Functional Analysis of the Primate Shoulder

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Abstract Studies of the shoulder girdle are in most cases restricted to morphological comparisons and rarely aim at elucidating function in a strictly biomechanical sense. To fill this gap, we investigated the basic functional conditions that occur in the shoulder joint and shoulder girdle of primates by means of mechanics. Because most of nonhuman primate locomotion is essentially quadrupedal walking—although on very variable substrates—our analysis started with quadrupedal postures. We identified the mechanical situation at the beginning, middle, and end of the load-bearing stance phase by constructing force parallelograms in the shoulder joint and the scapulo-thoracal connection. The resulting postulates concerning muscle activities are in agreement with electromyographical data in the literature. We determined the magnitude and directions of the internal forces and explored mechanically optimal shapes of proximal humerus, scapula, and clavicula using the Finite Element Method. Next we considered mechanical functions other than quadrupedal walking, such as suspension and brachiation. Quadrupedal walking entails muscle activities and joint forces that require a long scapula, the cranial margin of which has about the same length as the axillary margin. Loading of the hand in positions above the head and suspensory behaviors lead to force flows along the axillary margin and so necessitate a scapula with an extended axillary and a

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shorter cranial margin. In all cases, the facies glenoidalis is nearly normal to the calculated joint forces. In anterior view, terrestrial monkeys chose a direction of the ground reaction force requiring (moderate) activity of the abductors of the shoulder joint, whereas more arboreal monkeys prefer postures that necessitate activity of the adductors of the forelimb even when walking along branches. The same adducting and retracting muscles are recruited in various forms of suspension. As a mechanical consequence, the scapula is in a more frontal, rather than parasagittal, position on the thorax. In both forms of locomotion—quadrupedal walking and suspension—the compression-resistant clavicula contributes to keeping the shoulder complex distant from the rib cage. Future studies should consider the consequences for thorax shape. The morphological specializations of all Hominoidea match the functional requirements of suspensory behavior. The knowledge of mechanical functions allows an improved interpretation of fossils beyond morphological similarity.

Introduction

A general characteristic of the forelimb in all tetrapods is the mobility of the shoulder-thorax connection, that is, the forelimb's attachment to the trunk by muscles, mainly the m. serratus lateralis and m. levator scapulae, and the lack of a solid skeletal connection between the forelimb girdle and vertebral column. In addition to the muscles, a bone may connect the shoulder girdle to the trunk (the coracoid in reptiles and birds, and the clavicle in primates and bats), but this is not always the case (cursorial mammals). Textbooks note or emphasize the independence of the shoulder girdle from the trunk (Hildebrand and Goslow 2004; Romer 1956; Romer and Frick 1966; Starck 1979), a line of reasoning that is best illustrated by Klima and Maier (1988). For the morphology of primate shoulder blades, the studies of Graves (1921) and Frey (1923, 1924) give an overview, while Ashton and Oxnard (1964); Ashton *et al.* (1965, 1971), Oxnard (1963, 1967), and Young (2006) mark the standards. Primates show morphological characteristics of the shoulder that deviate from those of other mammals, and the special features of the primate shoulder complex—well developed clavicle, form of scapula with prominent acromion and marked spina, often acute caudal angle, a dorsally shifted position of the scapula on the wide thorax, and a rather straight humerus with globular head—have been described repeatedly (Mollison 1911; Schultz 1930, 1961), but are not yet completely understood. They are often attributed to the mobility of the forelimb, especially the wide excursions of the upper arm.

The biomechanics of the shoulder in quadrupeds are poorly known. Preuschoft (1973) calculated force equilibria for the glenoid joint of chimpanzees in various load cases. Badoux (1974) showed some basic conditions. Müller (1967) analyzed the functional loading of the scapula, interpreting it as a framework consisting of the reinforced margins alone. The vertebral margin in this model is simplified as a beam, supported by the cranial and the axillary margins and loaded by the weight-bearing m. serratus. The vertebral margin of the scapula actually shows the most marked

curvature where the weight-bearing m. serratus inserts. This curvature at the point of force application gives it the greatest strength without the necessity to deposit a great amount of heavy bone material, so that great strength is combined with minimum weight. In a remarkable study, Roberts (1974) used a variety of approaches to explain the scapula functionally. All of these were based on the locomotor classifications that were *en vogue* at that time, despite their inadequacy for biomechanical studies. In his most attractive experiments, he investigated plastic casts of (existing) scapulae covered by a thin photoelastic plastic film under loads created by muscle contractions. He modified the simulations of muscle forces until the stress flows were in accordance with scapular morphology (including the patterns of trabeculae). He concluded that "the... structure of the scapula blade reflects a pattern of muscular and gravitational force distribution consistent with joint stabilisation and limb function..." (Roberts 1974, p. 178/179). Although this statement is correct, the first factor is not demonstrated completely, and the second not defined exactly. The combination of muscle forces and weight forces in Roberts` experiments was not designed in accordance with the conditions of external equilibrium of the whole animal. Moreover, an approach that starts from existing shapes can never explain the shapes of skeletal elements (Preuschoft and Witzel 2005; Rayfield 2007; Witzel and Preuschoft 2005).

The movements of the shoulder girdle on the thorax are difficult to observe but have been clearly documented in a series of studies on small mammals by the Jena group (Fischer 1994; Schilling and Fischer 1999; Witte *et al.* 2002). These studies include primates (Schmidt 2001; Schmidt and Fischer 2000; Schmidt *et al.* 2002) and confirm or complement the results obtained earlier by Stern and Oxnard (1973), Rose (1974, 1979), Morbeck (1979), and especially Larson (1993) and Whitehead and Larson (1994). Larson (1993) reviewed and summarized functional explanations of the primate shoulder, including the important observations of Jolly (1967), Roberts (1974), and Rose (1974, 1983, 1989). The activity patterns of the muscles controlling the shoulder are fairly well known thanks to the work of Stern and Larson (Larson 1993, 1998; Stern *et al.* 1977). The remarkable variability of muscle activities corresponds to the redundancy of muscle functions that is shown in the text that follows. This provides a biologically reasonable way to avoid fatigue of particular muscle fibers and bridge lesions. Preuschoft *et al.* (2003) provided a biomechanical explanation for the divergent thorax shape of primates and their scapular position, as well as the persistence of the clavicle in contrast to most other mammals. However, a complete biomechanical analysis of the forces acting around the shoulder of primates, which connects form and function, is still missing. No study has yet undertaken to calculate, or at least estimate, the forces across this complex. The major prerequisite for evaluating the influence of mechanical stresses on the development of shape again is precise knowledge of the stresses acting inside the body, which we attempt in this paper.

The search for morphological adaptations to the mechanical function of the limbs can be confined to the phases of posture and locomotion in which the limbs are highly loaded. This is the case in the stance phase of walking, because the forces that act on the limb while supporting body weight are much higher than those acting during the swing phase. Likewise, the forces transmitted across the shoulder in balancing the body by the arms in resting, other postural behaviors, collecting food,

and manipulation, as emphasized by Rose (1974) and Roberts (1974), are necessarily smaller than those in locomotion; otherwise they would initiate movements of the body! Small loads can be sustained easily by the skeleton and the musculature and do not need special adaptations; they must, and can be, sustained by the given morphology.

We deduced the principles of biomechanical loading of the shoulder in characteristic stages of locomotion, and information concerning the directions and magnitudes of the forces that act on the humeral head, glenoid joint, and thoraco-scapular junction. We compared these data with the most obvious morphological adaptations of this complex and empirical information about muscle activity. Our major aim was to identify the mechanical factors that influence the shoulder complex and compare them with morphology. We wanted to understand (in terms of mechanics) what is known, namely morphology, movements, and muscle activities. We do not claim to present a complete analysis of the shoulder mechanics in all primates; instead, we aim to demonstrate basic conditions. A thorough consideration of the forces acting on the ribs and their relation to thorax shape will follow in another paper.

Once a relation between shape and function is confirmed, this begs the question of how the adaptations have been developed. The origin of morphological adaptations is not beyond debate. There is common agreement regarding the phylogenetic aspect: Mutants that fit best to the functional demands of daily life have a selective advantage over those that do not possess the essential traits. The crucial point in this context is: What are the selective advantages of morphological (skeletal) traits, the so-called adaptations? However, Wolff's (1892) law and the work of Pauwels (1940–1965, English version 1980) and Kummer (1972) suggest that the process of causal morphogenesis of bone during the lifetime leads to optimal shapes of the skeletal elements by bone remodeling under the influence of mechanical stress, as discussed in our papers on skull shape (Preuschoft and Witzel 2004, 2005; Witzel and Preuschoft 2002, 2005).

Materials and Methods

We estimated the forces acting in the musculo-skeletal system of the whole primate during characteristic phases of locomotion by means of theoretical statics, as described in Lehmann (1974–1977), using published substrate reaction forces where available. The standard locomotor repertoire of many primates, and therefore the phases of locomotor movements, are known from pioneering studies of, e.g., Rose (1974, 1979) and Morbeck (1979) and have been verified by a considerable number of film or video recordings accumulated in various laboratories. We selected from the data available in Bochum, Jena, and Leipzig examples that are in line with M. Schmidt's cineradiographic data. We used the reaction forces applied during locomotion by the substrate against the individual's hands, published by D. Schmitt (1998, 2003). In other load cases we estimated substrate reactions on the basis of published measurements (Demes *et al.* 1992, 1994; Hirasaki *et al.* 1993; Kimura *et al.* 1979; Nakano 2002). These measured reaction forces are very similar to those predicted from theory (Preuschoft 2002). We determined which muscles are

available for balancing the external forces based on our own or published anatomical dissections. We reduced muscle forces to their lines of action. By constructing parallelograms of forces, in which the external and the muscle forces represent the sides, while the diagonals represent the joint forces, we established equilibrium first in the shoulder joint, then in the thoraco-scapular junction. We compared the most obvious morphological traits of the humerus, glenoid joint, and shoulder blade to the forces determined. The distribution of forces within the scapula is difficult to estimate theoretically with sufficient exactness, so we investigated the stress flows under the action of those muscles and joint forces, which follow from the theoretical approach, experimentally using Finite Element (FE) analysis. Simple 2-dimensional analysis was sufficient to answer the given question. To facilitate comparisons, and to emphasize the influence of the joint force, we use the same model for both ways of loading. In contrast to the true glenoid surface, the joint surface at the lower margin of our model is semicircular and so can transmit forces in various directions. We calculated stress flows using the FE-program ANSYS 2000. Unlike in our studies of skulls (Preuschoft and Witzel 2004; Witzel and Preuschoft 2005), we did not intend to construct the complete, 3-dimensional shape of the shoulder blade.

Results

Substrate Reaction Forces and Their Effects on the Musculo-skeletal System in Side View

M. Schmidt's x-ray images of a walking *Saimiri* (Fig. 1) show the postures through which the forelimbs pass during a walking cycle and that we analyzed as a first step. The whole forelimb, forearm, and upper arm plus shoulder girdle can be taken as a
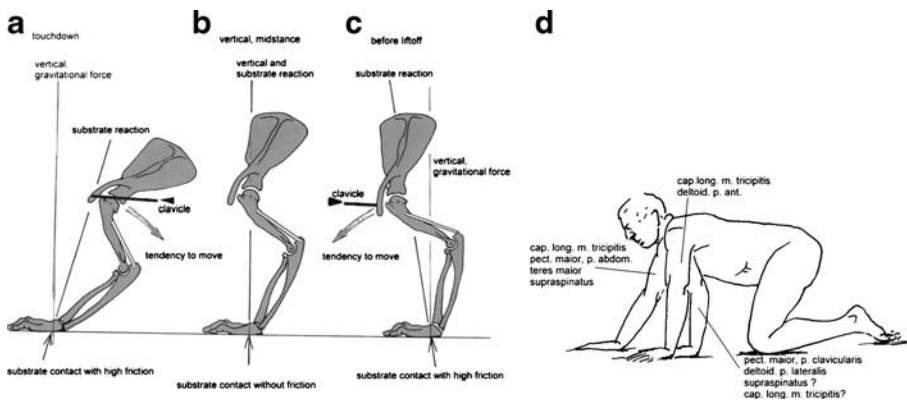

Fig. 1 (a, b, c) Three phases from of a walking cycle of the New World monkey *Saimiri*. Drawn after x-ray films by M. Schmidt *et al.* (2002) (Schmidt 2001). Note the anteverted position of the forelimb at the begin of the stance phase. If the elbow and shoulder joints are kept in balance by monarticular muscles (double lines), the whole limb is exposed to the tendency to give way either rearward or forward. These tendencies are countered without expenditure of energy by the clavicula (black bars), which is kept exactly in the positions it needs (arrowheads). (d) Aside from the stabilizing function of the clavicle, muscles of the shoulder girdle contract, as can be controlled in a simple experiment.

unit, rotating about the carpal joint, if the elbow and shoulder joints are kept in balance by monarticular muscles. The external substrate reaction force and body weight then pushes the shoulder either forward or rearward. Movements of the shoulder girdle can be blocked by either the clavicle, which has been observed to assume the positions shown in Fig. 1a and c and may transmit either compressive or tensile forces to the scapula, or by muscles, which can of course exert only tensile force. The activity of these muscles can be verified by the simple experiment shown in Fig. 1d: Depending on the positions of the hands, the muscles predicted in Figs. 1 and 2 are recruited. Empirically measured substrate reaction forces (SRR) in "more terrestrial" monkeys walking on more or less horizontal substrates according to D. Schmitt (1998, Fig. 2a) show—in spite of their considerable variability, and with the exception of propulsive steps—a constant position of the SRR anterior to the elbow and behind the shoulder joint. This allows a determination of the force equilibrium in the glenohumeral joint, scapula, and proximal humerus. We investigate the stance phases of walking that occur under these conditions in Fig. 2b and c. The shoulder joint can be controlled by only 1 muscle, first the m. supraspinatus (Fig. 2b) or second, the m. deltoideus (Fig. 2c). Larson and Stern (1989) and Larson (1998) observed activity of both muscles; activity of the latter muscle would yield a plausible explanation of the well-known retroflexion of the proximal humerus in quadrupedal monkeys. The joint forces that result from SRR and muscle forces pass in both cases through the more cranial part of the glenoid surface, and cranial to the scapular spine. As can be seen from Fig. 3a, the facies glenoidalis shows, especially in the more terrestrial monkeys, a marked, narrow extension cranially (Krause 2008; Larson 1993). The humeral head, on the other side, is cranially less curved (Fig. 3b),
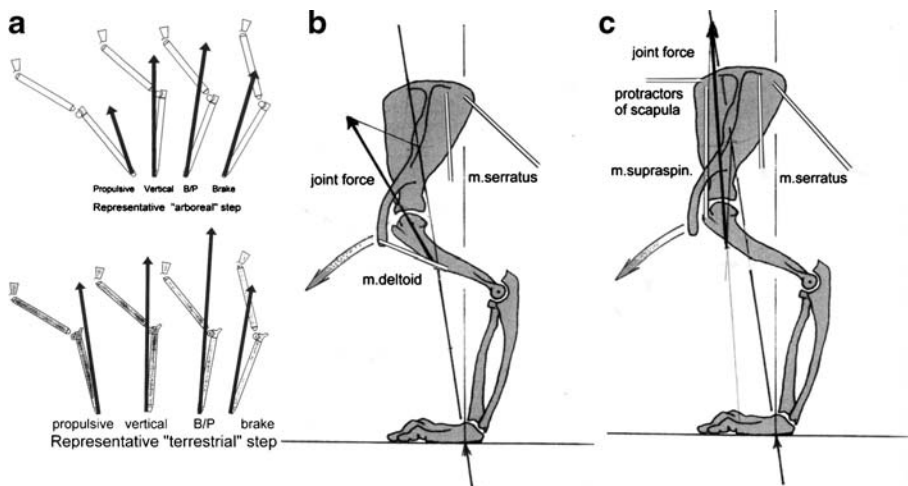

Fig. 2 (a) Substrate reaction forces in more terrestrial monkeys according to D. Schmitt (1998). These positions seem to be preferred in general by terrestrial Old World monkeys (Larson and Stern 2007; Schmitt 2003) in steady-state locomotion. (b) Joint resultant (arrow) and muscles (double lines) necessary for keeping the scapula in its place in relation to the thorax, if alone the m. deltoideus maintains equilibrium in the shoulder joint. (c) Joint resultant and muscles under the condition that the shoulder joint is balanced alone by the m. supraspinatus. For the sake of simplicity, the equilibrium in the elbow joint is taken for granted, without the illustration of the active muscles, as in all further figures.
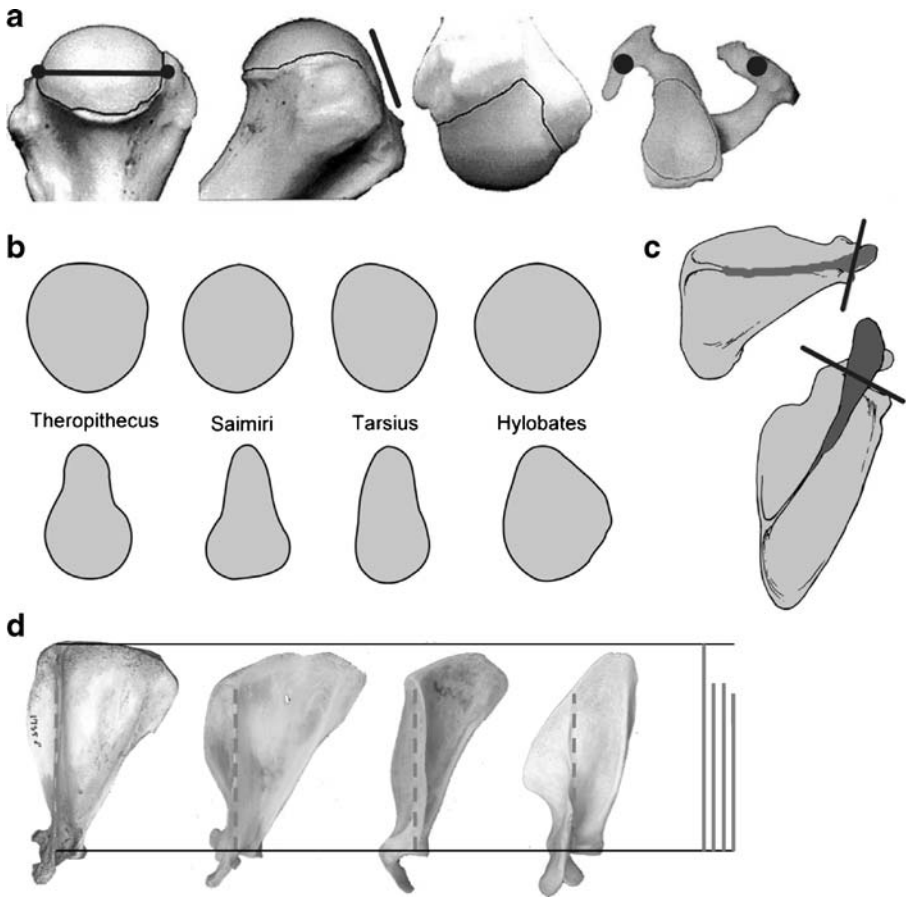
Fig. 3 Shapes of the humeral head, facies glenoidalis, and scapula in some primates to illustrate the adaptive traits. (**a**) Posterior, lateral, and cranial aspect of caput humeri; glenoid aspect of scapula in *Theropithecus*. The narrowness and flattening of the humeral head, as well as the distance of the coracoid and the acrominon from the joint, are emphasized. (**b**) Joint surfaces of caput humeri and facies glenoidalis. (**c**) Scapulae of a (terrestrial) baboon or macaque, and below of an (arm-swinging) gibbon to show the different orientations of the glenohumeral joint (modified from Larson 1993). (**d**) Scapulae in various locomotor types. From left to right: Terrestrial *Theropithecus*, arboreal walking and climbing *Saimiri*, clinging *Tarsius*, suspensory *Hylobates* (Krause 2008); the lengths of the spina scapulae in relation to total length of the scapulae are indicated, whereby the latter in the gelada is defined by spine length, but in the gibbon by the length of the axillary margin.

so that relatively large parts of the joint surfaces of humerus and scapula are in contact, offering, in spite of the narrow glenoid surface, a rather large surface for transmission of the joint resultant forces (Krause 2008; Larson 1993; Roberts 1974; Rose 1989).

If the shoulder joint is kept in equilibrium, the forelimb plus shoulder girdle must be stabilized on the thorax. This can be achieved by several muscles, pulling in the directions shown by red lines. The obvious redundancy of muscle functions allows the notorious variability of muscle activities, as emphasized by, e.g., Larson (1993) and D. Schmitt (2003).

Because of the illustrated direction of the joint resultant, the glenoid surface is set at nearly 90° to the cranial margin and the cranial part of the scapula receives much stress, and must be reinforced. Its length serves as a long lever for the foreswing of the limb (Fischer 1994), reduces the force necessary to keep the scapula in place, and also is long enough to offer bony insertions to many muscle fibers of the m. serratus. According to M. Schmidt *et al.* (2002) (Schmidt 2001), the length of the scapula contributes considerably to step length, because of its rotation. Both characteristics, strong cranial margin and length of scapula, are present in the more terrestrial Old World monkeys (Fig. 3c).

Another possibility for stabilizing the shoulder joint is contraction of the retractors of the shoulder: Mm. pectoralis maior, minor, and latissimus (Fig. 4a). This activity is comparable to the generally known technical principle realized in the lifting jack used in motor cars (Fig. 4b). This possibility is used preferentially by more arboreal monkeys, as documented by Larson and Stern (2007), who showed that New World monkeys tend to employ the retractors of the shoulder, whereas the more terrestrial Old World monkeys do not. This preference falls in line with the requirements of forelimb use in the more anteverted postures that are typical for arboreal activities. In most small mammals the forefoot is not more anteverted than below the eyes (Schmidt and Fischer 2000; Witte *et al.* 2002).

If the forelimb is more anteverted than usual in other mammals, the SRR may well pass cranial to the shoulder joint (Fig. 5). This also holds true if the limb is elevated and loaded above head level (as in Preuschoft *et al.* 2003), or if a pulling component is exerted by the arm, as typical of all more suspensory activities, as illustrated in Fig. 6. The glenohumeral joint alone may be balanced by the m. teres maior (Fig. 5), but if so, the scapula will tend to follow the resultant force of the
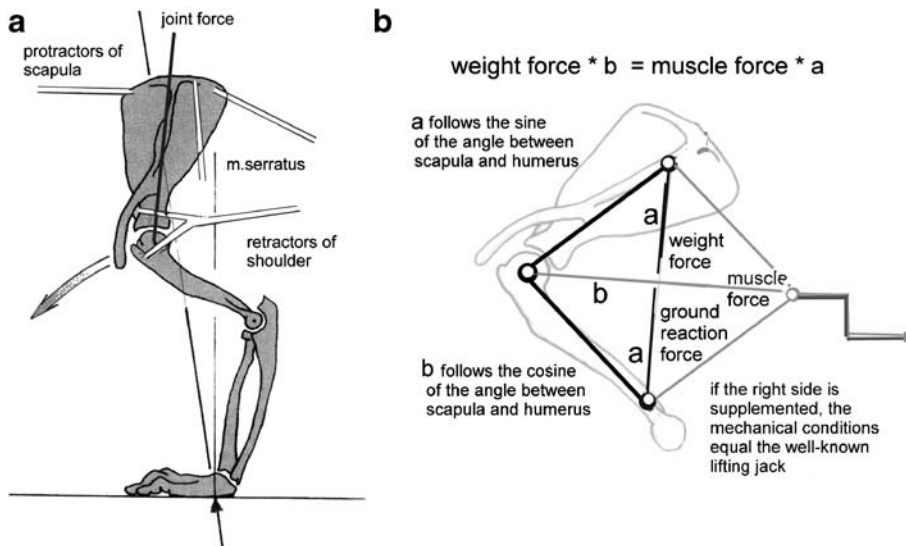

Fig. 4 (**a**) Shoulder kept in equilibrium by the retractor muscles of the shoulder (double lines). (**b**) The same technical principle is realized in the lifting jack. This way of controlling the shoulder seems to be preferred by some arboreal New World monkeys, as can be derived from EMG data of Larson and Stern (2007).
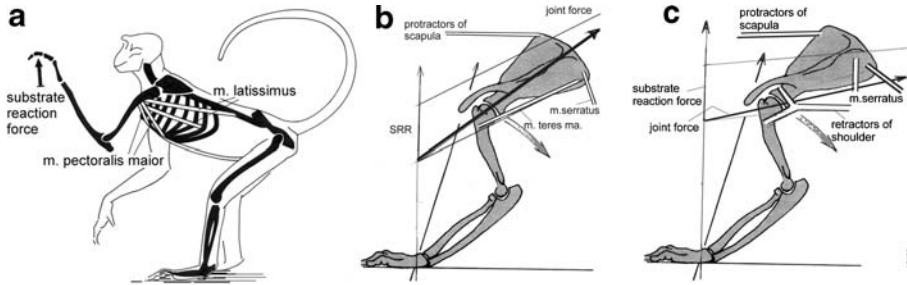
Fig. 5 (a) Elevation of the arm above the height of the shoulder in a Hanuman langur (Preuschoft *et al.* 2003). (b) Joint resultant of the shoulder joint (arrow) produced by SRR and the monarticular m. teres maior (double lines); shoulder girdle muscles are necessary to keep the scapula in its place on the thorax. (c) Joint resultant produced by the retractors of the shoulder. Again activity of shoulder girdle muscles is necessary to keep the scapula on the thorax. The loading of the clavicle in a comparable posture is shown in Fig. 1.

shoulder joint, and its place on the thorax must be controlled as well. The joint forces act against the center of the facies glenoidalis and are greater than during walking on level substrates, as analyzed in the preceding text. The relation between scapula and trunk can be controlled by the shoulder girdle muscles. Obviously, muscle forces pulling the scapula in cranial direction are absolutely necessary to compensate the rearward directed components of the shoulder retractors that cross the thoraco-scapular junction. This explains the observation of Larson *et al.* (1991)
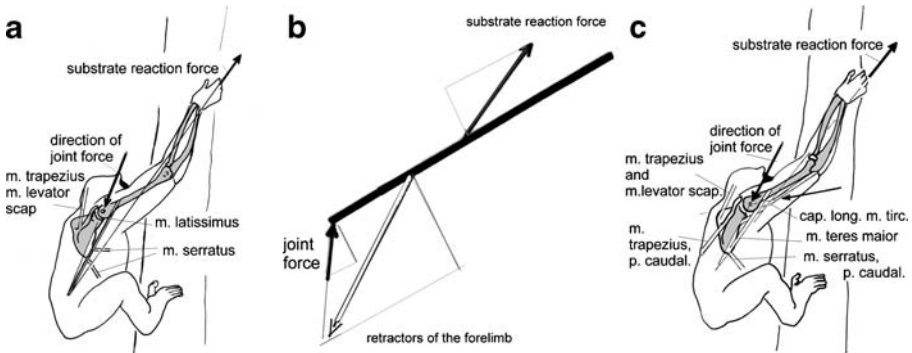

Fig. 6 Chimpanzee in vertical climbing as an example of suspended posture. (a) The glenohumeral joint is kept in equilibrium by the m. latissimus dorsi (double line). To prevent the scapula from moving caudally, a pull of the cranial m. trapezius (double line) or the m. levator scapulae, or both, is necessary. The resulting rotation of the caudal angle in dorsal direction is blocked by the caudal part of the m. serratus. (b) Illustration of the equilibrium of the humerus, pulled downward and to the left by the m. latissimus (double line), upward and to the right by the substrate reaction force (arrow) and so requires a force that must be directed upward and to the right like the joint force (arrow). (c) The shoulder joint is assumed to be balanced by the monarticular m. teres maior or the caput longum m. tricipitis. A joint resultant is evoked, which follows the axillary margin of the scapula and necessitates activity of m. levator scapulae and cranial m. trapezius, as well as the caudal m. serratus. In addition, the scapulae must be pulled dorsally by the caudal part of the trapezius.

concerning the activity of the cranial portion of the m. trapezius at the same time when the most caudal bundles of m. serratus are active. In this situation, which is typical of the more suspensory or acrobatic activities, the joint force is directed toward the caudal angle instead of along the spina scapulae.

The same becomes even more obvious in truly suspended postures and in upright clinging (Fig. 6). The SRR follows roughly the length of the arm, and is directed away from the trunk, so that the arm is under tension. The shoulder joint can be balanced by the m. teres alone, but if so, the most caudal portions of the m. serratus must be active (as was indeed observed by Larson *et al.* 1991). To prevent a pulling of the shoulder blade in the ventral direction, the caudal portion of the trapezius is also needed, and indeed active according to Larson *et al.* (1991). This part of the muscle is markedly developed in the apes (Maier 1971; Preuschoft 1965). If, however, the m. latissimus and m. pectoralis are used to balance the shoulder joint, their tendency to slide the scapula in caudal direction must be counteracted by the protractors of the shoulder blade, Larson *et al.* (1991) observed in electromyographical studies. Again the joint force of the scapula is passing along its axillary margin, which therefore must be enforced.

The stress distributions in a scapula under the conditions of terrestrial versus suspensory behavior is confirmed and illustrated by the simple 2-dimensional FE model in Fig. 7. The stresses in the terrestrial variant concentrate along the cranial margin, whereas the more suspensory variant shows higher stresses along the axillary margin. This experimentally documented stress concentration indicates a shift of the joint force along the vertebral margin in the cranial or caudal direction. The necessary reaction forces are provided by the m. serratus, which consequently needs to be enforced either in its middle or caudal portion. An elongation of the
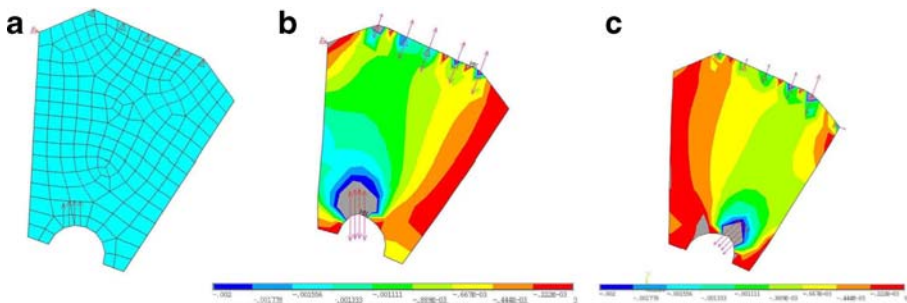

Fig. 7 FE models of the shoulder blade to show the flow of compressive stresses. (**a**) Two-dimensional network of finite elements in a schematic scapula. (**b**) Load case resembling the situation in terrestrial walking. (**c**) Load case resembling arboreal climbing or suspension, as shown in Figs. 5 and 6. The compressive stresses are color-coded: red = zero stress, blue or gray = very high compressive stresses. To facilitate comparisons, the same model is used for both ways of loading, and the joint surface at the lower margin semicircular, in contrast to the true glenoid surface. The cranial direction is on the left side; the joint force is applied from below, and its direction determines the distribution of reaction forces at the upper (= vertebral) margin. Stresses in terrestrial walking run primarily through the more cranial parts of the shoulder blade, due to the cranial position of the joint resultant. In arboreal climbing, the stresses are concentrated on the caudal part of the scapula, following the rearward directed joint resultant. As a consequence, the cranial portions of the m. serratus exert more force in the terrestrial monkey, whereas its caudal portion is more active in the arboreal monkey.

cranial or caudal part of the scapula allows a distribution of the compressive forces over a larger area and gives the active muscles longer lever arms. Indeed researchers frequently have observed the length, the enforcement of the axillary margin, extension of the fossa infraspinata, and especially the cranial angulation of the facies glenoidalis (as reviewed by Larson 1993) in more arboreal monkeys and in apes, especially gibbons (Fig. 3).

Substrate Reaction Forces and Their Effects on the Musculo-skeletal System in Frontal View

Thus far, we have considered only the lateral aspect. This emphasizes the features that all quadrupeds have in common. Differences among quadrupeds become obvious when we investigate the anterior aspect. There are 2 variants here: symmetrical 2-limb support as in standing, and asymmetrical 1-limb support as in walking. An external substrate reaction force applied to the "hand" lateral to the shoulder joint necessitates a contraction of adductor muscles, primarily the m. pectoralis maior, as shown on the right side in Fig. 8a. In symmetrical support, the joint resultant on the left side is constructed under the condition that only the m. latissimus keeps the shoulder joint in equilibrium. In any case, the resulting force acting between the humeral head and the shoulder blade is directed medially or at least has a marked medially directed component, depending on the muscles that are recruited. This holds true in symmetrical support by both forelimbs as well as in asymmetrical support by only 1 forelimb, where the external equilibrium is maintained with the aid of the hind limbs (Fig. 8b). The joint force pushes the shoulder blade medially, toward the vertebral column. As in the side view, it is kept in its place primarily by the m. serratus, which possesses a strong lateral component, thanks to the pronounced curvature of the ribs. While the m. serratus pulls the scapula laterally, the clavicle transmits medially directed compressive forces to the origin of the m. pectoralis, the anterior part of the chest, and the sternum. In asymmetrical support, as shown in Fig. 8b, the mm. trapezius and rhomboideus prevent the trunk from rolling downward along the shoulder blade and the supporting upper arm.

D. Schmitt (2003) has identified 2 variants of force transmission from substrate to animal during walking, that is, in asymmetrical support, in primates walking on flat ground and slender substrates, within a pronounced variability. One variant is preferred by the more terrestrial Old World monkeys, the other by more arboreal (or
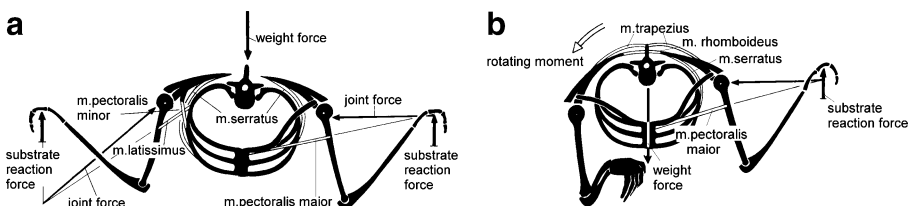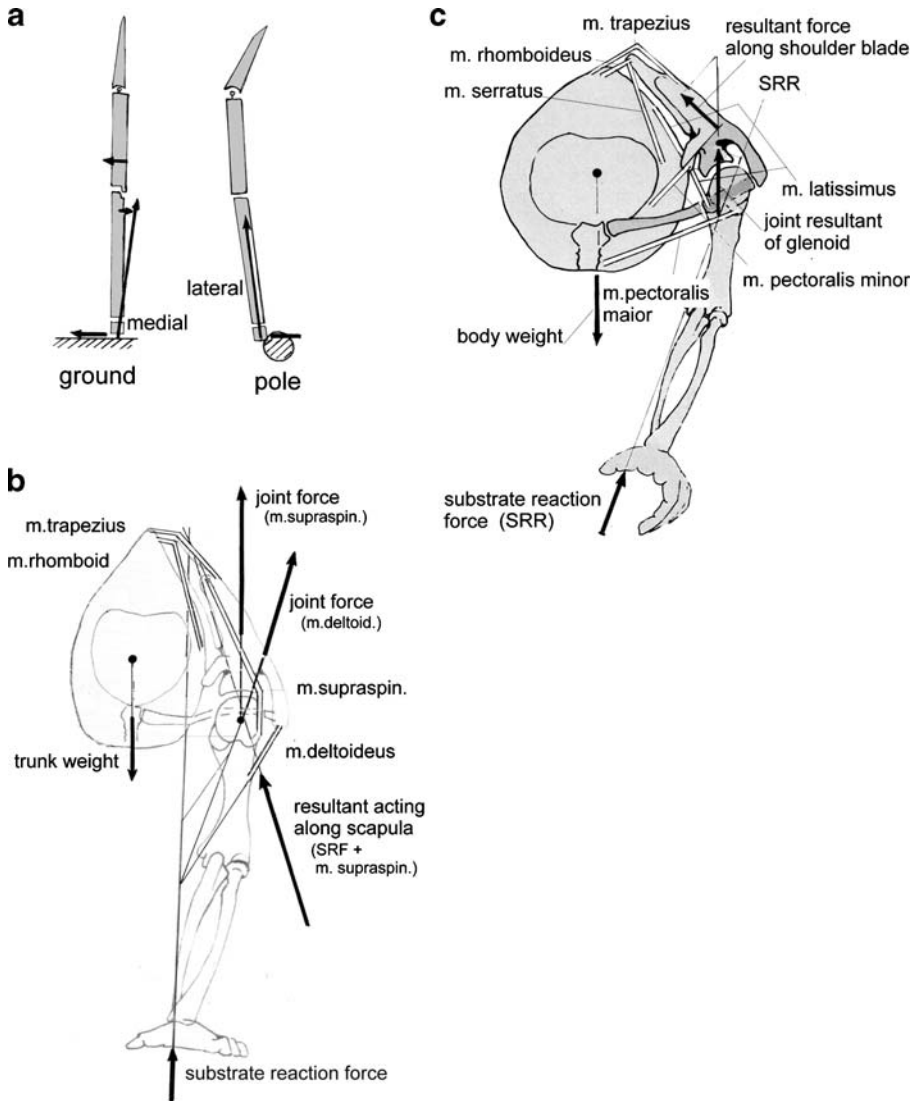

Fig. 8 Special ways of loading the shoulder in primates: carrying body weight in abduction (as in reptiles). (a) Symmetrical and (b) asymmetrical support. External equilibrium is maintained with the aid of the hindlimbs. (Modified from Preuschoft et al. 2003).

suspensory) New World monkeys: More terrestrial monkeys reduce the moment arm of trunk weight via a position of the SRR medial to the glenoid joint (Fig. 9a, b). They therefore need their shoulder abductors to keep balance. While the m. deltoideus evokes a laterally directed resultant, which makes the humeral head slide dorsolaterally on the glenoid surface, the supraspinatus redirects and centers the joint force, so that the joint force acting on the scapula is nearly vertical, falling perfectly in line with this element and keeping the bending moments along the scapula low. As mentioned previously, Larson and Stern (2007) found most marked EMG activity in the m. supraspinatus. There are no large mediolateral force components in the shoulder region. An upright position of the scapula, approaching a parasagittal plane,

◀ **Fig. 9** (**a**, **b**) Substrate reaction force as seen from in front, according to D. Schmitt (2003). In the more terrestrial monkeys (**a**), the ground reaction force passes from ground to a point between shoulder and median sagittal plane, while in more arboreal forms (**b**), walking along a pole, the SRR passes from the pole or branch more lateral, roughly through the shoulder joint. (**c**) Joint resultant and muscle forces necessary to keep the trunk and its weight in balance at the shoulder of a terrestrial monkey. If only the m. deltoideus balances the glenohumeral joint, the resultant is directed laterally, not to the center of the glenoid surface. If the m. supraspinatus keeps balance, the joint force is nearly vertical, and the resultant acting on the scapula falls perfectly in line with this element. (**d**) Forces acting in the shoulder complex of an arboreal monkey. The SRR passes through the shoulder joint, but activity of the m. pectoralis maior or m. latissimus is necessary to direct the joint force toward the center of the glenoid surface. The scapula is kept in its position by the m. pectoralis minor or the clavicle, or both. The resultant passes along the scapula, which here is more inclined than in the terrestrial monkey (**c**), but similarly exposed to compression and bending. Medially directed components of the muscle forces are neutralized by the clavicle. Note that the external equilibrium of the whole body in **C** and **D** is maintained by the hind limbs.

puts it in line with the joint resultant and therefore is advantageous. The mm. trapezius and rhomboideus prevent a rolling of the trunk downward along the supporting forelimb, and carry the swing limb of the contralateral side. These muscles cause a moderate bending of the shoulder blade, while the m. serratus causes compression by carrying the weight of the trunk. The shape of the scapula is suited to provide resistance against compression, and the existence of the spina scapulae gives it enormous bending strength. This is the more so because the mm. supraspinatus and deltoideus act as ties on the convex side of bending. The clavicula is not stressed much, but is in a perfect position to maintain the distance between the shoulder joint and the thorax.

More suspensory, arboreal monkeys tend to direct the SRR along the arm and through the shoulder joint (Fig. 9a, c). Although this seems to keep the joint in balance, sliding of the humeral head on the glenoid surface in the latero-dorsal direction must be excluded. In addition, this equilibrium is labile, and can be disturbed by any slight deviation of the substrate reaction force in lateral direction. A safe equilibrium can be accomplished by fixing the joint with the aid of the shoulder adductors, mm. pectoralis major et minor, and latissimus dorsi. An activity of the shoulder adductors and retractors indeed has been observed by Larson and Stern (2007), who put emphasis on rejecting a propulsive function of the shoulder retractors. In Fig. 9, the resultant passes through the joint and pushes the scapula in dorsal direction. A movement of the joint away from the trunk, or a lifting of the scapula in the dorsal direction under the influence of the joint force, is (and must be) excluded by the m. pectoralis minor and (perhaps) the m. coracobrachialis. If the former muscle activity is taken into consideration, or the m. latissimus/teres major complex, the resultant of all forces acts along the scapula, provided that it is placed more dorsal than lateral to the trunk. The medially directed sliding of the scapula on the thorax is countered and the scapula kept in the mentioned position by the clavicle and/or the m. pectoralis minor and the m. serratus, where both muscles at the same time help carrying trunk weight. A scapula in a dorsally shifted position and close to frontal orientation is well suited to receive the joint force resulting from this way of loading. The reduced length of the spina scapulae is a means to keep the balancing forces low. The lengths of the upper arm and the forearm in suspensory monkeys and in apes allow sufficient excursions of the forelimb in quadrupedal walking without

making use of a long scapular segment, which exists in the more terrestrial forms. Kimura (1985, *pers. comm.*) has observed that the angular excursions of the forelimbs in chimps are less than the excursions of the shorter hind limbs so that the same step length is reached.

Like the suspensory monkeys, the apes differ from the more terrestrial genera. The position of the scapula obviously correlates with the form of the thorax and the shoulder blade is therefore orientated more in a frontal instead of a sagittal plane. Their broad, and dorsoventrally flattened, thorax shapes have been well known for a long time (Kagaya *et al.* 2008a, b; Mollison 1911; Schultz 1930, 1961). Humans represent the extreme of widening and reduction of depth of the thorax, and of reorientation of the scapula.

Discussion and Conclusions

The dominant mode of locomotion among all tetrapods is walking, and the general conditions for symmetrical locomotion are well known (Mochon and McMahon 1980, 1981; Preuschoft and Christian 1999; Preuschoft and Günther 1994; Preuschoft *et al.* 1994; Witte *et al.* 1995a, b). During the stance phase, spatial limitations are given by the excursion angles; during the swing phase, the pendulum period sets limitations. These physical conditions explain a number of morphological characteristics: proportions, mass distribution on the limbs, position of the joints, speed, and the preference of the walk in contrast to the rarity of the trot in primates (Nakano 1996; Preuschoft and Günther 1994).

During the stance phase of walking, the forces exchanged through the limbs between the animal and its substrate are much higher than those acting during the swing phase. The same conditions as in walking hold true in the most frequent cases of arboreal locomotion, which is nothing else than a variant of walking, performed on inclined substrates (Morbeck 1979; Preuschoft 2002; Rose 1979). In truly suspended postural behaviors, the tensile forces acting on the forelimbs are also proportional to body weight, and therefore can assume high values. The search for morphological adaptations can be confined to cases in which high loads come into action. Small loads can easily be sustained by the skeleton and the musculature and do not need special adaptations; they must, and can, be sustained by the given morphology.

Our biomechanical analysis shows the dependence of the force flows in the shoulder region on the various locomotor habits of groups of primates: More terrestrial monkeys are rather similar to cursorial mammals (though much less specialized and 1-sided). The scapula assumes a lateral position on the narrow thorax; its outline is rather symmetrical and its fossa supraspinata wide. The glenoid surface is set at nearly 90° to the cranial margin. The spina scapulae ends in a prominent acromion. The length of the spina scapulae is about that of the axillary margin. The glenoid surface tends to be narrow. Correspondingly, the humeral head is narrow, elongate, and flattened in its most cranial part. In more arboreal monkeys, as well as in the apes and in some strepsirhines, the scapula assumes a more dorsal position on the wider, and less deep thorax. The scapula shows an elongated and wide fossa infraspinata; a protruding, acute caudal angle; and often a bony

enforcement in the form of a crest running along the axillary margin. The spina scapulae, and especially the cranial margin, are shorter than the axillary margin. The glenoid surface is tilted cranially, nearly at right angles to the axillary margin. The glenoid surface and the humeral head are symmetrical and spherical. All this is in perfect agreement with functional necessities of the respective forms, especially the frequent elevation and abduction of the arms in conditions that imply high loads. According to Young (2006), the variability of scapular morphology in terrestrial monkeys is less than in more arboreal forms. This seems to be related to the variable use made of the upper limbs in the arboreal forms. Suspensory locomotion, or more exactly the application of tensile forces to the arms, requires adaptations similar to those of abduction and anteversion of the arms in arboreal monkeys. Therefore, the shoulders of the apes among the hominoids are fairly close to those observed in the more arboreal monkeys. This is not in conflict with the preferred walking on ground or on large horizontal branches in large apes, because little weight is carried on the forelimbs during quadrupedal walking (Kimura 1985). Special adaptations to quadrupedal walking are not required in the African apes, while their suspensory behaviors imply that a large share of body mass is carried by the forelimbs (Kimura 2002), which cannot be sustained by shapes that are not well adapted. All traits typical of suspension serve as preadaptations to upright posture, according to Preuschoft (2004), Preuschoft and Witte (1991), and Witte *et al.* (1991).

All observed morphological traits imply biomechanical advantages for a specific locomotor or postural behavior. The combination of behavioral acts in primates, however, is extremely variable, not only among taxa, but also among individuals and among external conditions in which they move. In view of the notorious versatility of motor behavior, which is so characteristic of primates, it is impossible to attribute angles or proportions to special frequencies of locomotor behaviors at this time. The locomotor modes usually vary at the level of genus or subfamily (Preuschoft 1989), but the examples discussed here show that very similar biomechanical conditions may occur in widely separated forms, like New World and Old World monkeys, strepsirhines, and apes. This leads to the conclusion that the morphological variation of the shoulder in primates is adaptive instead of taxon-specific, and therefore not determined directly by phylogenetic relationships. Indeed, the even-sided triangular shape of the scapula in terrestrial monkeys approaches the scapular shape of cursorial mammals, which are also not at all closely related phylogenetically.

The adapted shapes of skeletal elements, or in other words, the existence of bone exactly where the mechanical stresses require compression-resistant material, may well be the direct consequence of mutations and subsequent selection. So far, our results confirm the commonly accepted phylogenetic explanation of morphology. The adapted shapes can also be a consequence of the ability of connective tissue to deposit bone under the influence of mechanic stress in the sense of Pauwels` causal morphogenesis (Kummer 1972; Pauwels 1965) or Wolff's law (Wolff 1892). Our Finite Element models of the scapula (Fig. 7) suggest the importance of causal morphogenesis (Pauwels 1965) for the development of skeletal structures. This is the more so in view of our detailed Finite Element Simulation studies of the skull (Preuschoft and Witzel 2004, 2005; Witzel and Preuschoft 2002, 2005), in which we investigated the flow of stresses within an unspecific, rather large bauraum. In a second step, we eliminated those parts of the latter that do not receive any stress, and

exposed a reduced model to the same stresses as before. As expected, the stresses concentrate in the reduced model, and again leave parts unstressed. The model's shape now approaches the real form of the skeletal element. A third step in the form of a reiteration of the reduction of the model and loading it again leads to fair coincidence with the real form. A similar study of the shoulder girdle is in progress Hohn (2007). This procedure parallels the process of causal morphogenesis described by Pauwels and used intentionally and explicitly or implicitly every day in bone surgery and orthopaedics.

The *intra vitam* development of the morphological traits under the influence of mechanical stress, and their adaptive nature, are emphasized further by the development of the marsupials, which immediately after birth use their forelimbs to crawl (in abducted postures of the forelimbs) to the marsupium. At this stage, they possess a complete ventral part of the shoulder girdle with a strong coracoid (Fig. 10), like monotremes, reptiles, birds, and amphibians (Klima 1987; Klima and Bangma 1987). This condition is connected with sprawling limbs and can be assumed to be ancestral for all land-living tetrapods. The massive ventral part of the shoulder girdle keeps the shoulder joint at a distance to the median sagittal plane, and the sprawled forelimbs lead to the application of external forces (SRR) lateral to
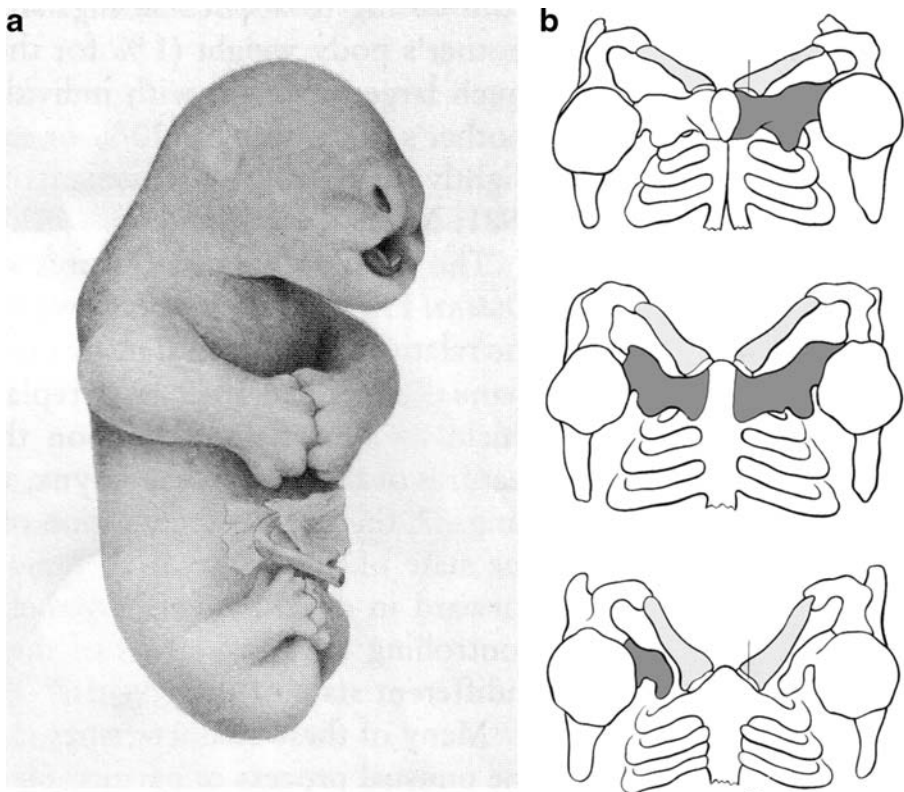

Fig. 10 Neonate (**a**) and three developmental stages of the shoulder girdle (**b**) in a pouch young of a marsupial (Koala, *Phascolarctos*). The earliest stage is at the top and the latest stage is at the bottom. (Modified slightly from Klima 1987; Klima and Bangma 1987).

the shoulder joint, similar to that in Fig. 8. Because of the origin of a large part of the m. pectoralis from the sternum, or the coracoid itself, the compressive force flows from the glenohumeral joint immediately through the coracoid. These mechanical conditions hold true for lower tetrapods (Preuschoft and Gudo 2005; Preuschoft *et al.* 2007) as well as for newborn marsupials. The interesting point is that pouch young marsupials reconstruct their shoulder girdle within few days after the newborn´s travel to the marsupium to the pattern existing in all other mammals. In particular, the cursorial mammals place their forelimbs close to the median plane and therefore do not need a medially directed pull of the m. pectoralis. Therefore the joint force in the shoulder joint has only very moderate medial components. A ventral element of the shoulder girdle is unnecessary and most mammals do not even possess a clavicle. Obviously, the development of the skeletal elements in marsupials gives an indication that these elements are functional adaptations, which change during life.

The traits listed in the preceding text allow reliable biomechanical interpretation of (sufficiently preserved!) fossils beyond correlation of morphological similarity, and without a closer look at taxonomic position. This, however, is beyond the scope of the present article. When interpreting fossils, one must always keep in mind that shape is connected with the exactly determined flow, size, and direction of mechanical forces, not with arbitrarily assumed so-called functions, like knuckle walking, manipulation, climbing, or the like (see also Preuschoft 2004). Our results can also serve as a reasonable basis for designing experiments for more detailed analyses of the mechanics in selected species, or for more detailed morphological study.

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