in the sediment increases dissolution. Below the lysocline, as depth increases, dissolution should continue to increase until the calcite compensation depth is reached. The results of this study differ from those of other published accounts of dissolution because below 4400 m dissolution decreases instead of becoming more severe.

The depth at which dissolution decreases appears to be controlled by a change in deep circulation. Using samples from the same data set, Bulfinch *et al.* (*15*) encountered the inshore margin of the high-velocity core of the Western Boundary Undercurrent (WBUC) on the lower rise, below about 4450 m. The increase in grain size and alignment that marks the high-velocity core of the WBUC coincides precisely with the decrease in dissolution. I conclude from these data that water in the high-velocity core of the WBUC is not corrosive with respect to carbonate. This conclusion is surprising in light of a recent report (*16*) that suggests that the WBUC below 4000 m is predominantly southern-source bottom water that should be corrosive to carbonate. These opposing conclusions may reflect a fundamental difference between physical oceanographic and geologic data. Physical oceanographic data reflect practically instantaneous events (*17*); geologic data are time-averaged, in this case incorporating data on sediments deposited over several hundred years.

WILLIAM L. BALSAM
Natural Science Division,
Southampton College of
Long Island University,
Southampton, New York 11968

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18. I thank all those who participated in the collection of core samples on R.V. *Eastward* cruise E4A-80. Support for R.V. *Eastward* samples was provided by NSF grant OCE 77-23278A02. This report was prepared while I was on sabbatical at the University of Georgia; use of the facilities there is appreciated. M. T. Ledbetter, B. B. Ellwood, and R. Thunell reviewed the manuscript and provided valuable criticisms. F. Balsam assisted in editing the manuscript. B. Daniel drafted the figures. This research was supported in part by the Climate Dynamics Program, Division of Atmospheric Sciences, under NSF grant ATM-7817854.

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Functional Morphology of *Homo habilis*

Abstract. *Olduvai hominid (O.H.) fossils 7, 8, and 35 represent the earliest species of the genus* Homo *dated at 1.76 million years. The O.H. 7 hand, jaw, and skull and the O.H. 8 foot come from one subadult individual, and the O.H. 35 leg are also those of* Homo habilis. *The skeleton represents a mosaic of primitive and derived features, indicating an early hominid which walked bipedally and could fabricate stone tools but also retained the generalized hominoid capacity to climb trees.*

Olduvai Gorge in northern Tanzania has yielded a wealth of early human fossils and cultural remains over the last 23 years (*1, 2*). None of the questions raised by the fossil finds has been more debated than whether or not an advanced hominid, early *Homo* (*Homo habilis*), existed contemporaneously with *Australopithecus boisei* (*3–5*). As a result of corroborative evidence from East Turkana, Kenya (*6, 7*), and the Omo River Valley, Ethiopia, *Homo habilis* has been accepted as a valid taxon (*8*). Although the taxonomic controversy has abated, our understanding of the anatomy and functional morphology of *Homo habilis* is still obscure. This is in part because of conflicting functional conclusions regarding fossils assigned to *Homo habilis* (*9–15*) and in part because of uncertainty over the associations of various parts of the postcranium with one taxon or another (*2, 3, 11, 16–19*).

The most important relevant postcranial remains from Olduvai Gorge come from sites FLK (level 22) and FLK NN (level 3) (*3, 10, 11, 20–22*). In early 1960 a tibia and fibula (O.H. 35) were found at the former site. Not much later, and nearby, a hand, skull, and jaw (O.H. 7) and a foot (O.H. 8) were recovered from FLK NN (level 3). The juvenile hand, jaw, and skull fragments became the holotype of *Homo habilis* (*3, 23*); the foot, purported to be that of an elderly female (*24*), became part of the paratype. The FLK tibia and fibula (O.H. 35) were placed in taxonomic limbo (*3, 10, 11, 16, 18, 19*). In the years that followed, O.H. 35 was assigned to *Australopithecus africanus* (*7*), *A. robustus* (*15*), and *Homo habilis* (*2*). Because one study of the O.H. 7 hand (*25*) suggested that the taxonomic assessment and assignments of the bed I material might be different from those originally reported, we undertook further study of the O.H. 7, 8, and 35 fossils in order to better understand the functional morphology and habitus of *Homo habilis*.

The O.H. 7 hand has 13 bones (*7, 20, 25*). The absence of epiphyses on the middle phalanges and the presence of fused basal epiphyses on the distal phalanges indicate that the individual was of a developmental stage equivalent to a modern human female of 13 years 6 months (*26*). The morphology and length of the distal phalanges resemble those of living humans (*25, 27*), but the fossil distal phalanges differ from humans principally in the greater diameter at midshaft. The middle phalanges differ from humans by being robust and curved, with well-marked flexor digitorum superficialis insertions that suggest powerful grasping potential, such as that of living apes (*25, 28*). The broken proximal phalanges with their thick cortices and marked curvatures also suggest a powerful grasping hand similar in overall configuration to chimpanzees and female gorillas.

Two wrist bones, a scaphoid and a

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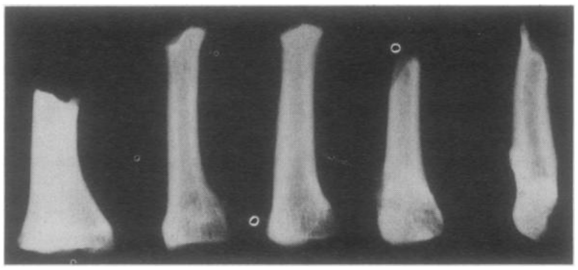

Fig. 1. Radiograph of O.H. 8 metatarsals I through V (left to right, lateral views). Although there is some postmortem erosion of the ends, epiphyseal lines can be seen on the distal ends of metatarsals II and III (which lack epiphyses). Metatarsals I, IV, and V have been broken, perhaps by carnivores.

trapezium, shed light on the thumb of *Homo habilis*. The scaphoid tubercle (partially broken) and articular surface for the trapezium are pongid-like, but the pollical carpometacarpal joint is distinctively human-like. The broad, flattened metacarpal surface on the trapezium indicates a strong, stout thumb. This morphology correlates with that of the distal phalanges and suggests that changes in the human direction are well advanced in the thumb and fingertips of *Homo habilis* but that power-grasping capabilities (*29*) are retained in the more proximal segments of the fingers (*25*).

The O.H. 8 foot, which has been extensively studied (*10, 13, 30*), was judged to that of an adult (*31*) and was thought to represent a different individual from O.H. 7. Our analysis indicates that the foot is that of a subadult individual. We base this conclusion on the fact that metatarsals IV and V (and perhaps I also) have been broken by carnivore biting, whereas metatarsals II and III give the appearance of bones that are simply lacking their epiphyses (*25*) (Fig. 1). That metatarsals II and III lack the heads can be adduced by two facts: the distal ends of the bones have been lost at the point where the epiphyseal plate is normally located (that is, at the epicondylar line), and radiographically the two bones retain trabeculae in their distal ends, indicating that they lack only the epiphysis. Metatarsals IV and V, broken further proximally, have no cancellous network in their distal ends, and their medullary cavities are open at the break points. Furthermore, the age of O.H. 8, as judged from the fused basal epiphysis of metatarsal I, together with the unfused heads of metatarsals II and III, is 13.7 to 13.9 years (*32*). This age for the foot concurs with the age estimate of 13.6 years for the O.H. 7 hand, which was found on the same surface and close by, and it thus appears that the hand and foot may be from the same individual.

The foot has a metatarsal robusticity formula fully commensurate with a bipedal striding gait (*33*). The plane of the first tarsometatarsal joint is human-like in that the articular surface of the medial cuneiform faces distally. Opposing tubercles for the attachments of the medial tarsometatarsal ligament prevent any significant abduction at that joint. This configuration is distinct from that in nonhuman primates where there is wide abduction of the halluces. The fossil hallux is stout, has proportions (relative to metatarsal II) that are within the human range and, as in humans, displays less axial torsion than that of apes. Metatarsal V, if its shape has not been distorted (*31*), shows a mediolateral flattening of its proximal portion similar to that of humans and distinct from apes. The calcaneus has an excavation on the inferomedial aspect of the distal surface. Into this excavation fits a projection of the cuboid which rotates into a close-packed position that prevents extreme supination of the forefoot at the midtarsal joint. The same condition of the calcaneocuboid articulation is present in humans, but apes and monkeys retain a more generalized pivot joint permitting greater mobility. The cuboid is narrower and more rectangular (in dorsal view) than that of African apes, and the peroneal groove is also narrower in the fossil and in humans than in the apes. As in humans, the inferior aspect of the navicular is expanded in the area which serves as the attachment site for the cubonavicular and plantar calcaneonavicular ligaments. The tuberosity of the navicular is also human-like in its relative reduction, unlike the African apes. The surface for the medial cuneiform is flat to concave in humans and O.H. 8; it is convex in the apes (and monkeys). The lateral cuneiform assumes a rectangular, human-like appearance and departs from the square shape (in dorsal view) of African apes.

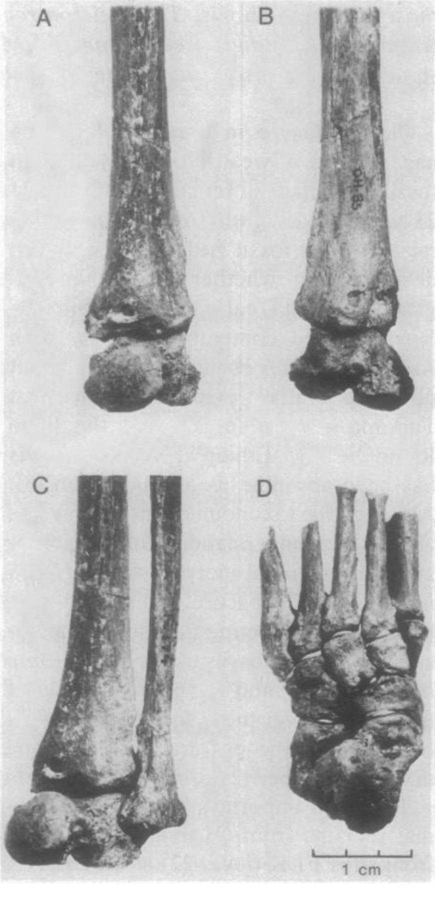

Fig. 2. (A) Anterior view of O.H. 8 talus and O.H. 35 tibia. (B) Posterior view of O.H. 8 talus and O.H. 35 tibia. (C) Anterolateral view of the O.H. 8 talus articulated with the O.H. 35 tibia and fibula. Note the congruent interosseous ridges at the location of the tibiofibular syndesmosis on the leg, and the fit of the fibular malleolus and talus. The patina on the bones is identical and the distal portion of the fibula and talus are eroded on their adjacent inferolateral surfaces. (D) The articulated O.H. 8 foot, dorsal view.

The O.H. 35 tibia and fibula also represent *Homo habilis*, as suspected by other workers (*3, 19*). The bones articulate perfectly with the O.H. 8 foot (Fig. 2, A to C), and their state of preservation, weathering, and patina and the relative dimensions compared to the foot (*34*) lead us to wonder if the O.H. 8 foot and O.H. 35 leg might represent the same individual (*35*).

The O.H. 35 specimens were first studied by Davis (*11*) who commented that the shaft of the fibula "in many ways resembles that of *H. sapiens*; indeed there are fibulae from modern human beings which resemble it almost exactly." Our observations on the O.H. 35 fibula indicate that, although certain traits found in the fossil are more typical of pongids than of modern humans (for example, the surface for the origin of the peroneus brevis is convex rather than concave, and there is a marked ridge between that region of the posterior surface devoted to origin of the flexor hallucis longus and the region of the medial surface devoted to the same muscle), Davis' statement is correct. Furthermore, the fossil has characteristics that are found in no ape (*36*). Some of these traits do not lend themselves readily to functional interpretation, but those concerning the articular facet for the talus suggest that the extreme plantarflexion potential which characterizes the ape ankle was absent (*37*).

Davis (*11*) found the O.H. 35 tibia to be less modern in aspect than the fibula. He drew attention to the rounded anterior border, the extensive origin of the tibialis posterior, supposedly atypical markings for the popliteus, and the apparent failure of the soleal line to reach the lateral border of the shaft. Lovejoy (*9, 38*) asserted that the fossil is atypical only in the particularly marked development of the crest between the origins of the tibialis posterior and flexor digitorum longus. Other traits of the O.H. 35 tibia that are less typical of modern tibiae are (i) the weak development of the interosseous ridge and (ii) the marked platycnemia associated with both a posterior pilaster between the subcutaneous surface and interosseous ridge at midshaft, and a laterally rather than posteriorly facing tibialis posterior origin. However, like Lovejoy (*9, 38*) we note that all the atypical traits of the O.H. 35 tibia can be matched in some modern humans with certain individuals possessing most, if not all, of them. Furthermore, there are characteristics of the fossil that are not seen among ape tibiae (*39*).

Thus our observations on the O.H. 35 tibia and fibula indicate that they have no features which cannot be readily found in a moderate sample of modern humans. The fossils have numerous features never observed in nonhuman primates. Some of these latter traits, particularly those relating to joint surfaces, are strong indicators of human-like bipedality (*37*), and there is little doubt that the O.H. 35 leg was that of an habitual biped.

From a functional viewpoint the implications of the determination that the O.H. 7 hand, O.H. 8 foot, and O.H. 35 leg belong to the same taxon (and perhaps the same individual) are that *Homo habilis* possessed a derived, bipedal morphology of the leg and foot together with a hand that, although advanced in its thumb and fingertip morphology (*20, 22, 25*), still retained climbing potential (*28*). Since *Homo habilis* was a small hominid, lacking large, projecting canines and with only rudimentary toolmaking skills (*1*), it is likely that a selective advantage would have derived from its ability to sleep (*28, 40*), escape, and perhaps occasionally feed in trees. The phenotypic plasticity of bone suggests that the thick-walled, robust, and heavily muscled character of the O.H. 7 hand is not simply a vestige of a suspensory (hominoid) heritage. Rather, certain features of the limbs of *Homo habilis* and other Pliocene-Pleistocene hominids (*37, 41*) suggest a significant component of climbing was present in the locomotor behavior of small Pliocene-Pleistocene hominids well beyond the point at which they became habitual bipeds.

RANDALL L. SUSMAN
JACK T. STERN
*Department of Anatomical Sciences,
Health Sciences Center, State
University of New York at Stony
Brook, Long Island 11794*

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31. The lateral tarsus and metatarsal bases display abnormal bony deposition (Fig. 1D). Originally thought to be a sign of age-related arthritis, the osteophytes on the lateral tarsus and metatarsals—at the joint margins rather than on the articular surface—are as likely the product of a traumatically induced pathology (*25*). The injury and subsequent pathology may also explain the flattening of the lateral tarsus [C. E. Oxnard and F. P. Lisowski, *Am. J. Phys. Anthropol.* **52**, 107 (1980)].
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34. When an index of foot length to tibia length is computed the value for O. H. 8/35 is 25 to 27; for modern human, 26.8 ($N = 10$; standard deviation, 1.32); *Pan troglodytes*, 34.9 ($N = 10$; S.D., 0.64); and for *Gorilla*, 35.9 ($N = 7$; S.D., 4.22). Foot length was measured from the proximal edge of the navicular to the epicondyle of metatarsal II, and the ratio was computed from Davis' (*11*) estimate of length for the O.H. 35 tibia and our own estimate. Lovejoy (9) noted an error in Davis' estimate of tibial length. On the basis of extrapolation from the position of the nutrient foramen, Davis predicted a length of the O.H. 35 tibia of 277 ± 10 mm. (By this same method we obtained a value of 274 mm.) But, the nutrient foramen of the fossil is located along the soleal line proximal to its juncture with the crest between tibialis posterior and flexor digitorum longus, an unusually high position which, as Lovejoy stated, will give a falsely high value for tibial length. We have two modern tibiae with virtually the same location of the nutrient foramen. Using these as a basis for predicting the length of O.H. 35, we obtain estimates of 251 and 262 mm respectively. If one assumes that the break at the proximal end of the shaft occurred at the inferior limit of the tibial tuberosity (as observation suggests), we obtain a length estimate for the O.H. 35 tibia of 259 mm. None of these estimates can be considered precise, but we believe they clearly indicate that Davis' value is too high.
35. One argument against this view is that the distal epiphysis of the O.H. 35 tibia is already fused. In human females the distal tibial epiphysis fuses at a mean age of 14.1 years, thus later than the metatarsal epiphyses. However, the standard deviation for fusion of the human distal tibial epiphysis is 1.1 years. A second argument against O.H. 35 and O.H. 8 coming from the same individual derives from stratigraphic considerations. The position of the FLK level 22 ("Zinj") floor from which O.H. 35 came is said to be 1 to 2 feet above the FLK NN level 3 occupation floor which yielded O.H. 7 and 8. However, the relevant levels at both sites are described as gray silty clays with nodular limestone inclusions and upper weathered components (*1*). In the description of level 22 at FLK it has been pointed out that "both the nature of the clay and the mode of occurrence of the remains on the occupation floor bear a close resemblance to the conditions pertaining in level 3 at FLK NN" (*1*, p. 49). The two sites are separated by a considerable distance of around 200 m or more, but such a wide distribution of the bones may reflect carnivore or scavenger activity which scattered the bones at a presumptive muddy lakeshore.
36. These traits include (i) an extreme anteroposterior slenderness of the neck; (ii) a marked buttress extending proximally from the area of origin of tibialis posterior; (iii) a prominent anterior expansion of the lateral malleolus associated with an acute angle between the articular facet for the talus and the subcutaneous surface, which acuteness causes the subcutaneous surface to face more laterally than anteriorly; (iv) the superior portion of the articular facet is directed medially rather than inferomedially; and (v) the superior edge of the facet runs an anteroposterior course rather than on an oblique downward course.
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39. These traits include (i) the inferior rather than inferolateral direction of the lateral segment of the articular surface for the talus, (ii) the anterior inclination of this same surface, (iii) the

lateral convexity of the lower shaft, and (iv) the anterior concavity of the upper portion of the shaft.

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Nucleotide Sequence of the p21 Transforming Protein of Harvey Murine Sarcoma Virus

Abstract. *Harvey murine sarcoma virus is a retrovirus which transforms cells by means of a single virally encoded protein called p21* has. *We have determined the nucleotide sequence of 1.0 kilobase in the 5′ half of the viral genome which encompasses the* has *coding sequences and its associated regulatory signals. The nucleotide sequence has identified the amino acid sequence of two additional overlapping polypeptides which share their reading frames and the carboxyl termini with p21 but which contain additional* NH_2*-terminal amino acids.*

The Harvey murine sarcoma virus (Ha-MuSV) is a replication-defective transforming retrovirus (*1*). The 5.5-kilobase genome contains a rat-derived sequence that is required for Ha-MuSV–mediated cellular transformation (*2, 3*). This conserved gene encodes a 21,000 dalton phosphoprotein [p21 *has*, formerly known as p21 Ha *ras* (*1*)] which has guanine nucleotide binding activity (*4*). The cellular rat DNA sequences coding for p21 *has* are represented by two genes, c-*has* I, which is composed of four exons and three introns, and c-*has* II, which is colinear (by heteroduplex analysis) with the viral *has* sequences (*5*). The p21 encoded by c-*has* I is closely related to, but distinguishable from, viral p21 *has* (v-*has*) (*5, 6*). Another related transforming retrovirus, Kirsten murine sarcoma virus (Ki-MuSV), also encodes a p21 which cross-reacts serologically with the p21 of Ha-MuSV; approximately two-thirds of the tryptic peptides of Ha and Ki viral p21 protein are the same (*7*). We have derived the nucleotide sequence for the transforming gene of Ha-MuSV from which the amino acid sequence of p21 *has* has been deduced. Oroszlan *et al.* have confirmed (*8*) the deduced amino acid sequence by direct sequencing of many peptides labeled with tritiated amino acids. Sequences important in the transcription and translation of this gene have been identified. Moreover, the structure of the gene p21 *has* has been compared (*9*) to the Ki-MuSV transforming gene (v-*kis*); (formerly known as Ki *ras*) (*7*).

The region between the restriction endonuclease cleavage sites Acc I and Pst I of Ha-MuSV for which we have obtained the nucleotide sequence is shown in Fig. 1. A larger fragment, extending from a Kpn I restriction endonuclease site 0.3 kilobase upstream from Acc I down to the same 3′ end (Pst I), previously had been cloned within the late region of SV40 (*10*). In studies on the messenger RNA (mRNA) transcribed from the chimeric SV40–Ha-MuSV molecule, the 5′ terminus of v-*has* mRNA was mapped to a location 160 bases upstream from the Hind III site in Fig. 1 (*10*). Accordingly, we analyzed the nucleotide sequences in this fragment for sequences related to the Goldberg-Hogness box TATAAA (*11*) (T, thymine; A, adenine). There are three such sets of sequences, around positions 45, 137, and 165. On the basis that the 5′ ends of RNA transcripts generally lie approximately 25 nucleotides downstream from the 3′ end of the consensus sequences (*11*), the putative 5′ ends of the transcripts (by RNA polymerase II) would map at approximately positions 70, 162, and 195. This is consistent with the approximate location observed for the primary transcript from the SV40–Ha-MuSV recombinant (*10*).

The sequence in Fig. 2 shows a fourth putative RNA polymerase II start site at position 16 downstream from a TATAAA box located around position 45; however, this transcript would be from the antisense strand. If this fourth RNA

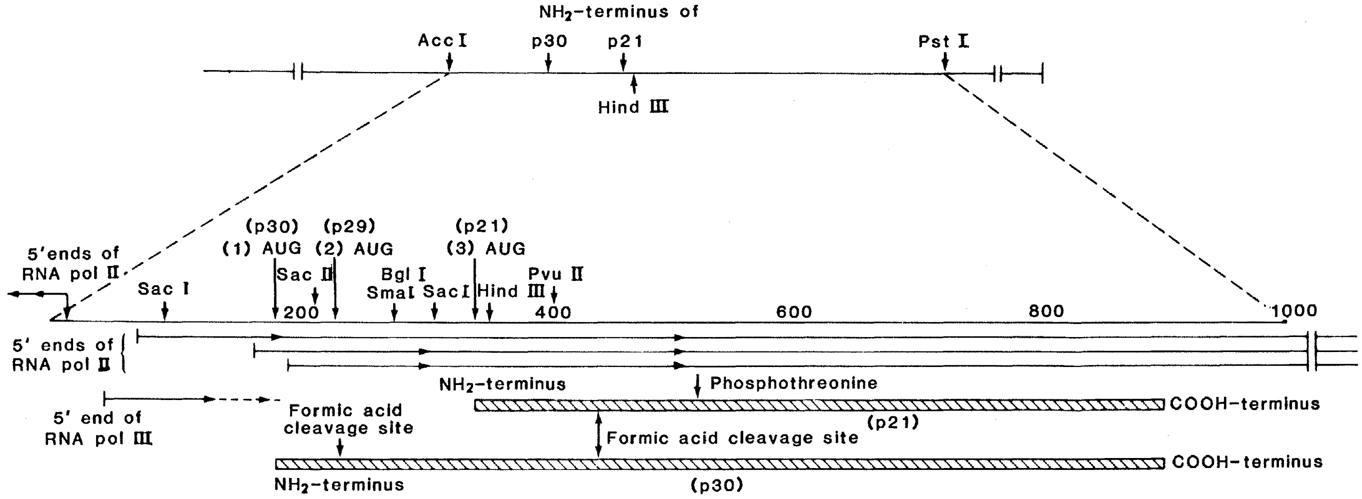

Fig. 1. Schematic representation of the 5′ half of the Ha-MuSV genome. The upper line denotes that part of the 5′ genomic half which contains the p21 *has* sequences. The locations of the NH_2-termini of p30 and p21 as well as of key restriction sites are marked. The region between the restriction sites Acc I and Pst I—map positions 3650 and 4710, respectively, as defined in (*2*)—is enlarged below. The numbers 0 to 1000 refer to the nucleotide positions in Fig. 2, and key restriction sites (Sac I, Sac II, Bgl I, Sma I, Hind III, Pvu II) are placed on this scale. The numbers (1), (2), and (3) next to AUG represent the initiation sites for the coding sequences of p30, p29, and p21, respectively. The putative 5′ ends and 5′ to 3′ directionality of transcripts initiated by RNA polymerase (pol) II and III are indicated. The hachured boxes represent the location of the p21 and p30 coding sequences; these proteins have a common COOH-terminus but distinct NH_2-termini. The locations of the formic acid cleavage sites and of the phosphorylation site (phosphothreonine) are denoted on the coding sequences by arrows.