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GENERAL BIOLOGY

Kinematics of the Shoulder Girdle in Bats

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Movements of the distal wing segments in bats are readily accessible to observation and are rather thoroughly investigated [9, 10, etc.]. On the contrary, movements of elements of the shoulder girdle are hidden from view and are difficult to study. Therefore, the concept of the chiropteran shoulder girdle functioning is far from perfect.

A well-known hypothetical scheme of wing movements in a flying bat was proposed by Hill and Smith [6]. This is probably a compilation of studies of Vaughan [7, 8, etc.] and original data of these authors. According to this scheme (Fig. 1), a significant contribution to flapping movements of wings is made by joint action of the shoulder girdle and humerus. A key element of this model is the clavicle which is presumed to be mobile in the transverse plane, with an amplitude more than 60°, from an almost vertical position of the clavicle at the beginning of the downstroke to an almost horizontal position at its end. The scapula connected to its distal end is presumed to slide over the surface of the thorax, circumscribing respective arch. The authors of this scheme believe that, in the upper position of the wing, the scapula lies horizontally on the dorsal surface of the thorax and, in the lower position, it is located lateral to the thorax in an almost vertical (parasagittal) position. Similar ideas were developed in [1, etc.].

However, the scheme considered is not based on actual morphological and experimental data and lacks cogent functional arguments for presumed movements. In addition, the only X-ray study of movements of the clavicle [5] which existed by the time of the development of this scheme was not cited in [6]. Thus, to date, an integrated picture of movements in the shoulder girdle of chiropterans during flight, which could have provided an understanding of functional features of their flying apparatus, has not been proposed. The purpose of the present study is to fill this gap.

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MATERIALS AND METHODS

The structure of forelimb joints was described based on dry skeletons of nine chiropteran species: *Cynopterus sphinx, Rousettus aegyptiacus, Pteropus lylei, Pteropus tonganus, Rhinolophus ferrumequinum, Rhinolophus borneensis, Hipposideros larvatus, Hipposideros armiger*, and *Myotis blythi*. The potential mobility of joints was examined using syndesmologic preparations of four species (*C. sphinx, R. aegyptiacus, R. ferrumequinum*, and *H. larvatus*) and fresh corpses of six species (*R. aegyptiacus, Myotis daubentonii, Myotis dasycneme, Plecotus auritus, Eptesicus nilssoni*, and *Carollia perspicillata*). In sum, representatives of five families of both chiropteran suborders were investigated.

Actual mobility of elements of the shoulder girdle was examined by X-ray filming of the flight of *Rousettus aegyptiacus.* When filming, a collar with a lead were put on the animal's neck to keep it in screen.

RESULTS AND DISCUSSION

Potentially Possible Movements of the Shoulder Girdle

Even at the beginning of morphofunctional analysis, we had to abandon the scheme of movements of the shoulder girdle of chiropterans proposed by Hill and Smith [2–4] for the following reason. It is evident that the swing of the clavicle in the transverse plane, presumed in this hypothesis (Fig. 1) is only possible in the presence of appropriate adaptations of the sternoclavicular joint for movements with a large amplitude. When studying the structure of this joint, relief of the articular surfaces and their orientation, we have not recognized features providing movements of this sort. The articular facets on the sternum and clavicle are flattened and ovate. Moreover, in addition to a thin synovial bursa, the joint has two well-developed ligaments considerably restricting mobility of the clavicle.

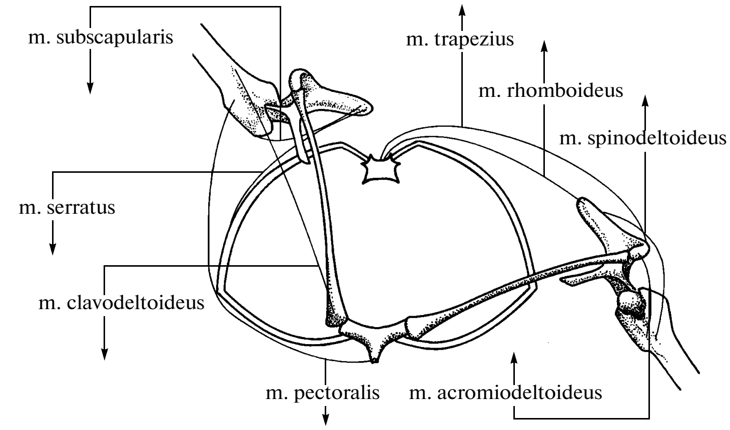

Fig. 1. Scheme of movements of the shoulder girdle of bats after Hill and Smith [6]. Muscles that presumably contract during upstroke and downstroke are marked by respective arrows.

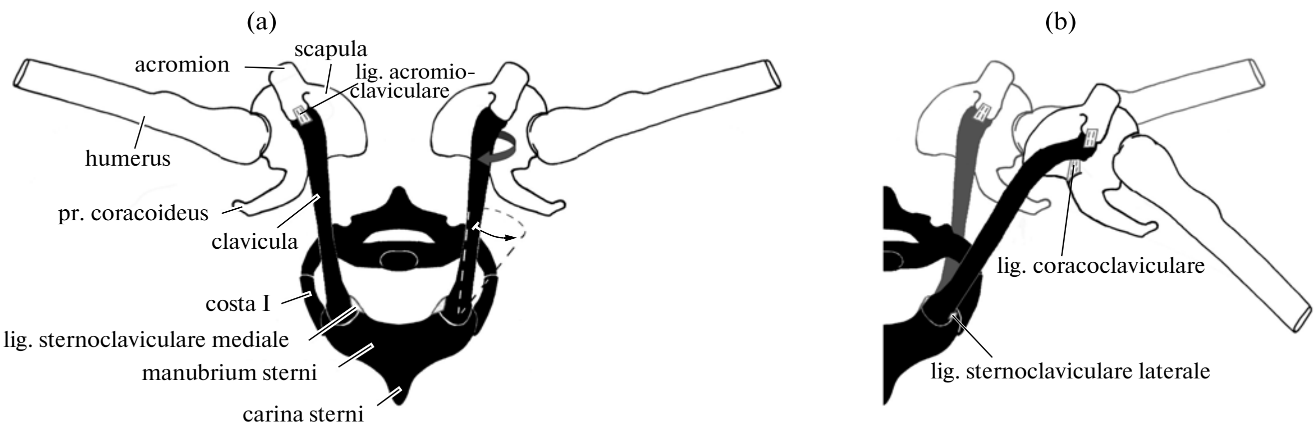

Fig. 2. Scheme of movements recognized of the shoulder girdle and humerus of chiropterans, anterior view: (a) beginning of a downstroke; the clavicle is in the medial position, the humerus is risen; arrows mark directions of further movement, and hatching shows limits of mobility of the clavicle; (b) the end of downstroke; gray outline shows the previous position.

One of them, the obliquely positioned medial sternoclavicular ligament (ligamentum sternoclaviculare mediale), connects the medial margin of the proximal head of the clavicle to the anterior margin of the manubrium of the sternum (Fig. 2). The second, lateral ligament (ligamentum sternoclaviculare laterale), is located on the opposite, lateral side of the joint (Fig. 2b). It is even shorter than the medial ligament and connects the margins of articular surfaces of the sternum and clavicle, which directly prop against each other. These ligaments restrict significantly disarticulation of the flattened articular facets, leaving, however, the ability for small inclination of the clavicle. The amplitude of lateromedial inclination is at most 30° (Fig. 2), that is, less than half of that presumed in the scheme of Hill and Smith. The amplitude of craniocaudal inclination is even lower. In sum, the two degrees of freedom provide movements of the clavicle within a cone outlined in Fig. 2a. A more prominent movement in the sternoclavicular joint is rotation of the clavicle about the longitudinal axis of its proximal part. The limits of rotation are determined by the length of the medial sternoclavicular ligament, which is wound on the base of the clavicle, as it turns. The amplitude of rotation of the clavicle varies somewhat in different chiropteran groups.

In addition to the mobility of the shoulder girdle relative to the axial skeleton, chiropterans possess some intragirdle mobility, i.e., that of the scapula relative to the clavicle. The character of this mobility is determined by two ligaments, the ligamentum acromioclaviculare and ligamentum coracoclaviculare. The acromioclavicular ligament (Fig. 2) is thick, frequently bears a sesamoid ossification (indicating high tension of the ligament). The coracoclavicular ligament (Fig. 2b) connects the cranial margin of the base of the coracoid process on the scapula and the caudolateral surface of the distal end of the clavicle.

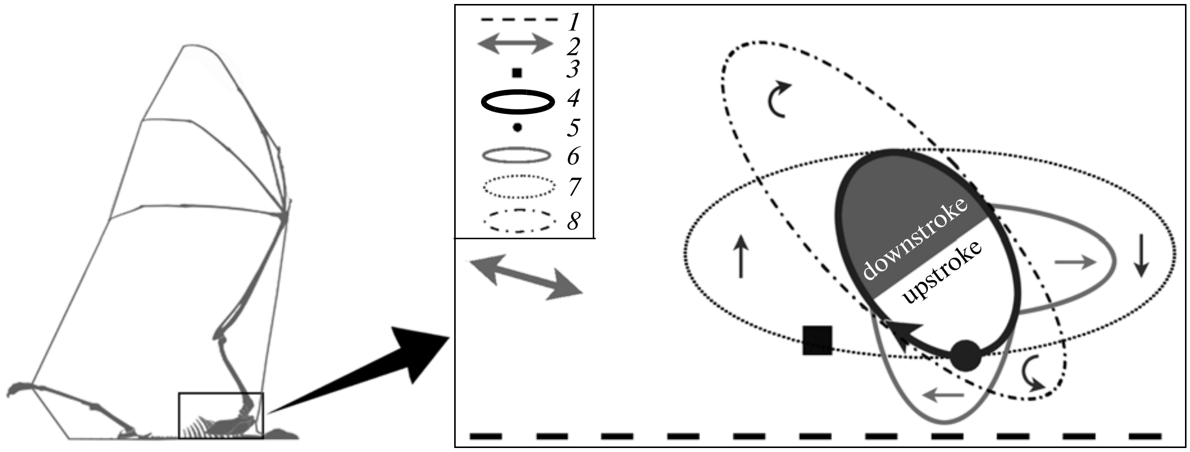

Fig. 3. Scheme of a complete motion cycle of the shoulder girdle in *Rousettus aegyptiacus* in flight (based on X-ray data); for the proper scheme polarity the general animal's outline is shown on the left. Designations: (*1*) midline of the body, (*2*) trajectory of dorsocaudal corner of the scapula, (*3*) sternoclavicular joint, (*4*) trajectory of the distal end of the clavicle, (*5*) extreme medial position of the acromioclavicular joint, (*6*) phases of craniocaudal deviation of the clavicle, (*7*) phases of lateromedial deviation of the clavicle, (*8*) phases of axial rotation of the clavicle; arrows indicate directions of movements.

Together, these two ligaments serve as guy ropes for the distal end of the clavicle bracing it between the acromion and cranial edge of the scapula. Although these ligaments allow for a relatively wide range of mobility, the basic scapular movement is its rotation about the longitudinal axis (Fig. 2b), passing through the acromioclavicular joint and dorsocaudal corner. In the course of these turns, the two ligaments are wound on the clavicle, limiting the range of scapular rotation.

Actually Used Movements of the Shoulder Girdle

The study of skeletons and syndesmological preparations is necessary but not sufficient for the revelation of actually used movements of the shoulder girdle, because a flying animal does not use the entire range of possible mobility. The movements of the shoulder girdle employed by chiropterans in flight were obtained directly by X-ray filming.

Movements of the shoulder girdle in flight are stably repeated in accordance with the wingbeat cycles (Fig. 3). Beginning from the second half of the upstroke and throughout the first half of the downstroke, the clavicle is deviating laterally. At the upstroke to downstroke transition, the clavicular supination is added, which increases lateral displacement of the acromion due to characteristic curvature of the clavicle. At the middle of downstroke, the acromion reaches its lateralmost position and the clavicle begins to deviate medially. At the downstroke to upstroke transition, the clavicle begins to deviate anteriorly, and its supination changes to pronation. When the acromion reaches the anteriormost point of its trajectory, the clavicle begins to deviate posteriorly. At the middle of the upstroke, its medial deviation changes to lateral one and the cycle repeats. It is noteworthy that craniocaudal movements of the clavicle are restricted to the upstroke, while, throughout the downstroke, the most loaded phase of flight, it remains in the caudal position.

Judging from X-ray data, the amplitude of axial rotation (supination–pronation) of the clavicle in *Rousettus aegyptiacus* is at least 45°, the amplitude of lateromedial deviations is at most 30°, and craniocaudal deviations are too small to be measured with certainty.

The scapula in the wingbeat cycle does not show significant deviations from the frontal plane, staying on the dorsal surface of the thorax. Since its acromial process is tightly attached to the clavicle, the position of the anterior part of the scapula is determined by movements of the distal end of the clavicle. The trajectory of the acromion approaches an ellipse (Fig. 3), the longer diameter of which is not strictly perpendicular to the vertebral column, so that the lateral pole of the ellipse is located somewhat caudal to the medial pole. Along the posterior half of the ellipse, the acromion moves away from the vertebral column and, along the anterior half, back towards the vertebral column. During an upstroke, the acromion passes along the craniomedial part of the ellipse and, during a downstroke, along the caudolateral part. The trajectory of the posterior end of the scapula (its dorsocaudal corner) differs considerably from the trajectory of its acromial part. It moves posteriorly and anteriorly, following a rectilinear trajectory almost parallel to the vertebral column. Thus, in the frontal plane, the dorsocaudal corner of the scapula moves reciprocally, and its acromial region "driven" by the clavicle moves circularly. The general principle of movements of the shoulder girdle resembles the kinematics of a crank mechanism, with the clavicle playing the role of crank and the scapula playing the role of connecting rod.

In summary it should be emphasized that all the above movements of the scapula and clavicle contribute very slightly to the amplitude of wing movements, because they are considerably smaller than the movement range of the humerus relative to the scapula in the shoulder joint.

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