

A Complete Skeleton of a Late Triassic Saurischian and the Early Evolution of Dinosaurs

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Characterizing the evolutionary history of early dinosaurs is central to understanding their rise and diversification in the Late Triassic. However, fossils from basal lineages are rare. A new theropod dinosaur from New Mexico is a representative of the early North American diversification. Known from several nearly complete skeletons, it reveals a mosaic of plesiomorphic and derived features that clarify early saurischian dinosaur evolution and provide evidence for the antiquity of novel avian character systems including skeletal pneumaticity. The taxon further reveals latitudinal differences among saurischian assemblages during the Late Triassic, demonstrates that the theropod fauna from the Late Triassic of North America was not endemic, and suggests that intercontinental dispersal was prevalent during this time.

By the Late Triassic (~230 million years ago), Dinosauria had diversified into three major lineages: Sauropodomorpha, Theropoda, and Ornithischia (1, 2). In comparison to the later Mesozoic, fossils of Triassic early dinosaurs and their closest relatives are generally rare, fragmentary, and incomplete (3, 4). Indeed, the record from the Ischigualasto Formation, which provides some of the most detailed information on early dinosaur evolution (1, 2, 5), reveals that dinosaur specimens constitute less than 6% of the tetrapod assemblage (6). This depauperate fossil record has limited our understanding of early dinosaur interrelationships, diversification, and paleobiogeography, and the origin of modern avian morphologies during a critical interval of Mesozoic climate change and faunal turnover (7–9).

Here we report on a new carnivorous dinosaur represented by two nearly complete skeletons and several other partial specimens collected in a tightly associated small grouping at a single locality. Characterization of this taxon's morphology and phylogenetic history enables us to solidify basal saurischian dinosaur relationships and bears directly on the evolution of early saurischian character systems, paleobiogeography, and diversification.

Systematic paleontology: Archosauria Cope 1869 *sensu* Gauthier and Padian 1985. Dinosauria

Owen 1842 *sensu* Padian and May 1993. Theropoda Marsh 1881 *sensu* Gauthier 1986. *Tawa hallae*, nov. taxa.

Etymology. *Tawa*, Hopi name for the Puebloan sun god; *hallae*, after Ruth Hall, who collected many of the specimens that formed the genesis of the Ghost Ranch Ruth Hall Museum of Paleontology (GR) collections. **Holotype.** GR 241. A nearly complete associated but disarticulated skull and postcranial skeleton. **Paratypes.** A nearly complete skeleton of a larger individual (GR 242) and at least six other individuals found in the same area of the quarry [see supporting

online material (SOM) (10)] including femora, pelvis, and tail (GR 155) and cervical vertebrae (GR 243). A complete right femur (GR 244) is from Hayden Quarry (HQ) site 3. **Locality and horizon.** Site 2, HQ, Ghost Ranch, Rio Arriba County, New Mexico, USA. The HQ has been dated to ~215 to 213 million years ago (11) and is in the lower portion of the Petrified Forest Member of the Upper Triassic Chinle Formation (12).

Diagnosis. A theropod diagnosed by the following combination of characters (autapomorphies are noted by an asterisk here and in Figs. 1 and 2): Prootics meet on the ventral midline of the endocranial cavity; anterior tympanic recess greatly enlarged on the anterior surface of the basioccipital and extending onto prootic and parabasisphenoid; deep recess on the postero-dorsal base of paroccipital process*; sharp ridge extending dorsoventrally on the middle of the posterior face of the basal tuber*; incomplete ligamental sulcus on the posterior side of the femoral head and semicircular muscle scar/excavation on the posterior face of the femoral head*; small semicircular excavation on the posterior margin of the medial posterior condyle of the proximal end of the tibia*; “step” on ventral surface of the astragalus*; and metatarsal I similar in length to other metatarsals. See SOM for differential diagnosis (10).

Description. The holotype material is a juvenile or subadult individual, based on comparison to the largest femur among the referred material and the open braincase and neurocranial sutures. The premaxilla (Fig. 1) is similar to that

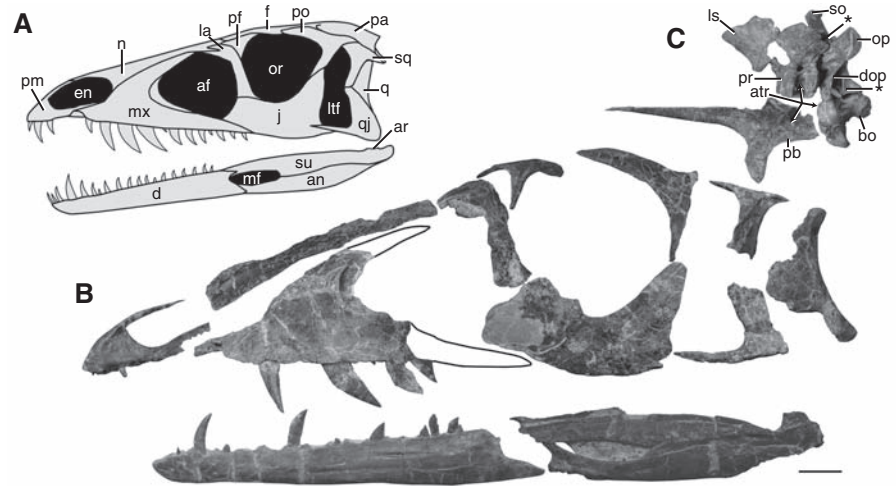


Fig. 1. The skull of *T. hallae* nov. taxa. **(A)** Reconstruction of the skull in lateral view. **(B)** The preserved skull elements of the holotype of *T. hallae* (GR 241) in left lateral view (j, qj, and the posterior portion of the mandible were reversed, and the matrix was digitally erased from the pm, mx, and n). The processes of the maxilla are present but obscured by matrix in lateral view, so they are represented here in outline. **(C)** Braincase of *T. hallae* in left lateral view (parabasisphenoid reversed). Abbreviations in the figure are as follows: antorbital fenestra (af), angular (an), articular (ar), anterior tympanic recess (atr), basioccipital (bo), dentary (d), descending process of the opisthotic (dop), external naris (en), frontal (f), jugal (j), lacrimal (la), laterosphenoid (ls), lower temporal fenestra (ltf), maxilla (mx), mandibular fenestra (mf), nasal (n), opisthotic (op), orbit (or), parabasisphenoid (pb), prefrontal (pf), premaxilla (pm), postorbital (po), prootic (pr), quadrate (q), quadratojugal (qj), supraoccipital (so), squamosal (sq), and surangular (su). Scale bar, 1 cm. Autapomorphies are noted by an asterisk.

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of coelophysids in possessing unserrated premaxillary teeth and a narial process of the premaxilla that is elongate and forms a low angle with the alveolar margin. It differs from neotheropods by having a relatively tall maxillary process that extends dorsally beyond the posterior border of the naris as in *Herrerasaurus*. In dorsal view, the premaxilla-nasal suture is simple, lacking the W-shaped morphology present in Neotheropoda. Like basal neotheropods (such as *Coelophysis bauri* and *Dilophosaurus wetherilli*), a subnarial gap is expressed between the premaxilla and maxilla, but unlike these taxa, *Tawa* and *Herrerasaurus* lack an extensive antorbital fossa on the lateral surface of the maxilla. A concave narial fossa is located on the anterolateral surface of the nasal. A lateral ridge on the nasal forms the dorsal border to the antorbital fossa, similar to *Eoraptor lunensis* and *C. bauri*. Unlike most basal neotheropods, in *Tawa* the jugal participates in the antorbital fenestra and lacks distinct lateral ridges on the maxilla and jugal. The lacrimal is anterodorsally inclined, as in *Herrerasaurus* and more basal dinosaurs. The anterior process of the quadratojugal is elongate as in *C. bauri* but unlike that in *Herrerasaurus*.

Tawa lacks several braincase character states present in most other dinosauriforms. Absent character states include a reduced and medially

recessed descending process of the opisthotic [the crista interfenestralis (10)] and a metotic strut. A weak parabasisphenoid recess is present on the ventral surface of the braincase, similar to that in *Herrerasaurus*, *Eoraptor*, and Neotheropoda.

The vertebral column (Fig. 2) shares several apomorphic features with neotheropods. Cervical vertebrae preserve anterior pneumatic pleurocoels (as rimmed fossae) and anterior and posterior infrazygapophyseal fossae; these features are present in all basal neotheropods. The diapophyses and parapophyses of the anterior to midcervical vertebrae are close together and nearly contact. *Tawa* shares with *Herrerasaurus* pronounced ventral keels on the cervical vertebrae and elongate prezygapophyses in the distal caudal vertebrae, as in neotheropods. The dorsal vertebrae possess hyposphene-hypantra articulations and there appear to be only two sacral vertebrae.

The complete forelimb (found in articulation) and shoulder girdle share numerous apomorphic features with *Herrerasaurus* and neotheropods such as *C. bauri* and *D. wetherilli*. The elongate manus is particularly theropod-like, with metacarpals abutting each other along their shafts (without overlapping margins) and the presence of weak extensor pits (traits also present in the basal ornithischian *Heterodontosaurus*). The shaft width of metacarpal IV is reduced in *Tawa*, and

the accompanying phalanges are greatly reduced. Moreover, digit V is completely absent, as in *Herrerasaurus* and other basal theropods. The manus of *Tawa* retains a plesiomorphically small medial-most distal carpal. The hand of *Tawa* also retains nine carpals, similar to the basal ornithischian *Heterodontosaurus*, whereas *Herrerasaurus* has seven and *C. bauri* has five.

The *Tawa* pelvis is generally plesiomorphic with respect to neotheropods. The preacetabular process of the ilium (GR 241) does not extend anterior to the pubic peduncle. Additionally, the anterior end is rounded, unlike the squared-off morphology of neotheropods. The supraacetabular crest projects laterally without any ventral deflection but is distally restricted in that it does not approach the articular facet of the pubic peduncle. The supraacetabular crest is continuous with the ventrolateral edge of the postacetabular process, as in coelophysoids. In contrast, the pubis displays a well-developed pubic boot similar to that present in neotheropods, *Herrerasaurus*, and *Staurikosaurus*.

The proximal articular sulcus of the femur, common to Dinosauriformes, is asymmetrically developed in *Tawa* and neotheropods. The fourth trochanter is symmetrical and bladelike in lateral outline, in contrast to the plesiomorphic saurischian condition of a thick asymmetrical ridge. The proximal condyles of the tibia align along the posterior

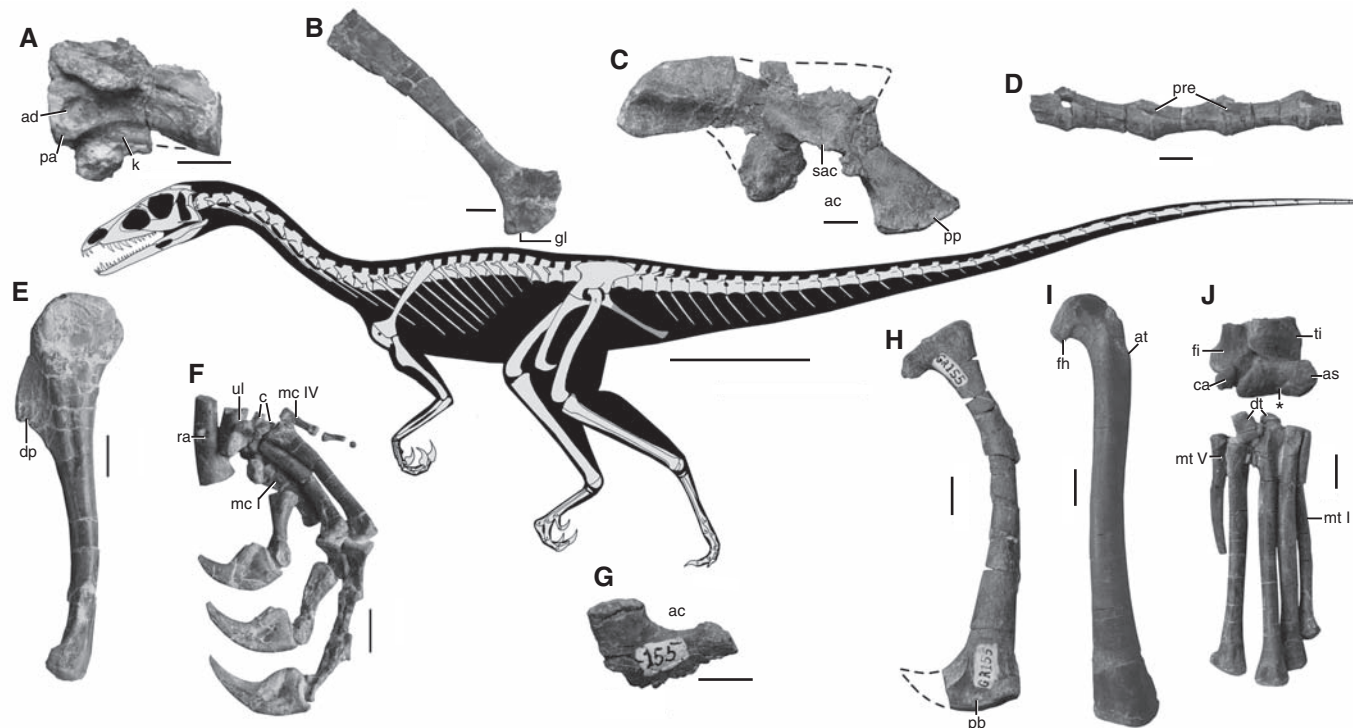


Fig. 2. Skeletal anatomy of *T. hallae* nov. taxa. (A) Anterior cervical vertebra (GR 243) in lateral view. (B) Right scapula (GR 242) in lateral view. (C) Right ilium (GR 155) in lateral view. (D) Middle caudal vertebrae (GR 155) in lateral view. (E) Left humerus (GR 242) in posterolateral view. (F) Complete right manus (GR 242) in posterior view. (G) Right proximal portion of the ischium (GR 155) in lateral view. (H) Right pubis (GR 155) in lateral view. The proximal portion of the apron is incomplete. (I) Left femur (GR 244) in anterior view. (J) Articulated right pes (GR 242) in anterior view.

Abbreviations in the figure are as follows: acetabulum (ac), anterior depression (ad), astragalus (as), anterior trochanter (at), carpals (c), calcaneum (ca), deltopectoral crest (dp), distal tarsals (dt), femoral head (fh), fibula (fi), glenoid (gl), keel (k), metacarpal (mc), metatarsal (mt), parapophysis (pa), pubic boot (pb), pubic peduncle (pp), prezygapophyses (pre), radius (ra), supraacetabular crest (sac), tibia (ti), and ulna (ul). Matrix was digitally erased from around the manus. Scale bars, 1 cm and reconstruction scale = 0.25 m. Autapomorphies are noted by an asterisk.

edge as in *Herrerasaurus* and neotheropods (such as *C. bauri*). The tibia lacks a fibular crest, and the cnemial crest is not proximally expanded above the proximal articular surface. Two neotheropod character states—an expanded medial edge and a distinct proximodistally elongate posterior ridge—are absent on the distal end of the tibia in *Tawa*. The pes of *Tawa* is plesiomorphic in having metatarsals I to IV elongated. As in other basal saurischians, the fourth tarsal lacks a rounded posterior edge and the astragalus and calcaneum are not co-ossified. The astragalus retains a rimmed basin on the proximal surface posterior to the ascending process. However, the calcaneum of *Tawa* is reduced relative to the astragalus in a manner similar to that of neotheropods. It is mediolaterally compressed and completely lacks a medial process. Metatarsal I retains contact with the ankle in *Tawa*, as in *Herrerasaurus* and *Eoraptor*.

Cladistic analysis identifies *T. hallae* as the closest taxon to Neotheropoda (Fig. 3). The transitional morphology of *Tawa* present in both the skull and the postcranium results in the recovery of *Herrerasaurus* and *Eoraptor* as definitive basal theropods. Although initially described as early theropods (1, 2), the phylogenetic affinities of these taxa have been debated, with some authors arguing for a nondinosaurian position for *Herrerasaurus* (13), a nontheropod, but basal saurischian position for *Herrerasaurus* and *Eoraptor* (14), a basal saurischian position for *Herrerasaurus* and a theropod position for *Eoraptor* (15), or a basal theropod position for both taxa (5). In our analysis, *Herrerasaurus* forms a monophyletic Herrerasauridae with *Staurikosaurus* and *Chindesaurus* at the base of Theropoda, although clade support is weak (10). It takes six steps to recover *Tawa* and *Chindesaurus* as sister taxa. *Eoraptor* and *Tawa* form successively closer sister taxa to Neotheropoda.

Despite the absence of postcranial skeletal pneumaticity in the basal saurischians *Saturnalia*, *Herrerasaurus*, and *Eoraptor*, the presence of anterior cervical pleurocoels in *Tawa* and *Chindesaurus* supports the hypothesis that the origin of cervical air sacs predates the divergence of Neotheropoda and may be ancestral for Saurischia or possibly even Ornithodira [(16) and references therein]. The disarticulated braincase of the holotype of *Tawa* also documents the earliest example of an expansive pneumatic anterior tympanic recess, and the caudal expansion of this recess into the basioccipital. The weak excavation on the ventral surface of the basisphenoid in *Tawa* relative to neotheropods also suggests that development of the cavities associated with the middle ear sac (such as the anterior tympanic recess) preceded the elaboration of the median pharyngeal system into an expansive basisphenoid sinus in neotheropods. Despite the extensive nature of the anterior tympanic recess of *Tawa*, an antero-medial border to the recess is still provided by the basisphenoid and prootic. This reinforces the hypothesis that contralateral connections of the tympanic diverticula are not homologous in crocodiles

and birds, and that the “interaural passage” used in sound localization by modern avians, and possibly some basal coelurosaurs (17), had not evolved by the time of the divergence of *Tawa* from Neotheropoda.

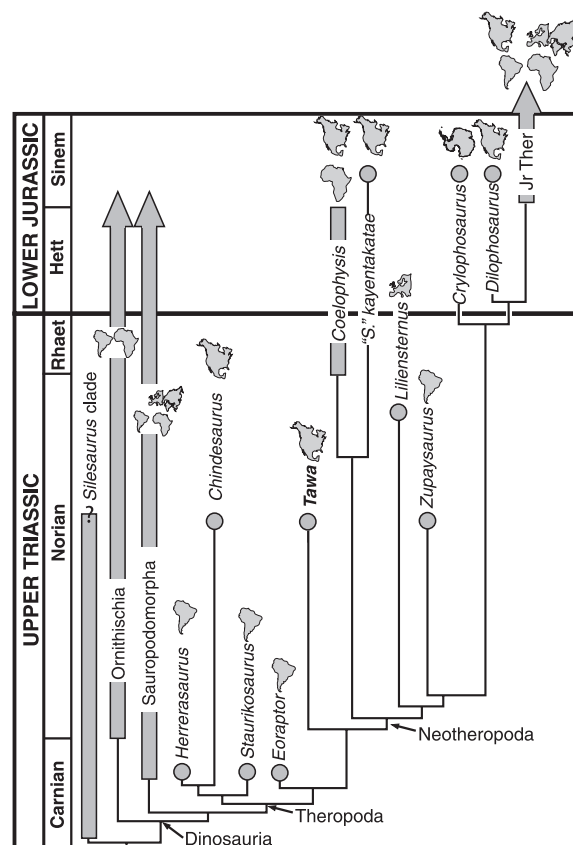
Coelophysoid monophyly is unsupported in our analysis. Without *Tawa* and *Eoraptor*, phylogenetic analyses support a variety of characters as synapomorphies of a clade of “coelophysoid” taxa (*Coelophysis*, “*Syntarsus*” *kayentakatae*, *Liliensternus*, *Zupaysaurus*, *Cryolophosaurus*, and *Dilophosaurus*), because they are absent in both tetanurans and neotheropod outgroups (10). With *Tawa*, these characters are more clearly inferred to have been primitive for Neotheropoda and later lost in the lineage leading to Tetanurae (10). Previous work (18) suggested that resolution of an inclusive Coelophysoidea may be artificial for two reasons: (i) the failure to sample Early Jurassic taxa that possess a mosaic of coelophysoid and more-derived neotheropod features, and (ii) the failure to recognize a broader distribution among basal dinosaurs of many coelophysoid synapomorphies. *Tawa* confirms these hypotheses because it possesses both coelophysoid traits (such as the low angle of the narial process to the premaxillary alveolar margin, the presence of a subnarial gap, and a strong ridge connecting the supraacetabular shelf and brevis shelf) and neotheropod plesiomorphies that collapse Coelophysoidea in our analysis (10). We suggest that the traditional basal theropod clade Coelophysoidea has acted as a phylogenetic vacuum cleaner, with deep thermo-

pod synapomorphies and ceratosaur/tetanuran reversals being “sucked up” and optimized as coelophysoid synapomorphies, because critical taxa were absent across the basal theropod tree. This result reiterates the centrality of new discoveries and increased taxon sampling to providing increased phylogenetic accuracy by breaking long branches [see references in (19)], is critically important for polarizing character evolution in more-derived theropod lineages, and bears directly on the magnitude of turnover in theropod faunas at the Triassic-Jurassic and Early-to-Middle Jurassic boundaries (7, 20).

The presence of multiple carnivorous theropod lineages (*Chindesaurus*, a coelophysoid-grade theropod, and *Tawa*) and an absence or rarity of sauropodomorphs suggest that the HQ saurischian assemblage was qualitatively more like that of the older Ischigualasto Formation (21), where only a single sauropodomorph specimen has been reported, than that of the overlying Los Colorados Formation, which is closer in age to the Hayden assemblage (21). In contrast, the Los Colorados saurischian assemblage contains diverse and abundant sauropodomorphs but only a single reported theropod. These patterns support the hypothesis that the evolution of Triassic dinosaur faunas was diachronous across Pangea (12).

The HQ taxa are spread throughout the stem of theropod phylogeny, and none are each other’s closest relative. This demonstrates that they do not represent a monophyletic Norian radiation endemic to the North American protocontinent. Instead, the

Fig. 3. Phylogenetic relationships of *T. hallae* among dinosaurs and the paleobiogeographic distribution of early dinosaur taxa [see SOM (10) for details of the analysis]. Relative temporal relationships for the early Mesozoic are indicated, with minimum ghost lineage extensions implied by phylogeny. The length of the gray bars indicates stratigraphic imprecision, and those with arrows continue through the Sinemurian. Abbreviations are as follows: Hett, Hettangian; Jr Ther, other Jurassic theropods; Rhaet, Rhaetian; and Sinem, Sinemurian.



HQ theropods are separated from each other by branches subtending taxa from other continental faunas, indicating that dispersal between these geographical regions probably occurred during the Camian-Norian. Other contemporaneous theropod assemblages from Europe (22) and South America contain only members of Neotheropoda and do not match the diversity of theropods at the HQ.

Both parsimony (23) and likelihood-based (24) biogeographic methods for ancestral range reconstruction reject scenarios of an endemic North American theropod radiation (10). Analyses differ slightly in support for range reconstructions at individual nodes, but provide high relative support for inferring the South American protocontinent as the ancestral range through the spine of the basal dinosaur tree (10). In most analyses, the distributions of the three HQ theropods are explained by either dispersal to North America from South America or allopatric and/or vicariant speciation from an ancestral widespread range encompassing North and South America (10). This pattern is apparent in many other clades during the Late Triassic, including actosaurs (25), crocodylomorphs (26), shuvosaurids (27), and “traversodont” cynodonts (28). The ubiquity of this phylogenetic pattern in clades encompassing markedly different ecomorphotypes argues against the presence of physiographic barriers isolating the Norian faunas of North America. Thus, the conspicuous absence of saurpodomorphs in the Norian of North America (3, 12) cannot be attributed to their inability to disperse to these areas but rather to their inability to become established in areas sampled by Late Triassic terrestrial sedimentary outcrops. Latitudinal differentiation of Norian faunas attributable to climatic

differences and climatic tolerances remains an intriguing explanation for the global ubiquity of basal theropod taxa such as *Tawa* and the North American absence of saurpodomorphs. Indeed, recent paleoclimate models and proxy data for the Late Triassic reveal a marked dichotomy between low and high paleolatitudes (29). Alternative explanations, including smaller-scale ecological differences, community-level interactions, or facies-dependent sampling biases, cannot be ruled out, nor are these explanations mutually exclusive (12). Explaining these patterns remains an outstanding problem in early dinosaur evolution at the nexus of phylogenetic, geologic, and paleoclimatic studies of the Late Triassic.

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Supporting Online Material

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SOM Text
Figs. S1 to S8
Tables S1 to S5
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An Analytical Solution to the Kinetics of Breakable Filament Assembly

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We present an analytical treatment of a set of coupled kinetic equations that governs the self-assembly of filamentous molecular structures. Application to the case of protein aggregation demonstrates that the kinetics of amyloid growth can often be dominated by secondary rather than by primary nucleation events. Our results further reveal a range of general features of the growth kinetics of fragmenting filamentous structures, including the existence of generic scaling laws that provide mechanistic information in contexts ranging from in vitro amyloid growth to the in vivo development of mammalian prion diseases.

Molecular self-assembly is the basis of phenomena ranging from the construction of materials for nanotechnology (1) to the formation of molecular machineries within living cells (2). The assembly of these frequently complex and highly intricate structures typically depends on a series of individual steps that are inherently simple and are therefore amenable in principle to a quantitative analysis

based on physical principles. An important class of molecular structures that emerges from the self-assembly of simpler components is that of filamentous assemblies of biological macromolecules. Many proteinaceous aggregates of this type, which are increasingly linked with normal and aberrant biological processes (2), form through a nucleation mechanism followed by a self-templated growth where the ends of exist-

ing filaments recruit soluble molecules into aggregates that can themselves multiply through secondary nucleation processes such as fragmentation (Fig. 1A).

One of the key questions in molecular self-assembly phenomena is to determine the relative importance of different microscopic processes and their contribution to the overall reaction (3, 4). Master equation approaches are particularly powerful in this context as they enable the explicit description of microscopic processes and have thus offered a series of insights (5–10) into phenomena including the formation of amyloid fibrils, species that are of increasing interest particularly because of their association with clinical disorders ranging from Alzheimer’s disease to type II diabetes (2). The lack of analytical

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