An elephant-sized Late Triassic synapsid with erect limbs
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Here, we describe the dicynodont Lisowicia bojani, from the Late Triassic of Poland, a gigantic synapsid with seemingly upright subcursorial limbs that reached an estimated length of more than 4.5 meters, height of 2.6 meters, and body mass of 9 tons. Lisowicia is the youngest undisputed dicynodont and the largest nondinosaurian terrestrial tetrapod from the Triassic. The lack of lines of arrested growth and the highly remodelled cortex of its limb bones suggest permanently rapid growth and recalls that of dinosaurs and mammals. The discovery of Lisowicia overturns the established picture of the Triassic megaherbivore radiation as a phenomenon restricted to dinosaurs and shows that stem-group mammals were capable of reaching body sizes that were not attained again in mammalian evolution until the latest Eocene.

The time interval from the end of the Permian to the beginning of the Jurassic (252 to 201 million years ago) coincided with a trophic and taxonomic restructuring of terrestrial ecosystems (1). During the middle Permian, the predominant large herbivores were dinocephalians—stem-group mammals (in the clade Synapsida, “mammal-like reptiles”) such as Tapinocephalus, which was up to 3 m in length and weighed an estimated 2 tons (2). These animals were associated with faunas of nonsynapsid pareiasaurian parareptiles and a rich variety of other synapsids. In the late Permian, the large-size synapsid herbivores (rhachiodophylid dicynodonts) and the last pareiasaurians played the role of largest terrestrial herbivores (2). By the Early Jurassic, no stem-group mammals were larger than a half meter in length, and most were much smaller (3, 4), whereas herbivorous dinosaurs exceeded 15 m in length and 10 tons in weight; virtually all mid-sized to large tetrapods were archosaurs. Until now, this pattern has appeared clear-cut, with Triassic synapsids approaching the largest Permian forms in size but with no forms reaching sizes of the first large sauropodomorphs.

Dicynodonts were among the most abundant and diverse synapsids from the middle Permian to the early Late Triassic (5, 6). There were two episodes of body size increase in their evolution: the first in the late Permian, exemplified by Rhachiodophylus, and the second in the Middle to Late Triassic, when dicynodonts such as Placerias were the dominant herbivores in some ecosystems (6). There have been comparatively few rigorous estimates of dicynodont or dinocephalian body masses presented in the literature. The largest of these dicynodonts (such as krammeyeriiforms) are estimated previously to have reached lengths of 3 to 3.5 m and weights of up to 1 to 2 tons (2, 7), which is very similar to the largest middle Permian dinocephalians, such as Tapinocephalus or Moschops (2).

Fossils of Triassic dicynodonts are extremely abundant in African, Asian, and North and South American deposits but are comparatively poorly known from other regions (5, 6). Dicynodonts were seemingly rare in the European Late Triassic, being known only from a single mandible (8) and questionable isolated bones (9). The Late Triassic dicynodont fossils described here, of Lisowicia bojani, are the first substantial finds from Europe (10, 11).

Many previous authors have analyzed the structure of the pelvic girdle of Triassic dicynodonts, resulting in the unanimous opinion that the posture of the hindlimbs was erect (12). By contrast, most authors agree that Triassic dicynodonts had sprawling forelimbs with the horizontal position of the humerus (10). Lisowicia has a relatively conventional dicynodont hindlimb construction but departs from the standard forelimb posture (Fig. 1). In many respects, its forelimb position resembles that of large quadrupedal dinosaurs, but forelimb elements of Lisowicia are morphologically similar to other dicynodonts (Fig. 2). The result is a subcursorial tetrapod with upright limb posture, unlike any other known stem-group mammal but comparable with that of large crown-group mammals such as rhinoceroses and hippopotami, as well as quadrupedal dinosaurs such as sauropodomorphs and ceratopsians.

Histological data from limb bones of Lisowicia provide life history data that complement its distinctness. Like other large dicynodonts, Lisowicia shows a large area of bone resorption in the inner cortex. However, unlike in other genera, there is no clear sign of growth-slowing later in life. The presence of potential lines of arrested growth in the studied tibia might be indicative of slower, more episodic growth. However, the lack of characteristic slow-growing tissue on the periphery

Fig. 1. The skeleton restoration of Lisowicia bojani. (A) Left humerus (ZPAL V.33/96) in ventral view. (B) Left radius (ZPAL V.33/665) in lateral view. (C) Cervical vertebrae (ZPAL V.33/720) in posterior view. (D) Dorsal vertebrae (ZPAL V.33/720) in lateral view. (E) Left pelvis (ZPAL V.33/720; ilium, pubis, and ischium) in lateral view. (F) Left femur (ZPAL V.33/75) in anterior view. (G) Left tibia (ZPAL V.33/75) in lateral view. (H) Left fibula (ZPAL V.33/75) in medial view. (I) Left ulna (ZPAL V.33/75) in lateral view. (J) Left scapulocoracoid (ZPAL V.33/468) in lateral view. (K) Fused quadrate and quadratojugal (ZPAL V.33/735) in posterior view. Scale bars, 10 cm (A) to (K); 1 m for the skeleton. (L) Light gray bones represent missing elements. il, ilium; pu, pubis; is, ischium.

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of the largest bones of *Lisowicia* suggests that the studied material represents either a fast-growing taxon or juvenile/subadult individuals of extremely large body size. However, the second explanation is rather unlikely because of its size and that these two bones are well ossified.

*Lisowicia* demonstrates that Late Triassic dicynodonts became specialized herbivores. It displays several features in the limb skeleton that suggest that this group evolved new postural adaptations. The massive scapula of *Lisowicia* lacks a distinct acromion process for articulation with the clavicle, the scapula articulates with the humerus on its posteroventrally (instead of posterolaterally) located glenoid, and distal articulation surfaces of the humerus are in the same plane instead of being rotated (formal taxonomic description is provided in the supplementary materials).

On the basis of published scaling relationships (14), we estimate an adult body mass of 9000 kg, which approaches that of an African elephant [the largest recorded individual stood 4 m at the shoulders and weighed 10,000 kg (15)]. This confirms that *Lisowicia* was certainly the largest Triassic nondinosaur tetrapod. Gigantism in herbivorous dinosaurs first emerged in the Late Triassic, with the evolution of the first large sauropodomorphs (16, 17) and then the earliest true sauropods (18). Until now, gigantism in the Triassic appeared to be entirely a dinosaur adaptation (19), and previously known Triassic dicynodonts were substantially smaller. The discovery of *Lisowicia* suggests that general ecological factors may have been driving the process, rather than clade-specific attributes of dinosaurs (20).

The find of *Lisowicia* shows that at least one dicynodont lineage also participated in the “push for gigantism” at the same time as the sauropodomorphs (20) but also suggests that their evolutionary history in the Late Triassic is poorly documented (Fig. 3A). In addition, recognition of *Lisowicia* as a placerine dicynodont together with the resurrection and recent description of *Pentasaurus* from South Africa (21) alters our understanding of the Late Triassic fossil record of dicynodonts. Although their relatively lower abundance and richness compared with those of Middle and early Late Triassic faunas suggest evolutionary decline, the concept of the Late Triassic kammeyeriforms as highly geographically restricted relicts is no longer valid (22). The recognition of dicynodonts in the late Norian–earliest Rhaetian of Europe (10) and Karoo Basin (27) conflicts with some ideas on early Late Triassic dicynodont extinction and survival, namely their supposed absence during the radiation of early sauropodomorphs (Fig. 3B).

Upright posture has been associated with decreased joint stress and energetic cost of locomotion (23). Selection pressures on some aspects of lifestyle or ecology were likely drivers of the evolution of the distinct posture of *Lisowicia* among dicynodonts. Increase in the body size of dicynodonts across the Late Triassic may have been driven by selection pressure to reach a size refuge from large predators (24). It is possible also that the gigantism of the latest dicynodonts was a metabolic adaptation that allowed these animals to maximize food retention time and consequently the energy gain (25). It took Late Triassic dicynodonts some 20 million years to produce giant forms (Fig. 3, B and C), and it was a rather gradual size increase and a similar pace

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**Fig. 2. Comparison of the reconstructed pectoral girdle of *Lisowicia bojani* with another dicynodont, dinosaur, and recent mammal.**

(A) Position of bones of *L. bojani* in anterior and lateral views. Some proportions of the bones were estimated by means of comparison with articulated skeletons of *Parakannemeyeria* (IVPP V. 979) and *Sinokannemeyeria* (IVPP V.974), but most were inferred from the size of articulation areas. (B) Reconstruction of large dicynodont *Stahleckeria* (GPIT/RE/8001) in anterior and lateral views. (C and D) Hypothetical flexibility of the humerus in protraction-retraction. (E) Reconstruction of rhinoceros *Diceros* in anterior and lateral views based on MPUWr 502223. (F) Reconstruction of *Triceratops* in anterior and lateral views based on (27). Scale bars, 10 cm.
to that observed in the evolution of herbivorous dinosaurs in the Mesozoic and mammalian lineages in the mid-late Paleogene (26). All suggest that in the Late Triassic, there was a substantial temporal overlap in the occurrence of very large herbivores: the previously dominant dicynodonts and their emerging ecological analogs among archosaurs, the sauropodomorph dinosaurs.

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Fig. 3. Phylogeny of kammerneyeriform dicynodonts and its relationship with the changes in femur length of dicynodonts and sauropodomorphs. (A) Time-calibrated phylogeny of the Triassic dicynodonts simplified after (22) (numerical ages for the base and top of Norian are based on the Chronostratigraphic Chart of the ICS v. 2018/8) with position of L. bojani. (B) Femur length (body size proxy) of sauropodomorph (black squares) and dicynodont (gray circles) taxa from the Middle to Late Triassic plotted at the stratigraphic range midpoints for each taxon. (C) Comparison of dicynodont femur bones (1, 2, ZPAL V.33/763, Ischigualastia; 3, UCMP 32394, Placerias; 4, MGZ 378 58M, Ischigualastia; 5, MCN PV 3600, Dinodontosaurus; 6, GPIT/RE/8002, Stahleckeria).

ACKNOWLEDGMENTS
We thank J. Dzik (Institute of Paleobiology, PAS) for proposing this research and support, M. Dec (Institute of Paleobiology, PAS) for help with preparation of dicynodont shoulder girdle virtual model, P. E. Ahlberg (Uppsala University) for discussion, D. Snitting (Uppsala University) for help with phylogenetic and computed tomography data, N. Campione (University of New England) for his help with body mass estimate, and K. Zaremba-Niedzwiedzka (Uppsala University) for help during preparation of the manuscript. We are very thankful to anonymous reviewers whose comments radically improved the final version of the paper. Funding: The study was supported by Polish grant (2012/01/B/NZ8/02707) and Swedish Vetenskapsrådet grant (2017-05248). Author contributions: T.S. designed the study. T.S. and G.N. performed the comparative and analytical work, participated in morphological studies, and wrote the paper. Competing interests: The authors declare no competing interests. Data and materials availability: All described specimens are accessioned at the Institute of Paleobiology, PAS (Poland).

SUPPLEMENTARY MATERIALS
www.sciencemag.org/content/363/6422/78/suppl/DC1
Materials and Methods
Supplementary Text
Figs. S1 to S16
Tables S1 to S7
References (28–74)
Movies S1 to S4
28 November 2016; resubmitted 4 August 2018
Accepted 29 October 2018
Published online 22 November 2018
10.1126/science.aal4853