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Preface

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PREFACE

The foothills of the Andes in northwest Argentina are the birthplace of knowledge of dinosaur precursors and the earliest dinosaurs. The first skeletal evidence complete enough to generate specific hypotheses regarding the origin and early evolution of dinosaurs came from the canyons and badlands in the Argentine provinces of La Rioja and San Juan. Two picturesque areas, one called 'Talampaya' and the other 'Ischigualasto' (Monetta and Mordo, 1995) (Fig. 1), are central to the story, the former for its Middle Triassic bipedal dinosaur precursors, namely *Lagerpeton talampayensis* and *Marasuchus* (= *Lagosuchus*) *lilloensis*, and the latter for its Late Triassic early dinosaurs. Both lie within the Ischigualasto-Villa Unión Basin, which is centered on a rift zone that accumulated thick terrestrial deposits during the Triassic (Romer and Jensen, 1966; Stipanicic and Bonaparte, 1979; Milana and Alcober, 1994).

Some 70 years ago, Cabrera (1943) described fragmentary therapsid fossils, and shortly thereafter Frenguelli (1948) described the nature of the sediments in the Ischigualasto Formation. Intensive paleontological study of the Ischigualasto and Chañares formations, however, began only in the late 1950s and 1960s with the realization of the extraordinary quantity and quality of the fossil vertebrates in these two formations. Fossils from Ischigualasto, a geographic name of uncertain origin, are the focus of the current memoir. Ischigualasto extends nearly 100 km northwest into the Andes Mountains as a sculpted, arid valley, which for centuries has served as a gateway for livestock crossing the mountains between Argentina and Chile.

Reaching a thickness of up to 700 m, the Ischigualasto Formation comprises alternating fluvial sandstones and overbank mudstones rich in fossil remains (Currie et al., 2009). Intercalated ash beds have yielded important radioisotopic dates (Rogers et al., 1993; Martínez et al., 2011), with ages near the bottom (231.4 ± 0.3 Ma) and top (225.9 ± 0.9 Ma) suggesting sediment accumulation in late Carnian–early Norian time during approximately 6 million years (Martínez et al., 2011).

Although the descriptive focus of this memoir is dinosaurs, non-dinosaurian vertebrates greatly outnumber dinosaurs among collected specimens, which now number in the thousands. This substantial collection of fossil vertebrates from Ischigualasto is housed principally at the Instituto y Museo de Ciencias Naturales of the Universidad Nacional de San Juan. Smaller collections are housed at the Instituto "Miguel Lillo" in San Miguel de Tucumán, the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" in Buenos Aires, and the Museum of Comparative Zoology at Harvard University in Cambridge, Massachusetts, U.S.A.

The chapters in this memoir focus, in particular, on the succession of vertebrate fossils within the formation, their taphonomy, and the osteology of basal sauropodomorph dinosaurs. The phylogenetic relationships of *Eoraptor lunensis* and other basal dinosaurs are considered elsewhere (Sereno and Martínez, in review). As background, a brief account is given here of the principal paleontological expeditions to the Ischigualasto Formation and the most important fossil discoveries that have been made with respect to dinosaur origins.

Institutional Abbreviations—**MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.; **PVL**, Paleontología de Vertebrados, Instituto "Miguel Lillo," San Miguel de Tucumán, Argentina; **PVSJ**, División de Paleontología de Vertebrados del Museo de Ciencias Naturales y Universidad Nacional de San Juan, San Juan, Argentina.

Harvard Paleontological Expeditions

A. S. Romer led two pioneering expeditions in 1958 and 1964–1965 to northwest Argentina late in his career, when he was 64 and 70 years old, respectively (Fig. 2A). The first 4 months of the 6-month expedition in 1958 was spent prospecting Permo-Triassic rocks in Mendoza Province, south of San Juan Province. That work produced almost no fossils, to the despair of the team, as recorded in a flamboyant account of the expedition by field assistant James A. Jensen (Jensen, 2001). They arrived in San Juan City, contemplating the rough 300-km drive north to Ischigualasto that ended as an ungraded track as it approached the valley. On April 22, 1958, Romer wrote in his field notebook: "Opinions vary as to whether we can get the car to Ischigualasto or not." A day later, however, they were setting up camp in the center of a picturesque valley at the mouth of a large arroyo with standing water (Agua de al Peña; Fig. 3B). Romer found a rhynchosaur skull the following day, and other fossil finds were reported by every crew member. Romer and Jensen proceeded to map by hand most of the southern exposure of the formation, dividing it (as in the present memoir) into four subunits (Fig. 3). On May 3, Romer wrote in his field journal: "I am getting out 2 skeletons of moderately large forms (1 a rhynchosaur) W of Jim's area, N of camp about 1 km." On May 14, Romer wrote: "more and more fossils coming in daily, in blocks and packages."

It is very probable that the second "moderately large" skeleton Romer mentioned that he was collecting on May 3 was the skull (Fig. 4; MCZ 7063) and partial postcranial skeleton (Brinkman and Sues, 1987; MCZ 7064) of a basal dinosaur soon to be named *Herrerasaurus ischigualastensis* (Reig, 1963). According to the typed collection record for 1958, field number 295 consists of "2 plaster blocks and a large bag containing much of an indeterminate skeleton" collected by Romer from a site located in "zone 1" about 1 km northwest of Agua de la Peña (Fig. 3B). On the field map, Romer's comments clearly narrow the location of the find to a small area labeled "Romer's Flat Valley" (Fig. 3B). Although the field record does not specifically mention that the "indeterminate skeleton" includes the skull, there are no other fossils in Romer's field notes or in the specimen list that would account for these fossils (MCZ 7063, 7064). They are matched in size and preservation and seemingly must be parts of the same specimen—the first skull and partial postcranial skeleton of a herrerasaurid dinosaur (Fig. 4).

Brinkman and Sues (1987) described some of the postcranial material pertaining to this specimen (MCZ 7064) and noted resemblances to *Staurikosaurus pricei*, a taxon based on a partial skeleton from the Santa Maria Formation of southern Brazil (Colbert, 1970). Comparisons to *Herrerasaurus ischigualastensis* were restricted to data from the preliminary account by Reig (1963). Brinkman and Sues (1987) identified MCZ 7064 in open nomenclature as cf. *Staurikosaurus* sp. They noted that the partial postcranium (MCZ 7064) might be associated with a partial skull (MCZ 7063), but the specimen was already removed from its

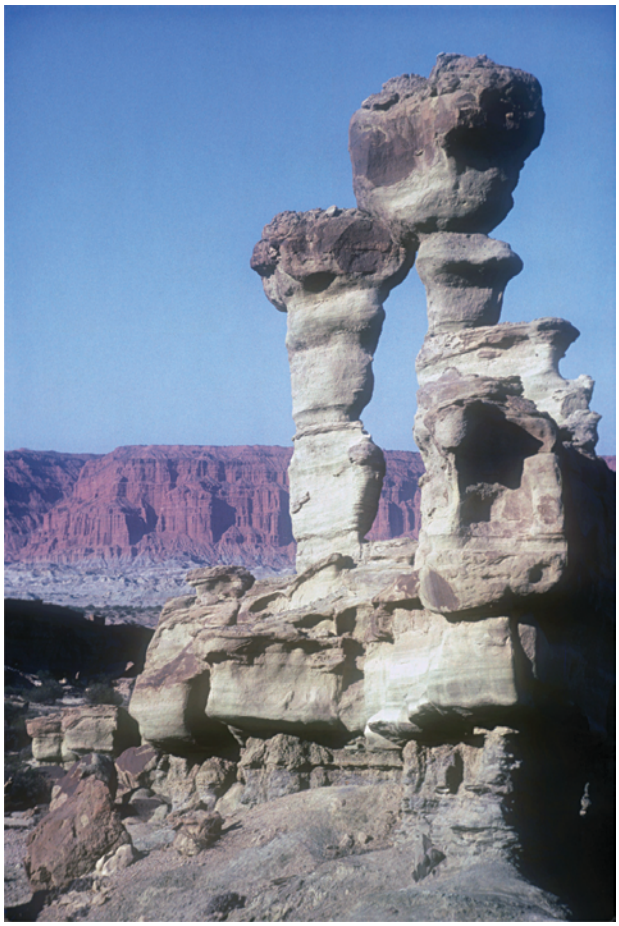

FIGURE 1. View northeast of prominent multi-story channel sandstone known locally as 'The Submarine' ('El Submarino'), which is located at the base of the Ischigualasto Formation in Ischigualasto Provincial Park (Parque Provincial Ischigualasto). In the middle ground are eroded badlands composed of alternating mudstones and thinner sandstone units. The cliff-forming red sandstones of the overlying Los Colorados Formation tower over the nearly barren outcrop of the uppermost member of the Ischigualasto Formation (photograph by P.C.S.).

field jacket and the field notes were ambiguous without confirmation from bridging specimens. Now we can confirm the close resemblance of both of these specimens (MCZ 7063, 7064) to *Herrerasaurus ischigualastensis* on the basis of articulated material (PVSJ 373, 407; Novas, 1994; Sereno, 1994; Sereno and Novas, 1994). MCZ 7063 and 7064 pertain to a single adult individual (Fig. 4), which has a skull length approximately 135% longer than that in PVSJ 407 (Fig. 6B).

Thus, the first skull and skeleton of *Herrerasaurus* were discovered by Romer in 1958 before Victorino Herrera led Argentine paleontologists to the partial postcranium in May of 1961 (Reig, 1963). The fossils from Romer's 1958 expedition, nevertheless, were impounded for two years at the port in Buenos Aires (Romer, 1967; Jensen, 2001). When they finally arrived at Harvard in 1960, they were set aside in favor of other specimens, and the association between the pair of jackets containing the skull and postcranial skeleton eventually was lost.

Argentine Expeditions

With news of the fossil discoveries at Ischigualasto, Argentine paleontologists O. A. Reig in Buenos Aires and J. F. Bonaparte (Fig. 2B) in San Miguel de Tucumán assembled a team and headed to Ischigualasto in 1959 and again in 1960, 1961, and 1964. During the 1961 field season, a local artisan and rancher named Victorino Herrera (Fig. 5A) led the Argentine crew to the posterior one-half of a skeleton in Valle Pintado (Fig. 3C). That specimen was later designated the holotype of *Herrerasaurus ischigualastensis* (PVL 2566; Reig, 1963). The type locality is situated about 4 km southeast of Agua de la Peña (Reig, 1963) in the Cancha de Bochas Member of the Ischigualasto Formation.

Bonaparte continued to work in the Ischigualasto Formation periodically in the late 1960s, describing a series of archosaurs and therapsids (e.g., *Chiniquodon*, Bonaparte, 1966; *Venaticosuchus*, Bonaparte, 1971), before turning his attention to the overlying Los Colorados (Bonaparte, 1972) and underlying Los Chañares (Bonaparte, 1975) formations.

Argentine-American Expeditions

In 1988, several of my students and I joined colleagues in San Juan on the first Argentine-American Expedition to renew paleontological work in the Ischigualasto Formation after some

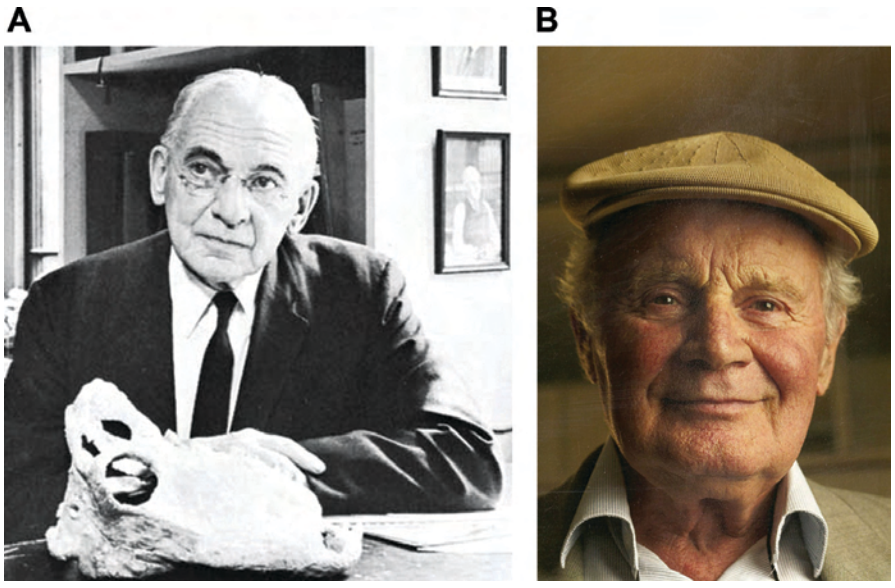

FIGURE 2. Two paleontologists that figure most prominently in the development of fieldwork and research on Ischigualasto fossil vertebrates. **A**, Alfred Sherwood Romer (1894–1973), formerly a professor at the University of Chicago and later at Harvard University (copyright© President and Fellows of Harvard College); **B**, José Fernando Bonaparte (born 1928), formerly curator at the Instituto "Miguel Lillo" in San Miguel de Tucumán and later curator and senior scientist at the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" in Buenos Aires (photograph courtesy of J. F. Bonaparte)

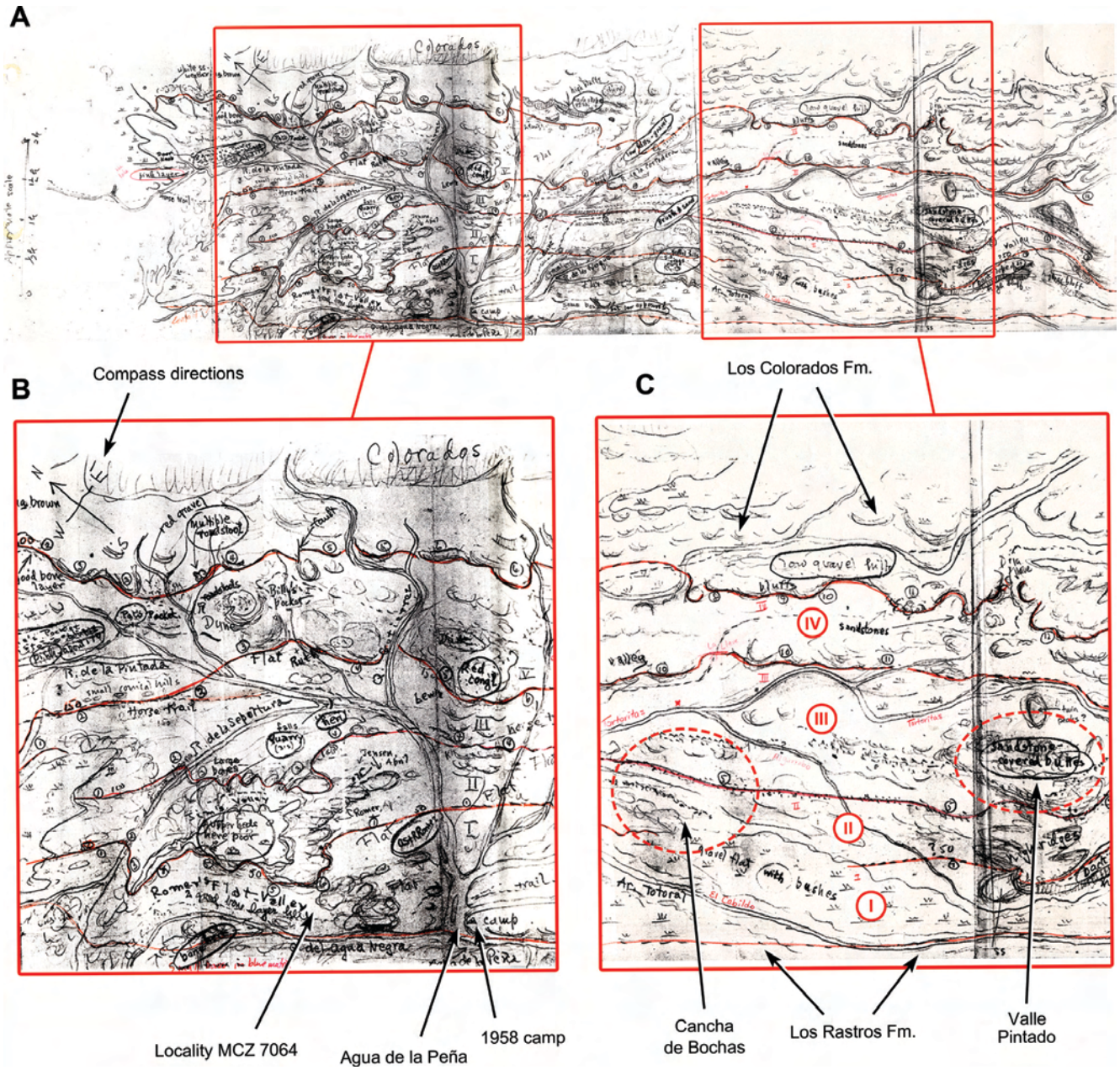

FIGURE 3. Copy of a hand-drawn field map from the 1958 Harvard Paleontological Expedition (courtesy of Harvard University Archives). **A**, map with distance scale to the left, compass direction in the upper left, the underlying Los Rastros Formation at bottom, and the overlying Los Colorados Formation at top. The boundaries between four units within the formation recognized by Romer were highlighted with red pencil by the author on a copy of the map. **B**, enlargement of the left (northwest) side of map showing the location of the first skull and skeleton of *Herrerasaurus ischigualastensis* (MCZ 7063, 7064) approximately 1 km northwest of the 1958 campsite, which was located adjacent to Agua de la Peña. **C**, enlargement of the right (southeast) side of map showing the location of Valle Pintado and Cancha de Bochas. **Abbreviations**: **I–IV**, four subunits of the Ischigualasto Formation recognized by Romer.

20 years with little activity. Argentine colleagues included R. N. Martinez, O. A. Alcober, F. N. Novas, and A. B. Arcucci, and American colleagues included C. A. Forster and C. L. May. J. F. Bonaparte joined us for several days as we entered the Valley of the Moon (Valle de la Luna), which by 1971 had paved access, a basic refuge building without electricity, and formal recognition as Ischigualasto Provincial Park (Parque Provincial Ischigualasto). In recent years, the route to the park and its facilities have improved dramatically to accommodate the many busloads of tourists that arrive each year to drive the unpaved loop within the valley.

FIGURE 4. Skull of *Herrerasaurus ischigualastensis* (MCZ 7063). Left lateral view of most of the preserved bones in the partial skull discovered in 1958 by the Harvard Paleontological Expedition. Skull bones are covered with a layer of hematite and appear to have been partially weathered when discovered. Scale bar equals 10 cm; maximum skull length equals 41.0 cm.

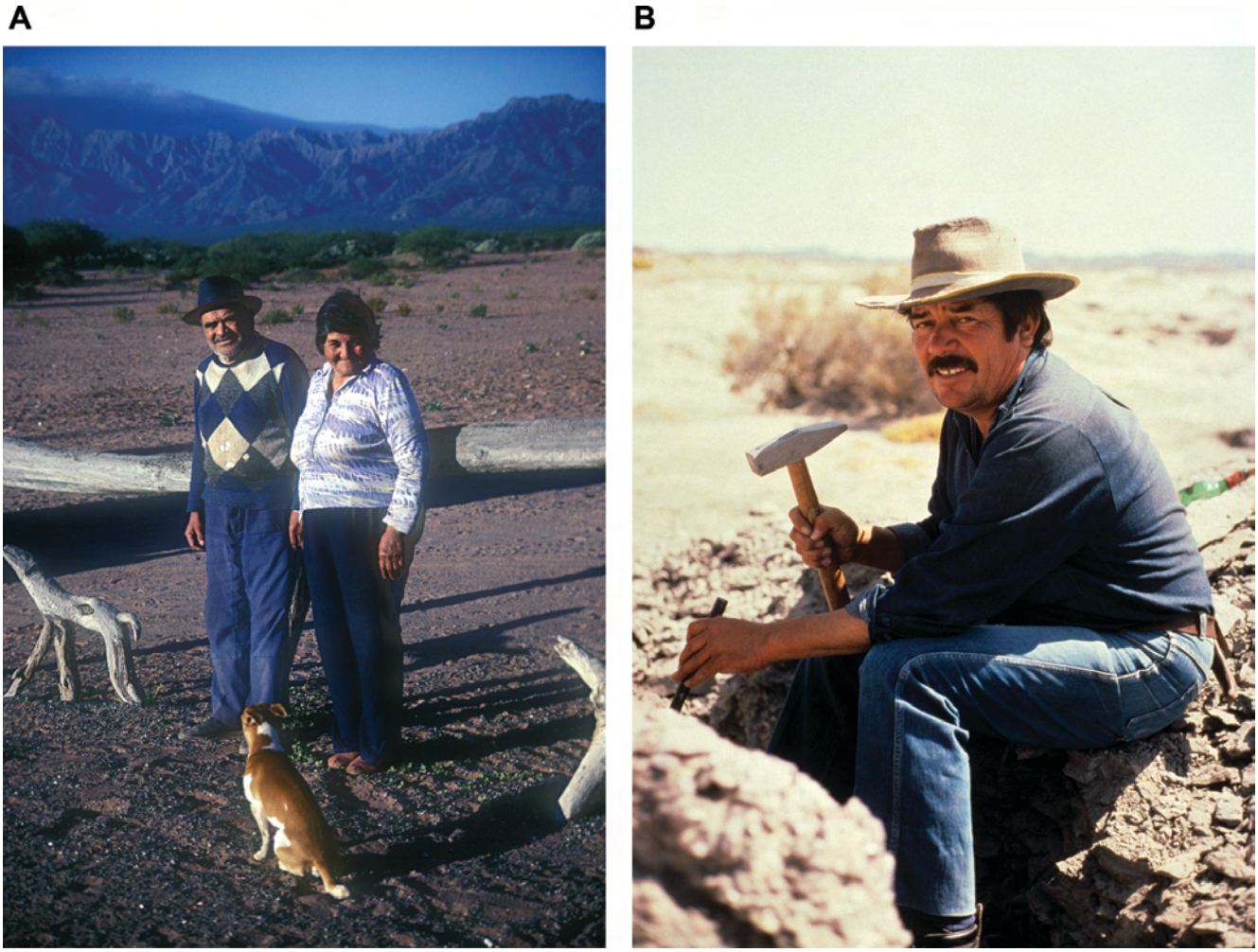

FIGURE 5. The Herrera family. **A**, Victorino Herrera (now deceased), his wife Magarita, dog, and wood carving (left side) in 1988 outside his home in Los Baldecitos, San Juan Province, Argentina; **B**, Dante Herrera, nephew of Victorino and key assistant and guide to the Argentine-American expeditions of 1988 and 1991 (photograph taken in 1991). Dante Herrera works as a ranger for Ischigualasto Provincial Park (photographs by P.C.S.).

FIGURE 6. Skull and postcranial skeleton of *Herrerasaurus ischigualastensis* (PVSJ 407). **A**, skeleton as discovered on May 10, 1988, on sandstone outcrop in the Cancha de Bochas Member of the Ischigualasto Formation (photograph by P.C.S.); **B**, skull after preparation showing some surface weathering of bone interpreted as subaerial exposure prior to burial. The sclerotic ring is preserved within the right orbit. Scale bar equals 5 cm; maximum skull length equals 30.0 cm.

Because we were unaware of Romer's hand-drawn map until after the Argentine-American expeditions and because there are no field maps with specimen localities for the previous Argentine expeditions, in 1988 we had little idea where any of the described vertebrates from the formation were found. Only general locations for a few important discoveries were available to us as we approached the myriad ravines and buttes that are exposed along more than 100 km of outcrop of the formation. We knew, for example, that the holotypic skeleton of *Herrerasaurus ischigualastensis* came from Valle Pintado ('Painted Valley'), and Reig (1963) had indicated a distance from Agua de la Peña to the type locality in kilometers. We used a satellite image of the outcrop to pinpoint our new fossil localities. We met Victorino Herrera, who at that time was still living in a small village (Los Baldecitos) on the edge of the valley (Fig. 5A). His nephew, Dante Herrera, would function as our guide and mechanic on both the 1988 and 1991 Argentine-American expeditions (Fig. 5B).

While prospecting in Valle Pintado 20 days into the 2-month 1988 expedition, I came upon the partially exposed skull and skeleton of *Herrerasaurus ischigualastensis* (PVSJ 407; Fig. 6). A short section from the middle of the neck had moved to the edge of the sandstone bluff that held the skeleton, poised to depart with the next heavy rain. I rolled it back into place. After preparation, the skull can be seen to have a length about two-thirds that of the skull that Romer found. The skull and neck of that 1988 specimen, which are better preserved than Romer's specimen, were prepared at the University of Chicago (Sereno and Novas, 1994); the remainder of the partial articulated skeleton was prepared in Buenos Aires and has not been figured. Except for the cervical series, new information on the postcranial skeleton of *Herrerasaurus ischigualastensis* came from a second important specimen, which was discovered only 2 days into the expedition. Although it lacked the skull and neck, much of the rest of the skeleton was preserved in articulation and nearly free of hematite (Novas, 1994), and it would provide substantial new information on the carpus, manus, tarsus, and pes (Novas, 1994; Sereno, 1994).

A more fragmentary specimen (PVSJ 845) was recovered later in the 1988 field season and described recently as a new basal sauropodomorph, *Chromogisaurus novasi* (Ezcurra, 2010). The specimen is described in more detail in this memoir (Martinez et al., 2013).

In 1991, we returned to Ischigualasto on the second Argentine-American Expedition to systematically explore the formation, continue to map our field localities, and search for ash beds for radioisotopic dating. While prospecting in an area known as Cancha de Bochas on October 1, R. N. Martínez picked up a fist-sized, hematite-encrusted nodule. Before tossing it away, he turned it and saw the edges of the crowns of two teeth peeking from under a covering layer of hematite. Gazing downward, he realized that he had just lifted the skull from the neck of an unusually small dinosaur (Gore, 1993). The specimen (PVSJ 512) remains one of the most complete vertebrate skeletons recovered from the Ischigualasto Formation (Fig. 7). Later it would be designated the holotype of *Eoraptor lunensis* (Sereno et al., 1993) and was initially regarded as a basal theropod. In the wall of the trench around the skeleton, a partial hind limb from a second larger individual was discovered (PVSJ 559), which preserves the crus and tarsus in exquisite detail. The holotypic site, its absolute age, and the local taphonomy and osteology of *Eoraptor* are described in detail in this memoir (Sereno et al., 2013). The relationships of *Eoraptor*, *Herrerasaurus*, and other basal dinosaurs are considered elsewhere (Sereno and Martínez, in review).

Universidad Nacional de San Juan

For 12 years (1994–2005) with support from the Earthwatch Institute, R. N. Martínez and O. A. Alcober of the Universidad

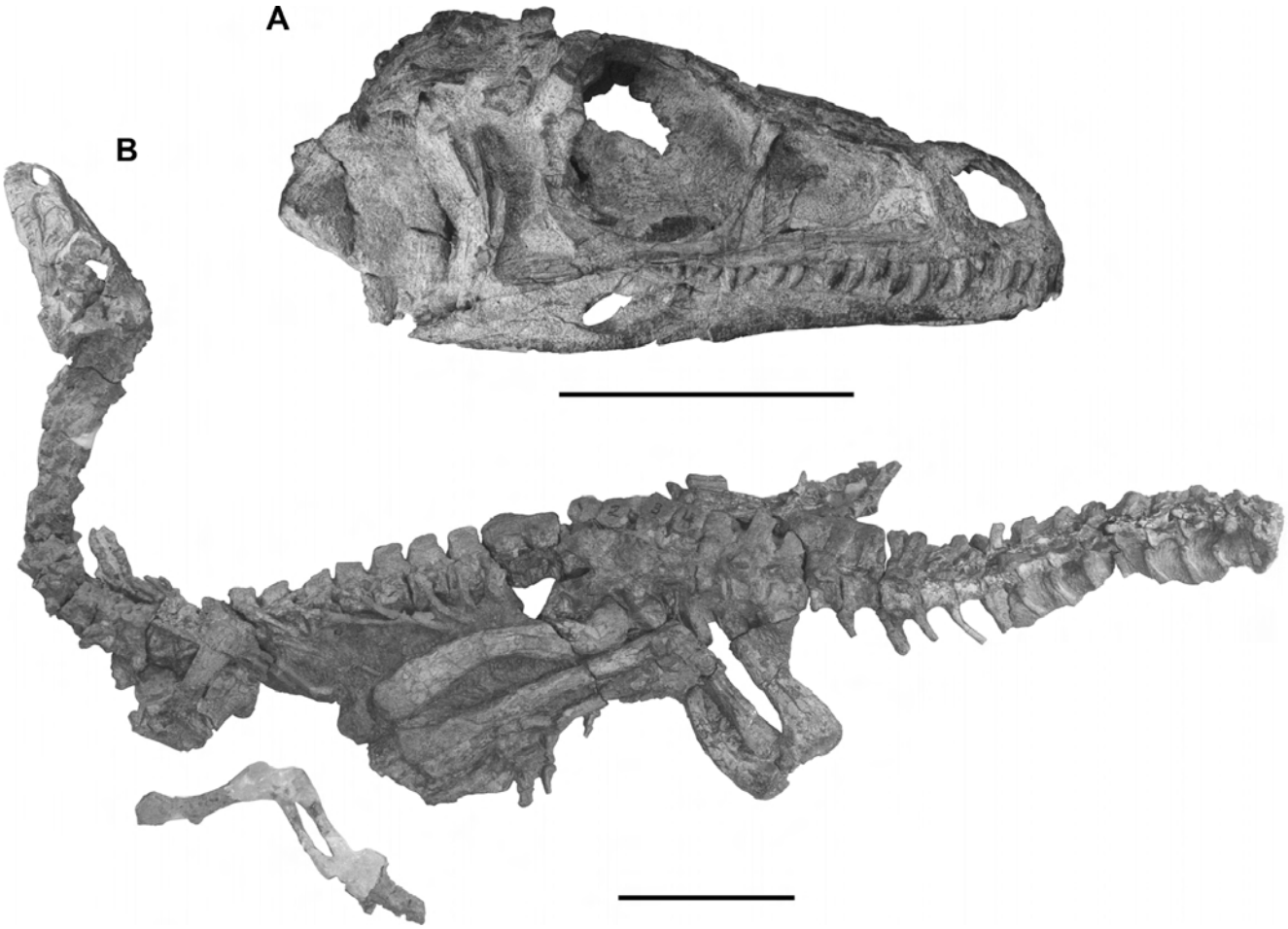

FIGURE 7. Skull and articulated skeleton of *Eoraptor lunensis* (PVSJ 512). **A**, skull in lateral view showing the better-preserved right side; **B**, skeleton as preserved lacking the distal one-half of the tail. Scale bars equal 5 cm in **A** and 10 cm in **B**; maximum skull length equals 12.3 cm.

Nacional de San Juan led teams of Argentine and foreign volunteers to work in the Ischigualasto and Los Colorados formations (Brightsmith et al., 2008). On October 8, 1996, American volunteer James Murphy and R. N. Martínez were prospecting along a ridge and spotted some delicate dinosaur bones in the crust of the surface of the outcrop. As they explored these bones the following day, Japanese volunteer E. Nagao was following a cynodont rib into the side of the same low ridge of mudstone a few meters away. She spotted some small vertebrae. After brushing aside a small amount of matrix, and articulated tail of a small dinosaur came into view.

The new dinosaur, virtually identical to *Eoraptor* in size, was discovered higher in the formation, about 200 m from its base in Cancha de Bochas Member. The locality, in addition, was situated farther up the valley northwest of Agua de la Peña near a rock formation called 'The Mushroom' (El Hongo) (Fig. 8A). A few weeks later, I joined R. N. Martínez and O. A. Alcober to excavate the specimen found by volunteer E. Nagao (PVSJ 560), which turned out to be a nearly complete skeleton (Fig. 9). It would be designated the holotype of *Eodromaeus murphi*, new genus and species of basal theropod (Martínez et al., 2011).

Prior to their preparation, however, we thought the new specimens belonged to *Eoraptor lunensis*. As also happened during the excavation of *Eoraptor lunensis*, a few bones of a second individual (PVSJ 561) were found in the trench wall around the holotype, including a well-preserved maxilla (Fig. 8B). The specimens collected by J. Murphy and R. N. Martínez also preserved many articulated portions of the skull and skeleton (PVSJ 562). Considerable preparation time was required to remove the hematite that coated most bone surfaces of the holotype. Only then did we understand that it represented a new taxon and eventually realize that we had discovered bones of this *Eoraptor*-sized dinosaur lower in the section during the second Argentine-American Expedition in 1991 (PVSJ 534, 877; Martínez et al., 2011). *Eodromaeus* and *Eoraptor* were contemporaries.

That seasoned paleontologists could ever mistake as the same taxon nearly complete skeletons of a basal sauropodomorph (*Eoraptor lunensis*) and basal theropod (*Eodromaeus murphi*) underscores the fact that the Ischigualasto Formation captures the roots of a great radiation—when the two great saurischian clades, Theropoda and Sauropodomorpha, lived side by side as

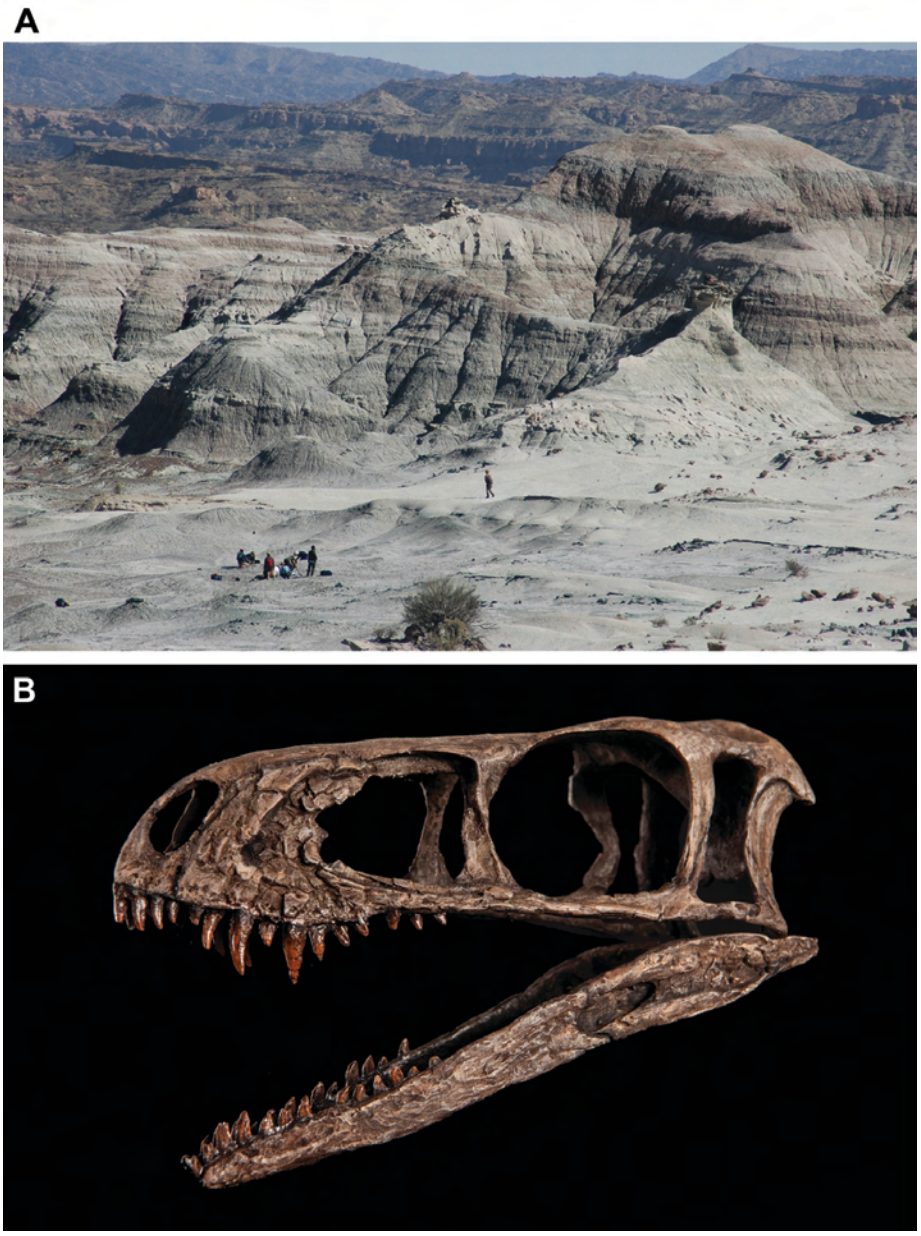

FIGURE 8. Excavation site and skull reconstruction of *Eodromaeus murphi*. **A**, site of the holotype (PVSJ 560) and most complete referred material (PVSJ 561, 562) of *Eodromaeus murphi* in the Valle de la Luna Member of the Ischigualasto Formation (photograph by R. N. Martínez); **B**, skull reconstruction of *Eodromaeus murphi* in left anterolateral view based on the holotype (PVSJ 560) and referred material (PVSJ 561, 562). Maximum skull length estimate equals 12.0 cm.

small-bodied, two-legged contemporaries but whose descendants eventually would include genera as disparate as *Diplodocus* and *Tyrannosaurus*, respectively.

Other discoveries in these years (1994–2005) include a partial skeleton of *Panphagia protos* (PVSJ 874), a close relative of *Eoraptor lunensis* discovered in the Cancha da Bochas Member of the formation in Valle Pintado (Martínez and Alcober, 2009) (Fig. 3A). A new herrerasaurid, *Sanjuansaurus gordilloi* (PVSJ 605), was discovered low in the section 40 m above the base of the formation in the Cancha de Bochas Member (Alcober and Martínez, 2010). Of special note is the discovery of fragmentary, but diagnostic, remains of lagerpetid and silesaurid dinosauromorphs in the Ischigualasto Formation, which are described in this memoir (Martinez et al., 2013). The first, based on a partial femur (PVSJ 883), extends the temporal range of bipedal lagerpetids in southern Pangaea from the pre-dinosaurian Middle Triassic (Ladinian) Chañares Formation into Upper Triassic (Carnian) levels of the Ischigualasto Formation. The second is a new silesaurid based on an ilium (PVSJ 884), which documents the presence of this small-bodied, quadrupedal clade in the Ischigualasto assemblage. Both of these taxa provide additional evidence of the global distribution of basal dinosauromorphs in association with the earliest dinosaurs during the Late Triassic (Irmis et al., 2007; Nesbitt et al., 2010).

FIGURE 9. Cast of the holotypic skull and skeleton of *Eodromaeus murphi* (PVSJ 560). Scale bar equals 10 cm.

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In closing this preface, this memoir would not have been possible without the encouragement and dedication of series editor J. A. Wilson, the timely comments and improvements of several colleagues, and the financial assistance from the Taylor & Francis Group and the Society of Vertebrate Paleontology. Special thanks are due to C. Abraczinskas of the University of Chicago for drafting and improving the final versions of the majority of the figures, and to W. Simpson and the superb fossil preparators in the Fossil Laboratory at the University of Chicago and the Museo de Ciencias Naturales at the Universidad Nacional de San Juan. We also thank the National Science Foundation (NSF BSR-8722586) for funding the 1988 Argentine-American Expedition, the National Geographic Society for funding the 1991 Argentine-American Expedition that resulted in the discovery of *Eoraptor lunensis*, the Earthwatch Institute for 12 years of field support, and the Universidad Nacional de San Juan and James Murphy for support of research and upgrading and expansion of paleontological laboratory and collections facilities.

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