

Biomechanics and functional preconditions for terrestrial lifestyle in basal tetrapods, with special consideration of *Tiktaalik roseae*

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The article is dedicated to the memory of Wolf Reif, the old friend and colleague, who influenced my (H.Pr.) thinking much more than becomes evident by the few investigations we published together.

The fossil *Tiktaalik roseae* from the Late Devonian induces clear definition of the biomechanical and functional preconditions for a terrestrial lifestyle including quadrupedal standing and locomotion on limbs. Therefore, we determined the internal stresses in this model organism under the influence of gravity using the finite element method. Stress patterns during symmetrical two-forelimb support result from bending of trunk and neck. During asymmetrical one-forelimb support, as occurs during terrestrial locomotion, torsional stresses are higher than those caused by bending. The observed patterns of compressive stresses correspond well with the arrangement of compression-resistant materials: vertebral column, shoulder girdle and ribs. The tensile stresses are in accordance with the arrangement of longitudinal and oblique muscles forming the body wall. Torsional stresses concentrate along the periphery of the trunk, leaving its cavity free from mechanical stresses. Theoretical mechanics indicate that the flat skull and the mobility of the neck were advantageous for lateral snapping, similar to crocodiles. The same movement on land requires sprawling and flexed forelimbs. Our results can be interpreted as explanations for the tetrapod bauplan as well as confirmation and refinement of existing hypotheses about the lifestyle at the border between water and land of this early predecessor of terrestrial tetrapods.

Keywords: functional morphology; tetrapod bauplan; finite element method; transition to land living; *Tiktaalik roseae*

1. Introduction

It is well established that limbed, land-living vertebrates are derived from members of the tetrapodomorph lineage of lobe-finned fishes (Cope 1887, 1892; Daeschler et al. 2006). The origin of tetrapod locomotion and the respective morphology, which is the tetrapod bauplan, was widely investigated under phylogenetic (Ahlberg and Johanson 1998; Long et al. 2006; Shubin et al. 2006), developmental (Shubin et al. 1997, 2004; Coates and Cohn 1998), physiological and ecological aspects (Carroll et al. 2005; Clack 2007).

Functional morphology of the observed features was considered in the reconstruction of the vertebral column and ribs of *Ichthyostega* (Ahlberg et al. 2005), the pelvic fin and girdle of *Panderichthys* (Boisvert 2005; Boisvert et al. 2008), and the functional investigation of the skull sutures of *Acanthostega* and *Eusthenopteron* (Markey and Marshall 2007). This raises the question whether the various traits can be traced back to one or few biomechanical requirements (Ahlberg and Johanson 1998; Janvier 1998).

The transition from water to land is one of the most dramatic changes within vertebrate paleontology. Conceivable reasons for this transition are not only escape from predators and acquisition of prey, but also climate dependent changes in oxygen concentration (Carroll et al. 2005) or the increase of control over body temperature by basking in the sun (Clack 2007). The lineage leading to modern tetrapods is commonly constructed on the basis of fossils such as the fish-like *Eusthenopteron* (Jarvik 1980, 1996a, 1996b), *Gogonasus* (Long et al. 2006) and the Latest Middle Devonian tetrapod-like fish *Panderichthys*, which are all about 385–380 my old (Ahlberg and Milner 1994; Ahlberg and Johanson 1998; Ahlberg and Clack 2006). It continues with the recently discovered *Tiktaalik*, which is about 382 my old (Daeschler et al. 2006), and *Elpistostega* from the same period. *Acanthostega* (376 my; Clack and Coates 1995; Coates 1996) and *Ichthyostega* (365 my; Ahlberg et al. 2005) from the Late Devonian are considered to be basal tetrapods. Morphological transitions are visible in the skull (feeding, respiration) and limb girdles (locomotion). *Tiktaalik* and *Elpistostega* are described as transitional forms bearing morphological

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features, which were not present in *Eustenopteron* and *Panderichtys*, but are still less pronounced than in later fossils (Daeschler et al. 2006). Special emphasis has been placed on the anterior limb and its autopodium (Shubin et al. 2006; Boisvert et al. 2008; Callier et al. 2009), a complex which in *Tiktaalik* seems less suitable for land living than in *Acanthostega*.

The transition from water to land raises new biomechanical problems concerning posture, locomotion, feeding as well as respiration. Neither the conditions nor the adaptations by which the animals can meet the mechanical requirements have yet been sufficiently investigated. In this study we will concentrate on locomotion and feeding, because both lead to the highest forces inside the animal's body, which can only be sustained by 'adapted' skeletal elements. We neglect the forces required for breathing, because they are not sufficiently known, but can be expected to be much lower than those used in locomotion and capturing prey. It is vital for an organism to sustain the highest among the regularly occurring forces, while lower forces can be sustained without 'adaptions' of the skeleton.

Higham (2007) postulated 'future studies that examine the morphological, physiological and functional evolution of locomotion involved in prey capture by aquatic and terrestrial vertebrates' and expects that they 'will provide insight into the origin and consequences of diversity'. To reach this aim, we regard it as absolutely necessary to understand and explain morphological features and to identify selective advantages on the basis of biomechanics to offer a solid base for an integrative approach to evolutionary biology.

Tiktaalik roseae seems to be a promising candidate for an investigation of the basic conditions of terrestriality and their possible relation to the tetrapod bauplan. The fossil possesses a pattern of morphological features intermediate between fish and land-living tetrapods (Ahlberg and Johanson 1998; Janvier 1998, vide above). Therefore, we analyse the basic biomechanical conditions of a semi-terrestrial or terrestrial mode of life, in which gravity plays a much greater role than in water. To withstand gravity and to maintain the shape of the body against gravity and without the support of surrounding water makes a number of morphological traits advantageous for land-living forms in general, distinguishing them from their purely aquatic predecessors. We focus on the structures forming the trunk (axial skeleton and ribs) and the pectoral girdle, as well as on the skull. These structures are connected to locomotion and/or prey capture. With the aid of biomechanical methods, we investigate how these traits are connected to each other and hypothesise a lifestyle for which they are biomechanically suited. The expected results are not *Tiktaalik*-specific, but reflect the constraints of terrestrial locomotion in general.

To address the question of adaptation for locomotion on dry land, an excursion into generalities was necessary. The investigation of at least two load cases: symmetrical and asymmetrical supports on the pectoral appendages, the latter being the extreme of non-symmetric loading which is inevitable under simulated natural conditions. The general relevance and applicability of these methods to species other than *Tiktaalik* have been shown in a previous paper, in which we applied a similar biomechanical approach, especially the FE technique to living forms (varanids; Preuschoft, Schulte, et al. 2007).

The immediate aim of this paper is to apply our approach to *Tiktaalik*, to see to what extent it could have functioned as a tetrapod. The biomechanical requirements posed to the body by external forces under the influence of gravity and during prey capture are investigated. Our more far-reaching goal was to apply FE techniques to the analysis of the tetrapod bauplan in order to find out which structures (muscular, skeletal) of a tetrapod are essential for a terrestrial lifestyle and quadrupedal locomotion.

2. Materials and methods

Our theoretical analysis of the stresses occurring in an animal's body is based on *Tiktaalik*. The published data on dimensions and proportions of this fossil (Daeschler et al. 2006; Shubin et al. 2006) were supplemented by our own measurements in Dr Shubin's laboratory. Our calculations are based on the data summarised in Table 1. Although these data come from only one individual, we use them as model to characterise without statistical routine treatment the general body shape we are attempting to understand. Two approaches were used: the finite element method [FEM, including finite element structure analysis (FESA) and finite element structure synthesis (FESS), see below] and application of mechanical laws (for formulae, see Lehmann 1974/1977; Dubbel 1981).

2.1 Finite element model

FESA is a technique to demonstrate stress, strain and deformation in solid and liquid structures (Zienkiewicz et al. 1971, 2005). It is commonly used in engineering sciences and orthopaedics, and recently also in paleontology and zoology (Carter and Beaupré 2001; Witzel et al. 2011). A survey of the applications of FEMs in biology and paleontology was recently given by Rayfield (2007). FESS (Witzel and Preuschoft 2005; Witzel et al. 2011) describes the virtual synthesis of skeletal structures out of a homogenous solid by applying external and muscle forces. The latter approach is essentially based on Wolff's law and the principles of remodelling of bone (Wolff 1892) and on the 'causal morphogenesis' *sensu* Pauwels (1965), which predict that bone only develops where

Table 1. Body measurements of *T. roseae* (NUFV 109).

Body measurements	Length (mm)
Total body length	800
<i>Trunk</i>	
Length	560
Width (max.)	180
Height (at the position of the shoulder)	120
<i>Skull</i>	
Length	240
Width (max.)	190
Width (min.)	20
Height (max.)	70
Height (min.)	20
<i>Neck</i>	
Width	170
Height	70
Length (distance occipital condyle → shoulder joint)	62
<i>Shoulder</i>	
Height	110
Width	170
Distance between shoulder joints	30
Distance shoulder joints and ground contact area of the forelimb	70
<i>Forelimb length</i>	
Humerus	100
Antebrachium and 'Fin rays'	30
	70

Notes: Dimensions of the skull and body length in mm were taken from the original publication (Daeschler et al. 2006). Dimensions of the shoulder girdle and forelimbs were measured on the original fossil by the first author.

compressive stresses occur. In this study we first used FESA to analyse the flow of stresses, which occur in a homogenous solid model, which has the morphological features of *Tiktaalik*. The model geometry was based on our own measurements of the original fossil and information reported in the original description (Table 1). Using the FE program ANSYS (ANSYS, Inc., Canonsburg, PA, USA), we determined the areas showing either compressive or tensile stresses, where bony material or muscular structures should be present to sustain the occurring forces and identify their anatomical analogues. Following FESS, we identify the skeletal elements and the muscular structures necessary for terrestrial statics and locomotion.

The material properties of the skeletal elements in *T. roseae* could not be determined precisely and appear to be heterogeneous. Therefore, the material properties chosen for the whole FE model, such as Young's modulus (10 GPa) and Poisson's ratio (0.3), are based on an average value for cortical (Rho et al. 1995) and cancellous bone (Ciarelli et al. 1991). These values represent bone material of different material properties and allow the stress flows to spread throughout the whole model. For simplicity, homogeneous isotropic linear elastic properties were assumed for the FE model. The volume was meshed with

10-node solid tetrahedral elements resulting in a total number of 6000 elements. Weight force was defined by the model's volume, density (1) and earth acceleration (1G).

Figure 1 shows the meshed model before calculation. Two different load cases were calculated by 'constraining' the model either at the distal ends of both forelimbs, or at the right forelimb alone. The first load case represents symmetrical support on both forelimbs. In the second load case, the model is supported by one (the right) forelimb alone, while downward directed forces (= weight of the lifted limb) are applied to the left forelimb, thus simulating the asymmetrical stance that occurs during walking, but also in any other form of uneven distribution of body weight (Figure 1). Due to lack of information about the hindlimbs, the model in both load cases rests on its hind quarters in the hip region. The occurring compressive and tensile stresses were plotted and described separately. The distribution of stresses is colour coded. Areas with high compressive stresses appear in blue, areas of low compressive stresses are in red. Grey colour shows regions in which stresses are significantly beyond the range of our coding. The reverse holds true in tensile stresses: high values of tensile stresses are shown in red, low stresses in blue. Grey indicates values beyond the range.

2.2 Head movements

The calculation is based on the measurements shown in Table 1. The values deviate slightly from the data given by Shubin et al. (2006). Head volume (area in top view × skull height) was calculated as 1490 cm³ and trunk volume as 5450 cm³. Assuming a specific density of the animal of about 1, a total body mass of about 6.94 kg

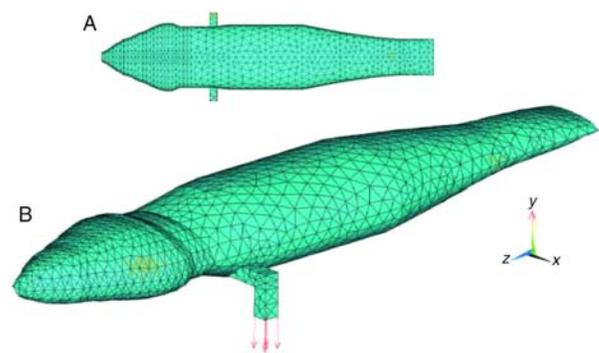


Figure 1. Simplified and meshed 3D FE model of *Tiktaalik* in oblique-lateral (A) and dorsal (B) views. The body is supported on the right forelimb and resting on its pelvic section. Downward acting forces indicate weight of the lifted left forelimb. Bearings are applied to the right forelimb and at the region of the pelvis, indicating ground contacts. These conditions show the asymmetrical support on only one forelimb, whereas in two limbs stance bearings must be applied to both pectoral appendages.

was estimated. The head was taken as a solid with trapezoidal ground plan, the trunk as an elliptical cone. The tail was neglected because its narrow shape means low influence on mass estimates and its compliance makes it unimportant for passive water resistance.

In aquatic animals, two kinds of resistance must be overcome during locomotion: (a) mass inertia F_i and (b) water resistance F_w .

- (a) For linear movements, the resistance F_i of each body segment is calculated as

$$F = m \times a, \quad (1)$$

where F is the force exerted by mass inertia, m is the mass and a is the acceleration.

Angular movements of the head have to overcome the resisting moment (M), calculated as

$$M = \dot{\omega} \times l^2 \times m, \quad (2)$$

where M is the mass moment of inertia in an angular movement, l is the distance from the pivot of movement (here the distance from the base of the neck to the centre of head mass) and m is the mass.

- (b) Water resistance is calculated as

$$F_w = c_w \times A_p \times \rho \times \frac{v^2}{2}, \quad (3)$$

where F_w is the water resistance, c_w is the friction coefficient, depending on shape and surface structure of the moved body, A_p is the cross-sectional area normal to the direction of movement, ρ is the density of water and v is the speed of the moved body.

The rotations of the whole body take place about the body's centre of mass (COM). The forces that the animal must produce to overcome the resistance offered by inertia and lateral surface of the parts anterior and posterior to the body's COM depend upon the speed of movement.

3. Results

3.1 *FE model, symmetrical support on both forelimbs and hindquarters*

In symmetrical stance, the model indicates rather low stress values of about -0.9 MPa. The highest compressive stresses occur in the supporting limbs and their insertions at the trunk. A flow of stresses is directed dorsally and crosses the midline (Figure 2(A),(B)). On the ventral side, compressive stresses exist between the supporting limbs (Figure 2(C)) and on the lower margin of the neck in the region with the shortest diameters (Figure 2(A),(C)). High values of compressive force can also be found on the dorsal side of the trunk, rising from the supporting limbs along the

back to the resting hindquarters (Figure 2(B)), where the compressed region near the posterior support is separated from that in the shoulder region. Cross sections are taken at the level of the hip, the middle of the trunk and the supporting forelimbs (Figure 3). The most caudal (hip) section (Figure 3(A)) shows high stresses in the dorsal third of the diameter. In the middle of the trunk (Figure 3(B)), the stresses decrease in layers from the highest values on the dorsal margin to a stress-free plane in the centre of the cross section. At the level of the forelimbs (Figure 3(C)), stresses are concentrated at the lateral sides of the trunk and, to a lesser degree, on the ventral and dorsal sides, leaving the central part of the volume free of compressive stresses.

Tensile stress values reach a maximum of about 0.1 MPa and are therefore significantly lower than the above-described compressive stresses. They commonly alternate with the occurring compressive stresses. Maximum tensile stress values are found at the ventral side of the middle and caudal trunk regions and at the dorsal side of the neck (Figure 4(A)–(C)). Rather low tensile stresses are located between the supporting forelimbs (Figure 4(B)).

3.2 *FE model, asymmetrical support on one forelimb and hindquarters*

As soon as the animal lifts one of its pectoral appendages from the ground in asymmetrical support, tension occurs on the dorsal side, which is sustained by the mm. rhomboideus and trapezius, which also carry the swing limb (Figure 11(B)). The insertions of these muscles into the spinous processes of the vertebrae are distributed over several segments, so that they do no exert too much force on each segment. In contrast, the ventral side shows a marked increase of compression (Figures 2–7), and the skeletal elements of the ventral side establish a compression-resistant contact.

In comparison to symmetrical stance, the values of compressive stresses are significantly higher, reaching up to -43 MPa. Between the forelimbs the values are 10 times greater than in symmetrical standing. Again maximum values are located in the supporting limb and its insertion to the trunk, that is the pectoral girdle (Figure 5(A),(D)). Clearly, the supporting (right) limb receives higher stresses than the swing limb (Figure 5(C),(D)). The major differences to symmetrical stance are the remarkably high compressive stresses between the forelimbs on the ventral side of the trunk (Figure 5(D)) and the asymmetrical expansion along the dorsal side. The latter stress flow begins at the right shoulder joint and spreads from the supporting forelimb obliquely across the trunk to the contralateral half of the ground-contacting belly (Figure 5(A),(C)). In quadrupeds, this would of course be the contralateral hindlimb. The observed stress distribution is the result of superimposition of bending (see above) and torsional stresses. Torsional stresses have tensile as well as compressive components and can best be viewed on

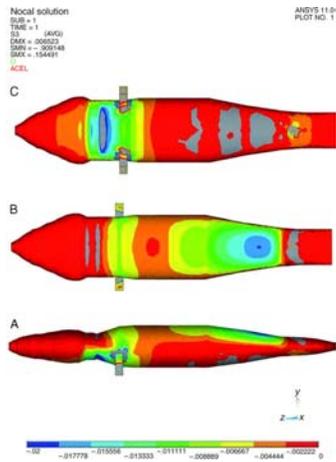


Figure 2. Distribution of compressive stresses in the 3D FE model of *Tiktaalik*, shown in lateral (A), dorsal (B) and ventral (C) views. Both limbs are constrained as in symmetrical support. The coloured scale at the bottom indicates compressive stress values from 0 MPa (red) to 0.02 MPa (blue). Absolute stress values are shown in the heading legend. Highest compressive stresses occur at the insertions of the limbs, spreading dorsally across the midline of the trunk. In the caudal part of the dorsum, close to the constrained pelvic region, compression also reaches high values (A, B). In ventral view (C), compressive stresses are most evident between the supporting limbs, and spread cranially to the neck region with the shortest diameter. In contrast, the ventral aspect of the trunk is nearly free of compressive stresses.

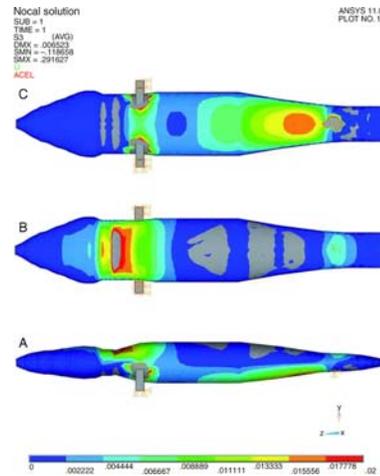


Figure 4. Distribution of tensile stresses in the FE model, shown in lateral (A), dorsal (B) and ventral (C) views. Both limbs are constrained as in symmetrical support. Coloured scale at the bottom indicates tensile stress values from 0 MPa (blue) to 0.02 MPa (red). Absolute stress values are shown in the legend on top. The highest tensile stresses occur ventrally near the pelvic region (C), and dorsally at the neck basis (B). Moderate tensile stresses exist on the ventral side between the supporting limbs (C).

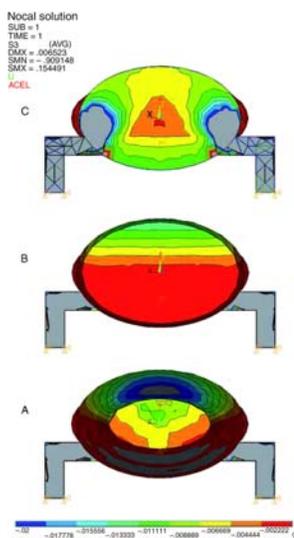


Figure 3. Frontal sections through the FE model in symmetrical support showing the distribution of compressive stress. The scale at the bottom indicates compressive stress values (0 to -0.02 MPa). Numerical stress values are shown in the heading legend. (A) At the level of the supporting hindquarter, stresses spread symmetrically from the bearing towards the back. (B) In the middle of the trunk, compressive stresses increase linearly from the centre to the dorsal surface. (C) At the level of the supporting forelimbs, high stress values occur at the insertions of the limbs and ventrally between the limbs. At the dorsal side the stress values are low, and the centre is left unstressed.

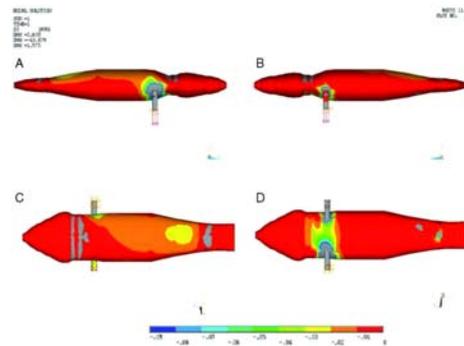


Figure 5. Distribution of compressive stresses in the FE model of *Tiktaalik* in asymmetrical support. Note that the absolute values of compressive stresses are significantly higher in asymmetrical than in symmetrical support, so that Figures 2 and 4 cannot be compared directly! (A) Lateral view, right side; (B) lateral view, left side; (C) dorsal and (D) ventral view. The supporting right forelimb is constrained, whereas the dangling left limb (B) is loaded with its weight. The scale at the bottom indicates compressive stresses from 0 to -0.09 MPa. Absolute stress values are shown in the legend on top. Stresses reach their peak values at the insertion of the weight-bearing limb, while the hanging limb is less stressed. Stress flows spread dorsally from the supporting limb to the bearing at the hindquarter (C). High stress values are observed ventrally between the forelimbs and most pronounced within the supporting limb.

cross sections (Figure 6), where they concentrate along the periphery (Figure 6(A),(B)), leaving the interior of the trunk (the abdominal cavity) free from stress. The concentration of the occurring stresses at the supporting limb

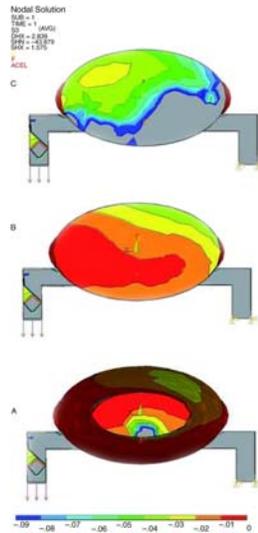


Figure 6. Frontal sections through the FE model in asymmetrical support showing the distribution of compressive stress. (A) At the level of the supporting most posterior (hip) section of the trunk, stresses spread asymmetrically from the bearing towards the dorsal side. (B) In the middle of the trunk, the compressive stresses are asymmetrically concentrated near the dorso-lateral surface. If forelimb support is changed, the pattern is inverted and the left side of the cross section receives the same high stress as the right side. In both cases, an unstressed area remains in the centre of the cross section, where the trunk cavity is located. (C) At the level of the supporting forelimbs, the highest stress values (grey, exceeding -0.09 MPa) occur at the ventral side and between the forelimbs, because of the insertion of the supporting limb. The scale at the bottom indicates compressive stress values (0 to -0.09 MPa). Absolute stress values are shown in the legend on top.

is best visible at the foremost cross section (Figure 6(C)), where compressive stresses connect both sides ventrally. In addition, moderate stresses spread dorsally, connecting the swing limb with the trunk.

Like compressive stresses, maximum values of tensile stress are significantly higher in asymmetrical than in symmetrical stance. In both postures, however, the values of tension are significantly lower than those of compression. Stress patterns show an increase of tensile stresses dorsal to the supporting limb (Figure 7(A),(B)), where they reach and cross the midline (Figure 7(C)). Slightly lower tensile stresses occur at the ventral side, where they spread dorso-caudally towards the resting hindquarters (Figure 7(A),(B),(D)).

3.3 Skull shape

Skull height influences positively the strength necessary for biting (Figure 8). Bending strength of a massive, akinetic skull is defined by the area moment of inertia I_x :

$$I_x = \int dA \times y^2, \quad (4)$$

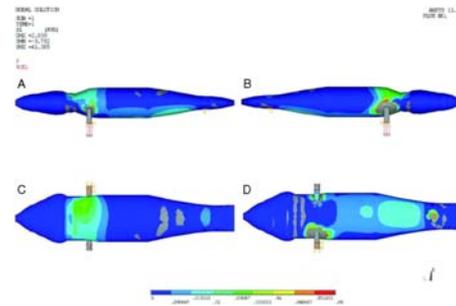


Figure 7. Tensile stresses in the FE model in asymmetrical support. (A) Left side of the model. The highest stresses occur ventrally near the weight-bearing hip region, and at the pendant forelimb, from where they extend towards the back. (B) Right side of the model. Stresses in the shoulder region are much greater than on the unloaded side, whereas the ventral strip of tensile stress is narrower than on the left, indicating the asymmetry which becomes obvious in dorsal and ventral views. (C) Dorsal view, showing the asymmetry. The highest stresses on the dorsal side can be found between the right and left half of the shoulder girdle. (D) Ventral view, showing again the asymmetrical stress distribution. The highest stresses occur at the load bearing shoulder. The scale at the bottom indicates compressive stress values (0 to -0.09 MPa). Absolute stress values are shown in the heading legend. Again the stresses are concentrated near the periphery of the trunk, leaving the centre unstressed.

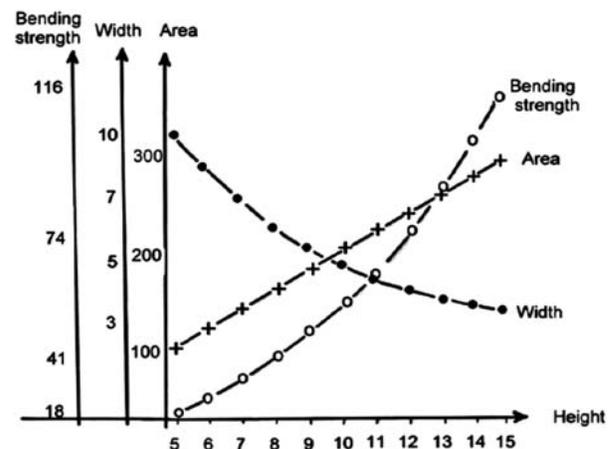


Figure 8. Influence of skull height on bending strength (open circles), cross-sectional area (crosses) and width (filled circles) in a simplified skull. Especially bending strength grows rapidly with increasing height. Therefore, a higher skull may contain less material and therefore have less weight than a flat skull.

where dA is a very small part of the cross-sectional area and y is its distance from the neutral line.

The greater the height of the skull, the greater is its bending strength. Skull width may decrease, while cross-sectional area (which is proportional to weight at a given length) grows linearly. Therefore, flat skulls as in crocodiles or in *Tiktaalik* need a greater amount of bone material (thicker walls, greater breadth) than higher skulls

to sustain the bending moments during biting and are, therefore, heavier.

3.4 Prey capture

Prey acquisition by a lateral movement of the head alone (Figures 9(A) and 10) requires energy to overcome the head's water resistance, which is proportional to its lateral surface, perpendicular to the movement (Equation (3), Figure 9(A), grey). Due to the depressed skull shape, the lateral surface area is not more than 0.0137 m^2 in *Tiktaalik* and water resistance (F_w) is rather low ($F_w = 10.1 \text{ N}$).

The lateral movement is also resisted by rotational inertia M_i (Equation (2)). If tangential acceleration is 1.5 G (as assumed by Preuschoft and Witzel 2005) at the COM, mass moment of inertia (M_i) is about 1.60 Nm. Together with the greatest possible lever length of the nuchal muscles of 0.08 m, the force required for rotation is 31.88 N.

If the snapping movements involve the whole body, rotation of the entire body takes place about the COM (Figure 10). The total resistance to be overcome, therefore, consists of the mass moment of inertia ($M_i = 14.62 \text{ Nm}$) and the moment of water resistance ($M_w = 18.83 \text{ Nm}$) of the entire body. Again, the greatest possible lever length of the muscles is 0.08 m, so that the total force required for rotation is 418.13 N.

Rushing forward requires axial acceleration of the total body mass in addition to overcoming water resistance. We calculated a body mass of 6.94 kg and an acceleration of 1.5 G (Preuschoft and Witzel 2005). Overcoming inertia, therefore, requires a force F_w of about 102.12 N. The water resistance force F_w is defined by Equation (3). Together with a water resistance value of $c_w = 0.06$, a cross-sectional area of the animal of 0.017 m^2 and an assumed speed of 2 m/s for our early tetrapod, we calculated a value of 2.04 N to overcome water resistance and a total of 104.16 N for propulsion of the body.

To close the jaws (Figure 9(B)), water resistance and inertia must be overcome. The area of the lower jaw moved against water resistance during jaw closure is 0.0267 m^2 . For calculation of the forces necessary for closing the jaws, we assumed an angular speed ω of $997^\circ/\text{s}$ as was observed during feeding in a caiman (Cleuren and De Vree 1992). The total force for overcoming inertia and water resistance in closing the jaws amounted to 32.87 N. The value results from the large jaw area exposed to water resistance. If the oral floor is very compliant and the bottom of the mouth lags behind the quick movement of the lower jaw, the area moving against water resistance is reduced in the case of *Tiktaalik* by half. The force required for closing the jaws under these conditions is 16.44 N (Figure 9(B)).

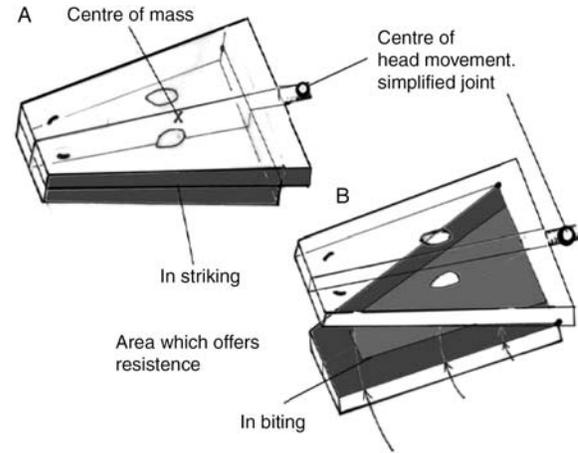


Figure 9. Schematic head of a Devonian tetrapod. (A) The base of neck is assumed to be the pivot for lateral striking. The COM of the head is indicated by X. In a flat skull, the lateral surface (grey) offers a minimum of water resistance. (B) The mandibular joints near the posterior margin of the head (dots) define the axis of the closing movement of the jaws. The anterior teeth cover a longer distance per time unit than the posterior teeth (arrows). The lower jaw consists of the mandible (dark grey) and the oral floor (light grey). Assuming a thickness of the mandible of 2.5 cm, each part has the same area.

3.5 Neck mobility and trunk shape

An immobile base for rapid movements of the mobile head is provided by the mass moment of inertia of the trunk (Figure 10). Mass of the head here is assumed as one-fourth of the trunk, and distance between the head's and trunk's COMs is one-third of the body stem. This mass distribution reduces recoil of the trunk during a strike but may not prevent it completely. The trunk can be further stabilised by water resistance either passively by enlarging the body's lateral aspect by unpaired fins, or actively by producing an impulse by their forelimbs (Preuschoft and Gudo 2005). In the shoulder region, the body is flexed laterally mainly by the same muscles, for example the m. levator scapulae in extant reptiles, which move the head towards a prey into the same direction, but to a lesser degree (Figure 10). Thus, the neck-shoulder region will tend to move into a direction opposite to the direction of the lateral strike, because the pivot of the movement is the animal's COM. Anterior fins can be used to suppress this movement by actively producing an impulse against the recoil of the head's movement (Figure 10(B)).

3.6 Limbs

Water resistance grows linearly with the area of a moved body part (Equation (3)), so fins need long and/or wide surfaces to evoke sufficient resistance when moved. The total reaction force acting against unit area of the fin depends on the speed of fin movement. The distribution of

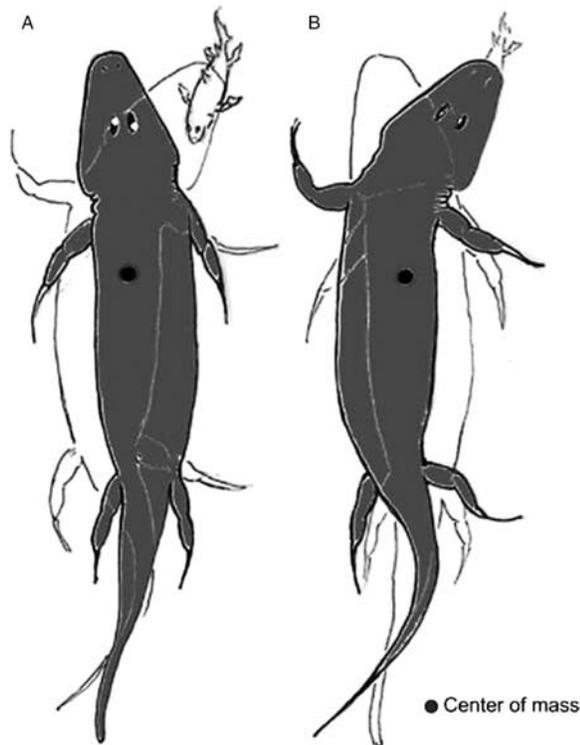


Figure 10. *Tiktaalik* bouyant in water, snapping sideways towards a prey. (A) Animal lying in wait for prey or swimming slowly. The potential prey is spotted at its right side. (B) Striking to the right is inevitably coupled with reactive recoil of the trunk to the left. The pivot of both movements is the COM (dot). The recoil can be suppressed either passively by the trunk's mass moment of inertia, or by active movements of the fin-shaped forelimbs.

reaction forces over a large area leads to a parabolic increase of the bending moments along the length of the fin (see Figure 11(A), right side), so that it is exposed to lesser bending moments than the dactylous autopodium in a terrestrial animal (Figure 11(A), left side). Consequently, the rays of land-living forms need to be shorter and stronger than the rays of fins to sustain the bending stresses. Furthermore, moving and controlling short free extremities, or their segments, requires less energy than long limbs, because the lever arms of external forces remain shorter. Shortness also reduces the danger of overstraining in accidents (Preuschoft 1990).

In *Tiktaalik*, the shoulder joint is shifted towards the ventral margin of the body, near the level of the belly (personal observation and communication with N. Shubin). The caudo-ventro-laterally directed movement of the humerus in the socket-like, though shallow glenoid surface and a corresponding expansion of the humeral head offer a close-packed position which allows the transmission of high joint forces. This position and shape of the glenoid joint implies a mechanical advantage because of two reasons: first, the lateral head strike can also be used by a

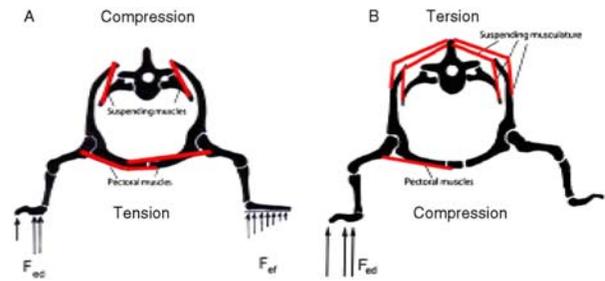


Figure 11. Schematic cross sections through the shoulder region of a generalised tetrapod. The model is designed like a reptile. The morphologically, but not mechanically, divergent situation in lissamphibians has been investigated by Preuschoft and Gudo (2002). (A) Symmetrical stance. Skeletal elements black. Grey lines indicate structures suspending the trunk on the limbs and sustaining transverse compression between the shoulder blades. On the left side, the ground reaction force (F_{ed}) is acting on a foot with digits. The pectoral muscle on the ventral side of the coracoid is shown as common among limbed vertebrates. On the right side, the ground reaction force (F_{ef}) acts against a fin with elongated rays and the pectoral muscle is shown on the dorsal surface of the skeletal elements, as assumed for *Tiktaalik*. In this situation, in which the trunk is supported by both forelimbs, the dorsal side is under compression, whereas the ventral side has to sustain tensile forces. (B) Tetrapod in asymmetrical support, standing alone on the left forelimb. Now the dorsal side is under tension, the ventral side is compressed.

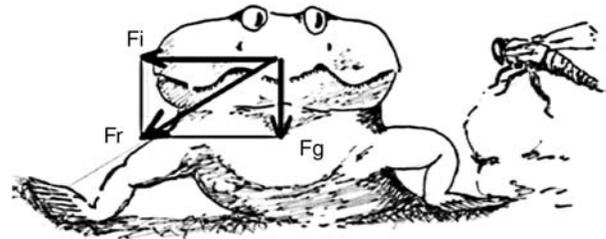


Figure 12. Primitive tetrapod on firm ground in frontal view, snapping sideways at a prey. F_g is weight force, F_i is inertia and F_r shows the resultant. To counterbalance the latter, the supporting limb has to be abducted, otherwise the animal would lose balance. Finlike or digitated autopodia fulfil the same requirements.

land-living animal for capturing prey. The mechanical conditions are shown in Figure 12. The essential factors are weight (F_g) and acceleration (F_i) of the head. According to former observations in various living animals, the accelerations of limb and head movements are often about two times earth acceleration, that is 20 m/s^2 , in rare cases up to 30 m/s^2 (Demes and Günther 1989a; Günther 1989; Busbey 1994; Preuschoft and Witzel 2004a, 2004b). The resultant of weight force and inertia (F_r) acts opposite to the direction of the strike between the median plane and the lateral support. For maintaining balance, F_r must hit the ground medial to the supporting autopodium. If the resultant acts lateral to the forefoot, the

animal loses its balance. The resultant F_r is larger than weight force (F_g) alone and larger than the load supported in lifting the anterior part of the body from the ground or in slow forward crawling. The same conditions hold true in changing the direction of locomotion. Second, like in land-living extant forms, a rather deep, ventral position of the shoulder joint requires less muscle force in situations like those depicted in Figure 1, because the muscles are not compelled to change their direction. In each case, the forelimbs are under higher stress and need to be stronger if the animal is on land. The torques in the joints become lower and less muscle force is needed if the joints are close to the resultant F_r .

Finally, the propulsive effect of the limb in contact with a firm substrate is most pronounced if the autopodium is positioned forward with its digits directed cranially. To permit this position, a considerable degree of dorsiflexion in the wrist is needed which indeed has been considered possible in *Tiktaalik* (Daeschler et al. 2006; Shubin et al. 2006).

4. Discussion and conclusions

In the following discussion, we will not focus on homologies of bony or muscular elements in the early tetrapod body, but highlight the necessity of certain structures to fulfil the basic mechanical requirements if a tetrapod body is supposed to act on land or in water. For the description of structural analogues, we relied on the widespread terminology used for amphibian and reptilian bones and muscles. Regarding the muscles of the pectoral girdle, we refer to recent comparative anatomical studies of the pectoral girdle in bony fish and tetrapods by Diogo and Abdala (2007). Note that the stress patterns revealed by the FE analysis do not depend on morphological details as absolute dimensions, exact distribution of body mass, outline of cross section, limb posture, angle of joints or shape of individual bones.

In general, we have to start from the assumption that (new) behaviour antedates the evolution of shape – as proposed for the digital bones by Ahlberg and Clack (2006). As soon as an animal leaves the aquatic surroundings, it comes under the influence of gravity. The necessities to balance its body and to provide strength of its limbs create strong selective pressures, and these seem to determine the common tetrapod bauplan. Selective advantages will appear, if the same effects can be reached with less energy, or if greater effects are achieved by a morphological modification.

4.1 General bauplan characteristics in land-living forms: body stem

The statics of the trunk in mammals were investigated by Slijper (1946) and Kummer (1959), who established the

bow string theory. Preuschoft (1976) modified it slightly by emphasising the influence of the neck and introducing quantitative aspects. Preuschoft, Falaturi, et al. (1994) and Preuschoft, Witte, et al. (1994) extended the analysis on the kinetic conditions, which occur in locomotion. The rib cage was analysed by Preuschoft et al. (2005), Preuschoft, Schulte, et al. (2007), Preuschoft, Hohn, et al. (2007), and Fujiwara et al. (2009).

The stress distribution found in our FE analyses is characteristic for a solid body supported by two or four limbs on firm ground and resembles the stress patterns in other quadrupedal animals (Preuschoft et al. 2005; Preuschoft, Hohn, et al. 2007; Preuschoft, Schulte, et al. 2007). Downward directed body weight (or the reciprocal, upward directed ground reaction force) is the dominating factor. The lack of hindlimbs in the FE model does not lead to stresses essentially different from being supported on all fours. The characteristic distribution of bending as well as torsional stresses in all tetrapods is, as a biomechanical necessity, connected with a specific morphology, because the compressive stresses can be sustained only by compression-resistant skeletal materials, regardless of its tissue (bone or cartilage), origin (dermal or cartilaginous) and phylogenetic homology. The best-known and best-preserved skeletal structures are of course bony elements. Indeed, compressive stresses in the model occur regularly at places where the skeletal elements are located in vertebrates: along the dorsal outline of the trunk, the vertebral column, at the sides of the anterior trunk, the rib cage.

The arrangements of tension-resistant tissues, mostly muscles, and also collagenous structures, correspond exactly with the occurrence of tensile stresses in the FE model: the m. rectus abdominis and its sheath.

The larger the distance between the compression-resisting vertebral column and the straight abdominal muscles, the smaller the stresses. In other words, large dorso-ventral depth of the trunk leads to long lever arms of the m. rectus, thus reducing the muscle forces necessary for balancing bending moments. A dorso-ventrally flattened cross section is not advantageous for a land-living animal (see also below).

At the height of the shoulders and at the base of the neck, the vertebral column often is shifted towards the ventral side, and compression resistant elements on the ventral side of the pectoral girdle, such as an interclavicle or a sternum, are developed (Preuschoft 1976; Hohn et al. 2007a, 2007b; Preuschoft, Hohn, et al. 2007; Preuschoft, Schulte, et al. 2007). On the dorsal side of the anterior trunk and posterior neck, where tensile forces (Figures 4 and 7) occur, many living quadrupeds possess a nuchal ligament and/or reinforced parts of the dorsal musculature (e.g. m. semispinalis cervicis), and muscles of the shoulder girdle (m. rhomboideus and trapezius, both possessing remarkable longitudinal components). Like in the trunk, long lever arms (= dorso-ventral diameters) save force.

Lifting one forelimb from the ground – which is a precondition for walking – leads in our FE model to a shift of the highly compressed area at the back towards the supporting side. This is a consequence of superimposition of bending and torsional stresses. The flows of compressive stresses cover a field broader than the axial skeleton composed of the notochord, or vertebral column itself. In the case of *Tiktaalik*, the area exposed to compression is equipped with broad, imbricated ribs. In this particular trait, *Tiktaalik* differs from living quadrupeds which either possess marked lateral processes of their vertebrae (lissamphibians), or true ribs (reptiles and mammals), which articulate with the vertebrae so that movements in longitudinal direction are possible (reptiles, mammals). Longitudinal compression, however, can be transmitted neither between transverse processes nor between true ribs.

The major function of ribs is sustaining the compressive force components of torsional stresses. The unusual arrangement in *Tiktaalik* may have been a necessary consequence of the lack of a bony vertebral column, as noted by Daeschler et al. (2006). If imbricated ribs are connected by tough connective tissue, they can sustain longitudinal compression of the dorsum. This notion is in accordance with Jenkins' (1970) suggestion that imbricated ribs contribute to 'stiffening' the trunk in terrestrial locomotion.

Because torsional stresses have not only compressive, but also tensile components, not only compression-resistant elements (ribs), but also tension-resistant structures (oblique muscles) in the trunk wall are required. These muscles are surprisingly constant among extant terrestrial vertebrates and their aquatic descendants (Guibé 1970) consisting of longitudinal, transverse and oblique fibres, no matter whether their arrangement is considered to correspond to the layers found in mammals or not. A rather deep, ventral position of the shoulder joint requires less muscle force in situations like those depicted in Figure 12.

In fossils, tension-resistant 'soft' structures are not preserved, but can be reconstructed by analogy with extant animals and – sometimes – by muscular marks on the skeleton. Because many muscles insert into extended fascia, or merge with other muscles' insertions, muscle marks do not necessarily represent muscle morphology completely.

The stresses in the ribs and oblique muscles become smaller with an increase of the trunk's diameter (Preuschoft et al. 2005; Hohn et al. 2007b; Preuschoft, Hohn, et al. 2007; Preuschoft, Schulte, et al. 2007). Because torsional forces concentrate along the periphery of a body, the interior of the trunk remains unstressed, leaving space for the abdominal cavity (Figures 3 and 6). Skeleton and muscles wrap in the trunk cavity, filled with the soft and deformable intestines which cannot resist

mechanical loads. The dorso-ventrally depressed cross section as observed in fossil *Tiktaalik* turns out to be not optimal for living on land, because it requires greater muscular forces in the rectus abdominis and an axial skeleton which is stronger than in a deep trunk. The depressed trunk shape, however, makes sense in shallow water or in a swampy environment (see Section 4.3). Possibly the cross-sectional outline of *Tiktaalik* was variable like in modern crocodiles and lizards, in which the resting trunk is wider than in walking, by which its depth is increased. The existence of the 'knee' between the bony and cartilaginous ribs allows such a change in living animals. The short bony ribs of *Tiktaalik*, which are confined to the dorsal side, do not contradict such a hypothesis.

Strong and diversified ribs, which are suited to sustain the torsional stresses on the dorsal and lateral periphery of the trunk, exist only in land-living tetrapods and their secondary aquatic descendants. An exception is some lissamphibia, in which transverse processes functionally replace the ribs. The reinterpretation and subsequent rearrangement of the vertebral column in *Ichthyostega* by Ahlberg et al. (2005) also shows a regional diversification of segmental elements depending on the functions of the vertebrae. In general, diversification is coupled with the extent of terrestrial locomotion. The opposite is most obvious in secondary aquatic animals like whales and sea cows, which have almost uniform ribs (Preuschoft and Kuschel, in preparation).

As shown with FESS (see Section 2.1), the skull shape in living and extinct tetrapods depends essentially upon mechanical conditions, mainly the stress flows evoked by bite forces (Preuschoft and Witzel 2002, 2004a, 2004b, 2005; Rossmann et al. 2005; Witzel and Preuschoft 2005; Gössling et al. 2008; Gössling 2010; Witzel et al. 2011). Any deviation from this general rule, like flatness of the skull, needs an explanation. The latter was identified in this study by a possible habit of lateral snapping under water. Under terrestrial conditions, there is no reason to develop a flat shape, although the same lateral head strike can be advantageous.

4.2 General bauplan characteristics in land-living forms: pectoral girdle and limbs

Maximal compressive stresses occur near the attachments of the limbs to the trunk. There are two stress flows spreading from the glenoid joint, which receives the highest stresses: one is directed dorsally and slightly caudally along the side of the trunk, corresponding to the location of the scapula and suprascapula of recent tetrapods. The second stress flow is directed ventrally towards the midline of the trunk (Figures 2(A) and 5(A)). In extant amphibians and reptiles, the coracoid and

procoracoid are located at this position and may be completed by a bony sternum and interclavícula (Figures 3(C), 6(C) and 11(B)). The quality of stresses in the pectoral girdle changes depending upon the position assumed by the animal. In symmetrical support, the dorsal margins of both sides are pressed against each other (Figures 2(B) and 3(C)), while the ventral margins are pulled apart (Figure 4(C)). The vertebral column is hung up from both scapulae. In living forms, the serratus muscle connects the ribs (reptiles) or transverse processes of the vertebrae (lissamphibia) to the scapula or suprascapula. To transmit compressive force components directed medio-laterally, this muscle needs its characteristically inclined line of action. A suspension of the trunk by the m. serratus, as shown in Figure 11(A), and common among all living tetrapods, can sustain compression from one side to the other because of the inclined direction of the m. serratus, which gives it a horizontal component. The ribs of *Tiktaalik* are not as well developed as in true tetrapods and do not reach the ventral midline of the trunk (Daeschler et al. 2006). Nevertheless, trunk weight transmission seems to have taken place in the same way as shown in Figure 11(A).

In lateral head striking under semi-aquatic or terrestrial conditions, the forelimbs of lower tetrapods could be used to counteract the recoil of the anterior trunk (Figure 10). In contrast, fishes stabilise their trunk by using water resistance either passively by enlarging their lateral aspect with unpaired fins or actively by producing an impulse by their forelimbs (Preuschoft and Gudo 2005). Undue rotations about the longitudinal axis are avoided if the shoulder joint is located at mid-depth of the trunk, halfway between dorsal and ventral contour. Under terrestrial conditions, a laterally directed, 'sprawled' position of the forelimbs is useful and adaptive for rapid lateral movements. For locomotion on land, a position of the glenoid joint close to the ventral margin of the trunk gives more freedom from the ground than a lateral position. It also shortens the load arms of the pectoral adductor (Figure 11(A),(B)), while excluding losses of force, which are caused by changes in the direction of muscle force. Consequently, the shoulder joint in land-living forms is optimally positioned if shifted towards the ventral margin of the body. This also holds true in *Tiktaalik* (own observation, N. Shubin, personal communication). Its glenoid facet allows transmission of high forces and is separated into two areas, indicating a tight connection of the humerus to the glenoid joint during action (Shubin et al. 2006).

Due to the wide-gauged, sprawling position of the forelimbs, weight force exerts a considerable torque in the shoulder joint. In all modern amphibians, reptiles, birds and mammals, this is countered by the adductor of the humerus. This muscle (Figure 11(A),(B)) is present in all modern tetrapods. It takes its origin at the ventral side of

the trunk, which is coracoid, procoracoid, sternum or ribs (Figure 11(A), left side, (B)). In *Tiktaalik*, a muscle that may fulfil the function of stabilising the glenoid joint seems to originate on the dorsal side of the coracoid (Figure 11(A), right side) and inserts into the humerus (Shubin et al. 2006). Such an arrangement of the m. pectoralis differs from the situation in living quadrupeds, but works well if the tendon passes ventral to the shoulder joint – which seems to be the case.

The tensile stresses on the ventral side of the shoulder girdle in symmetrical support are largely sustained by the mm. pectorales. If the origins of m. pectoralis do not reach the contralateral side, a tension-resistant ligamentous connection between both sides is an absolute necessity.

In all recent tetrapods, a bony or cartilaginous skeletal element (sternum, interclavícula) exists along the midline of the body between the coracoids and permits transmission of compressive as well as tensile stresses. Elements like this are mechanically necessary for supporting the body on forelimbs (Hohn 2010). In *Tiktaalik*, similar ventral elements of the pectoral girdle have not been observed, but they may have existed in cartilaginous form, and the transmission of compressive forces may have taken place through the adjacent, well-developed clavicles (Shubin et al. 2006). In general, sternum-like elements evolved late in evolution (Romer and Parsons 1977; Starck 1979), but at least partly cartilaginous elements between the coracoids are highly probable in so huge terrestrial animals like sauropod dinosaurs (Hohn 2010, 2011).

If symmetrical and asymmetrical supports alternate, the compressive forces flowing from the humerus to the midline can be supported by the coracoid plates. Compressive stresses are also evoked at the base of the neck by bending the trunk under the influence of gravity. Thus, a continuous structure that can transmit compression and tension in transverse as well as longitudinal direction on the ventral side of the shoulder girdle is a mechanical requirement for terrestrial postures as well as locomotion.

In *Panderichthys* and *Tiktaalik*, as well as in the earliest tetrapods, an increase of the endochondral elements (scapula, coracoid) of the shoulder girdle can be observed (Shubin et al. 2006). At the same time, the dermal elements (cleithral series) of the shoulder girdle functionally involved in aquatic locomotion and feeding are reduced (Romer and Parsons 1977). The gradual nature of these changes during evolution could indicate that basal stem tetrapods were semi-aquatic (Clack and Coates 1995; Coates et al. 2002; Shubin et al. 2006). The correlation of the altered construction of the shoulder girdle with an enhanced terrestrial support coinciding with increased body weight and counteracting muscle force has been recognised long ago. The reasons assumed as causes of the changes, however, are sometimes not convincing. For

example, Romer and Parsons (1977) attributed the enlargement of the ventral elements to the downwards acting body weight which otherwise would push both coracoids apart. Our data indicate that the skeletal elements increased as a result of the mechanical stresses occurring during terrestrial locomotion, no matter whether they were originally dermal or endochondral. According to Wolff's law and the rules of causal morphogenesis (Pauwels 1965), the compressive stresses occurring between the origins of muscles and their insertion lead to the modelling and remodelling of bone. The bigger reaction forces on land are responsible for the greater strength of the bones of zeugopodia, stylopodia and the shoulder girdle in comparison to aquatic forms.

The compressive stresses in our FE model reach up to -20 MPa, or 10% of the ultimate strength of 'haversian' bone, which is 172–220 MPa (Wainwright et al. 1976). This value would be two times greater than that necessary for deposition of bone material in a living body (Frost 1988). The values of widely distributed stresses in the FE models in symmetrical support were relatively low (see Figures 2–4, legends: -0.02 to 0.004 MPa). The compressive stresses in asymmetrical support are higher (Figures 5–7, legends: 0 to 0.09 MPa). This comparison of symmetrical and asymmetrical support indicates the relevance of locomotion for the forming of the entire musculoskeletal system.

Although shortness of the free extremity saves force in moving and allows better control of the limb in cases of emergency, greater length from shoulder joint to ground contact implies for terrestrial animals the advantage of greater step length and therefore faster locomotion – but requires much greater muscle forces.

4.3 Biomechanical conditions posed by divergent environments

The tetrapodomorph fishes seem to have lived in 'deep' water (in terms of hydromechanics; Prandtl et al. 1969; Lighthill 1977; Ungerechts 1980; Gersten 2003), that is water deeper than two times the body height of the animal. Propulsion resulted mainly from horizontal undulation of the body axis. A rather large lateral plan yields the greatest area for propulsion in relation to mass of the animal (compare Equation (3)). Height of the body may be expanded at the expense of breadth. Undulating movements are performed by segmented musculature and require a compression-resistant longitudinal structure (notochord or vertebral column). This axis receives the same compression along its entire length (Preuschoft and Kuschel, in preparation). Active and passive appendages control the position in space, the paired, active extremities reduce undue rotations about the longitudinal axis best if attached to the trunk halfway between the dorsal and ventral outlines.

The biotope closer to land is shallow water, with stems of plants, stones or other stiff objects on the ground. Living forms that inhabit such biotopes are, for example, crocodiles and newts. As long as an animal is fully submerged, its weight is carried by water and does not evoke vertical reaction forces from the ground. Each unit of body volume which sticks out of the water exerts a weight force which must be supported by the ground. A depressed trunk with larger transverse diameters (breadth) than dorso-ventral height saves energy. Propulsion can again be produced by horizontal undulation and/or by bracing the limbs or part of the body against stiff objects. The former may be confined to the laterally compressed, flat tail, the latter leads to concentrated attack of external forces, mainly against the appendages. All external force components contributing to propulsion are confined to the mediolateral plane, not to the dorso-ventral, as in truly terrestrial forms. Similar conditions exist on semi-rigid surfaces such as fine-grained mud or masses of vegetation in swamps. However, vertical forces resulting from gravity come into play. The large ventral surface of trunk, neck and head distributes body weight over a large area. This area is particularly large, if the trunk is depressed dorso-ventrally. As a rough approximation, the dimensions assumed for *Tiktaalik* may be used. Its elliptical cross section has a breadth of 18 cm and a height of 12 cm. The elliptical cross-sectional area is $A = \pi \times h/2 \times b/2$, a circular cross section is $A = \pi \times r^2$. If the area is constant, its breadth b depends on r^2/h . Therefore, the area on which body weight is distributed in the case of *Tiktaalik* is 12.2% larger than that of a circular cross section. The limbs do not give reliable supports on very soft (e.g. muddy) surfaces, and, therefore, are less suitable for carrying body weight. The resulting high friction between belly and ground requires propulsion at each step. This is neither the case in swimming nor the case in walking on limbs, because in both modes of locomotion, the impulse of the body once accelerated is maintained with minimal loss. In the case under consideration, the extremities are mainly used for propelling, not carrying the animal. For sustaining the external forces concentrated mainly on the autopodia, these need to be reinforced. Fin-like autopodia may do, they just need to be strong enough. However, claws or other structures to increase friction are clearly of advantage – but again lead to a concentration of external forces. In any case, the movements of the limbs can be largely restricted to a transverse plane. If the most proximal joints (shoulder and hip) are on the level of the belly (as described for *Tiktaalik* by Shubin et al. (2006)), force transmission from the external support to the trunk is without loss. Rotation about a longitudinal axis (as discussed above) is of minor importance if ground contact is frequent or continuous.

Water resistance grows linearly with the area of a moved body part (Equation (3)); therefore, fins need long

and/or wide surfaces, including long digits to evoke high resistance. For a purely aquatic animal, fin-like autopodia are advantageous because the numerous, long and compliant rays distribute the external forces over a large surface. This distribution of reaction forces leads to a parabolic increase of the bending moments along the length of the fin (see Figure 11(A), right side), so that it is exposed to lesser bending moments than the dactylous autopodium in a terrestrial animal (Figure 11(A), left side). Consequently, the rays of land-living forms need to be shorter and stronger than the rays of fins. The total reaction force acting against unit area of the fin depends on the speed of fin movement. Shortness of stylopodia and zeugopodia requires less energy for moving and controlling the limbs under aquatic conditions.

4.4 Reconstructing *Tiktaalik's* lifestyle

Some conclusions concerning the lifestyle of one of the earliest transitory forms between aquatic and terrestrial lifestyle can be suggested, which go beyond Daeschler et al. (2006).

The head shape of *Tiktaalik* is somewhat reminiscent of crocodiles which use the lateral strike of the head without moving the whole body for prey capture and in intra-specific encounters (Busbey 1994; McHenry et al. 2006). Fishes usually have an immediate connection between head and shoulder girdle, which inhibits head and neck movements (Gudo and Homberger 2002; Preuschoft and Gudo 2005). In *Tiktaalik* the opercular series is reduced and no bony connection exists between skull and pectoral girdle (Daeschler et al. 2006; Shubin et al. 2006; Downs et al. 2008), thus permitting free movements of the head.

Long jaws allow long reach and fast closing movements at the jaw tips, facilitating capture of evasive prey (Preuschoft et al. 1985, 1986, 1987). The disadvantages of increased jaw length are, first, decreasing bite forces with increasing distance of the bite point from the articular-quadrates joints, and second, increased water resistance. There are two ways to reduce water resistance and energy required for movement: first, the jaws could be narrow and slender, as in modern *Gavialis*, *Thomistoma* or porpoises. Slender shape of the jaws, however, reduces the probability of capturing swift prey by poorly aimed snapping and requires a high standard of coordination that may have not been present in tetrapodomorphs, nor in early tetrapods. We, therefore, assumed the acceleration of the whole animal to be as low as 1.5 G, whereas more than 2 G has been observed in horses (Preuschoft et al. 1987) and more than 4 G in animals the size of, or smaller than, *Tiktaalik* (Günther 1989; Demes and Günther 1989a, 1989b). Likewise, the closing speed of the jaws was assumed in our calculations to be nearly 1000°/s, whereas

measurements of Herrel et al. (1995) yielded a value of 1437°/s and a closing time of 32 ms in lizards at a maximal opening angle of 46°.

A second way to improve the chances for capturing a prey is increasing the gape and width of the mouth while reducing water resistance. A soft and compliant floor of the oral cavity (as in modern rorquals) would lag behind the fast movement of the mandible, reducing water resistance in the calculated case of *Tiktaalik* to about one half.

Our calculations revealed that *Tiktaalik* may have acquired prey by lateral snapping because increasing length and width of the jaws improves the chance of engulfing the prey, but at the same time reduces the speed of the water flow entering the mouth, making suction less effective (Higham et al. 2007). This is in line with former studies predicting that *Tiktaalik* had already made the shift from suction to snapping feeding behaviour (Ahlberg and Clack 2006; Markey and Marshall 2007).

The energy demands for the lateral head strike, as observed in crocodiles (Busbey 1994; McHenry et al. 2006), are less than for turning the whole body about the centre of gravity, or rushing forward. *Tiktaalik* possesses all the essential traits to perform this behaviour if submerged in water. The flat shape of the head keeps water resistance low at the expense of bending strength. Under aquatic conditions *Tiktaalik* may have used its fin-like pectoral appendages to counteract the recoil of the anterior trunk (Figure 10). In contrast, fishes use their forelimbs for moving their head while passively stabilising their trunk through water resistance by enlarging their lateral aspect by unpaired fins (Preuschoft and Gudo 2005).

Living near the bottom of shallow water or in swamps allows bracing the body against vegetation and the use of limbs primarily for propulsion – like in salamanders and crocodiles (though not in the amphibious hippos, as observed by Niemitz, unpublished). A ‘sprawled’ position of the forelimbs and the ventral location of the glenoid are advantageous, fin-like as well as dactylous autopodia can be useful in such an environment. The dorso-ventrally depressed body form suggested by the fossil fits well to this sort of biotope, but may be exaggerated by post-mortem influences and seems to be a variable trait. Flatness, however, would be less suited for sustaining the stresses that occur during standing, or walking on firm ground.

The location of ossified skeletal elements in the post-cranial skeleton of *Tiktaalik* coincides with compressional stresses that would occur during standing, crawling or walking on firm ground. The positioning and the obvious strength of the scapula also indicate that *Tiktaalik* was capable of supporting at least the anterior part of the body above the ground. Lateral snapping is clearly practicable in land-living animals as well. It leads to mechanical advantages for forelimbs in sprawled and flexed postures of the free limb and requires a particularly strong shoulder girdle plus forelimb. The position of the anterior

extremities is suitable for stabilising the body during these strikes in water as well as on land.

To sum up, our results indicate that *Tiktaalik* could behaviourally handle foraging and moving on land better than its ancestors, though it was not fully adapted to terrestrial life.

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