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An Earful of Jaw

If you read this whole essay, you'll deserve and get a reward

by Stephen Jay Gould

The most sublime of all beauties often proceed from the softest or the smallest—the quadruple pianissimos of Schubert's "Schöne Müllerin," as sung by Fischer-Dieskau (and penetrating with brilliant clarity to the last row of the second balcony), the tiny birds of brilliant plumage depicted in the marginalia of medieval manuscripts. But even the most refined and intellectual character may succumb without shame to the sheer din employed now and then by great composers to overwhelm the emotions by brute force rather than ethereal loveliness—Ravel's orchestration of the "Great Gate of Kiev" at the end of Moussorgsky's *Pictures at an Exhibition*, or the last scene of Wagner's *Die Meistersinger*.

I once had the privilege of singing with the Boston Symphony at Tanglewood in the midst of *numero uno* among musical dins—the *Tuba mirum* of Berlioz's *Requiem*. I had listened to the piece all my adult life; we had rehearsed (without orchestra) for weeks. I knew exactly what was coming as the dress rehearsal began. The four supplementary brass choirs enter one after the other, building and building to a climax finally joined by the timpani—eight pair, I think, although they seemed to extend forever in an endless row before the choral risers. And against this ultimate crescendo, the basses alone (including me) must sing the great invocation of the last judgment:

Tuba mirum spargens sonum
Per sepulchra regionum
Coget omnes ante thronum

(The wondrous sound of the trumpet goes forth to the tombs of all regions, calling all before the throne.)

So it should go, and so it went—but not for me. I had devolved into tears and spinal shivers—not in ecstasy at the beauty, but in awe at the volume. (Forewarned is

forearmed; I was fine at the performance itself.) Great composers have every right to exploit the physiology of emotional response in this way, but only sparingly, for timing is the essence (and most of Berlioz's *Requiem* is soft).

My memory of this extraordinary incident in my emotional ontogeny focuses upon a curious highlight of mixed modalities. The sound of the brass assaulted my ears, but the thunder of the timpani followed another, unexpected route. It entered the wooden risers under my feet and rose from there to suffuse my body; sound became feeling.

I am no disciple of Jung, and I do not believe in distant phyletic memory. Yet, in an odd and purely analogical sense, I had become a fish for a moment. We (and nearly all terrestrial vertebrates) hear airborne sound through our ears; fish feel the vibrations of waterborne sound through their lateral line organs. Fish, in other words, "hear" by feeling—as I had done through a set of wooden risers with a density closer to water than to air.

For an optimal combination of fascination with excellent documentation, no saga in the history of terrestrial vertebrates can match the evolution of hearing. Two major transitions, seemingly impossible but then elegantly explained, stand out at opposite ends. First, at the inception of terrestrial life, how can creatures switch from feeling vibrations through lateral lines running all over their bodies to hearing sounds through ears? How, in other words, can new organs arise without apparent antecedents? Second, at the last major innovation in vertebrate design, how can bones that articulate the upper and lower jaws of reptiles move into the mammalian ear to become the malleus and incus (hammer and anvil) in the chain of three bones that conduct sound from the eardrum (the tympanum in anatomical parlance, recalling my Berlioz story in

the singular) to the inner ear? How, in other words, can organs switch place and function without destroying an animal's integrity as a working creature? How can we even imagine an intermediary form in such a series? You can't eat with an unhinged jaw. Creationists have used this difference between reptiles and mammals to proclaim evolution impossible a priori—I mean, really, how can jawbones become ear bones? Get serious, fellas. Yet, we shall see, once again, that the domain of conventional thought can be much narrower than the capabilities of nature—although ideas should be able to extend and soar beyond reality.

The key to the riddle of both these transitions lies in the major theme of my Berlioz story—multiple modalities and dual uses. You can pat your head and rub your stomach, fart and chew gum at the same time, feel and hear sound, chew and sense with the same bones.

Nature writing in the lyrical mode often exalts the apparent perfection and optimality of organic design. Yet, as I frequently argue in these columns, such a position plunges nature into a disabling paradox, historically speaking; if such perfection existed as a norm, you might revel and exult all the more, but for the tiny problem that nature wouldn't be here (at least in the form of complex organisms) if such optimality usually graced the products of evolution.

I recently made my first trip to Japan to deliver a lecture at the opening of an annual series that will bring one American scholar to Japan and a Japanese counterpart over here to speak on a common topic. I was both pleased and intrigued by our assigned theme for this initial year (largely at Japanese request)—creativity. (Some Japanese apparently fear—although my superficial impressions included nothing to sustain such anxiety—that their scholars and industrialists excel

at efficiency and alteration, but not at innovation.)

I had no words of wisdom on Japanese life (I would not dare, not even by the old criterion that experts are folks who have lived in a country either more than twenty years or less than two days); nor do I understand the sources of creativity in the human psyche of any culture. So, following the fine maxim that a shoemaker must stick to his last (a wooden model of a foot, not a final goal), I spoke on the evolutionary meaning of creativity—specifically, on the principles that permit major transitions and innovations in the history of life. I don't know that my message was well received in this land of supreme artistry in the efficient use of limited space, for I held that the watchwords of creativity are sloppiness, poor fit, quirky design, and above all else, redundancy.

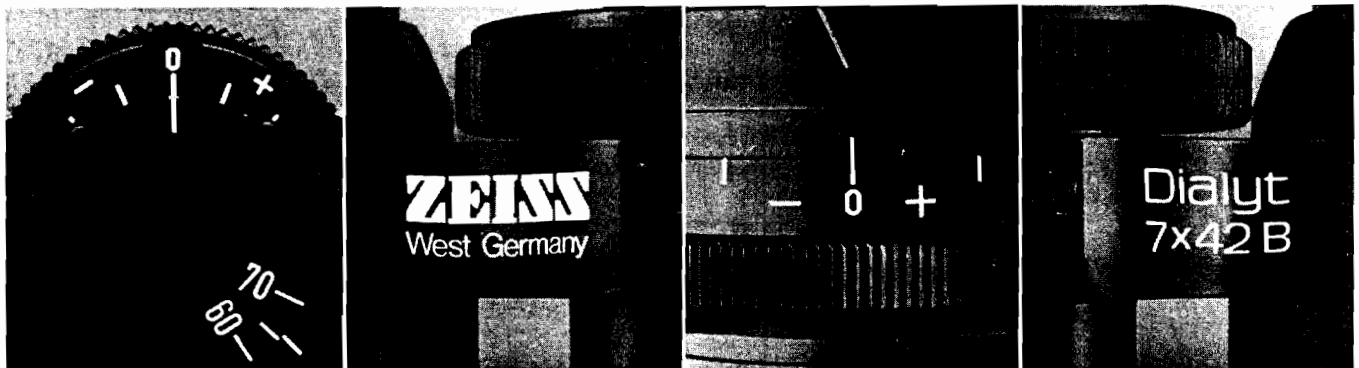
Bacteria are marvels of efficiency, simple cells of consummate workmanship, with internal programs, purged of junk and slop, containing single copies of essential genes. But bacteria have been bacteria since life first left a fossil record 3.5 billion years ago—and so shall they probably be until the sun explodes. Such optimality provokes wonder, but provides no seeds

for change. If each gene does one, and only one, essential thing superbly, how can a new or added function ever arise? Creativity in this sense demands slop and redundancy—a little fat not for trimming but for conversion; a little overemployment so that one supernumerary on the featherbed can be recruited for an added role; the capacity to do several things imperfectly with each part. (Don't get me wrong. Bacteria represent the world's greatest success story. They are today and have always been the modal organisms on earth; they cannot be nuked to oblivion and will outlive us all. This time is their time, not the "age of mammals" as our textbooks chauvinistically proclaim. But their price for such success is permanent relegation to a microworld, and they cannot know the joy and pain of consciousness. We live in a universe of trade-offs; complexity and persistence do not work well as partners.)

To build a vertebrate along the tortuous paths of history, evolution must convert the poet's great metaphor into flesh and bones. "I hear it," writes Yeats, "in the deep heart's core." I don't mean to be excessively literal, but if creatures couldn't occasionally hear with their lungs

(as some snakes do) or with their jaws (as our immediate reptilian ancestors probably did), we would not now have ears so cleverly wrought that they fool us into the attractive but untenable vision of organisms as objects of optimal design. Consider the first and last major steps in anatomical construction of the mammalian middle ear—for we know no better or more intriguing story in the evolution of the vertebrates.

1. *The origin of hearing bones in the first terrestrial vertebrates.* The hearing of sound in thin air poses a major physical problem: how can low-pressure airborne waves be converted into high-pressure waves suitable for transmission by fluids in the cochlea of the inner ear? Terrestrial vertebrates use two major devices to make the necessary conversion. First, on the "stiletto heel" principle (quoting a metaphor from my colleague T. S. Kemp), they collect sound on the relatively large area of the eardrum, but eventually transmit the waves into the inner ear through a much smaller opening called the *fenestra ovalis* (oval window). Second, they pass the vibrations from eardrum to oval window along a bone or series of bones, called in mammals, the malleus, incus, and sta-



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pes, or hammer, anvil, and stirrup to honor a truly uncanny resemblance. These bones act as levers to increase the pressure as sound waves travel toward the brain.

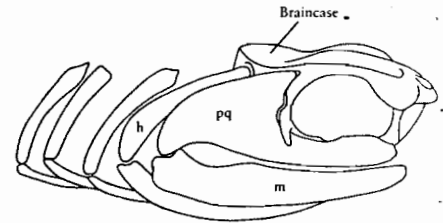
Fish have an inner ear, but no eardrum or middle-ear bones; they "hear" primarily through their lateral line organs by detecting the movement of water produced by sound waves in this dense medium. How then could middle-ear bones arise in terrestrial vertebrates, apparently from nothing?

The first vertebrates had no jaws. Modern lampreys and hagfishes survive as remnants of this first vertebrate radiation; their formal name, Agnatha (or jawless), embodies their anatomy (or partial lack thereof). In agnathans, a series of gill openings lies behind the boneless mouth—and this arrangement foreshadows the evolution of jaws. In the first jawed fishes, gills are supported by a series of bones, one set for each gill slit. Each set includes an upper and lower bar, pointing forward and hinged in the middle. Obviously, this arrangement, although evolved for supporting gills, looks uncannily like the upper and lower jaws of a typical vertebrate. We do not know for certain whether jaws arose from a functioning gill arch that moved forward to surround the mouth or whether jaws and gill arches just represent two specializations, always separate, but generated from the same system of embryological development. In either case, we do not doubt that gill supports and jaws are homologous structures (that is, evolved from the same source and representing the "same" organ in different forms—like arms and legs or fingers and toes). The evidence for homology is multifarious and overwhelming: (1) the embryo builds both jaw precursors and gill arches not from mesoderm, the source of most bones, but from migrating neural crest cells of the developing head; (2) both structures are made of upper and lower bars, bending forward and hinged in the middle; (3) the muscles that close the jaw are homologues of those that constrict the gill slits.

If vertebrate jaws represent an anterior gill arch, then another crucial element of the skull also derives from the gill supports just behind. The upper bar of the next gill arch in line becomes the hyomandibular of jawed fishes, a bone that functions in support and coordination by linking the jaws to the braincase.

All this detail may seem distant from the origin of hearing bones, but we are closing in quickly (and shall arrive before the end of this paragraph). Mammals have three middle-ear bones—hammer, anvil, and stirrup, or stapes. And the sta-

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In this classic figure of gill arch-jaw homologies, from Robert L. Carroll's Vertebrate Paleontology and Evolution, the upper and lower jaws (pq and m) have the same position and form as all the gill arches behind them. Also, the upper element of the gill arch just behind the jaws articulates with the braincase. This bone becomes the hyomandibular (h) and later the stapes in terrestrial vertebrates.

pes is the homologue of the hyomandibular in fishes. In other words—but how can it happen?—a bone originating as a gill support must have evolved to brace the jaws against the braincase, and then changed again to function for transmission of sound when water ceded to air, a medium too thin to permit "hearing" by the lateral line.

As usual in a world of encumbrances, we must flush out an old and conventional concept before we can understand how such an "inconceivable" transition might actually occur without impediment in theory or practice. We must forget the old models of horses and humans mounting a chain of improvement in functional continuity—from small, simple, and not-so-good to larger, more elaborate, and beautifully wrought. In these models, brains are always brains, and teeth always teeth—but they get better and better at whatever they do. Such schemes may work for the improvement of something already present, for a kind of stately continuity in evolution. But how can something original ever be made? How can organisms move to a truly novel environment, with needs imposed for functions simply absent before? We need a different model for major transitions and innovations, for King Lear was correct in stating that "nothing will come of nothing."

We need, in other words, a mechanism of recruitment and functional shift. Evolution does not always improve a rudiment. It must often take a structure functioning perfectly well in one capacity and shift it to another use. The original middle-ear bone, the stapes, evolved by such a route—changing from a stout buttressing bone to a slender hearing bone.

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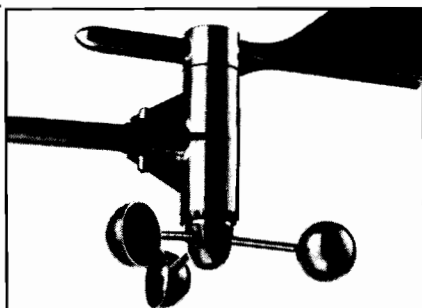
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each person has but one vote, then evolution would generate no structural complexity, and bacteria would rule the world. But we (and our fellow creatures of elaboration) are here by virtue of slop, multiple use, and redundancy. The hyomandibular, once a gill support, then braced jaw and braincase. But this bone happens to lie right next to the otic capsule of the inner ear—and bone, for reasons incidental to its evolution, can transmit sound with reasonable efficiency. Thus, while functioning primarily as a brace, the hyomandibular also acquired other uses. Skates and rays take in water through a round opening, called the spiracle, located in front of the other gill slits. The hyomandibular then helps to pump this water into the mouth cavity, and thence out and over the gill slits. Closer to our phyletic home, the hyomandibular may help to ventilate the lungs of modern lungfishes.

I have wanted to write about the origin of middle-ear bones ever since I began this series, for we have no finer story in vertebrate evolution. But I like to wait for a handle in new information, and one just came my way. In a recent issue of *Nature* (the leading British journal in science), J. A. Clack described her finding of the oldest stapes (“Discovery of the Earliest Known Tetrapod Stapes,” *Nature*, vol. 342, pp. 425–27). The first known tetrapods (four-legged terrestrial vertebrates) hail from eastern Greenland in rocks 360 million years old. They have been known for some time under the names *Ichthyostega* and *Acanthostega*, but their stapes had not been well resolved before. Clack found six stapes of *Acanthostega*, four preserved in their life positions.

Clack suggests not only a dual but a triple function for the stapes of these first land vertebrates. The bone is stout and dense, not slender and delicate as in stapes adapted largely for hearing. This original stapes must still have functioned in its earlier role as a brace (other early tetrapods, including mammalian ancestors, also had stout stapes). Clack also advocates a supplementary role in respiration. Finally, she makes a key observation based on the stapes’s location: “The stapes is likely to have had some auditory function because of the close association between the footplate [a part of the stapes] and the otic [ear] capsule.”

Such a multifarious bone nearly bursts with evolutionary potential. The stapes may have braced for a hundred million years, but it also worked for respiration and hearing if only in an incipient or supplementary way. When the cranium later lost its earlier mobility, and the braincase became firmly sutured to the skull—as

occurred independently in several lineages of terrestrial vertebrates—the stapes, no longer needed for support, used its leverage and amplified a previously minor role in hearing to a full-time occupation.

2. *The origin of mammalian middle-ear bones.* The odyssey of the stapes (stirrup) is extraordinary enough, a tale worthy of Scylla, Charybdis, and all the wiles of Circe—from gill support to a brace between jaws and braincase to a hearing bone for airborne sound. Yet the other two bones of the mammalian middle ear, named long ago by an age that knew the blacksmith’s forge, have an even more curious history. The hammer and anvil (malleus and incus), as elements of the gill arch in front of the hyomandibular, became parts of the jaw in early vertebrates. In fact, they took up the central role of connecting and articulating the upper and lower jaws—as they still do in modern amphibians, reptiles, and birds. The quadrate bone of the reptilian upper jaw became the incus of mammals, while the articular bone of the lower jaw became the malleus. The transition, so improbable in bold words, is beautifully documented in the fossil record and in the embryology of all modern mammals.

The homology of reptilian jawbones to mammalian ear bones was discovered by German anatomists and embryologists well before the advent of evolutionary theory. In 1837, C. B. Reichert made the key observations and expressed the surprise that this tale has elicited ever since. With these words, Reichert introduced his section on the *Entwicklungsgeschichte der Gehörknöchelchen* (developmental history of the little hearing bones). (German looks so God-awful for its massive words. But these tongue twisters are usually made of little words compounded, and the system becomes beautifully transparent, even charming, once you break the big items into their elements. The Germans have preferred to construct technical terms as compounds of their ordinary words, rather than from fancy and foreign Latin or Greek. A rhinoceros is a *Nas-horn*, or nose horn as rhinoceros actually says in Greek; a square is a *Viereck*, or four-corner. Our technical literature refers to the hammer, anvil, and stirrup as “auditory ossicles”; don’t you prefer the German *Gehörknöchelchen*, or little hearing bones?) In any case, Reichert wrote: “Seldom have we met a case, in any part of animal organization, in which the original form of an early [embryological] condition undergoes such extensive change as in the ear bones of mammals. We would scarcely believe it . . . nevertheless, it happens in fact.”

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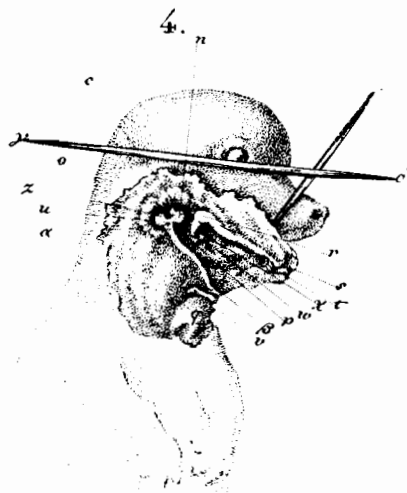
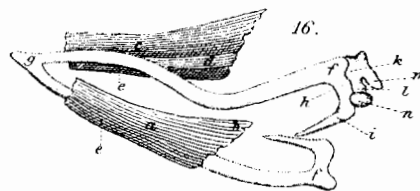
David Morgan

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Reichert recognized all key outlines of the story: that all the ear bones derive from the first two sets of gill-arch bones, the hammer and anvil from the first arch (forming the jaw of vertebrates), and the stirrup from the second arch (forming the hyomandibular of fishes). He noted that the lower jaw first forms with a precursor called Meckel's cartilage (in honor of another great German anatomist of the generation just before, J. F. Meckel). The mandible or jawbone then ossifies on the side of Meckel's cartilage. Meanwhile, the posterior end of Meckel's cartilage, forming the back end of the jaw in the early pig embryo, ossifies and then detaches to become the malleus of the middle ear. One could hardly ask for more direct evidence, and Reichert's observations have been affirmed thousands of times since.

(As a tangential comment in my continuing campaign against textbook copying, the accompanying illustration shows Reichert's original figure of a developing lower jaw in the embryonic pig; *h* and *i* represent parts of the future malleus forming at the back end of Meckel's cartilage (*g*); the ossifying mandible (*a*) begins to surround and supplant the cartilage.

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From Archiv für Anatomie,
Physiologie, 1837

Meanwhile, the incus (*k*) and the stapes (*n*) form as bones separate from the lower jaw. This figure has been copied and degraded, like xeroxes of xeroxes, ever since this 1837 original. I last saw its clone in a vertebrate anatomy textbook published in 1971. Two bits says that the author of that text [who undoubtedly copied the figure from a book just slightly older than his] would be shocked to learn that his figure dates from 1837. This time, everyone lucks out because Reichert was a great anatomist and his figure is basically correct; but think of the capacity for compounded error inherent in this procedure of mindless copying. I also include, to give an interesting [if gory] flavor of common styles of illustration during the early nineteenth century, one of Reichert's graphic preparations of a pig embryo, dissecting pins and all.)

Thus, every mammal records in its own embryonic growth the developmental pathway that led from jawbones to ear bones in its evolutionary history. In placental mammals, the process is complete at birth, but marsupials play history postnatally, for a tiny kangaroo or opossum enters its mother's pouch with future ear bones still attached to, and articulating, the jaws. The bones detach, move into the ear, and the new jaw joint forms—all during early life within the maternal pouch.

Paleontological and functional evidence join the embryological data to construct a firm tripod of support, giving this narrative pride of place—by combining strength of documentation with fascination of content—among all transitions in the evolution of vertebrates. One theme stands as the coordinating feature of this narrative (and of my entire essay): redundancy and multiple use as the handmaiden of creativity.

We might employ this theme to make an abstract prediction about the character of intermediary forms in the fossil record. Contrary to creationist claims that such a transition cannot occur in principle because hapless in-betweens would be left without a jaw hinge, the principle of redundancy suggests an obvious solution. Modern mammals hinge their jaws between squamosal (upper jaw) and dentary (lower jaw) bones; other vertebrates between quadrate (upper jaw) and articular (lower jaw) bones destined to become the incus and malleus of the mammalian ear. Suppose that mammalian ancestors developed a dentary-squamosal joint while the old quadrate-articular joint still functioned—producing an intermediary form with a double jaw. The old quadrate-articular joint could then be abandoned, as its elements moved to the ear, while the jaw

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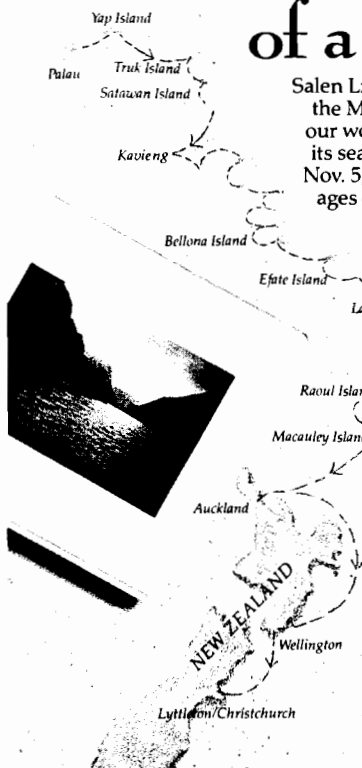
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continued to function perfectly well with the new linkage already in place.

Our woefully inadequate fossil record is not brimming with intermediary forms, for reasons often discussed in these columns. But the origin of mammals represents a happy case of abundant evidence. The abstract predictions of the last paragraph (actually advanced by paleontologists before the discoveries, so I am not just making a rhetorical point here) have been brilliantly verified in abundant fossil bone. The cynodont therapsids, our ancestral group among the so-called mammal-like reptiles, show numerous trends to reduction and loosening of both quadrate and articular bones in the old reptilian jaw joint. Meanwhile, the dentary of the lower jaw enlarges and extends back to contact the upper jaw. (In mammals, the dentary forms the entire lower jaw; reptilian jaws contain several postdentary elements, all reduced and then suppressed or dispersed in mammals.) Many cynodonts develop a second articulation between the squamosal and a postdentary element of the lower jaw called the surangular. (This joint is not the later mammalian dentary-squamosa link, but its formation illustrates a multiple evolution of the intermediacy proclaimed impossible by creationists.) Finally, two or three genera of advanced cynodonts develop a second articulation of truly mammalian character between the dentary and squamosal. One such genus (although the evidence has been disputed bears the lovely and distinctive name *Diarthrognathus*, or two-jointed jaw.

Moreover, the earliest true mammal does not yet have a fully independent malleus and incus. These bones remain affixed to the jaws, and continue to participate in articulation, in both *Morganucodon* and *Kuehneotherium*, the two best known early mammals. "In this sense," writes Edgar F. Allin, "the earliest mammals did not yet possess a 'mammalian middle ear.'" (See Allin's excellent article on "Evolution of the Mammalian Middle Ear," *Journal of Morphology*, 197: vol. 147, pp. 403-38.) By Upper Jurassic times, still well within the early days of mammalian life in a world dominated by dinosaurs, these bones had entered the ear, and an exclusively dentary-squamosal joint had formed.

Embryology and paleontology provide adequate documentation of the "how" but we would also like more insight into the "why." In particular, why should such a transition occur—especially since the single-boned stapedial ear seems to function quite adequately (and, at least in some birds, every bit as well as the three-boned mammalian ear)? We are nowhe-

near the full answer to this complex question, but one hint conveys special interest and also illustrates the principle of redundancy one more time.

Pelycosaurs, those sail-backed creatures included in every set of plastic dinosaurs and every box of chocosaurs cookies, are not dinosaurs at all, but our distant ancestors—forebears of the therapsid reptiles that eventually evolved into mammals. The stapes of pelycosaurs lies in close contact with the quadrate bone of the upper jaw (forerunner of the incus that now articulates with the stapes in the mammalian middle ear). This linkage continues and sometimes intensifies in descendant therapsids—the more immediate ancestors of mammals. This anatomical connection strongly suggests that the quadrate of mammalian ancestors, while working primarily as a jaw articulation, already played a subsidiary role in the transmission of sound. Allin argues: "From the nature of its junction with the stapes, the cynodont quadrate obviously took part in sound conduction."

Unfortunately, we cannot experiment on extinct animals and have no direct evidence for quadrate hearing in the actual ancestors of mammals. However, we do know that reptilian quadrates can transmit sound while still acting as part of a jaw joint, for several modern reptiles use an important quadrate path to their inner ear. (These creatures are not mammalian ancestors to be sure, but they do demonstrate the possibility, indeed the actuality, of this crucial multiple modality in the evolution of mammalian hearing.) Snakes, for example, have no external ear or eardrum, and many scientists had considered them entirely deaf, until recent studies illustrated sensitivity to sound over most of the body, especially around the large lung that can transmit sound to the inner ear. But another route offers special advantages to a creature so close to the substrate by God's direct decree: "... upon thy belly shalt thou go, and dust shalt thou eat all the days of thy life." Snakes hear primarily by placing their heads on the ground and passing vibrations from the lower jaw to the quadrate and finally to the stapes—thus closely following the eventual mammalian pathway for bones still in the jaw. In addition, direct experiments on several lizards, and on the tuatara of New Zealand, show that vibrations directed at the quadrate are passed to the stapes and recorded in the brain.

May I confess an ulterior motive in closing, for complex and abstract excursions can be mere glosses upon simpler aims. In-jokes have delicious qualities because they

are inaccessible to all but the initiated. But sometimes, in-jokes are so good that we long to share them, but despair for the volume of background required. Well, this essay can be read as nothing but an extended pony for understanding one of my favorite humorous poems. My colleague John Burns, a lepidopterist now in Washington but formerly at Harvard, used to introduce our weekly seminars with his punny doggerel. We loved the poems and came more to hear his introductions than to suffer with the subsequent speeches. John finally published his verses in a volume called *Biograffiti* (Demeter Press, 1975), with an introduction by yours truly. My favorite is a pithy epitome of mamma-

lian ear evolution, entirely incomprehensible to 99 percent of the population, but now vouchsafed to you, my dear readers, as a small reward for your persistence, and as a dessert after this ponderous dissertation:

Evolution of Auditory Ossicles

With malleus
Aforethought
Mammals
Got an earful
of their ancestors'
Jaw.

Stephen Jay Gould teaches biology, geology, and the history of science at Harvard University.

What does it take to be the world's best aerobic exerciser?

It takes a total-body exerciser.

A machine capable of exercising all the major muscle groups in your body, not simply your legs like treadmills exercise bikes and stairclimbers.

It takes a cardiovascular exerciser.

A machine that utilizes enough muscle mass to readily exercise your heart, not simply specific muscle groups like weight machines.

It takes a weight-bearing exerciser.

A machine that utilizes the standing position to exercise the joints and long bones of the skeleton, not simply a few muscle groups like sit-down exercisers.

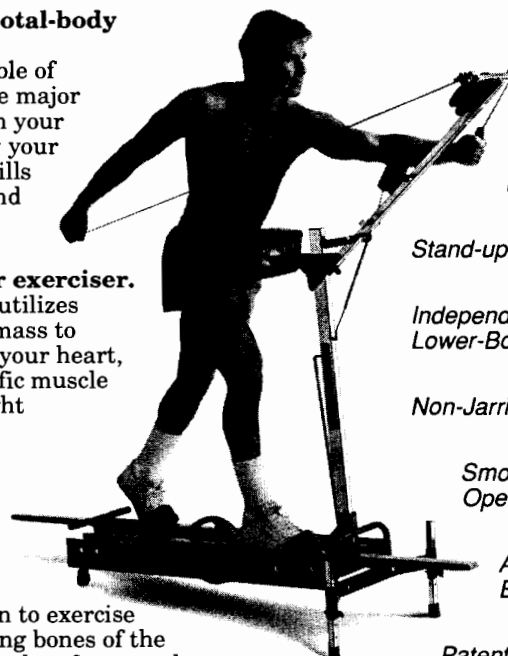
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