

Evidence of hominid-like precision grip capability in the hand of the Miocene ape *Oreopithecus*

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ABSTRACT Functional and allometric analyses of the hand of the late Miocene ape *Oreopithecus bambolii* (Tuscany, Italy) reveal a series of features that reflect an improved grasping capability including firm pad-to-pad precision gripping that apes are unable to perform. Related features such as hand length, relative thumb length, a deep and large insertion area for the tendon of the long thumb flexor, and the form of the metacarpal 2/capitate articulation are not present in extant or fossil apes. In these features, the *Oreopithecus* hand closely matches the pattern of early hominids, presumably as a response to similar functional demands.

Within nonhuman primates, great apes and cercopithecine monkeys are known to perform a variety of precise gripping techniques, including the classical “precision grip” that involves the thumb tip and one or more finger tips (1). However, tests of primate grasping behavior and manipulatory skills demonstrate that only humans are able to apply the considerable force (2, 3) necessary for holding objects securely and steadily between the pads of the thumb and one or more fingers (3). This ability is considered to be an important ingredient in the hominid hand/brain/tool complex (4) and is not expected to be found in nonhominid primates. In the fossil record, anatomical features indicative of human-like precision grip[§] capabilities are known from bipedal hominids only and are not documented before 3.5 million years ago (*Australopithecus afarensis*). Hand bones of the fossil Miocene ape *Oreopithecus bambolii* now provide evidence that the “acme of precision” (1) evolved independently from the hominid lineage and as much as 5 million years before (2).

O. bambolii (Tuscany, Italy) is a late Miocene hominoid (8 million years ago) of modern aspect, with an orthograde body structure comparable to that of extant apes and humans (4–7). It is considered to be closely related to the European late Miocene genus *Dryopithecus* (8, 9). The hand of *Oreopithecus* has never been studied in detail and is considered as morphologically similar to the hand of climbing and suspensory apes (10). However, a revision of the large and almost unpublished collection of *Oreopithecus* hand specimens not only uncovered ape-like features (e.g., strong flexor insertions in the phalanges, deep insertion notches for ligaments between carpals and between metacarpals), but brought to light a combination of unexpected features indicative of improved manipulative skills hitherto thought to be characteristic of early hominids only. This calls for a reconsideration of the hand function of *Oreopithecus*. Our study is based on the largely unpublished Basel collection and the recently restored left hand of the skeleton IGF 11778 from Florence, Italy. The Basel collection includes, in addition to many isolated specimens, several

partial hands (BA#151; BA#89; BA#200; BA#85) and a nearly complete right hand (11) (Ba#140).

An essential characteristic of the locomotor and postural mechanism of primates is hand length (12). In comparison to the pronograde monkeys, all apes with the exception of *Gorilla* have elongated hands relative to their body weight (Fig. 1a) or in relation to humerus length (Fig. 1b). This is attributable to their climbing and suspensory behaviors that require a secure handhold [e.g., maximized palmar friction to prevent sliding (13)]. The same holds for fossil primates. Although *Proconsul* falls within the allometric trend of pronograde monkeys, the orthograde *Dryopithecus* fits the proportions of extant apes. Contrary to previous suggestions (13), the orthograde *Oreopithecus* has short hands relative to its estimated body weight (Fig. 1a, based on the skeleton IGF 11778, which has a nearly complete hand and body weight estimations for this skeleton of refs. 14 and 26). In an allometric context, its hand length falls close to that of pronograde monkeys, gorillas, and hominids and not, as expected, to that of apes.

Thumb/finger proportions significantly reflect the quality of precision grip capabilities (1, 2). In spite of the differences in hand length/body weight ratio, chimps, hylobatids, and gorillas maintain a similar thumb/index finger ratio with a short thumb in relation to the index finger (Fig. 2). Although the thumb of *Dryopithecus* is not known, that of *Proconsul* is completely preserved (15). In an allometric context, its thumb/index finger ratio fits that of colobines and apes. The *Oreopithecus* hand (BA-140) preserves a complete thumb and nearly complete second and third rays (Fig. 3a). Thumb/index finger proportions of *Oreopithecus* are only comparable with those of humans, *Australopithecus*, baboons, and *Theropithecus* and differ from all other fossil or extant monkeys and apes (Fig. 2b). Also, the length of the proximal phalanx of the thumb compared with the length of that of the index finger clearly indicates that both *Oreopithecus* specimens (BA#140 and IGF 11778) are long in comparison with most of the primates (Fig. 2a). These characters are considered to be diagnostic for hominid hands and a basic requirement for human-like pad-to-pad precision grips (1, 2). Within nonhuman primates, only some specialized terrestrial cercopithecids (*Papio* and *Theropithecus*) achieve these proportions (1).

The application of considerable force to precision grips [precision pinching sensu (2)] is a distinctive human character,

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[§]In this study, we use the term “human-like precision grip,” based on the classic definition proposed by Napier (1) and the recently expanded definition of Cristel (3) as far as it is applicable to our material. Thus, in this study the term “precision grip” refers to every type of grip that involves thumb and one or more fingers for fine manipulations, but without applying force. The term “human-like precision grip” refers to the pad-to-pad grip that apes are not able to perform. This capability is determined by morphology and the size relationships of the components of the thumb. “Power grip” is the firm pinching of large objects by using the full or partial volar surface of the hand. This grip depends on the stability and probably on the robusticity of the hand as a whole (21) and is not a subject of this study.

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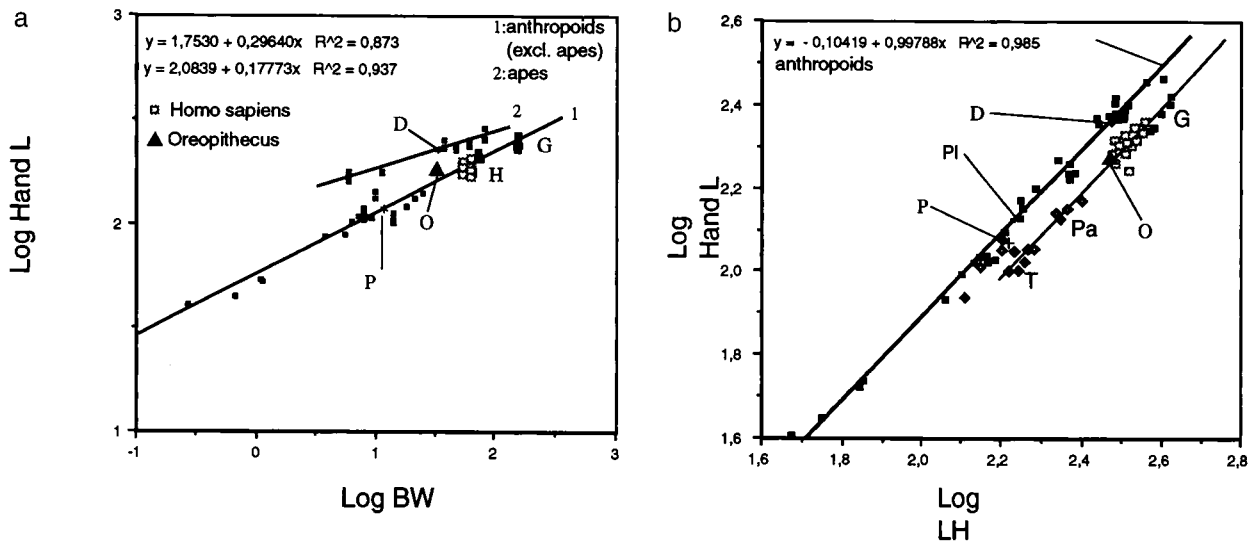


FIG. 1. Size and proportions of the *Oreopithecus* hand. (a) Relation between hand length (carpals, metacarpals, and phalanges of the third digit) and body weight in anthropoid primates (log₁₀; body mass, refs. 14 and 26). Hands of orthograde anthropoids (apes) are considerably longer than those of pronograde anthropoids because a large friction surface is needed to secure a firm hold during vertical climbing and hanging from branches. Both Miocene hominoids that yielded hand remains show the expected proportions: the pronograde *Proconsul* (P) has relatively short hands whereas the orthograde *Dryopithecus* (D) has long hands, as in extant apes. Four orthograde genera, however, do not follow this rule, as they have shorter hands than expected for their body weight: in *Gorilla* (G), this is attributable to the great body weight and the primarily terrestrial quadrupedal locomotion (22) whereas in *Homo* (H) it is attributable to the shift from a mainly locomotor to a more manipulative use of the hands. The reduction of hand length in *Oreopithecus* (O) presumably occurred for similar reasons as in hominids (see discussion in the text). (b) Relation between hand length (carpals, metacarpals, and phalanges of the third digit) and humerus length in anthropoid primates, *Oreopithecus*, and other fossil anthropoids. T, *Theropithecus*; Pa, *Papio*; Pl, *Pliopithecus*.

and it largely depends on the strength of the flexor pollicis longus, the main muscle that flexes the thumb. All distal thumb phalanges of *Oreopithecus* (IGF 11778, BA#85, BA#140, BA#130, and BA#170) are broad-based and flat proximally, as in hominids and baboons. They show a large, deep, and rough excavation for the insertion of the flexor pollicis longus tendon (Fig. 4 b and c), comparable in size and depth only to that of hominids. Although

apes and monkeys are reported to lack this pit (16), a weak and shallow excavation is found in hylobatids (17), *Papio*, and *Theropithecus* (S.M.-S., M.K., and L.R., unpublished observations). However, it is never as deep as in *Oreopithecus*. All other primates, including *Proconsul*, lack this pit. In *Oreopithecus*, the size and depth of the pit suggest considerable strength for the flexor pollicis longus muscle.

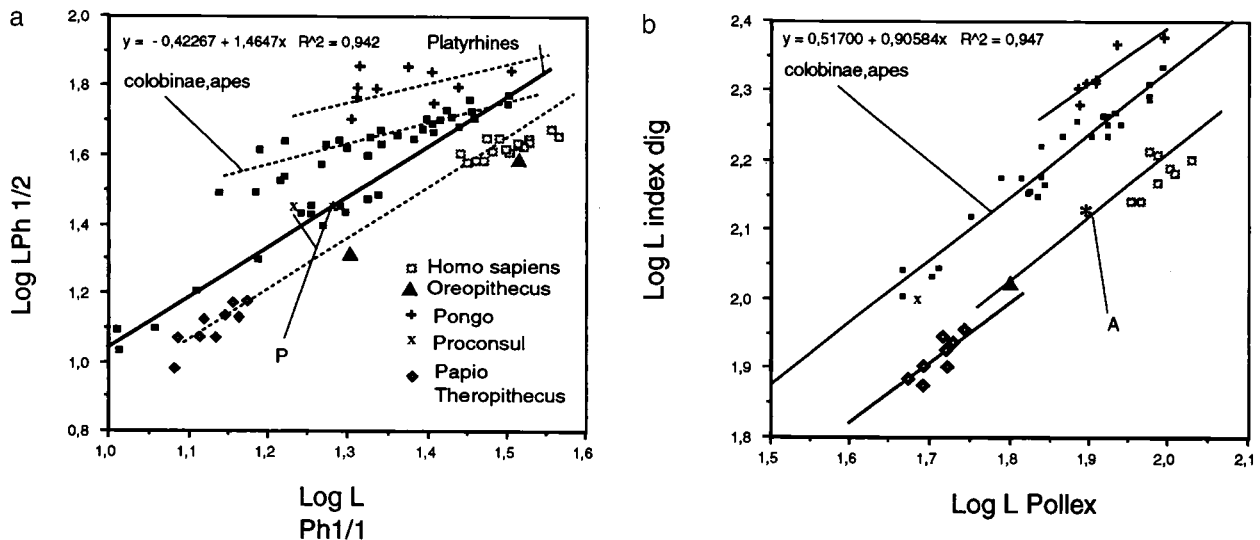


FIG. 2. (a) The length of the proximal phalanges of the thumb set against the length of the proximal phalanges of the index finger of anthropoids, for the two complete hands of *Oreopithecus* (BA#140 and IGF 11778) and other forms. In an allometric context, the platyrrhine condition (solid line) is likely to be primitive for anthropoids while there are two derived characters: the relatively long first phalanx of the thumb in *Papio*, *Theropithecus*, *Homo*, and *Oreopithecus*; and the relatively short proximal thumb phalanx in colobinae, apes, and, especially, *Pongo*. The *Proconsul* specimens considered are KNM-RU 2036 and the subadult individual I from the channel deposit at Kaswanga Primate Site (27). (Lph 1/2, length of the first phalanx of the second ray; Lph 1/1, length of the first phalanx of the thumb.) (b) Relation between thumb (pollex) length (metacarpal 1 and phalanges) and index finger length (metacarpal 2 and phalanges; log₁₀). Colobines, hylobatids, chimps, and gorillas show an allometric relationship. Only *Pongo* falls above the regression line, with a relatively very long index finger in relation to its short thumb. *Oreopithecus* (BA#140), however, shows the same proportions as *A. afarensis* (A:AL#333) and *Homo sapiens*. The length of the *A. afarensis* thumb is reconstructed from the known lengths of metacarpal 1 and proximal phalanx and with a length for the distal phalanx estimated at 20.1 mm (based on the relationship between the lengths of the mc 1 and distal phalanx in modern humans).

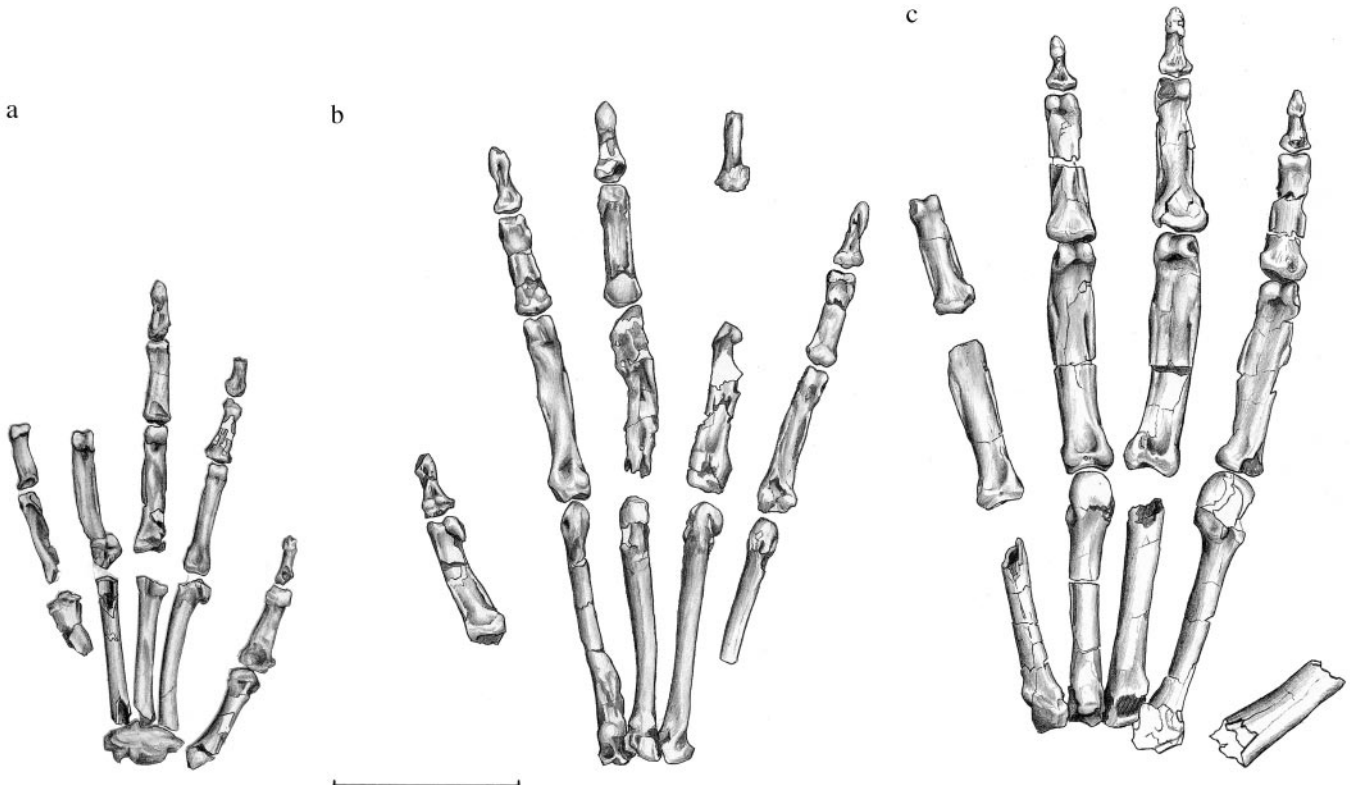


FIG. 3. The hand of *O. bambolii* from Baccinello. (a) Hand of a small animal (BA#140). This specimen belongs to a young adult because some epiphyses are still unfused. The thumb/index finger ratio can be considered to be definitive because intrinsic proportions of the hands remain unchanged during growth (28, 28). (b) Hand of the Florence skeleton (IGF 11778). (c) Hand of *Dryopithecus laietanus* (skeleton from Can Llobateres). Note that the hand of *Oreopithecus* (IGF specimen) and that of *Dryopithecus* (CLL-18800) differ greatly in size despite the comparable estimated body mass and the similar arm lengths of both individuals (30).

In hominids, the capitate/metacarpal 2 articulation is considered to be uniquely specialized (2). The facet for the capitate on the metacarpal 2 is proximally directed, nearly perpendicular to the facet for the metacarpal 3, as a response to the compressive forces generated by pad-to-pad thumb-index finger gripping (2, 18) (Fig. 5*h*). Correspondingly, the facet for the metacarpal on the capitate points distally (Fig. 5*m*). In extant apes, these facets are oriented in a sagittal plane in prolongation of the facet for the metacarpal 3 (Fig. 5*j*). Also,

in fossil hominoids [*Dryopithecus* (S.M.-S., M.K., and L.R., unpublished observations)] and *Proconsul*, the capitate/metacarpal 2 facets are oriented sagittally (Fig. 5*i*) whereas in pronograde monkeys, they are slightly deviated from the sagittal plane as a response to the axial stresses generated by quadrupedal locomotion. In *Oreopithecus*, the facet for the capitate on the metacarpal 2 shows a hominid-like transversal orientation, perpendicular to the facet for the metacarpal 3 (Fig. 5 *g*, *k*, and *l*). Furthermore, the capitate of *Oreopithecus*

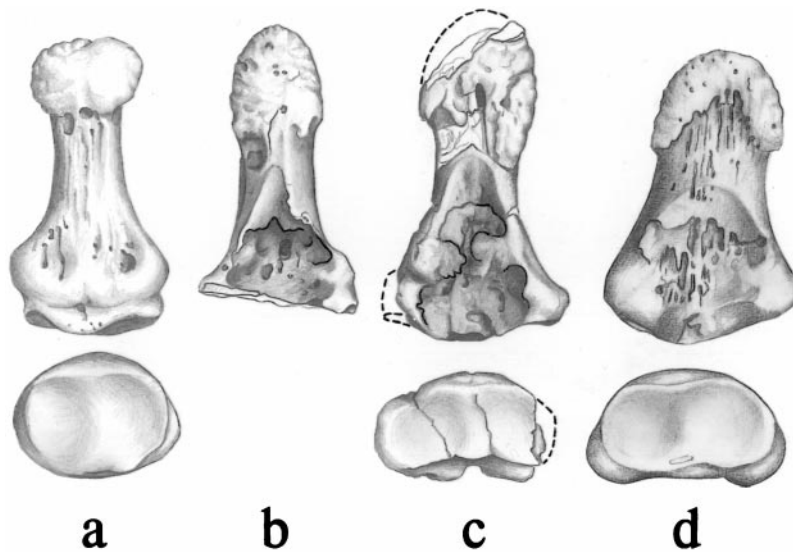


FIG. 4. The distal phalanx of the thumb. (a) *Pan* (right). (b and c) *Oreopithecus* (b, BA#130; c, IGF 11778, left). (d) *Homo* (right). Upper, palmar view; lower, proximal view. Note the strong impression for the flexor pollicis longus tendon.

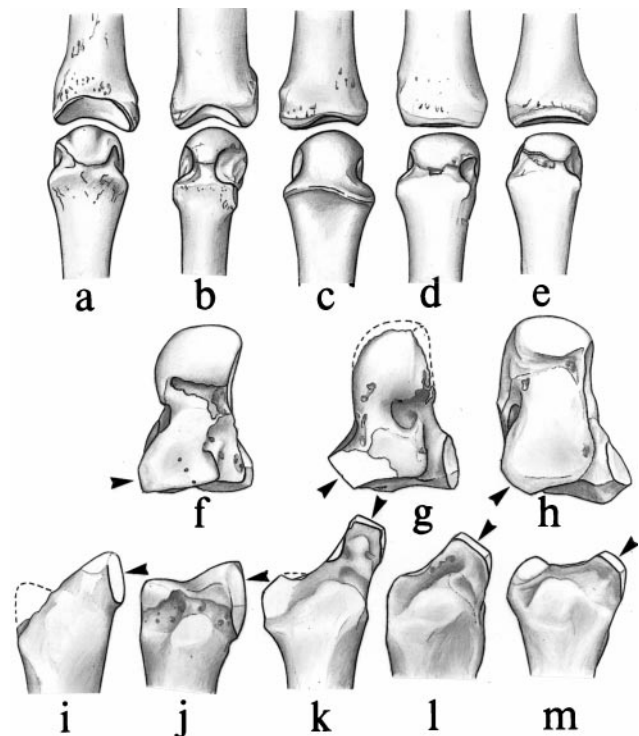


FIG. 5. (a–e) Right third metacarpal and proximal phalanx. (a) *Papio*. (b) *Dryopithecus*. (c) *Pan*. (d) *Oreopithecus* (proximal phalanx undetermined). (e) *Homo*. For comments, see text. (f–m) Capitate/metacarpal 2 morphology in apes, hominids, and *Oreopithecus*. (i) *Proconsul*. (f and j) *Pan troglodytes*. (g, k, and l) *O. bambolii* (BA#151 capitate; BA#165 Mc2; and BA#208 Mc2). (h and m) *H. sapiens*. Arrows indicate the orientation of the facets for the metacarpal 2 on the capitate and for the capitate on the mc2. Note the human-like (proximal) orientation of the facet for the capitate in *Oreopithecus* and in *Homo* and the ape (medial) orientation in *Pan*. Note the lack of waisting on the *Oreopithecus* capitate and the *Homo* capitate and its presence in *Pan*.

lacks the ape-like waisting (Fig. 5g), considered as an adaptation to withstand the tensile stresses caused by climbing and arm hanging (18). This feature is still present in *Australopithecus* (18).

Primate hand shape reflects specific locomotor behaviors because locomotion and powerful grasping exert higher external stresses than any kind of precision handling (19, 20). These constraints strongly determine hand morphology and thus grip performances (3). Most primates are unable to perform the pad-to-pad grip, considered an important component of skillful grasping techniques, because it depends on an appropriate thumb/index finger ratio (2, 3). This is the case for the orthograde apes. Because of their climbing and suspensory behavior, their second-through-fifth fingers are elongated in relation to the body mass (Fig. 1a) whereas the thumb length remains unchanged. The difference in length between the thumb and index finger makes a precision pad-to-pad grip impossible (1, 3). In apes, orthograde body structure and elongated hands are linked inseparably, as they form part of the same adaptive complex functionally related to suspension and vertical climbing. Conversely, in highly specialized terrestrial monkeys (*Papio* and *Theropithecus*), the lengths of the second-through-fifth fingers are reduced as a response to the stresses caused by habitual cursorial locomotion. In these forms, this reduction leads to an approximation of the lengths of the index finger and the thumb and thus to proportions that allow improved dexterity and even pad-to-pad gripping. Hominids show similar proportions. However, these proportions do

not result from locomotor constraints but from an adaptation to manipulation-related tasks (1, 2).

The thumb–index finger proportions of *Oreopithecus* are comparable to those of both the baboons and the hominids and thus are indicative of the capability to exert pad-to-pad grips. This raises the question of whether the hand morphology of *Oreopithecus* is convergent with either baboons or hominids. A series of features excludes the possibility that the proportions of the *Oreopithecus* hand might reflect an adaptation for pronograde locomotion. In monkeys and Miocene hominoids, the dorsally concave shape of the proximal articular surfaces of the proximal phalanges allows a high degree of hyperextension of the metacarpo-phalangeal joints indispensable for baboon-like digitigrady or palmigrady of arboreal monkeys, *Proconsul* or *Dryopithecus* (see Fig. 5 a and b, *Papio* and *Dryopithecus*). In *Oreopithecus* and *Homo*, the rather flat shape of these joint surfaces allows little, if any, hyperextension (see Fig. 5 d and e). Knuckle walkers (*Pan*, *Gorilla*) show a swollen transverse crest on the distal metacarpals, marking the “stop” that prevents dislocation of the hyperextended joints during knuckle walking (see Fig. 5c, *Pan*). *Oreopithecus* lacks these crests (see Fig. 5).

If the outstanding features of the *Oreopithecus* hand cannot be interpreted as adaptations to terrestrial quadrupedalism, then the similarities with hominids must be considered. Recently, eight features have been proposed as distinctive of modern human precision grips and precision handling (2). Australopithecine hominids do not show all of these features but, rather, a combination of some of them that suggests improved finger control, the capability to exert greater force, and the tolerance of new stresses (2). Three features are found in *A. afarensis*. These are the uniquely specialized orientation of the capitate/metacarpal 2 joint, the long thumb relative to the remaining fingers, and the pronation of the index finger (first phalanx/metacarpal articulation) (2). A fourth feature, namely, a deep impression for the flexor pollicis longus tendon on the volar surface of the distal thumb phalanx, is found in *Australopithecus africanus* (2, 3, 21). Similar to *A. afarensis*, *Oreopithecus* shows the specialized orientation of the carpo-metacarpal joint as well as the thumb–index finger proportions. Furthermore, *Oreopithecus* shares with *A. africanus* (21) the strong impression for the tendon of a well developed long flexor muscle on the thumb (not known in *A. afarensis*). The functional resemblances with the australopithecine pattern suggest for *Oreopithecus* similar manipulative skills, with improved finger control and the capability to hold objects securely and steadily between the pads of thumb and index finger. The *Oreopithecus* pattern of orthograde body structure combined with features exclusively related to manual dexterity is not known in any extant or fossil primate except for bipedal hominids. This strongly suggests that the hand morphology of *Oreopithecus* is derived for apes and convergent with that of early hominids.

We now have a model with which early hominids can be compared because *Oreopithecus* combines bipedality and enhanced manipulative abilities as inferred for australopithecines. This may help to answer the vexed question of what might have been the main adaptive causes leading to bipedality. *Oreopithecus* is an endemic ape from the Miocene island of Tuscany/Sardinia (Italy) (22). The evolution of the paleoenvironmental conditions of Mediterranean islands is known to have followed a cyclical pattern. In times of overpopulation, limitation of trophic resources led to increased inter- and intraspecific competition for food (22, 23) and occasionally to mass starvation (23). This generated specific selective pressures that favored an increase in efficiency of those organs that are involved in harvesting and feeding, mainly the masticatory apparatus and, in particular, the teeth (23). Bipedal positional and locomotor behavior, facultative or habitual, hence proves to be of immediate advantage because it permits the efficient

exploitation with free hands of those vegetation levels that are less accessible for other mammals (24). However, only habitual bipedality really frees the hands from locomotor tasks and thus from those biomechanical constraints that would impede any modification to hand morphology necessary to further improve harvesting (25), complex bimanual food processing, and other manipulative capabilities. Selection for a skillful hand might have been one of the factors leading to habitual bipedality.

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