

The Giant Crocodyliform *Sarcosuchus* from the Cretaceous of Africa

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New fossils of the giant African crocodyliform *Sarcosuchus imperator* clarify its skeletal anatomy, growth patterns, size, longevity, and phylogenetic position. The skull has an expansive narial bulla and elongate jaws studded with stout, smooth crowns that do not interlock. The jaw form suggests a generalized diet of large vertebrates, including fish and dinosaurs. *S. imperator* is estimated to have grown to a maximum body length of at least 11 to 12 meters and body weight of about 8 metric tons over a life-span of 50 to 60 years. Unlike its closest relatives, which lived as specialized piscivores in marginal marine habitats, *S. imperator* thrived in fluvial environments.

A partial skull of an enormous crocodyliform was discovered in 1964 by geologists mapping a remote section of the Ténéré Desert in Niger. Named *Sarcosuchus imperator* (1), its paleontological significance has never been fully explored, despite the recovery of many additional specimens (2).

We outline the skeletal anatomy of this giant among crocodyliforms with newly discovered skulls and partial skeletons from the Lower Cretaceous (Aptian-Albian) El Rhaz Formation in Niger (Fig. 1). The snout is proportionately long (about 75% of skull length) but is considerably broader than in the living gharial and other narrow-snouted crocodyliforms (Fig. 2, A to C). The subtriangular supratemporal fossae

are only slightly larger than the orbits, which are dorsally oriented and moderately telescoped. On the roof of the snout, the slender tips of the

nasals maintain contact with the premaxillae, which form an expansive bulla around the large and undivided external naris. The sidewall of the snout lacks any trace of antorbital or maxillary fossae [contrary to previous reports (1, 2)]. In palatal view, the relatively large internal nares are divided by a narrow pterygoid septum. They are positioned posterior to the suborbital fenestra and are bounded by the palatines anteriorly and pterygoids posteriorly.

There are 5 premaxillary teeth, which angle posteroventrally, and 30 maxillary teeth (Fig. 2A). The third and fourth premaxillary teeth are the largest teeth in the jaws; the 10th maxillary tooth is also enlarged (Fig. 2, A and C). There are 31 dentary teeth, the third and fourth of which are enlarged (Fig. 2, D and F). All of the dentary teeth occlude inside the maxillary tooth rows (Fig. 2D). Both upper and lower crowns have carinae fore and aft but are otherwise smooth and remarkably stout (Fig. 2E).

The lower jaw is noticeably shorter than the upper jaw, which overhangs the flared anterior

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Fig. 1. Mid-Cretaceous (Aptian-Albian, about 112 million years ago) paleogeographic map showing the position of Africa and location of fossils (white cross; Mollweide projection, latitude and longitude lines at 30° intervals with longitude greater than 120° omitted) (32).

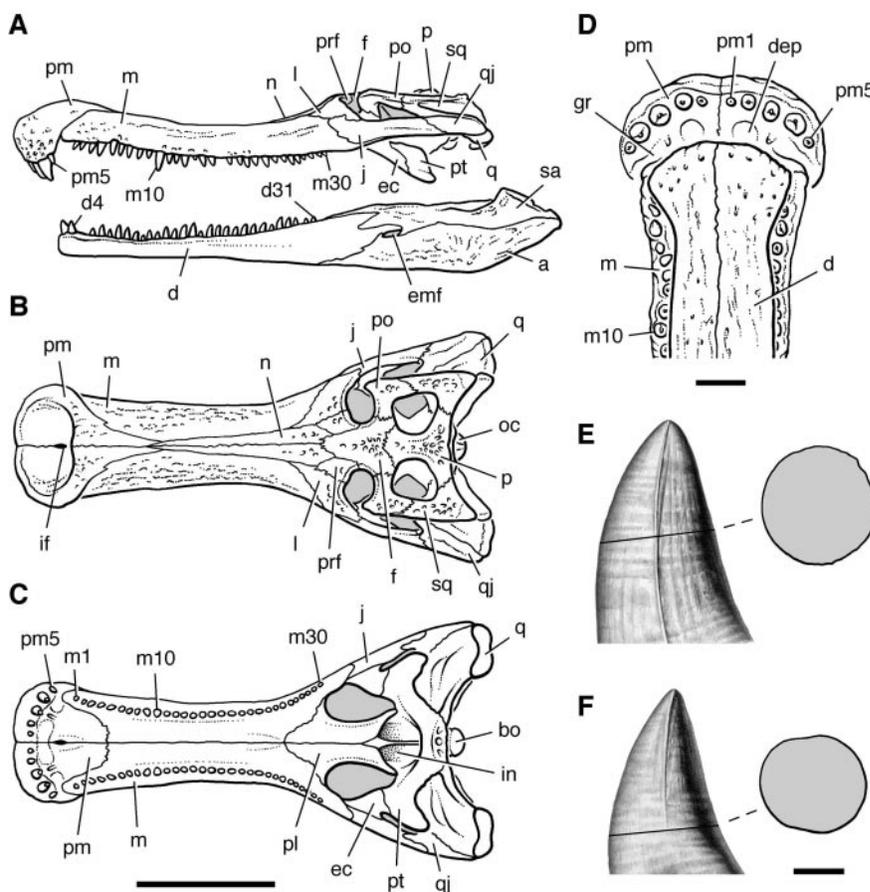


Fig. 2. Skull of *S. imperator* (MNN 604). (A) Skull and lower jaws in left lateral view. Cranium in (B) dorsal and (C) ventral views. (D) Anterior end of the jaws in ventral view. Right dentary tooth 4 (E) and 17 (F) in anterior and cross-sectional views. Scale bars: (A) to (C) 50 cm; (D), 10 cm; and (E) and (F), 1 cm. Abbreviations: 1-31, tooth number; a, angular; bo, basioccipital; d, dentary; dep, depression; ec, ectopterygoid; emf, external mandibular fenestra; f, frontal; gr, groove; if, incisive foramen; in, internal nares; j, jugal; l, lacrimal; n, nasal; oc, occipital condyle; p, parietal; pl, palatine; pm, premaxilla; po, postorbital; prf, prefrontal; pt, pterygoid; q, quadrate; qj, quadrate-jugal; sa, surangular; sq, squamosal.

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end of the dentary. A 10-cm gap is present between the premaxillary tooth row and the anterior margin of the lower jaw (Fig. 2D). Moreover, none of the enlarged upper or lower teeth occlude with palatal depressions or insert into the sizable diastemata in upper and lower tooth rows (Fig. 2D).

Several of these jaw features characterize *S. imperator* (3) and contrast sharply with the proportionately narrower snouts and more elongate, interlocking teeth of extant crocodylians that are primarily ichthyophagous (4). Terrestrial mammals comprise a substantial proportion of the diet of large extant crocodylians such as *Crocodylus niloticus* (4). Adult *S. imperator* may well have had a similar generalized diet that included large terrestrial prey such as the abundant dinosaurs that cohabited the region.

All of the vertebral centra are amphicoelous (Fig. 3, B and C), in contrast to the procoelous condition in Crocodylia or the incipiently procoelous condition in a few crocodylian outgroups (e.g., atoposaurids). Cervical vertebrae

have shallow ventral keels and short overlapping ribs. Dorsal vertebrae have long transverse processes but stout neural spines. The scapulae, coracoids, and pubes are strongly flared, and the iliac blade has a broad dorsal surface (Fig. 3G). Little is known of the limbs except the femur. The osteoderms resemble those of the goniopholidids *Sunosuchus* (5) and *Goniopholis* (6). Cervical and trunk osteoderms have low laterally positioned keels, hook-shaped anterolateral processes, and overlapping articular surfaces (Fig. 3, D and E). Caudal osteoderms are quadrangular or subtriangular and lack anterolateral processes and keels (Fig. 3F). The osteoderms formed a continuous surface from the anterior cervical vertebrae to the middle of the tail, as in *Araripesuchus* (7) and other basal crocodylians, but unlike extant crocodylians that exhibit discontinuity between the dermal armor of cervical and trunk regions (8).

In juvenile skulls of *S. imperator* up to 1 m in length (Fig. 4A, left) (9), the maxillary portion of the snout tapers in width anteriorly

as in *Gavialis* and the most slender-snouted living crocodylians. With maturity, the snout becomes substantially more robust and expands in width anteriorly, a very unusual snout shape (Fig. 4A, right). In addition, the narial bulla expands in width and invaginates, and the premaxillary teeth and alveolar margin turn inward (Fig. 2A and Table 1).

We used skull length (10) to estimate maximum body length in *S. imperator*, because no single skeleton is complete enough for direct measurement (Fig. 4B). In extant crocodylians, skull and total body lengths of subadult and adult individuals are strongly correlated and show negligible sexual variation (11–16). Linear equations show that the skull is proportionately longest relative to the body in the slender-snouted *Gavialis gangeticus*, intermediate in crocodylians such as *Crocodylus porosus*, and shortest in the broader snouted alligatorids such as *Alligator mississippiensis*.

Using a large adult skull of *S. imperator* (17) and the mean of total body length values based

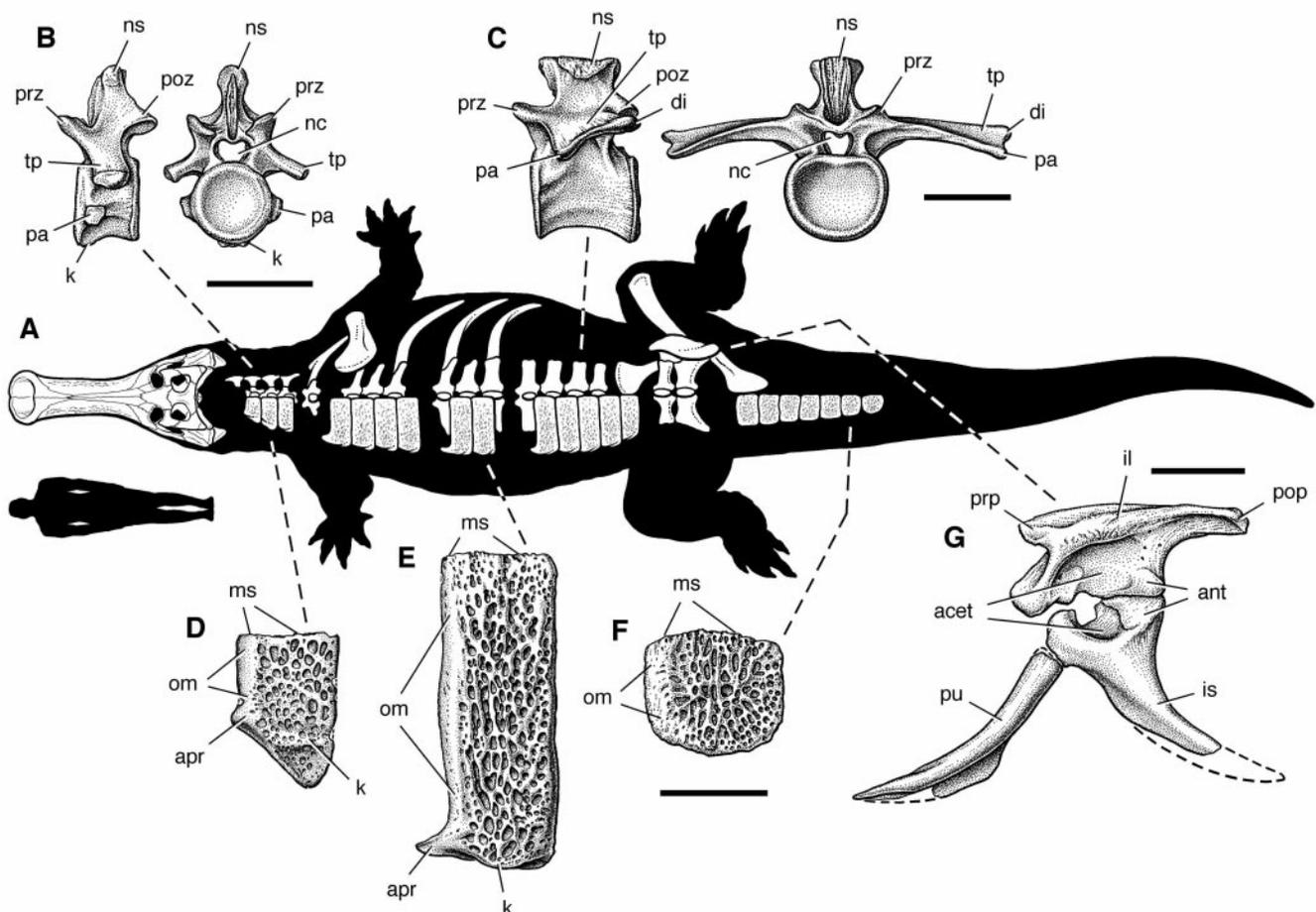


Fig. 3. Skeletal reconstruction of adult *S. imperator* showing (A) preserved bones (right side) and scutes (left side) (length 11.65 m, or 38 feet, 3 inches). Individual bones: (B) mid cervical vertebra in left lateral and anterior views (juvenile MNN 605), (C) posterior dorsal vertebra in lateral and anterior views (subadult MNN 606), (D) mid cervical scute in dorsal view (subadult MNN 607), (E) trunk scute in dorsal view (MNN 605), (F) caudal scute in dorsal view (MNN 607), and (G) pelvic recon-

struction (juvenile MNN 606, subadult MNN 607). Scale bars in (B) to (G), 10 cm; human silhouette is 1.68 m (5 feet, 10 inches) tall. Abbreviations: acet, acetabulum; ant, antitrochanter; apr, anterolateral process; di, diapophysis; il, ilium; is, ischium; k, keel; ms, median suture; nc, neural canal; ns, neural spine; om, overlap margin; pa, parapophysis; pop, postacetabular process; prp, preacetabular process; prz, prezygapophysis; pu, pubis; tp, transverse process.

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on regressions for *G. gangeticus* and *C. porosus* (18), we estimate maximum adult body length in *S. imperator* to be at least 11 to 12 m (or 37 to 40 feet) (Fig. 4B). This is slightly greater than previous estimates for *S. imperator* (2) and for the enormous Miocene crocodylid *Rhamphosuchus* (19). The Late Cretaceous crocodylian *Deinosuchus* may have achieved a similar maximum body size (20, 21), although this has yet to be established from reasonably complete cranial remains. Using a regression for body weight in *C. porosus* (22), we estimate that an adult *S. imperator* with a body length of about 11.5 m

would have a body weight of about 8.0 metric tons (or 17,500 pounds).

Thin sections of trunk osteoderms from a subadult individual (80% of maximum adult size) show about 40 annual growth rings or lines of arrested growth. This count suggests that a maximum adult size was achieved only after a duration of 50 to 60 years. Because extant crocodylians do not actively grow or typically survive this long in the wild (16, 23), *S. imperator* appears to have achieved its enormous body size by extending the duration of rapid growth as has been shown to be

the case in the giant crocodylian *Deinosuchus* (20), rather than accelerating the rate of bone deposition.

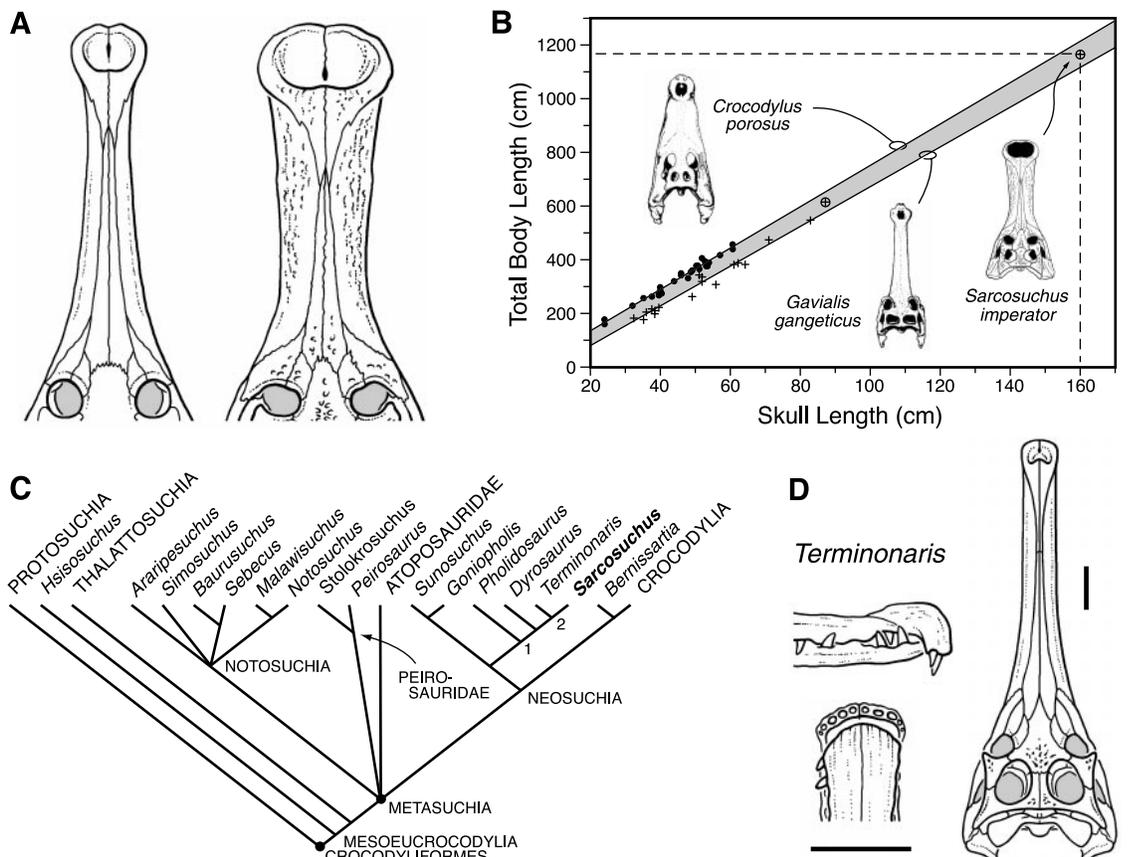
A suite of unusual features of the snout unites *Sarcosuchus* with a similar age, smaller bodied North American relative *Terminonaris* (24) (Fig. 4C, node 2). These features include the transverse expansion and ventral offset of the snout end (Figs. 2, A and D, and 4D) (25). The anterior snout is unknown in the earlier European relative *Pholidosaurus* (26), and so it is united more loosely with *Sarcosuchus*, *Terminonaris*, and *Dyrosaurus* (Fig. 4C, node 1). Linking *Dyrosaurus* with the aforementioned pholidosaurids as a clade is an interesting result supported previously by only one study (24). With one exception, members of this clade are slender-snouted, fish-eating specialists adapted to near-shore marine habitats. The giant crocodyliform *Sarcosuchus* stands in sharp contrast to its closest of kin, its jaws and teeth those of a generalist predator unearthed from fluvial deposits within a terrestrial setting.

At higher levels within Crocodyliformes, phylogenetic analysis placed the long-snouted thalattosuchians as the basal sister group to Metasuchia, a clade comprising an array of moderate or small-bodied taxa, some more closely related to *Notosuchus* and others to Crocodylia (Fig. 4C). Within this phylogenetic

Table 1. Measurements (in millimeters) and ratios of the crania of juvenile and adult *S. imperator* (Fig. 4A). Parentheses indicate estimated measurement.

Measurement or ratio	Juvenile	Adult
Cranial length (midline)	870	1500
Snout length	645	1150
Snout width, mid length	99	270
Snout width, anterior end of maxillae	117	365
Snout width, premaxillary narial rim	130	(440)
Occiput, width across paroccipital processes	326	520
Occiput, height at quadrate condyles	104	230
Dentary rami width, neck before distal flare	–	176
Dentary rami width, distal flare	–	285
Snout length/cranial length	0.74	0.77
Snout width: anterior end of maxillae/mid length	1.18	1.35
Snout width: premaxillae/mid length	1.31	1.63
Mandibular flare: flare/neck width	–	1.62

Fig. 4. (A) Outline of juvenile (left) and adult (right) snouts of *S.* (drawn to the same size) (for measurements, see Table 1). (B) Scatter plot and regression lines for total body length versus skull length in *Gavialis gangeticus* (crosses) and *Crocodylus porosus* (dots) with an estimate of maximum body length for an 87-cm juvenile skull of *Sarcosuchus imperator* (cross in circle) and the largest recorded adult skull (160 cm) (cross in circle with dashed lines) (18). (C) Strict consensus tree based on three minimum-length trees of 196 steps for 20 crocodyliform taxa based on maximum parsimony analysis of 72 characters (CI 0.52; RI 0.61) (33). *Sarcosuchus* (bold) and *Terminonaris* are united by seven unambiguous synapomorphies (node 2); another six unambiguous synapomorphies unite these taxa, *Pholidosaurus*, and *Dyrosaurus* (node 1) (characters and data matrix available at Science Online) (29). Dots at nodes for Crocodyliformes and Metasuchia signify node-based definitions of node-stem triplets (30). (D) Skull of *Terminonaris robusta* (98 cm length) in dorsal view (right), with the end of the snout shown in right lateral (top left) and ventral (bottom left) views. Scale bars in (D), 10 cm.



framework (27), *Sarcosuchus* and its closest relatives are understood as basal neosuchians, allied with but outside Crocodylia and the radiation that gave rise to all living crocodylians.

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17. The holotypic skull of *S. imperator* in the collections of the Musée National du Niger (MNN) has a length of 160 cm (2) and is the largest verified skull length on record (the same reference reported a 170-cm skull, but there are no figures of this specimen).
18. Regressions of body length (y) against head length (x) for *G. gangeticus* ($y = -69.369 + 7.4x$, $r^2 = 0.972$) and *C. porosus* ($y = -20.224 + 7.717x$, $r^2 = 0.98$) yield total body length estimates of 11.15 m and 12.15 m, respectively, for a skull length of 160 cm. Mean total body length equals 11.65 m (38 feet, 3 inches) (Fig. 4B). Data for *G. gangeticus* ($n = 17$) include measurements taken by P. Sereno from captive bred gharials in the Kukrail Picnic Center and Katerniaghat National Reserve in northern India and available measurements for individuals greater than 1.5 m long (11). Data for *C. porosus* ($n = 28$) come from wild individuals in northern Australia (A. Britton) and from available measurements for individuals greater than 1.5 m long (11) (excluding one suspicious record with body length of 4.91 m) (for measurement data, see supplementary material) (29).
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ARR1, a Transcription Factor for Genes Immediately Responsive to Cytokinins

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Cytokinins are a class of phytohormones involved in various physiological events of plants. The *Arabidopsis* sensor histidine kinase CRE1 was recently reported to be a cytokinin receptor. We used a steroid-inducible system to show that the transcription factor-type response regulator ARR1 directs transcriptional activation of the *ARR6* gene, which responds to cytokinins without de novo protein synthesis. This fact, together with characteristics of *ARR1*-overexpressing plants and *arr1* mutant plants, indicates that the phosphorelay to ARR1, probably from CRE1, constitutes an intracellular signal transduction occurring immediately after cytokinin perception.

Cytokinins induce a variety of physiological events, including cell division, chloroplast development, and shoot formation (1, 2). These cytokinin responses in *Arabidopsis* are at least partly triggered through the recognition of cytokinins by the sensor protein CRE1, which is a member of the protein histidine kinase family (3, 4). In bacteria, histidine kinases participate in His-Asp phosphorelays, which respond to environmental stimuli, usually in association with cytoplasmic response regulators, the majority of which are transcription factors (5). If

the His-Asp phosphorelay is also the case in plants, an intracellular signal transduction pathway starting from the CRE1 sensor may involve response regulators. The *Arabidopsis* genome codes for 22 response regulators (ARRs), 12 of which contain a Myb-like DNA binding domain called ARRM (type B) (6–9). The remainder (type A) possess no apparent functional unit other than a signal receiver domain containing two aspartate and one lysine residues (DDK) at invariant positions, and their genes are transcriptionally induced by cytokinins without de novo protein synthesis (7, 9, 10). The type B members, ARR1 and ARR2, bind DNA in a sequence-specific manner and work as transcriptional activators (11, 12).

We analyzed the morphological characteristics of transgenic plants carrying *35S::ARR1* and *35S::ARR1ΔDDK* genes (13), in which the full-length ARR1 and its truncated version missing

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