reassessments of the balance between pelagic production and respiration in lakes (11). Our data suggest that the transport of carbon from land to water is an important control on the carbon budget in most lakes.

We can use the frequency distribution of $P_{CO_2}$ to estimate the potential contribution of CO$_2$ from lakes to the atmosphere. We assume an evasion coefficient of 0.2 day$^{-1}$ for all lakes, and for underestimated lakes an enhancement factor of 3 (12). Globally, lakes (an area of 2 $\times$ 10$^{12}$ m$^2$) could contribute CO$_2$ to the atmosphere in the amount of 0.14 $\times$ 10$^{12}$ g of carbon per year. This flux is slightly less than half as great as the total export of organic plus inorganic carbon from rivers to the sea (13), is larger than recent estimates of total organic carbon burial in lake sediments (0.06 $\times$ 10$^{12}$ g (14)), and is comparable to organic carbon burial in reservoirs (0.2 $\times$ 10$^{12}$ g (14)). Lakes have longer hydrological residence times than do flowing waters and may allow for both the degassing of CO$_2$ derived from soil respiration and possibly for increased respiration of organic materials derived from the catchment.

REFERENCES AND NOTES

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6. D. H. Landers, W. S. Oort, R. A. Linturth, D. A. Brakke, Environ. Sci. Technol. 22, 128 (1988); R. A. Linturth et al., Environ. Prot. Agency (U.S.) Publ. 600/4-91-009 (1991). A study of a number of redundant chemical measurements were made, and $P_{CO_2}$ can be computed in several ways, all of which lead to the same conclusions. For example, a linear regression of $P_{CO_2}$ calculated from the change in DIC before and after air equilibration against $P_{CO_2}$ calculated from noncalibrated pH and DIC has a slope of 0.99 + 0.03 and a correlation coefficient, $R^2$, of 0.7.
7. During the calculation of $P_{CO_2}$ from pH and ANC, overestimation of true $P_{CO_2}$ may be caused by the presence of noncarbonate ANC. This effect is strongest at low values of ANC; we excluded from our ANC-based calculations samples with ANC below 40 meq L$^{-1}$ to minimize this effect.
8. We found a strong, uncorrected relation between $P_{CO_2}$ directly measured versus $P_{CO_2}$ calculated from pH and DIC. A linear regression of measured versus calculated $P_{CO_2}$ (N = 330 samples) has an $R^2$ of 0.88 and a slope of 1.03 + 0.01.
12. Evasion of CO$_2$ from supersaturated water was calculated as:

$$\text{Flux} = \frac{D}{2}(2) \left(\text{CO}_2\right)_{\text{air}} - \left(\text{PCO}_2\right)_{\text{water}}$$

where $K_a$ is Henry's constant, $D$ is the temperature-dependent diffusivity coefficient, and $z$ is the surface boundary layer. An evasion coefficient [2/2(2)] of 0.5 m day$^{-1}$ would be equivalent to $z = 300$ µm at 22°C (or $z = 200$ µm at 10°C) and is well within published values for lakes. In undersaturated atmospheres, atmospheric CO$_2$ may react chemically with hydroxyl or carbonate ions more rapidly than it would diffuse physically (J. B. Emerson, Limnol. Oceanogr. 20, 743 (1975)]. We used an enhancement factor of 3 to compute flux into undersaturated waters.

17. References for seasonal data for the 69 lakes are too numerous to list and are available upon request.
19. We thank C. Driscoll, K. Postek, C. Bowier, and D. Armstrong for assistance with the computations and M. Pace, G. Likens, and G. Kipp for thoughtful discussions throughout this work. We thank C. Sandgren, R. Axler, G. Fahnestock, C. Driscoll, C. Ellis-Evans, M. Mehl, S. Nodic, and P. diGloria for preparation of tables and unpublished data. We thank D. Buso, C. Mason, and E. Morency for making the $P_{CO_2}$ measurements at Mirror Lake and G. Likens, P. Lihe, G. Stewart, R. Miller, P. Raymond, J. Reed, and P. Troell for $P_{CO_2}$ measurements at other sites. Financial support was provided by the National Science Foundation (NSF-CEED 9211775, 9024169, 9317698, 9011690, 9019752). This is a contribution to the Institute of Ecosystem Studies; the Hubbard Brook Ecosystem Study; and the North Temperate Lakes LTER program.

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Fossil Evidence for Early Hominid Tool Use

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Although several Plio-Pleistocene hominids are found in association with stone and bone tools, it has been generally assumed that at any one time the hominid with the largest brain was the toolmaker. Fossils recovered over the last decade suggest that early hominids subsequent to 2.5 million years ago all might have used tools and occupied "cultural" niches. A test for humanlike precision grasping (the enhanced ability to manipulate tools) is proposed and applied to australopithecines and early Homo. The results indicate that tools were likely to have been used by all early hominids at around 2.0 million years ago. The earliest australopithecines, which predate the appearance of stone tools in the archaeological record, do not show signs of advanced precision grasping.

Approximately 2 million years ago (Ma) Africa was home to at least two, and probably more, hominid species (1). At least one, but perhaps all, early hominids at this time used implements of bone and stone, but the question of which Plio-Pleistocene hominids engaged in tool behavior (2) has been unresolved since the early 1960s (3-5). Oldowan tools are found throughout Africa beginning around 2.5 to 2.7 Ma. In 1960, the discovery of a partial hand of Homo habilis (Olduvai Hominid 7) from Bed I, Olduvai Gorge, prompted the inference that early Homo was a toolmaker (6) on the basis of anatomical features shared with modern humans. No diagnostic hand fossils of other fossil hominids from East or South Africa were then known. As a result, and because H. habilis had a large brain (7) and more advanced, humanlike teeth (8) and feet (9), H. habilis was considered to be the principal toolmaker in Bed I, roughly 2 Ma (10).

The idea that H. habilis, and not the australopithecines, was the exclusive toolmaker of the Plio-Pleistocene (11) was based on the assumption that the first stone toolmakers had relatively large brains (5-7). This idea has persisted up to the present (12). In this report, I test the assumption that brain size is somehow linked to tool behavior and that only one hominid could be a toolmaker at any one point in time, by an analysis of the functional morphology of ape and human hands and relevant hominid fossils. A major problem in determining which hominids made tools stems from a poor knowledge of which traits in the bones of living animals might be diagnostic of tool behavior. After a discussion of morphological correlates of precision grasping in hu-
mains (and their absence in non–toolmaking apes), I apply the test to fossil hominids from Africa, Europe, and the Middle East.

In living hominoids (apes and humans), there are a number of anatomical features that are linked to apelike power grasping and others that are related to humanlike precision grasping (5, 13). Apes have hands with, among many other characteristic traits, long, curved fingers with narrow fingertips (14), diminutive thumbs (15, 16), and elongate pisiform bones in the palm (17). Humans and our more advanced hominid ancestors have relatively short, straight fingers with broad fingertips and relatively long, stout thumbs with broad, fleshy tips. Humans have pea-like, rounded pisiform bones in the palm. These and other changes are seen in the adaptive shift from a principally power grasping hand, such as that used by apes in the arboreal setting, to a largely precision grasping, humanlike hand that is adapted for enhanced precision grasping and tool behavior (18).

Napier established the principle that precision grasp (the acme of which is seen in human hands that engage in tool behavior) could be identified in certain early hominid hands.

He recognized that the thumb metacarpal contained critical information about the evolution of tool behavior, but he also noted that thumb bones were lacking in the fossil record 30 years ago (5). First metacarpals are well represented in the fossil record at this time, and we can now examine thumb morphology in a comparative-functional analysis to address the question of which Plio-Pleistocene hominids engaged in tool behavior.

I compared the pollical metacarpals of Australopithecus afarensis, Paranthropus robustus, Homo erectus, and Homo sapiens neanderthalensis to those of 12 pygmy chimpanzees, 49 common chimpanzees, and 41 modern humans (19). A number of morphological and metrical differences in the pollical metacarpals of humans and apes can be related to an emphasis on either precision grasping or power grasping, respectively. Great apes have relatively shorter thumbs than do humans, with metacarpals that are reduced in relative length and diameter. In apes, the pollical metacarpal has a small base and a narrow distal articular surface, or head. When metacarpal head breadth is plotted against metacarpal length in pygmy chimpanzees, common chimpanzees, and humans, the relatively small head of the apes is apparent (Fig. 1A). In the range where apes and humans overlap in length (area between the two hatched lines, Fig. 1A), the head breadth proportions of the pollical metacarpal in apes are consistently less than in humans. Metacarpal head breadth in humans exceeds that of chimpanzees at each given length (for the ANCOVA slope test, \( P = 0.072 \), and for the intercept test, \( P = 0.000 \)) (Fig. 1A).

In addition to the size of the metacarpal head, a feature that distinguishes pollical metacarpals in humans from those of chimpanzees is the presence of a relatively narrow, parallel-sided shaft in the apes (Fig. 2E). Also, the pollical distal phalanx of apes has a reduced tuft (Fig. 3) (20) and, most notably, lacks a ventral-based depression for the insertion of the flexor pollicis longus muscle, which is lacking in non-human primates (21).

The relatively small bones of the ape thumb are surmounted by concomitantly reduced soft tissues. Not only do great apes lack a flexor pollicis longus muscle, but they also normally lack both a deep head of the flexor pollicis brevis muscle and the first volar interosseous muscle of Hulse (that is, the first palmar interosseous muscle) (Fig. 3). In both chimpanzee species, three developmentally ventral muscles cross the metacarpophalangeal joint in addition to a pollical tendon from the flexor digitorum profundus muscle mass (22). Human thumbs have three additional muscles that add strength as well as refined motor control to thumb movements. In humans, six ventrally derived muscles cross the metacarpophalangeal joint (Fig. 3). In humans, there is a separate flexor pollicis longus muscle, a first volar interosseous muscle (of Henle), and a deep head of flexor pollicis brevis (in addition to the adductor pollicis, the flexor pollicis brevis proper, and the abductor pollicis brevis). The presence of enhanced thumb musculature in humans, by the addition of these three muscles, increases the transarticular forces crossing the metacarpophalangeal joint. Expansion of the metacarpal head in humans (Figs. 1A and 2A) reduces stress in the pollical metacarpophalangeal joint that results from the increased forces from the added thumb musculature (23).

Applying the ratio of metacarpal head expansion to fossil hominid pollical metacarpals confirms the expectation that toolmakers have expanded metacarpal heads. The hand of A. afarensis possesses a narrow, anelike pollical metacarpal (Figs. 1B and 2D). The geological time range that encompasses A. afarensis (4.0 to 3.0 Ma) is, likewise, devoid of durable (stone and bone) tools. However, thumbs of later hominids from time ranges, and in some cases sites, associated with stone and bone tools do manifest the toolmaking criterion in their

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**Fig. 1.** (A) A plot of metacarpal I length versus metacarpal I head breadth in modern humans (H. sapiens), pygmy chimpanzees (Pan paniscus), and chimpanzees (Pan troglodytes). Humans have broader metacarpal heads than apes, with increased articular surface area. In humans, metacarpophalangeal joint expansion and the presence of increased musculature crossing this joint are linked to an enhanced potential for precision grasping. The human major axis regression equation is breadth = 4.91 + 0.226 (length) with an SE slope of 0.044 and an SE intercept of 2.026. The chimpanzees major axis regression equation is breadth = 3.777 + 0.131 (length) with an SE slope of 0.026 and an SE intercept of 1.071. (B) A plot of metacarpal I head ratio in the above human and ape sample, together with a like ratio in fossil hominids. This plot shows that (i) values for African apes and modern humans do not overlap and that (ii) A. afarensis (AL 333w-39), an early hominid that predated the occurrence of tools in the fossil record, plots within the 95% fiducial limits of the ape population. Three later hominids found with stone and bone tools, P. robustus (SKX 5020), H. erectus (SK 84), and H. s. neanderthalensis (Shanidar 4), plot near the human mean, outside the 95% confidence limits of the population. Sample sizes are in parentheses.
pollical metacarpals (24). These hominids include P. robustus in South Africa (1.8 Ma) (Fig. 2B), H. erectus in South Africa (1.8 Ma) (Fig. 2C), and H. s. neanderthalensis in Europe and Asia (around 50,000 years ago (not pictured, but see Fig. 1B)).

Given the distinctive morphology of precision grasping thumbs, it should now be possible to detect the capability for refined, humanlike precision grasping (and its correlate, tool behavior) in fossil hominid species of the Plio-Pleistocene that are represented by pollical metacarpals (25). The morphological criteria for toolmaking proposed by Napier in the early 1960s, including, among others, a fully opposable thumb with increased relative thumb length and broad distal phalanges of the thumb and fingers, are extended by this study. While Napier’s work has stood the test of time, the application of his test has been limited (i) because it relies on fossils that are rare and delicate (for example, manual distal phalanges) and (ii) because it has been limited to individual hominid specimens that are represented by associated hand bones (necessary to calculate thumb and finger proportions). The test I propose relies on a single thumb element and one that is well represented in the fossil record. Prudent application of the proposed diagnosis should help resolve the question of which Plio-Pleistocene hominids were responsible for the earliest tool assemblages of the Oldowan industrial complex.

REFERENCES AND NOTES

5. Napier studied the functional morphology of primate hands and the relation between structure and function. He observed that certain features of the human hand were correlated with an enhanced precision grasp. Napier noted that the presence or absence of these features in primates (including fossil hominids) indicated, “...within limits, the capacity of those hands in the cultural realm of tool-use and toolmaking.” J. R. Napier, Sci. Am. 206, 56 (December 1962).
7. L. S. B. Leakey, P. V. Tobias, J. R. Napier, Nature 202, 7 (1964); P. V. Tobias, ibid., p. 3.
10. L. S. B. Leakey initially proposed that Australopithecus (Zinjanthropus) boisei made the tools found in Bed I at Olduvai [L. S. B. Leakey, ibid., 184, 491 (1958)]. He later equivocated [ibid. 191, 417 (1961)] when H. habilis was recovered a few months later. Finally, Leakey argued that H. habilis was the more likely toolmaker in Bed I [Leakey et al., in (7)].
11. “Australopithecine” refers to the earliest hominids beginning with A. afarensis at around 4.0 Ma and including later A. africanus, P. robustus in South Africa, and P. boisei in East Africa. The latter two species are commonly referred to as the “robust” australopithecines because of their well-developed chewing apparatus, including massive jaws and expansive post-canine dentition.
17. M. Spinner, Kaplan’s Functional and Surgical Anat-
24. The oldest stone tools associated with reliable radiometric dates are from East Africa, members E and F of the Shungura formation of the lower Omo Valley, and at Hadar, from the Kada Hadar member along the Gona River in Ethiopia. These sites are dated at around 2.5 Ma [H. Roche and J.-J. Tiercelin, C. R. Acad. Sci. Paris 284, 1871 (1977); J. W. K. Harris, Afr. Archæol. Rev. 1, 3 (1980); F. C. Howell, P. Hare, J. de Heinzelin, J. Hum. Evol. 16, 665 (1987)].

25. The question of whether refined precision grasping is indeed related to tool behavior and not simply small-object feeding is settled by the fact that Theropithecus gelada, the quintessential non-tool-using small object feeder [C. J. Jolly, Man 6, 6 (1970)] lacks a hominid hand.