COMMENTARY

Dating the origin of dinosaurs

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The Triassic

In 1834, the salt-mining expert Friedrich von Alberti applied the name "Trias" to a succession of sedimentary rocks in Germany, which (from oldest to youngest) are the Buntsandstein ("colored sandstone"), Muschelkalk ("clam limestone"), and Keuper (derived from a word for the characteristic marls of this unit) (1). The Buntsandstein and Keuper each comprise predominantly continental siliciclastic strata, whereas the Muschelkalk is made up of carbonates and evaporites deposited in a shallow epicontinental sea. Alberti's threefold rock succession more or less corresponds to the standard division of the Triassic into Lower, Middle, and Upper Triassic series.

Marsicano et al. postulate that dinosaurs gradually diversified at middle to high paleolatitudes.

Later researchers used fossils of marine invertebrates to correlate carbonate units exposed along the northern and southern flanks of the European Alps with the Triassic strata in the Germanic Basin. Starting in the late 19th century, geologists, mostly working in the Austrian Alps, established the global standard marine stages of the Triassic Period (from oldest to youngest): Scythian, Anisian, Ladinian, Carnian, Norian, and Rhaetian (2). The Scythian was later further divided into the Induan and Olenekian stages.

Correlating continental and marine strata is always fraught with issues, and absolute age controls are essential for this purpose. In recent decades, improved methods of radiometric dating, especially uranium–lead (U–Pb) dating of detrital zircons, have led to the development of an increasingly robust chronostratigraphic framework for the Triassic (3).

The Triassic Period (252–201 Ma before present) represents a critical time interval in the history of life (4). Many of the dominant present-day groups of animals and (to a lesser extent) plants or their close relatives first appeared in the fossil record during this period. One of these groups is the dinosaur–bird clade of archosaurian reptiles. The oldest undisputed dinosaurs are known from the early Late Triassic, about 231 Ma (5, 6). Late Carnian strata of the lower portion of the Ischigualasto Formation of the Agua de la Peña Group in the Ischigualasto–Villa Unión Basin of northwestern Argentina have yielded skeletal remains representing the two major clades of dinosaurs, Saurischia and Ornithischia, including multiple taxa referable to each of the two major saurischian subclades, sauropodomorphs and theropods, and a nondinosaurian dinosauriform (7). This unexpected diversity indicates that the origin and initial evolutionary radiation of dinosaurs clearly predated the deposition of the Ischigualasto Formation. The Agua de la Peña Group also encompasses several other Triassic-age continental deposits, one of which, the Chañares Formation, has yielded a diverse assemblage of tetrapods including a variety of archosaurs closely related to dinosaurs (Dinosauriformes) (8). The latter are small-bodied forms with long, slender hindlimbs suitable for cursorial locomotion and comprise *Marasuchus* (formerly "*Lagosuchus*"), *Pseudolagosuchus*, and *Lewisuchus* (9). The Chañares Formation was dated as Middle Triassic (Ladinian), but this age was based on faunal comparisons and its low position in the Agua de la Peña succession. Its faunal assemblage became the quintessential example of a Middle Triassic vertebrate community from Gondwana (8).

Temporal Framework for Dinosaurian Origin

Now, Marsicano et al. (10) report high-precision chemical abrasion thermal ionization mass spectrometry U–Pb zircon ages for the Chañares Formation, which indicate a much younger, early Carnian age (234–236 Ma) for this unit—some 5–10 million years younger than previously assumed. Their samples bracketed the main fossil-bearing interval of the Chañares Formation. Marsicano et al. use these new dates to argue that the transition from the dinosauromorphs in the Chañares assemblage to the diverse dinosaurian community of the Ischigualasto Formation assemblage occurred rapidly within the intervening 5 million years. They also point out that there is otherwise little difference in faunal composition between the two assemblages, both of which are dominated numerically by nonmammalian synapsids (cynodonts and dicynodonts). This suggests that the initial appearance of dinosaurs was not linked to profound changes in the composition of these ecosystems. Marsicano et al. postulate that

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Author contributions: H.-D.S. performed research and wrote the paper.

The author declares no conflict of interest.

See companion article on page 509.

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dinosaurs gradually diversified at middle to high paleolatitudes, a view consistent with a recent study by Whiteside et al. (11) that argued for a considerably delayed rise to dominance of dinosaurs at tropical paleolatitudes. Based on the currently available information, dinosaurs did not become dominant in many ecological roles in continental ecosystems until after the end-Triassic extinction event (12). Thus, the "Age of Dinosaurs" really commenced at the beginning of the Jurassic Period.

Although the new results are intriguing, their geographic generality and the temporal framework require much additional research. We still know little about Middle and early Late Triassic tetrapod assemblages across Pangea, especially at lower paleolatitudes, and it is premature to make broad generalizations from two data points in a single geographic region. Furthermore, age assessments for most known Triassic tetrapod assemblages are dated based solely on faunal comparisons. As Marsicano et al. reiterate, such dates require independent verification by nonbiostratigraphic means of stratigraphic correlation. As an example, they cite a study by Ottone et al. (13) that found an early Carnian age for the Puesto Viejo Group in Argentina. The latter has long been dated as early Middle Triassic (Anisian) based on the presence of nonmammalian therapsids shared with the *Cynognathus* Assemblage Zone of the Karoo Basin in South Africa. Marsicano et al. use this work along with their new data to suggest that many or all of the Middle Triassic tetrapod assemblages from Gondwana might actually be much younger, early Late Triassic in age. This conflicts with traditional views about the evolutionary history of continental tetrapods at the beginning of the Mesozoic Era and thus would have major implications for the interpretation of the latter. The tetrapods from the *Cynognathus* Zone Assemblage of South Africa represent more basal members of their respective lineages (e.g., Archosauriformes) than those from the Chañares Formation, and it seems unlikely that they are more or less coeval with the latter. McKay et al. (14) cautioned that U–Pb zircon data from tuffs from the Karoo Basin should not be interpreted as actual depositional ages but must be understood in terms of the magmatic history of their volcanic source. Weighted U–Pb data from the Puesto Viejo Group range from about 260 to about 230 Ma, although there is general agreement that the Puesto Viejo volcanism took place between 241 and 230 Ma (14). Thus, just like the biostratigraphic evidence requires careful reassessment, additional high-precision U–Pb dates and other means of nonbiostratigraphic age determination are needed for allegedly Middle and early Late Triassic continental tetrapod assemblages across Pangea to permit rigorous testing of hypotheses about faunal history and heterogeneity in time and space.

Recent decades have witnessed a revolution in our understanding of the diversification of the two principal evolutionary lineages of archosaurian reptiles, the crocodile line (Pseudosuchia) and the dinosaur–bird line (Ornithodira) (15). Current data suggest that these two lineages had already diverged from each other at the beginning of the Triassic or perhaps even during the latest Permian. Thus, we could expect early occurrences of dinosauriforms, and perhaps even dinosaurs, although none of the numerous reports of pre-Late Triassic dinosaurs so far has withstood critical scrutiny. The Manda beds of Tanzania, long considered early Middle Triassic in age, have yielded skeletal remains of an undisputed dinosauriform (*Asilisaurus*) (16) and an enigmatic taxon, *Nyasasaurus*, which is known only from a fragment of a remarkably dinosaur-like humerus and some vertebrae (17). Precise temporal calibration of the Manda beds and correlative units elsewhere is critical for testing whether dinosaurs and their closest relatives have a long but as yet largely unrecorded history or, as suggested by Marsicano et al. (10), dinosaurs appeared and rapidly diversified at middle to high paleolatitudes in Gondwana at the beginning of the Late Triassic.

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