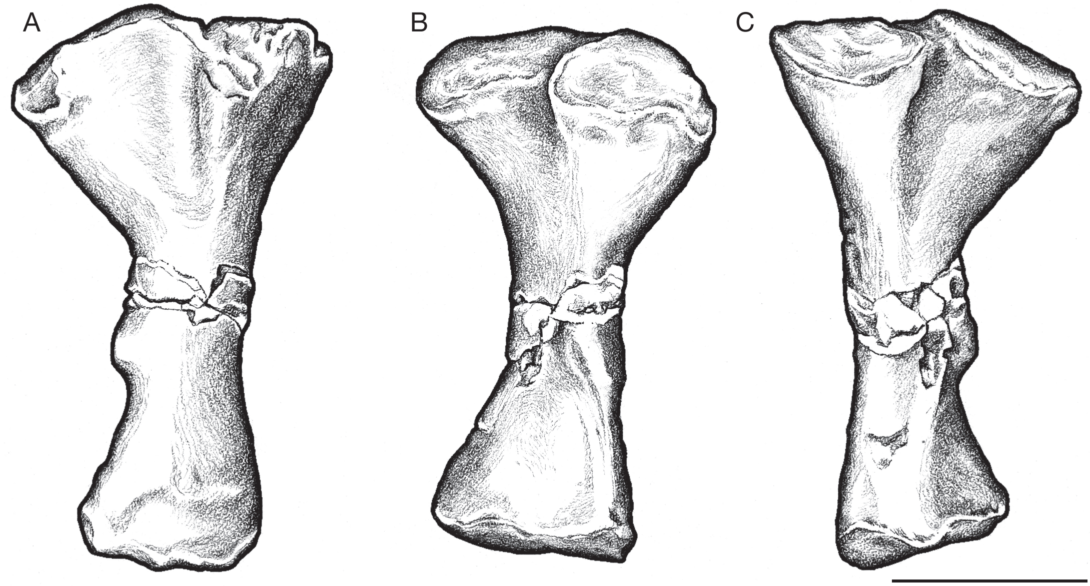

FIG. 9. — Right tibia of *Ruthenosaurus russellorum* n. gen., n. sp. (MNHN.F.MCL-1): **A**, lateral view; **B**, posteromedial view; **C**, medial view. Scale bar: 5 cm.

head. The distal head is significantly narrower than the proximal head. It bears a single articular surface for the calcaneum. Only a fragment of a right fibula is preserved in MNHN.F.MCL-1 next to the tibia, and shows no distinctive feature.

DISCUSSION

The material preserved, despite the absence of the highly diagnostic skull, is sufficient to definitively assign MNHN.F.MCL-1 to Caseidae. The absence of a sharp keel on the ventral surface of the vertebral centra precludes its assignment to the more derived eupelycosaurs such as varanopids and sphenacodontids (Romer & Price 1940; Stovall *et al.* 1966; Reisz 1986). In contrast, the distinct flat ventral surface of the vertebral centra is typical for caseids (Olson 1968). Additionally, the ribs project dorsally before bowing ventrally to form the characteristic large, barrel-like torso of caseids. MNHN.F.MCL-1 is characterized by the presence of three distinct sacral vertebrae, a number that is higher than in ophiacodontids and basal varanopids, but common to caseids, varanodontine varanopids, edaphosaurids, and sphenacodontians among non-therapsid synapsids (Maddin *et al.* 2006). The coracoids are large and plate-like, in contrast to the more slender coracoids of more derived eupelycosaurs. The proximal head of the humerus bears an accessory ridge that extends from the articular surface to the pectoralis process. The lack of a ledge associated with the accessory ridge makes the morphology seen in MNHN.F.MCL-1 different from that of derived eupelycosaurs such as varanopids. The presence of a large, well-developed entepicondyle in the distal head of the humerus also supports the assignment of MNHN.F.MCL-1 to Caseidae, as all caseid taxa possess a large robust, well-ossified distal head of the humerus (Reisz 1986). The pelvis is also characteristically caseid with respect to the size and morphology of the puboischiadic plate and the ilium. In particular, MNHN.F.MCL-1 possesses a plesiomorphically large posterior process on the ilium similar to that of *Casea broilii*, but in contrast to the narrow but tall iliac blade of more derived caseids (Olson 1968). Also, the iliac blade is mediolaterally wide, similar to those of other caseids, and different from those seen in other more derived synapsids. In addition, the weakly sphinx-like shape of the femur in anterior and posterior views, and the specific morphology of the internal trochanter on the proximal head is further indication that MNHN.F.MCL-1 pertains to a caseid. At the distal end of the femur, the anterior condyle is slightly shorter than the posterior one and they are clearly separated from one another.

While the material represents a caseid, its position within Caseidae is less well understood at this time. Interestingly, despite its relatively large size and robustness, several features indicate that MNHN.F.MCL-1 represents a juvenile individual, like the lack of fusion of the neural arches to their respective centra, the presence of distinct intercentra in the sacral region, and the poorly developed olecranon process. The latter trait is especially indicative of an immature caseid specimen, as a well-developed olecranon process is characteristic of all other caseid taxa for which the ulna is known (Olson 1968). This characteristic, along with other features of the forelimb, has lead to the hypotheses that caseids were diggers (e.g., Olson 1968; Maddin & Reisz 2007) and informally even as burrowers (see Olson 1968: 321). Therefore the absence of an olecranon could be related to a relatively early ontogenetic stage in this individual.

Although size is a dubious character in taxonomy, the dramatic difference in size between MNHN.F.MCL-1 and the only other currently described caseid from France, "*Casea*" *rutena* (Sigogneau-Russell & Russell 1974), is consistent with the assignment of MNHN.F.MCL-1 on the basis of morphological autapomorphies to a new genus and species.

The lack of preserved cranial material makes it difficult to include MNHN.F.MCL-1 in the only currently available data matrix used for caseid phylogeny, as most of the characters in the matrix of Maddin *et al.* (2008) pertain to the cranium. When MNHN.F.MCL-1 is scored in this matrix and the analysis re-run using the branch-and-bound algorithm (PAUP*4.0b10 [Swofford 2002]), only the derived clade containing *Ennatosaurus* Efremov, 1956, *Cotylorhynchus* and *Angelosaurus* Olson & Beerbower, 1953 is retrieved, with the position of *Ruthenosaurus* n. gen. remaining unresolved. At this time, the only available set of morphological features appear to be either autapomorphic or conflicting, thus preventing resolution of the tree. This issue will only be resolved by scoring more characters for MNHN.F.MCL-1, and this is dependent on the recovery of more material. For this purpose, systematical excations and prospections in the Rodez Basin are organized by Georges Gand (University of Dijon), J. Sébastien Steyer and an author of this contribution, Jocelyn Falconnet (both CNRS/MNHN).

Several features appear to be autapomorphic for MNHN.F.MCL-1, supporting the erection of the new genus and species, *Ruthenosaurus russellorum* n. gen., n. sp. The anteriorly tilted neural spines in the dorsal region and the short, massive neural spines that are the result of the presence of massive ridges in the "lumbar" and sacral regions are autapomorphies of MNHN.F.MCL-1. The distal head of the first sacral rib is unusually massive in comparison to other caseids, bearing an articular surface that is nearly twice as large as that of the second sacral rib and more than three times as large as that of the third sacral rib. Additionally, the sacral ribs extend straight laterally instead of curving ventrally at their lateral terminus, as in other caseid taxa. The iliac blade, while exhibiting distinctly caseid traits, displays a morphology that distinguishes MNHN.F.MCL-1 from other caseids. *Ruthenosaurus* n. gen. shows a large, well-developed, ventrally curved posterior process that creates a strongly concave posterior edge of the pelvis between the iliac blade and the body of the bone, somewhat reminiscent of the condition seen in *Casea broilii*. However, *Ruthenosaurus* n. gen. has a greatly reduced anterior process that seems to be intermediate in size and shape between that of *Casea broilii* and more derived caseids.

Unfortunately, the two Rodez caseids have only four skeletal elements in common, the posterior coracoid, humerus, radius, and ulna. Nonetheless, in addition to the size difference discussed above, several other features further distinguish MNHN.F.MCL-1 from "*Casea*" *rutena* (MNHN.F.MCL-2). These include the shape of the distal end of the humerus, shape of the ulna, and the overall much more robust nature of MNHN.F.MCL-1 in comparison to the more gracile "*C.*" *rutena*. In particular, the lack of an entirely enclosed ectepicondylar foramen, but rather the development of an ectepicondylar notch, separating the ectepicondyle from the supinator process, distinguishes MNHN.F.MCL-1 from MNHN.F.MCL-2. Moreover, beyond the unossified olecranon process in MNHN.F.MCL-1, this element is different in overall shape from the ulna of "*C.*" *rutena* and more similar in shape to the massive, robust element of *Cotylorhynchus romeri*. Specifically, the ulna of *Ruthenosaurus* n. gen. is more robust than the unusually slender element of "*C.*" *rutena,* and its shaft is rather asymmetrical in anterior and posterior views, with a concave medial side only rather than displaying a concave side medially and laterally. Finally, the overall robustness of *Ruthenosaurus* n. gen. (MNHN.F.MCL-1), when compared to the gracile appearance of "*C.*" *rutena* (MNHN.F.MCL-2), and the markedly larger size despite its clearly immature status, suggests that the two specimens indeed represent distinct taxa. A phylogenetic analysis would either confirm or refute this hypothesis; however, as mentioned above, the limited amount of preserved material prevents this type of analysis at this time.

TAXONOMIC STATUS OF "*CASEA*" *RUTENA*

The features that initially lead Sigogneau-Russell & Russell (1974) to assign MNHN.F.MCL-2 to the genus *Casea* included its relatively small size compared to other caseid genera, the lesser degree of specialization of the skull relative to other genera, the presence of dentition on the coronoids, and a higher phalangeal formula than in the other, presumably more derived genera. The small size and presumed lesser degree of specialization may be considered to be of dubious taxonomic value, as size is generally a poor character and morphological variation in the group is not well known at this time. The presence of coronoid dentition has since been reported in another caseid taxon, *Ennatosaurus tecton* Efremov, 1956 (Maddin *et al.* 2008), suggesting that coronoid dentition may be more widespread in caseids than previously thought. This leaves the phalangeal formula as the single potential synapomorphy uniting MNHN.F.MCL-2 with the other species of the genus *Casea*. The manual phalangeal formula of MNHN.F.MCL-2 is 2-3-4-4-3, which is the highest and thus most primitive phalangeal count of any caseid. It is closest to that of *Casea nicholsi* Olson, 1954 with a phalangeal formula of 2-3-3-4-3. However, *C. nicholsi* is the only member of *Casea* with a completely preserved manus. Therefore, the utility of the phalangeal formula as a diagnostic character for the genus appears doubtful.

The first computer-assisted analysis of the phylogenetic relationships within Caseidae rendered the genus *Casea* paraphyletic (Maddin *et al.* 2008). Therein "*C.*" *rutena* formed the sister taxon to the derived clade containing *Ennatosaurus tecton*, *Cotylorhynchus romeri*, and *Angelosaurus dolani* Olson & Beerbower, 1953, but to the exclusion of the type species of *Casea*, *C. broilii*. In this analysis, the node uniting "*Casea*" *rutena* with these derived caseid taxa was very well supported. Six unambiguous cranial synapomorphies united "*Casea*" *rutena* with the derived caseid clade composed of *Ennatosaurus*, *Cotylorhynchus*, and *Angelosaurus*, and thus divided the putative sister species of the genus *Casea* in the analysis of Maddin *et al.* (2008). These characters are: 1) the anterior location of the tallest point of the postnarial process of the maxilla; 2) the contribution of the postparietal to the posttemporal foramen; 3) the lacrimal being taller than it is wide; 4) the supratemporal having approximately the length of the parietal at its midline; 5) the length of the lateral temporal fenestra being about 30% of the skull length; and 6) the dorsoventral deepening of the splenial at the midline.

However, Maddin *et al.* (2008) refrained from providing a new generic name for "*C.*" *rutena*, as this task should be part of a focused investigation of the original material from Rodez, France, as is provided in this contribution. In light of this recent phylogenetic analysis, we propose the removal of MNHN.F.MCL-2 ("*C.*" *rutena*) from the genus *Casea* and suggest the erection of a new genus for this specimen. This conclusion implies that the caseid diversity in Europe is currently represented by at least three and possibly five distinct taxa, including the two caseids from Rodez, an undescribed caseid from Lodève (France), *Ennatosaurus* from Northern Russia, and another undescribed caseid from the German Bromacker Quarry (D. Berman pers. comm. 2006). This results in a total level of caseid diversity in the European deposits that approaches that of North America.

SYNAPSIDA Osborn, 1903
CASEASAURIA Williston, 1912
Family Caseidae Williston, 1911

Genus *Euromycter* n. gen.

Diagnosis. — As for the type and only known species, given below.

Type species. — *Casea rutena* (Sigogneau-Russell & Russell, 1974).

Etymology. — The new generic designation refers to the location of the taxon in Europe, and "mycter" = nose, refers to the enlarged external naris that characterizes this caseid.

Euromycter rutenus
(Sigogneau-Russell & Russell, 1974) n. comb.

Holotype. — MNHN.F.MCL-2, complete skull with lower jaws and hyoid apparatus, six cervical vertebrae with proatlas, anterior part of interclavicle, partial right clavicle, right posterior coracoid, distal head of right humerus, left and right radius, left and right ulna, and complete left manus. A cast of the skull is deposited at the MGPV.

Type horizon and age. — Top of the red pelitic beds of the M1 Member, Grès Rouge Group of the Rodez Basin, "Saxo-Thuringian", upper Sakmarian to lower Lopingian (Lopez *et al.* 2005, 2008), middle Early-early Late Permian.

Type locality. — 1 km east to the village of Saint-Christophe-Vallon, town of Valady, departement of Aveyron, Southern France.

Emended diagnosis. — A small caseid with the following autapomorphies: an unusually broad skull, large temporal fenestra, and lack of expansion of the axial neural spine. In addition, it can be distinguished from other caseids by presence of an supernumerary blade-like intranarial bone located posteromedially to the septomaxilla, proportional differences in forelimb and manus, presence of an accessory proximal articulation between metacarpals 3 and 4, medial recurvature of metacarpal, and its manual phalangeal formula of 2-3-4-4-3.

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