its splicing of an HIV-1 pre-mRNA. This pre-mRNA contains an intron that is also part of the coding region for the envelope protein. Several studies (*24, 25*) reported cis-acting sequences that influence the levels of splicing of genomic retroviral RNAs that when removed inhibit splicing. It is very unlikely, however, that the inhibitory splicing effect we have shown was due to the lack of either intron-deleted sequences (Fig. 1) or HIV-1 upstream sequences, since the synthetic SP6/HIV pre-mRNAs were spliced normally in extracts from uninfected cells. A trans-regulatory modulation of RNA splicing has been postulated for a number of viral and cellular genes (*26, 27*). However, the demonstration of inhibitors of RNA splicing encoded by HIV-1 is without precedents in retroviruses or other systems. The HIV-1 viral-encoded inhibitors of RNA splicing in the *env*-coding region might be one of the control mechanisms operative in the switch from long latency to a cytopathic virus. The cytopathic effect of HIV-1 directly correlates with the expression of high levels of viral envelope proteins by an infected cell (*8, 16*). The regulatory control mechanism of viral RNA splicing affords the virus a means of rapidly responding with efficient production of viral structural proteins for virion assembly.

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A Cineradiographic Analysis of Bird Flight: The Wishbone in Starlings Is a Spring

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High-speed x-ray movies of European starlings flying in a wind tunnel provide detailed documentation of avian skeletal movements during flapping flight. The U-shaped furcula (or "wishbone," which represents the fused clavicles) bends laterally during downstroke and recoils during upstroke; these movements may facilitate inflation and deflation of the clavicular air sac. Sternal movements are also coupled with wingbeat, ascending and retracting on downstroke and descending and protracting on upstroke in an approximately elliptical pathway. The coupled actions of the sternum and furcula appear to be part of a respiratory cycling mechanism between the lungs and air sacs.

CURRENT UNDERSTANDING OF THE mechanisms of bird flight is based largely on conventional photography (*1*). The mechanics of a wing's musculoskeletal structure, however, can only be inferred by these techniques. The action of the shoulder girdle, which is obscured by plumage, has remained unresolved. Our analysis of radiographic films of birds in flight provides detailed data on the excursions of the bones in the wing and shoulder and demonstrates that the furcula (the "wishbone") acts as a spring.

European starlings (*Sturnus vulgaris*) were radiographed in both lateral and dorsoventral projections at 200 frames per second as they flew in a wind tunnel at air speeds of 9 to 20 m/s (20 to 45 mile/hour) (*2*). For descriptive purposes the wingbeat cycle as seen in x-ray films can be divided into four phases: (i) upstroke-downstroke transition (ii) downstroke, (iii) downstroke-upstroke transition, and (iv) upstroke. During the upstroke-downstroke transition, the longitudinal axis of the humerus comes to lie in a sagittal or nearly sagittal plane (Fig. 1A, top). Thereafter the wing protracts (that is, moves craniad); in this movement the angular intersection of the longitudinal axis of the humerus and the longitudinal body axis increases from an acute angle (Fig. 1A, bottom) to about 50°. As downstroke begins, the humerus is further protracted another 5° to 10° and the elbow and carpal joints extend. During the downstroke (Fig. 1, B and C) the humerus depresses some 110° but is maintained at a relatively constant angle (55° to 60°) with respect to the longitudinal body axis.

The downstroke-upstroke transition is characterized by humeral elevation and adduction and by nearly simultaneous flexion of the elbow and carpus.

During flight the shafts of the furcula are bent laterally during downstroke (Fig. 1, A through C, top) and recoil during upstroke (Fig. 1, D through A, top). The mean excursion of the dorsal ends of the furcula in four birds was 5.8 mm (SD, 1.0 mm), an increase of 47% over the resting distance, which averaged 12.3 mm (SD, 0.2 mm) (Fig. 2A). The minimum intrafurcular distance during flight averaged 12.9 mm (SD, 0.6 mm), and the average maximum intrafurcular distance was 18.7 mm (SD, 0.9 mm) (*3*). Furcular spreading begins as the distal end of the humerus moves craniad

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during the upstroke-downstroke transition, before the initiation of humeral depression, and continues throughout downstroke. The dorsal ends of the strut-like coracoids and the cranial ends of the scapulae, both of which are intimately bound to the furcula, are also displaced laterad. The coracoid displacement occurs not through bending but by a caudolateral translation at the coracosternal joint. Each scapula appears to rotate on the thoracic wall about an axis located at the junction of the posterior and middle thirds of the bone's length. As a result, the posterior end of the scapula translates medially as the shoulders spread.

The sternum also exhibits cyclical movement with each wingbeat. During downstroke the sternum ascends and retracts caudodorsad, and then during the subsequent upstroke it descends and protracts cranioventrad (Fig. 1, bottom). These excursions are not simple linear displacements; they differ in their pathways and in the relative displacement of the cranial and caudal ends of the sternum. Typically the pathway of sternal ascent-retraction lies cranial to the pathway of descent-protraction so that one complete cycle of movement is approximately elliptical (Fig. 2B). An average total craniocaudal displacement was 2.7 mm, but some excursions exceeded 5 mm. Dorsoventral movement of the sternum was almost invariably asymmetrical, with the posterior end typically moving through a range 50% longer than that of the anterior end. An average total dorsoventral displacement of the anterior and posterior parts of the sternum was 2 and 2.9 mm, respectively; displacements up to 3.8 mm for the anterior sternum and 7.3 mm for the posterior sternum were observed (*4*).

The furcula, in addition to serving as the most cranial origin of the pectoralis, has generally been regarded as a strut or "spacer" between the shoulder girdles, although Norberg and earlier workers alluded to the possibility that this bone might be capable of storing elastic energy (*5*). We determined that the force required to bend fresh, excised starling furculae through their normal range of excursion is 0.6 to 0.8 N (Fig. 3); these furculae appear to act as lightly damped linear springs (*6*).

The pectoralis muscle appears to have a mechanical advantage appropriate for bending the furcula. Some pectoralis fibers originate from the furcular shaft, although most arise from the sternum and lateral aspect of the thorax. However, neither rhythmic nor tetanic contractions of the pectoralis, which were elicited by electrical stimulation in anesthetized birds, produced furcular spreading; in fact, the furculae were slightly compressed upon tetany. Similar stimula-

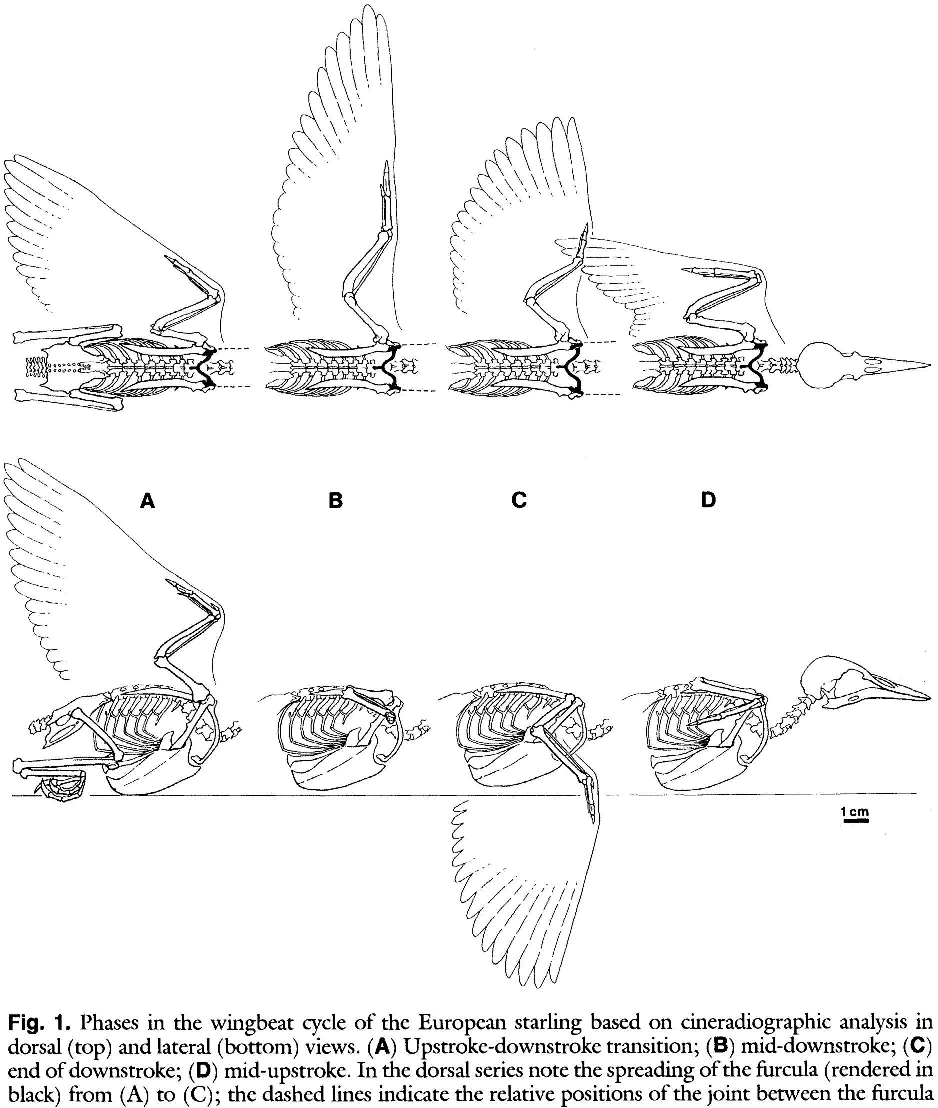

Fig. 1. Phases in the wingbeat cycle of the European starling based on cineradiographic analysis in dorsal (top) and lateral (bottom) views. (**A**) Upstroke-downstroke transition; (**B**) mid-downstroke; (**C**) end of downstroke; (**D**) mid-upstroke. In the dorsal series note the spreading of the furcula (rendered in black) from (A) to (C); the dashed lines indicate the relative positions of the joint between the furcula and coracoid. The lateral series depicts the excursion of the sternum relative to the bird's spinal column and a horizontal plane.

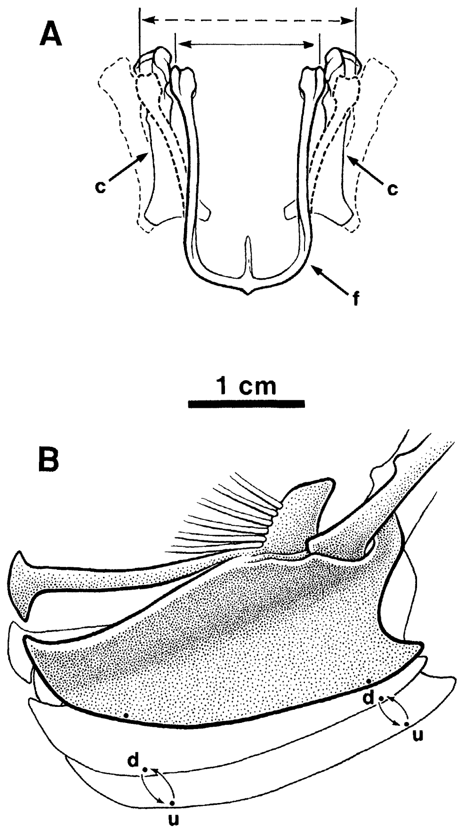

Fig. 2. (**A**) The furcula (*f*) and coracoids (*c*) of the European starling in anterior view exhibiting a typical intrafurcular resting distance of about 12.3 mm (solid horizontal arrow). As a result of furcular bending during downstroke (dashed lines), intrafurcular distance typically reaches 18.7 mm (dashed arrow) or more. (**B**) Sternal excursion in the European starling was determined by means of markers (represented as dots) implanted in the carina. The arrows indicate a typical movement from *u*, the position at the end of upstroke, to *d*, the position at the end of downstroke, and return. An average anteroposterior displacement was about 2.7 mm; sternal ascent was usually greater posteriorly (2.8 mm) than anteriorly (2 mm). The position of the stippled sternum relative to the markers at *u* depicts one of the largest excursions observed; the total dorsoventral movement of the posterior part of the sternum was 7.4 mm.

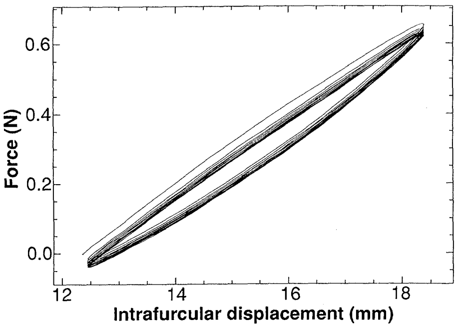

Fig. 3. Force versus displacement record of a freshly excised furcula from a European starling. Cycles of furcular bending and recoil were measured at 14 Hz. Other furculae gave slightly larger values for maximal force (up to 0.8 N).

tion of the sternocoracoideus did effect a distinct lateral bending of the furcula, widening the intrafurcular distance several millimeters (*7*). This muscle crosses the posterior aspect of the coracosternal joint and retracts the coracoid along the arcuate, posterolaterally directed pathway of the joint surface. With this movement the dorsal ends of the coracoids are abducted and the furcula is bent. Centrifugal forces generated by the extended wings during downstroke may also contribute to furcular bending (*8*).

The shafts of the furcula lie in intimate relation to the walls of the clavicular air sac. We tested the hypothesis that bending of the furcula may also occur as the result of inflation of this air sac under positive pressure by intubating the sac with a polyethylene cannula (inner diameter, 3.5 mm) inserted through the skin of the anterior chest wall. The ability of the bird to pressurize the air sac was thus compromised. No significant alteration of furcular excursion was observed in intubated birds during flight (*9*). Nonetheless, the intimate association of the clavicular air sac and the furcula is clear; artificial inflation of this sac through a tracheal cannula results in a spreading of the furcula.

Although the furcula in starlings bends and recoils over a wide range, the clavicles of some birds undoubtedly do not act in this manner. In barbets, toucans, and some parrots, for example, the clavicles are unfused ventrally and therefore cannot act as a spring. The clavicles of flightless birds (ratites and scrub-birds) are typically either absent or vestigial. The furculae of certain soaring birds, such as raptors, are so robust that they would appear to be far less compliant (if the bone bends at all). Thus, the structural diversity of avian clavicles may vary with body size, wingbeat frequency, or flight mode. The condition observed in starlings is probably common to most passerine and other small to medium-sized birds with similarly designed furculae. It is unlikely that the boomerang-shaped furcula in the Jurassic bird *Archaeopteryx lithographica* (*10*) acted as a spring because its greatest cross sectional diameter is aligned transversely and would resist bending.

The physiological significance of furcular and sternal movements during flight remains to be determined, but it is reasonable to hypothesize that these movements serve some respiratory function. Present interpretations of the mechanics of avian respiration are derived primarily from observations on stationary birds and are based on the supposition that all of the air sacs are simultaneously inflated and then deflated (*11*). Our observations on resting starlings, in both anesthetized and alert states, are that positive pressure in the clavicular air sac follows upon compression of the posterior thoracoabdominal region. This finding is consistent with our kinematic data that demonstrate coupling between furcular spreading (presumptive inflation of the clavicular sac) and sternal ascent and retraction (presumptive compression of the posterior air sacs). In a few birds (pigeons and crows) the primary respiratory cycle of inhalation:exhalation is coupled 1:1 with wingbeats, but in all others that have been studied this ratio varies from 1:2 to 1:5 and even includes odd ratios where the phase of breathing shifts relative to wingbeats (*12*). Starlings are therefore not unusual in exhibiting asynchrony between their respiratory rate during flight of approximately 3/s (*13*) and wingbeat frequencies of 12 to 16 Hz. Our observations, however, have established that furcular and sternal movements are synchronized 1:1 with wingbeat. We hypothesize that the furcular "spring" and sternal "pump" might represent a secondary respiratory cycling mechanism between the air sacs and the lungs that is capable of operating independently of inhalation and exhalation and that might serve the increased metabolic demands of flight.

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2. Siemens cineradiographic apparatus (grid-controlled tube with a 0.06-mm focal spot; 27.94-cm Sirecon image intensification system) was coupled with an Eclair GV 16 high-speed 16-mm cine camera. Adult starlings (65 to 75 g) were surgically implanted under deep anesthesia (ketamine, 2.5 mg/kg; xylazine, 2 mg/kg, by intramuscular injection) with carbide steel pin markers (0.3 mm) as an aid to kinematic analysis. Markers were placed in the anterior and posterior ends of the sternal carina, both acrocoracoids, and the deltopectoral crest of one humerus. Other skeletal features (for example, coracosternal joint, bones of the antebrachium and carpometacarpus) were readily visualized without markers. A stiff wire (0.9 mm in diameter, 1 cm long) was inserted subcutaneously along the vertebral column in the mid-dorsal region to serve as a scale. Flight sequences were analyzed frame by frame with a Vanguard M-CIIP film analyzer coupled with a Graf/Pen Sonic digitizer and Apple II computer.
3. Furcular excursions were determined from films of four birds taken in dorsoventral projection. The changing positions of the markers in the acrocoracoids were plotted from 963 frames of film representing 63 wingbeats. These measurements were adjusted to true intermarker distances with reference to the 1-cm scale; we then converted them to intrafurcular distances by subtracting the distance between the centers of the dorsal ends of the coracoids and furcula. Plots of intrafurcular distances exhibit symmetrical, sinusoidal oscillations. The ranges observed were 11.5 to 20.7 mm, 11.6 to 18.6 mm, 11.2 to 21.2 mm, and 10.8 to 21.2 mm; the resting intrafurcular distances were, respectively, 12.1, 12.3, 12.2, and 12.6 mm.
4. Sternal excursions were determined from films of four birds taken in lateral projection. The locations of the anterior and posterior carinal markers relative to the subcutaneous 1-cm scale on the bird's back were plotted from 706 frames of film representing a total of 41 complete wingbeats. The craniocaudal (CC) and dorsoventral (DV) excursions of the markers (in millimeters) were:

	Cranial marker		Caudal marker	
	CC	DV	CC	DV
	Bird 1 (n = *14*)			
$\overline{X}$	2.31	1.69	2.39	2.11
SD	0.58	0.53	0.60	0.44
Range	1.43–3.52	0.81–2.39	1.43–3.56	1.57–3.07
	Bird 2 (n = *6*)			
$\overline{X}$	2.39	2.60	2.47	3.57
SD	0.56	0.67	0.63	0.53
Range	1.67–3.33	1.96–3.77	1.67–3.47	3.14–4.58
	Bird 3 (n = 7)			
$\overline{X}$	2.44	1.54	2.52	2.39
SD	0.56	0.66	0.69	1.12
Range	1.75–2.93	0.66–2.43	1.75–3.64	1.52–4.81
	Bird 4 (n = *14*)			
$\overline{X}$	3.29	2.26	3.34	3.50
SD	0.88	0.57	0.86	1.46
Range	1.76–5.21	1.58–3.54	1.76–5.21	1.70–7.29

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6. In a device designed by N. C. Heglund and J. D. Harry, one dorsal flange of the furcula was secured with a minature bolt (0-80 size) to a stationary force transducer (Kistler 9207); the other flange was similarly affixed to the end of a lever whose position was governed by an electromagnetic ergometer (Cambridge Technology 300). The force generated by the furcula was recorded while the intrafurcular distance (that is, the lever position) varied over the range observed experimentally. Cycling from resting to maximum intrafurcular distance was undertaken at frequencies ranging from 0 Hz (stepped stages) to 14 Hz, a normal wingbeat frequency.
7. Starlings were deeply anesthetized as in (*2*). Two electrodes (0.51-μm-diameter Evanohm wires) were stripped of insulation and threaded through the length of the pectoralis bilaterally (two birds). In two other birds the brachial plexus was exposed through a dorsal approach and a set of electrodes attached directly to the pectoralis nerve. In another two birds the pectoralis was cut bilaterally and reflected along the carina to expose the sternocoracoideus, and its nerve was stimulated with single bipolar electrodes. All birds were suspended to simulate a flight posture with wings spread. Tetanic contractions were produced by stimulation pulses of 0.1-ms duration at above threshold voltage delivered at 100 Hz for 1 s (Grass S44 stimulator). Our negative results on the pectoralis contradict a report by K. Zimmer [*Zoologica* (*Stuttgart*) **88**, 32 (1935)] that electrical stimulation of the pectoralis in a domestic pigeon produced a lateral deflection of the

coracoid. Zimmer may be credited, however, with the observation (based on external measurements from a flying crow) that the dorsal ends of the coracoids diverge during downstroke.

8. Each wing in a starling was calculated to generate about 0.5 N of centrifugal force; this calculation is based on data from amputated wings (each weighing 4.95 g) of a 78-g starling that were quick frozen in an extended position. From this preparation the centers of mass and gyration were determined to be 3.2 and 3.6 cm, respectively, from the shoulder joint (C. Ellington and S. A. Rasmussen, personal communication).
9. Birds were implanted with markers in both acrocoracoids as in (*2*). Excursions of the furcula were determined from films taken in dorsoventral projection before intubation and compared with a similar analysis undertaken after intubation.
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Symmetrical Erosive Peripheral Polyarthritis in the Late Archaic Period of Alabama

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Rheumatoid arthritis was first described unambiguously in 1800, but its etiology and historical origins are still obscure. Definite rheumatoid arthritis has not been demonstrated in pre-19th century Old World skeletal remains. Six individuals who lived 3000 to 5000 years ago in northwestern Alabama and present erosive polyarthritis characteristic of rheumatoid arthritis are described. The diagnosis raises the possibility that rheumatoid arthritis can be associated with a New World pathogen or allergen.

RHEUMATOID ARTHRITIS, FIRST recognized in Europe, appears to be a relatively new disease (*1*). Except for Sydenham's (*2*) ambiguous description, Landre-Beauvais (*3*) provided the earliest documentation of rheumatoid arthritis in 1800, followed by Charcot's (*4*) in 1853 and Garrod's (*5*) in 1859. Published assertions of rheumatoid arthritis in skeletons antedating 1800 describe lesions or patterns of lesions that are not characteristic only of rheumatoid arthritis, being instead even more characteristic of osteoarthritis or spondyloarthropathies (*6–13*). We describe six prehistoric native Americans, each exhibiting a pathological pattern consisting of the presence of several kinds of lesions accompanied by the absence of several other kinds of lesions, all arranged in a particular anatomical distribution; rheumatoid arthritis is characterized by this pattern.

We examined skeletons of 84 adults who lived during the Late Archaic Culture Period, 3000 to 5000 years ago, along 19 miles of the Tennessee River immediately below Florence, Alabama. Each skeleton is directly or stratigraphically associated with distinctive Late Archaic artifacts. The excellent bone preservation derives from interment in acid-neutralizing mussel shell middens at Late Archaic riverine encampments.

While investigating paleopathologies in this group, we discovered lesions in six skeletons corresponding to lesions noted in contemporary rheumatoid arthritis patients. Although the consistent anatomic distribution of lesions in six individuals contraindicates postmortem artifact, we examined each lesion (magnification to ×40) for post-mortem artifact (pseudolesion). Four of the six affected individuals are female and two are male. Two (including one male) died at ages between 30 and 40 years, two (including the

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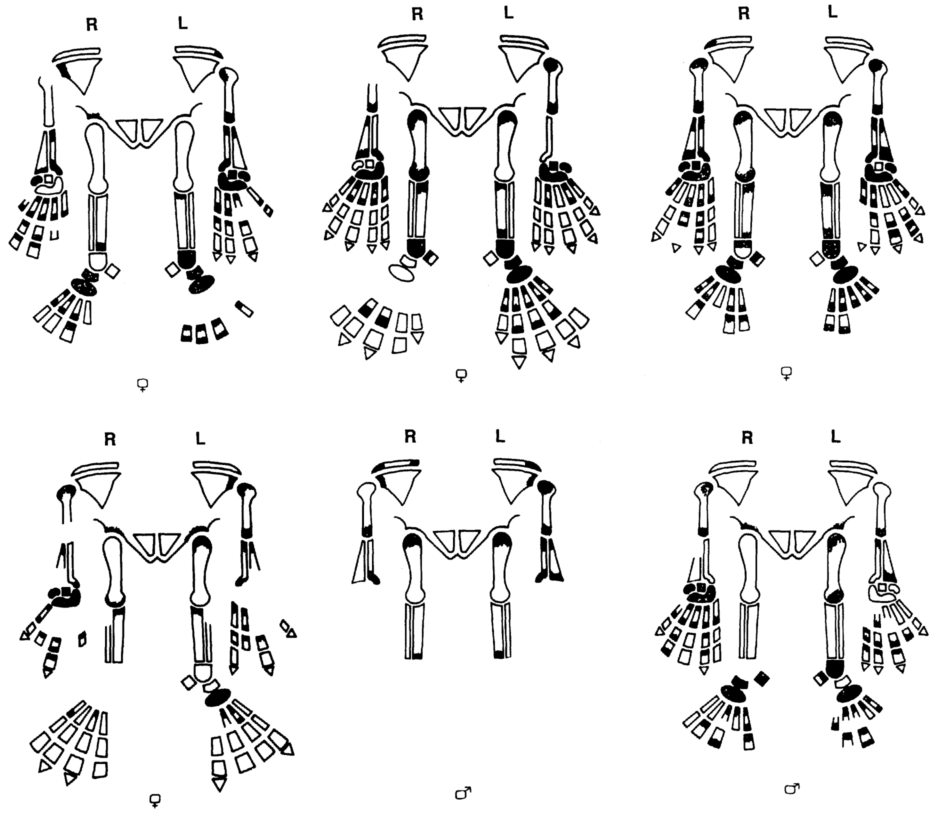

Fig. 1. Homunculi illustrating skeletal distribution of erosive lesions in individual Late Archaic native Americans. Nonvisualization of a bone indicates missing skeletal material, except for the spine and sacroiliac joints. Spine and sacroiliac joints, though present in all skeletons portrayed, contained no evidence of erosion or fusion.