electronic characteristics of a dislocation will vary depending on which atomic species is present at the dislocation core (21). From the image data alone, it is clear that both dislocations shown here are of the glide set (as were all 60° dislocations analyzed), indicating the presence of Cdterminated dislocations along [110] and Te-terminated dislocations along [110].

In a manner similar to that of Fig. 2. Lomer dislocations viewed along [110] and [110] are shown in Fig. 3, A and B, respectively, with their corresponding core structures in C and D. As in the case of 60° dislocations, two possible configurations can exist that possess identical Burgers vectors. In this case, the core structure viewed along [110] is situated above the interface and is asymmetric in nature, best described as consisting of five irregular sixfold rings surrounding a fourfold ring. The experimental evidence shows that the observed structure is unlike that of the Hornstra model (1), which can be described as a sevenfold ring coupled to a fivefold ring. However, atomic arrangements similar to the Hornstra model were observed along [110] but with the dislocation located exactly at the interface, implying that the two columns common to both the five- and seven-membered rings (marked α' and β') were occupied by Ga atoms. The most likely rationalization of the observed atomic arrangements in the asymmetric structure is that Cd columns α and β each possess one dangling bond per atom and that there is also a small shear (positive for α and negative for β or vice versa) of each column along $[1\overline{1}0]$ (parallel to the dislocation line direction) to accommodate a skewed tetrahedral bonding configuration for atoms in Te columns γ and δ . These data suggest that, possibly as a result of the highly polar nature of the CdTe, the Hornstra structure is not energetically favored when a dislocation occurs entirely within the material.

The nature of the observed structures in both the 60° and Lomer dislocations gives rise to a number of questions relating to, for example, dislocation energy, the chemical bonding in each region, the electrical activity, and the possible existence of a small number of stabilizing impurity atoms at dislocation cores. Such phenomena can now also be investigated experimentally with atomic resolution paralleldetection electron energy-loss spectroscopy (22). It should be stressed that although asymmetric Lomer dislocation core structures in both Si (5) and compound semiconductor (2) systems have been proposed, they differ from that observed here because it has not hitherto been possible to obtain direct evidence of column arrangements solely from experimental data.

A key advantage of the Z-contrast technique is that further theoretical and experimental investigations into the physics and chemistry of such atomic configurations can use the directly observed structures as a firm foundation from which to proceed. Our observation that core structures in polar materials can be significantly different from those in nonpolar materials should enhance the understanding of compound semiconductor heterostructures. The ability to determine dislocation core structures directly is expected to have a major impact in many other fields of materials science, leading perhaps to the understanding and control of brittleness, the key factor limiting the performance of structural materials.

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Sterkfontein Member 2 Foot Bones of the Oldest South African Hominid

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Four articulating hominid foot bones have been recovered from Sterkfontein Member 2, near Johannesburg, South Africa. They have human features in the hindfoot and strikingly apelike traits in the forefoot. While the foot is manifestly adapted for bipedalism, its most remarkable characteristic is that the great toe (hallux) is appreciably medially diverged (varus) and strongly mobile, as in apes. Possibly as old as 3.5 million years, the foot provides the first evidence that bipedal hominids were in southern Africa more than 3.0 million years ago. The bones probably belonged to an early member of *Australopithecus africanus* or another early hominid species.

 \mathbf{B} ipedalism was attained early in hominid evolution. Skeletal adaptations for this form of stance and gait are apparent in the pelvic girdle, hip complex, knee joint, and foot of African apemen, the australopithecines (1). The locomotor apparatus of early hominids was derived from that of quadrupedal, arboreal ancestors (2). There is debate whether arboreal adaptations persisted in australopithecines and, if so, whether arboreal activities were part of their locomotor repertoire or whether

such traits were simply evolutionary baggage (3, 4).

A discovery at Sterkfontein near Johannesburg, South Africa, of four foot bones provides evidence that the australopithecine foot possessed an apelike great toe that diverged from the other toes and was highly mobile. The foot bones (Stw 573) were found among mammalian remains that had been extracted from Dump 20 in 1980. Although they were not found in situ, there is no doubt that they came from Member 2 of the six-member Sterkfontein Formation (5, 6). The approximately 670 hominid specimens recovered from Sterkfontein to date have come exclusively from Members 4 and 5 (7).

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Member 2, which is much deeper and older than Member 4, is rich in fossilsespecially of cercopithecoids and carnivores-but has not previously yielded hominid remains. Its dating could not be less than 3.0 million years ago (Ma) and is more likely about 3.5 Ma (Fig. 1). Thus, the foot bones are the oldest hominid specimens in the Sterkfontein sequence. They are most probably older than Member 3 hominids (3.0 Ma) from Makapansgat, Northern Transvaal, which are the most ancient South African hominid fossils previously reported (8). They therefore provide the oldest signs of the presence of hominids in South Africa. Moreover, the Sterkfontein foot may be as old as, or even older than, the earliest Hadar foot bones and possibly nearly as old as the Laetoli footprints (9). They probably belong to a species of Australopithecus, possibly the earliest available A. africanus, or to another early hominid species. Stw 573 comprises a hominid talus, navicular, medial cuneiform, and first metatarsal, which articulate together perfectly as part of the medial longitudinal arch of a left foot. The four bones constitute the oldest tarsometatarsal ray of a hominid foot yet discovered.

The left talus, Stw 573a (Fig. 2), resem-



Fig. 1. Schematic section through Sterkfontein Formation near the east end of Silberberg Grotto, showing five of the six members. In this position Member 6 is not present. The shaded members have yielded hominids; the new foot bones are from Member 2. F, flowstone; EU, erosional unconformity. Probably appreciable lapses of time are evidenced by extensive flowstone between Members 1 and 2 and between Members 2 and 3, and by an erosional unconformity between Members 4 and 5 that forms a clear stratigraphic break (27).

bles the human rather than the ape form of talus in almost all respects: It is a squat, foreshortened bone with a small talar neck angle, more human in this respect than the Olduvai OH8 (10). It shows an elevated medial trochlear margin, a nearly vertical sulcus for musculus flexor hallucis longus, and absence of anterior cupping of the medial malleolar facet.

The left navicular, Stw 573b (Fig. 3), shows an interesting mixture of humanlike and apelike features. The tuberosity differs from that of African apes and resembles those of OH8, *Homo sapiens*, and Hadar specimens AL 333-36 and AL 333-47. As in apes, the facet for the medial cuneiform is convex over the superolateral two-thirds and concave over the inferomedial onethird (11, 12). Features on the lateral half suggest that the medial and intermediate cuneiform bones were oriented toward the axis of an abducted forefoot (13, 14).

The left medial cuneiform, Stw 573c (Fig. 3), is the best preserved medial cuneiform bone of an early African hominid, save for that of OH8 (15-17). It shows one human feature: a single L-shaped facet for the intermediate cuneiform on its lateral surface, rather than two facets as in apes. In all other morphological features, Stw 573c is apelike and different from OH8 and modern humans (18-20). The implications are that (i) the medial cuneiform of Stw 573 (like that of apes) lay in a medially diverged position in line with an abducted hallux, (ii) the strong m. peroneus longus adducted the hallux as in grasping movements (3), (iii) a wide range



Fig. 2. (**A** and **B**) Left first metatarsal of Stw 573 and other hominoids [(A), lateral aspect; (B), proximal aspect of base]. The bilobate facet in Stw 573 and OH8 contrasts with the reniform facet in *H. sapiens*. (**C**) Dorsal aspect of foot bones, showing greatest divergence of the hallux in Stw 573, modest divergence in OH8, and fully adducted position in *H. sapiens*. Contributors to the varus set in Stw 573 are (i) the set of the medial cuneiform on the navicular, (ii) the medial torsion of the dorsodistal part of the medial cuneiform, (iii) the marked curvature of the distal facet of the medial cuneiform, and (iv) the angulation of the first metatarsal at the first cuneometatarsal joint.

SCIENCE • VOL. 269 • 28 JULY 1995

REPORTS

of movements was possible at the first tarsometatarsal joint, and (iv) a locking mechanism was available by means of the screwing of the base of the first metatarsal into a close-packed position.

The left first metatarsal, Stw 573d (Fig. 2), has a highly concave proximal facet to receive the convex facet of the medial cuneiform (21), which implies a mobile first cuneometatarsal joint. When the metatarsal is locked in position on the medial cu-

neiform, it is angled medialward in the varus position (Fig. 2C); this provides powerful evidence that the hallux diverged from the other toes. The proximal facet is indented on both the medial and lateral margins and forms a bilobate or 8-shaped surface, as in Hadar AL 333-54 (12, 15). In humans, the medial indentation is slight or absent and the facet is reniform. There is a strongly marked impression for m. peroneus longus, which probably played an im-



Fig. 3. (A and B) Medial cuneiform bones of Stw 573 and other hominoids [(A), lateral aspect; (B), medial aspect]. On the lateral aspect, Stw 573 has an L-shaped facet for the intermediate cuneiform as in other hominids, while Pan (chimpanzee) has two separate facets. The "overflow" of the distal facet onto the medial surface in Stw 573 and Pan is shown; the dotted line indicates its proximal limit. The extent of this overflow may be determined as the projected distance of the dotted line from the distal surface, expressed as a percentage of the projected proximodistal diameter of the bone measured on its medial aspect. The greater overflow in Stw 573 than in OH8 and H. sapiens reflects more medial divergence of the first metatarsal on the medial cuneiform. The markedly convex distal facet connotes a highly mobile joint at the base of the great toe, as in Pan but unlike the flattish facet and limited mobility of the joint in humans. (C and D) Navicular bones of Stw 573 and other hominoids [(C), dorsomedial aspect; (D), posterior or proximal aspect]. Lateral thinning and strong recurvation in Stw 573 and Pan are shown in (C), in contrast with thicker, nearly straight lateral parts in OH8 and H. sapiens. In Stw 573, the medial splaying of the forefoot begins as far back as the cuneonavicular joint, as shown by a marked angle between the facets for intermediate and lateral cuneiform bones (arrow) and the convexoconcave facet for the medial cuneiform. The tubercle in Stw 573 is proximodistally elongated (C) and lacks the dorsal protrusion seen in Pan (D). In these respects Stw 573 resembles OH8 and the human specimen and differs from Pan.

portant part in adducting the hallux (4). An ill-defined smooth area lies on the proximolateral margin, but it is doubtful that this was for articulation with the second metatarsal (22).

The Sterkfontein Member 2 foot is small, the foot bones being similar in size to those of OH8 but smaller than matching bones from Hadar, save for the talus of AL 288-1 (23). Stw 573 provides a mixture of hominid features associated with bipedalism and primitive traits associated with a divergent, mobile, opposable hallux (Fig. 4). The hominid characters are evident in the talus, navicular tuberosity, and lateral articular surface of the medial cuneiform. The many apelike characteristics are evident in the lateral half of the navicular and its medial cuneiform facet, most features of the medial cuneiform, and the proximal facet of the first metatarsal. The first cuneometatarsal joint is a mobile, trochoid articulation, as in Hadar (12), with a built-in locking mechanism in close-packed alignment; in this state the metatarsal lies in an impressively varus position (Fig. 2C). The humanlike hindfoot contrasts surprisingly with the Pan-like forefoot. In contradistinction, the OH8 foot from Olduvai is Pan-like in its hindfoot and less so in its forefoot, from which Lewis (19) inferred that it had di-





minished hallucial divergence. Our evidence points to greater hallucial divergence in Stw 573 than in OH8.

Although the talus of Stw 573 has undergone remodeling appropriate to habitual bipedalism, the medial cuneiform and first metatarsal retain primitive, Pan-like features, whereas the navicular shows compromise morphology, to use Rose's term (2). Thus, there is evidence for a degree of adaptation intermediate between the hominoid arboreal foot and the human foot adapted for habitual bipedalism. The change from one form to the other developed in a mosaic evolutionary fashion; seemingly, in the lineage of A. africanus, locomotor changes in the hindfoot preceded those in the forefoot. Of opposite direction are the mosaic changes in OH8, where "locomotor specialisations tend to appear peripherally and progress centrally" (24). The features of the Stw 573 talus, like those of Hadar AL 288-1, are the result of changes during the transition to habitual bipedalism. Our study of the foot of Stw 573 demonstrates that, in the Sterkfontein Member 2 species, the foot has not sacrificed arboreal competence or hallucial opposability. Contrary to the view of Latimer and colleagues (3) that arboreal capability in early hominids should not be discussed in terms of "degrees" of adaptation, our studies support the conclusions of Christie (25), Day, Deloison, Senut and Tardieu (26), Stern, and Susman that the leg and foot of A. afarensis retain Pan-like features and connote an intermediate degree of adaptation. Likewise, we now have the best available evidence that the earliest South African australopithecine, while bipedal, was equipped to include arboreal, climbing activities in its locomotor repertoire. Its foot has departed to only a small degree from that of the chimpanzee. It is becoming clear that Australopithecus was likely not an obligate terrestrial biped, but rather a facultative biped and climber. The exact proportion of its activities spent on the ground and in the trees is at present indeterminate.

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- The angle between the navicular facet and the up-18. right limb of the L-shaped facet on the lateral surface is c90°, as in Pan and unlike the obtuse angle in OH8 and modern humans. This indicates that the Stw 573 medial cuneiform is oriented closer to the axis of an abducted hallux, whereas in OH8 and modern humans it is appressed laterally against the intermediate cuneiform, in conformity with an adducted hallux. The facet for articulation between the medial cuneiform and the second metatarsal is well developed in Stw 573, as in Pan, and is more extensive than in OH8 and modern humans. On the medial surface, the first metatarsal facet overflows from distal to proximal, as in apes where this encroachment conforms with hallucial divergence. The proximal encroachment in Stw 573 extends for some 33% (projected distance) of the proximodistal surface diameter; it reaches 35 to 40% in a small sample of Gorilla and nearly 50% in Pan (see Fig. 3B). OH8 and humans show virtually no such encroachment. The dorsal part of the medial surface is twisted on itself dorsomedially, carrying the metatarsal facet with it. This feature is striking in Gorilla and, to a lesser degree, in Pan, whereas this part of the medial surface leans laterally in humans and OH8. The facets for m. peroneus longus are strongly developed on the Stw 573 medial cunei-

form and first metatarsal. The large facet for the first metatarsal is highly convex with a rounded hump running along the long axis of the facet, as in Hadar AL 333-28 (15–17). In Stw 573 the upper part of this surface is markedly convex and is confluent below with a concave area, as in OH8 (19). These primitive characteristics are shown by *Gorilla* and *Pan*.

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- 21. In its concave proximal facet, Stw 573d resembles Sterkfontein Member 4 homolog Stw 562, as well as Hadar AL 333-54 (*12*, *13*) and *Pan*, but differs from SKX 5017 and modern human homologs with slightly concave or plane facets.
- 22. Such impressions are commonly sites for attachment of oblique ligaments on the lateral aspect of the hallucial tarsometatarsal joint (*19*). Lewis found such markings in *Gorilla*, which we have confirmed on one specimen, and we have located them in several *Pan* specimens. Thus, the presence of an impression is not directly relevant to the set of the hallux (*19*).
- 23. Some dimensions of Stw 573 in comparison with those of isolated Hadar homologs: maximum length of talus, 42.8 mm (AL 288-1, 35.7 mm); greatest mediolateral diameter of navicular, 34.0 mm (AL 333-36, 37.0 mm; AL 333-47, 36.3 mm); maximum proximodistal diameter of medial cuneiform, 17.0 mm (AL 333-28, 21.4 mm); greatest dorsoplantar diameter of first metatarsal base, 21.0 mm (AL 333-54, 23.5 mm). The Hadar measurements are from (15) and (16).
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