

## The functional significance of the lower temporal bar in *Sphenodon punctatus*

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Accepted 20 October 2008

### SUMMARY

One of the major conundrums in the evolution of vertebrate cranial design is the early loss and frequent redevelopment of the lower temporal bar in diapsids. Whereas it has been proposed that the reduction of the lower temporal bar allows for an increase in jaw adductor mass and bite force, this has never been tested experimentally. As the sole recent representative of the Rhynchocephalia, *Sphenodon punctatus* is different from other extant lepidosaurians in having a fully diapsid skull and in using translation to shear food rather than using the typical puncture-crushing of other lizards. In the present study, we show that *S. punctatus* has lower bite forces compared with extant lepidosaurians. Moreover, dissection of the jaw muscles of an adult *S. punctatus* shows that the mass of the external jaw adductor muscle is significantly smaller than that of lizards, probably accounting for the lower measured bite forces. An analysis of the transport cycles suggests a less efficient prey transport in *S. punctatus* compared with an agamid lizard of similar size in terms of handling time and number of cycles needed to crush similar prey. Modelling of biting in *S. punctatus* suggests a different role of the jaw adductor muscles during biting and a clear functional role for the lower temporal bar. Future finite element models may provide better insights into the function of the lower temporal bar in *S. punctatus*.

Key words: *Sphenodon punctatus*, lower temporal bar, feeding behavior, bite force, static bite model.

### INTRODUCTION

The evolution of the diapsid skull in vertebrates is marked by the early loss and frequent evolutionary redevelopment of the lower temporal bar (Müller, 2003). In the past, the loss of a contact between jugal and quadratojugal was interpreted as unique for squamates and, therefore, many ancient diapsids (e.g. *Prolacerta*, a Triassic archosaur; *Paliguana*, a Permian reptile) were considered to be squamates (Müller, 2003; Wu, 2003). However, modern cladistic analysis has shown that the absence or loss of the lower temporal bar should be considered an ancestral trait for many diapsids (Gauthier et al., 1988; Müller, 2003).

Despite the importance of the lower temporal bar in debates regarding basal amniote relationships, the functional significance of the presence or absence thereof remains obscure. One often cited hypothesis suggests that reduction of the lower temporal bar allowed for an increase in the volume of the external jaw adductor leading to an increase in bite force (Rieppel and Gronowski, 1981). Yet, the loss of the lower temporal bar probably also affects the stability of the jaw suspension, as reaction forces on the jaw during biting will induce moments at the jaw and quadrato–squamosal joints that could be resisted by a complete bar (Herrel et al., 1998a).

The redevelopment of the lower temporal bar in animals such as *S. punctatus* has been argued to stabilize the quadrate and allow precise occlusion (Wu, 2003; Lu et al., 2008), or to facilitate the development of a propalinal power stroke (Gorniak et al., 1982), enabling these animals to break down relatively large or tough prey. However, these advantages may have come at the cost of a reduction in bite force capacity and feeding efficiency if indeed jaw adductors are constrained by the presence of a lower temporal bar.

Lepidosaurians provide an excellent test case for these hypotheses as *S. punctatus*, the only extant representative genus of the

Rhynchocephalia, has a complete lower temporal bar (Fig. 1). Lizards, by contrast (the closest extant relatives of *S. punctatus*), are characterized by the lack of the lower temporal bar (Rieppel and Gronowski, 1981) (Fig. 1) and their feeding mechanics are relatively well known (e.g. Smith, 1982; Smith, 1984; Bels et al., 1994; Herrel et al., 2001c; Schwenk, 2000; Bels, 2003). In the present study, we explore the functional role of the lower temporal bar by comparing data on morphology, bite force and feeding kinematics in *S. punctatus* as well as in squamates with a generalized cranial morphology. We test whether *S. punctatus* has: (1) less jaw adductor muscles, (2) lower bite forces, and (3) needs more jaw cycles to process prey compared with lizards. Additionally, we use a static bite model to explore whether the redevelopment of a complete lower temporal bar in *S. punctatus* is a consequence of the reorganization of the jaw adductors and/or the development of the musculus pterygoideus atypicus (Wu, 2003) and may be associated with the presence of a unique shearing bite.

### MATERIALS AND METHODS

#### Muscle masses and fiber lengths

Data on the mass of the external jaw adductor were obtained by dissection of the jaw muscles of one adult ethanol preserved specimen of *S. punctatus* (Gray 1842) [snout-vent length (svl), 22.23 cm; cranial length (cl), 5.82 cm] from the collection at the Prague Natural History Museum. Data on jaw adductor muscle mass were also collected for one adult of the following species of lizards: *Pogona vitticeps* (Ahl 1926), *Chameleo calyptrotus* (Duméril and Duméril 1851), *Corucia zebrata* (Gray 1855), *Tiliqua scincoides* (White 1790) and *Gekko gecko* (Linnaeus 1758) (see also Herrel et al., 2007). All jaw muscle bundles of one side were removed and stored in 70% ethanol until weighed at the

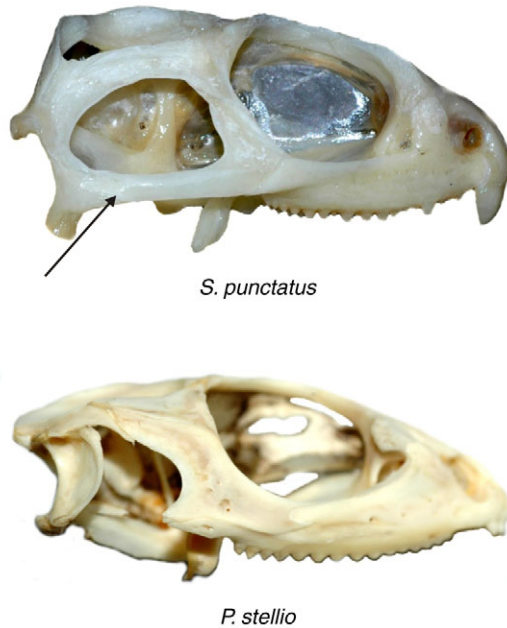


Fig. 1. Lateral view on the skull of *Sphenodon punctatus* (top) and *Ploceoderma stellio* (bottom). Note how the major difference between the two skulls is the absence of the lower temporal bar in *P. stellio*. Arrow indicates the lower temporal bar in *S. punctatus*.

Functional Morphology Laboratory at the University of Antwerp. Muscles were blotted dry and weighed on a Mettler MT5 electronic balance (accuracy,  $\pm 0.01$  mg; Mettler-Toledo Inc., Columbus, OH, USA) (Table 1).

Next, muscles were transferred to a 30% aqueous nitric acid solution and left for 20–24 h after which the solution was replaced by a 50% aqueous glycerin solution. Individual fibers were teased apart using blunt-tipped glass needles, and 10 fibers were selected randomly and drawn using a binocular microscope with attached camera lucida (MT5 Wild, Wild Heerbrugg Ltd., Heerbrugg, Switzerland). Drawings were scanned and fiber lengths determined using Image TpsDig software (Rohlf, 2001) (freeware available at <http://life.bio.sunysb.edu/morph>). The mean fiber length per bundle was determined and the physiological cross-section of each bundle was approximated by the ratio of the mass over the mean fiber length, assuming a muscle density of  $1000 \text{ kg m}^{-3}$  (Table 2).

#### Animals and husbandry

Data on bite forces and feeding behavior for *S. punctatus* were obtained from a series of juveniles maintained at the Otorohanga Kiwi house, Otorohanga, New Zealand. The animals were housed

in a large glass vivarium on a 12h:12h light:dark cycle and were offered water and food *ad libitum*. The environmental temperature varied from 20°C during the daytime to 10°C at night.

#### Bite forces

An isometric Kistler force transducer (type 9203, Kistler, Wintherthur, Switzerland) mounted on a purpose-built holder and connected to a Kistler charge amplifier (type 5058A, Kistler) was used to measure bite forces (for details, see Herrel et al., 1999a; Herrel et al., 2001a; Herrel et al., 2001b). Measurements were repeated five times for each animal ( $N=14$ ). The maximal value recorded out of the five trials was considered the maximal bite force for each animal. Data for *S. punctatus* were compared with previously unpublished bite force data for a wide array of agamid species (87 individuals belonging to nine different species) collected using similar methods.

#### Feeding behavior

Data on feeding behavior for *S. punctatus* were collected for three individuals. As previous recordings of jaw movements indicated that these were slow (Gorniak et al., 1982), feeding behavior was recorded at 25 Hz using a digital camcorder (Sony, Tokyo, Japan). Video recordings were reviewed using Midas Player software (Redlake, San Diego, CA, USA; v. 2.1.7), and only feeding sequences where animals remained perpendicular to the camera, and in which all the phases of a transport cycle (slow open, SO; fast open, FO; fast close, FC; slow close/power stroke, SC/PS) were present, were used in further analysis. A total of 26 feeding sequences ranging from 5 to 29 cycles were retained to calculate the transport and swallowing stage duration, the number of transport and swallowing cycles, the mean transport cycle duration and the mean swallowing cycle duration while eating a mealworm. Two externally visible landmarks, the anterior tip of the upper jaw and the anterior tip of the lower jaw, were digitized on each frame for 120 transport cycles of the three individuals using Didge (Image Digitizing Software v. 2.2.0; Alistair Cullum). Based on the  $x$ - $y$  coordinates from these markers gape distance was calculated. Velocities and accelerations associated with the changes in gape distance over time were calculated from the filtered displacement data (using a zero phase shift, fourth-order low pass Butterworth filter at 25 Hz; implemented by Sam Van Wassenbergh) by numerical differentiation.

To delineate the kinematic phases of a transport or swallowing cycle, we used the jaw acceleration data: the duration of the slow open phase was defined as the time between the beginning of a transport or swallowing cycle and the first pronounced acceleration peak during jaw opening, the fast open phase was defined as the time between the first acceleration and the deceleration peak, the fast close phase was defined as the time between the peak

Table 1. Data on jaw adductor muscle mass for different species

Genus	Species	svl (mm)	cl (mm)	MDM (g)	MAME (g)	MPSt (g)	MAMP (g)	MPt (g)	MPPt (g)	MLPt (g)	Total (g)
<i>Pogona</i>	<i>vitticeps</i>	193.30	35.21	258.95	1487.50	314.90	112.85	1650.00	17.13	9.77	3565.25
<i>Chameleo</i>	<i>calyptratus</i>	141.00	36.50	101.47	1382.30	87.50	35.34	359.50	—	—	1864.64
<i>Corucia</i>	<i>zebrata</i>	240.00	51.10	150.00	2360.00	730.00	230.00	1330.00	30.00	20.00	4650.00
<i>Tiliqua</i>	<i>scincoides</i>	310.00	65.80	270.00	4520.00	1270.00	870.00	3510.00	90.00	30.00	10170.00
<i>Gekko</i>	<i>gecko</i>	130.67	36.71	133.90	1480.80	114.40	17.40	530.30	66.90	33.00	2142.90
<i>Sphenodon</i>	<i>punctatus</i>	223.39	58.23	455.90	1721.18	683.42	137.60	1638.90	21.39	4.83	4181.10

svl, snout-vent length; cl, cranial length; MDM, m. depressor mandibulae; MAME, m. adductor mandibulae externus; MPSt, m. pseudotemporalis; MAMP, m. adductor mandibulae posterior; MPt, m. pterygoideus; MPPt, m. protractor pterygoideus; MLPt, m. levator pterygoideus; Total, total adductor mass.

Table 2. Jaw adductor muscle mass, fiber length and physiological cross-section of *Sphenodon punctatus*

Muscle	Data Gorniak et al. (1982)			Data Prague Museum Specimen		
	Mass (g)	Fiber length (cm)	Physiol. cross-section (1/cm <sup>3</sup> )	Mass (g)	Fiber length (cm)	Physiol. cross-section (1/cm <sup>3</sup> )
MDM	0.49	1.50	0.33	0.46	2.01	0.23
MAMES	0.90	1.25	0.72	0.90	1.09	0.83
MAMEM	1.04	1.32	0.79	0.59	0.87	0.68
MAMEP	0.10	0.80	0.13	0.24	0.50	0.48
MPsT	0.72	1.43	0.50	0.68	1.10	0.62
MPttyp	2.03	1.35	1.50	1.64	0.71	2.32
MPtatyp	0.11	1.65	0.07	0.09	1.34	0.07

Data were obtained from Gorniak et al. (1982) and by dissection of the jaw muscles of one adult fluid preserved specimen of *S. punctatus* from the collection at the Prague Natural History Museum.

deceleration and peak acceleration during jaw closing, and the slow close phase was defined as the time from the peak acceleration during closing until the end of the cycle (see Schaerlaeken et al., 2007; Schaerlaeken et al., 2008).

Static bite model

The analysis of biting in *S. punctatus* relied on the computation of the static force equilibrium. The model used was a modified version of the one applied by Cleuren and colleagues (Cleuren et al., 1995). Muscle forces were simply scaled to their physiological cross-section (250 kPa) (Herzog, 1994). Bite forces thus calculated are in remarkable correspondence with *in vivo* bite forces in some groups (Herrel et al., 2008), supporting the validity of this method. Muscle orientation was defined by the 3D-coordinates of the centres of origin and insertion. This spatial information was gathered from prepared skulls and our dissection. Bilaterally symmetrical muscle activation patterns are assumed (see Gorniak et al., 1982). As a result, only sagittal components of the muscle forces must be considered because transverse components will cancel each other out. Mean fiber lengths, muscle masses and coordinates of origin and insertion of jaw muscles for one additional *S. punctatus* individual (svl, 22.1 cm; cl, 5.68 cm) were obtained from the paper by Gorniak and colleagues (Gorniak et al., 1982).

For the simulations, three groups of muscles were considered: the bi-articular muscles crossing both the jaw and the quadrato–squamosal joint (or the equivalent junction in *S. punctatus*), and two groups of mono-articular muscles, crossing either the jaw or the quadrato–squamosal joint/junction. Calculation of the moment exerted by all jaw closers about the quadrato–mandibular joint allowed the determination of magnitudes of the food reaction forces at selected bite points. This was done for a range of orientations of food reaction forces [set to vary between –42 and –138 deg. with respect to the lower jaw (see Herrel et al., 1998a)], as the actual orientation of the food reaction force is often unpredictable and may depend upon the shape, texture and position of the food item, as well as the shape and position of the teeth. Biting points (=point of application of the food reaction forces; one on the anterior-most dentary tooth and one on the posterior-most dentary tooth) were selected on the basis of observational studies of feeding in unrestrained animals. These observations also showed small gape angles during forceful biting. To standardize the simulations and allow a comparison with previously published data (Herrel et al., 1998a; Herrel et al., 1998b), a fixed gape angle of 10 deg. was used in our simulations.

Each food reaction force also exerts a moment about the quadrato–squamosal joint/junction, which must be annulled to maintain the static equilibrium condition. The moment required to counteract the effect of the food reaction force at the

quadrato–squamosal joint/junction was calculated and termed the ‘required’ moment. Bi-articular muscles used for biting inherently also exert a moment about the quadrato–squamosal joint/junction. This moment was calculated and summed to the moment generated by mono-articular muscles when present. Premising a static quadrato, the difference between this moment and the required moment (i.e. remaining required moment) must therefore be induced by structures other than muscles (e.g. ligaments or bone as in *S. punctatus*). Joint forces are those forces acting from the jaw on the quadrato with the opposite sign and direction of the joint reaction forces. Conventionally, counter-clockwise moments in lizards facing to the right are regarded positive, clockwise moments as negative.

Statistical analyses

All kinematic data were log<sub>10</sub> transformed prior to analyses to meet the assumption of homoscedascity and normality for regression analyses (Sokal and Rohlf, 1981; Kachigan, 1991). To test for differences in muscle mass between *S. punctatus* punctatus and other lizards (see above), we used an analysis of co-variance with cranial length as covariate. Bite force differences between *S. punctatus* and agamid lizards were assessed using analysis of co-variance with head length as covariate. Finally, differences in prey transport behavior were tested using MANOVA coupled to univariate *F*-tests to explore which behavioral elements differed between *S. punctatus* and *Ploceoderma stellio* (Linnaeus 1758) (a generalized agamid lizard) (see Herrel et al., 1996) of similar body size (see results below).

RESULTS

Data on the mass of the external jaw adductor obtained by dissection of the jaw muscles of one adult preserved specimen of *S. punctatus* and a suite of representative lizards of similar size show that lizards have a larger external jaw adductor muscle than *S. punctatus* ( $F_{1,4}=61.4$ ,  $P<0.01$ ). Previously reported literature data for *S. punctatus* (Gorniak et al., 1982) confirm this finding (Fig. 2). In contrast to lizards, *S. punctatus* appears to invest more muscle mass into the pterygoideus group, which is also reflected in the presence of a novel m. pterygoideus atypicus (Gorniak et al., 1982) (Table 1).

*In vivo* bite forces in juvenile *S. punctatus* averaged 8.7 N ( $\pm 3.1$  N) for animals with a mean snout-vent length of 96 mm ( $\pm 9.1$  mm). As predicted, *S. punctatus* bites significantly less hard than agamid lizards of similar body or head length ( $F_{1,93}=40.6$ ,  $P<0.01$ ). For example, an agamid lizard of similar size (*P. stellio*; svl=98.14 $\pm$ 5.1 mm) generates a mean bite force of 21.12 $\pm$ 5 N, more than twice that of *S. punctatus* (see also Fig. 3).

Transport gape profiles are typical, with well-defined kinematic phases (see above). In each cycle, the mouth first opens slowly (SO) and then more rapidly (FO) until the maximal gape is

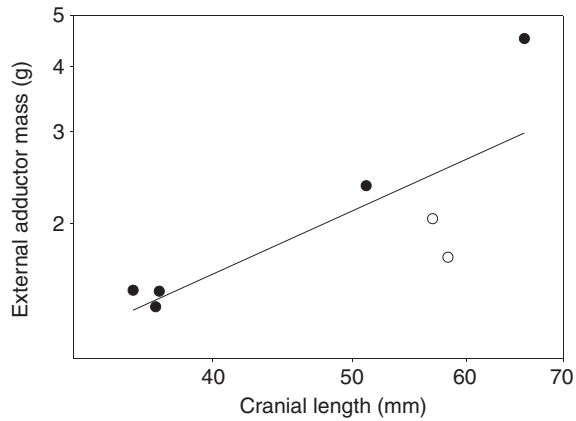


Fig. 2. Graph illustrating the mass of the external adductor for a given cranial length in lizards from three different families (agamids, scincids and geckos; closed circles) and *Sphenodon punctatus* (open circles). Note how *S. punctatus* has a significantly smaller jaw adductor for its cranial length than the lizards examined. Data include both masses from Gorniak et al. (Gorniak et al., 1982) and newly obtained data by dissection of an adult male specimen.

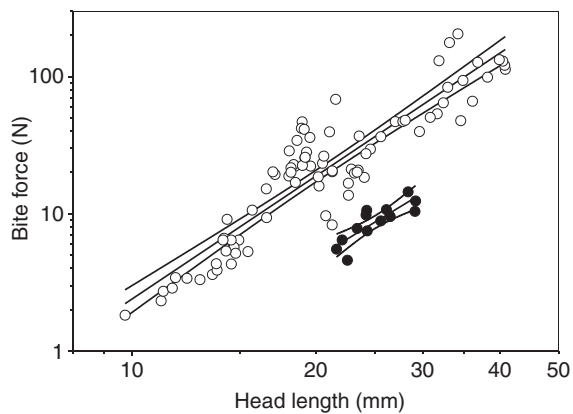


Fig. 3. Graph illustrating the differences in bite force between *Sphenodon punctatus* (closed circles) and agamid lizards (open circles). Note how bite forces are significantly lower in *S. punctatus* compared with agamid lizards.

reached. Next, the jaws close rapidly (FC) and jaw closure slows down (SC) as the food is contacted. During the power stroke, the lower jaw first continues to move upward slowly and then moves anteriorly (propalinal movement) (see Gorniak et al., 1982). Our kinematic data show that *S. punctatus* needs an average of 11 transport cycles lasting 10.75 s to crush and transport a mealworm. Swallowing was quicker and took only three cycles, lasting 4.6 s on average. Feeding behavior in *S. punctatus* differs from that in

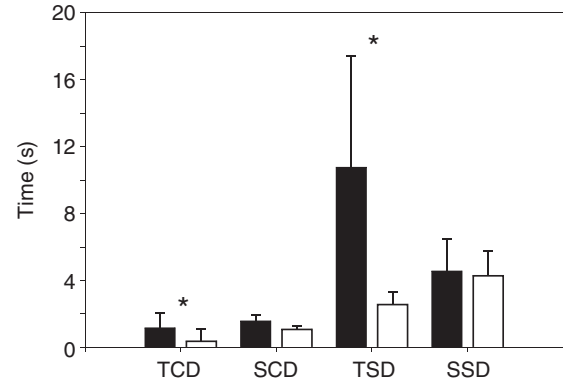


Fig. 4. Bar diagram illustrating differences in feeding behavior between *Sphenodon punctatus* (closed bar) and an agamid lizard (*Ploceoderma stellio*; open bar) feeding on the same prey (mealworm). Note how both the duration of a single transport cycle (TCD; transport cycle duration;  $F_{1,28}=25.29$ ;  $P<0.01$ ) and the transport stage duration (TSD;  $F_{1,28}=6.01$ ;  $P=0.02$ ) are significantly larger in *S. punctatus*. The duration of a single swallowing cycle (SCD) and the duration of the swallowing stage (SSD), by contrast, are not different between species ( $P>0.5$ ).

agamid lizards of similar size (Wilks' Lambda=0.254,  $F_{6,23}=11.23$ ;  $P<0.001$ ). *S. punctatus* is slower (transport stage duration  $F_{1,28}=6.01$ ;  $P=0.02$ ) and tends to use significantly more transport cycles (compared with *P. stellio*: seven transport cycles), each of which lasts almost four times longer than in *P. stellio* (1158 vs 365 ms<sup>-1</sup>, respectively;  $F_{1,28}=25.29$ ;  $P<0.001$ ) (see Fig. 4). Unexpectedly, a comparison of the relative gape cycle phase durations during transport (SO, FO, FC and SC) (Table 3; Fig. 5) demonstrated that longer transport cycles were caused by increased duration of the entire transport cycle rather than by an increase in specific phase durations. The number of swallowing cycles needed and the swallowing phase durations, however, are more similar in both species (*P. stellio*: three cycles lasting 4.28 s on average). However, overall swallowing cycle duration is still significantly longer in *S. punctatus* ( $F_{1,28}=6.29$ ;  $P=0.02$ ).

Our static bite model indicates significant differences in the relative participation of the different muscles groups in generating moments around the jaw joint. Whereas the pterygoideus group comprises 40% of the total adductor mass in *S. punctatus*, it generates only about 19% of the total moment around the jaw joint. The external adductor by contrast generates 55% of the total moment despite only being 42% of the total adductor mass. Interestingly, the m. pterygoideus in *P. stellio* generates even less (9.8%) of the jaw moment despite comprising nearly 54% of the total adductor mass (Herrel et al., 1998a) (Tables 1 and 4).

The orientation of the joint forces is also different in the two species. For any given bite point or orientation of the food reaction forces, the angle of the joint forces in *S. punctatus* tends to be slanted

Table 3. Comparison of the durations of gape cycle phases during transport (SO, FO, FC and SC)

	<i>P. stellio</i> (N=6)		<i>S. punctatus</i> (N=3)	
Avg dSO (s)	0.07±0.02	20%	0.26±0.17	22%
Avg dFO (s)	0.07±0.03	20%	0.20±0.05	18%
Avg dFC (s)	0.07±0.01	19%	0.22±0.04	19%
Avg dSC (s)	0.15±0.05	41%	0.48±0.76	41%

Note that longer transport cycles in *S. punctatus* were caused by increased duration of the entire transport cycle rather than by an increase in specific relative phase durations.



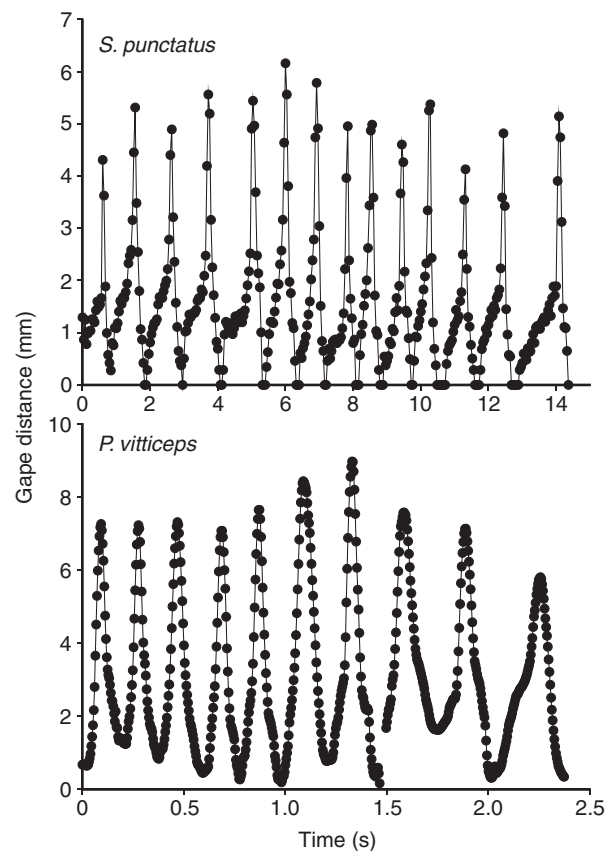


Fig. 5. Representative gape profile of prey transport in *Sphenodon punctatus* and *Pogona vitticeps* eating a mealworm. Note how the transport stage duration in *S. punctatus* is significantly longer than in *P. vitticeps* (1440 vs 237 ms<sup>-1</sup>, respectively) and consists of a greater number of cycles. Note also the difference in the scale of the two x-axes. Data for *P. vitticeps* were taken from Schaerlaeken et al. (Schaerlaeken et al., 2008).

more antieriad than in *P. stellio* where the orientation of the joint forces is more consistently aligned with the quadrate (Herrel et al., 1998b) (Table 5). Together with a counter-clockwise remaining moment (Table 6), these data suggest an antieriad compressive loading of the quadrate onto the jugal in *S. punctatus*.

DISCUSSION

Our data unambiguously show that the external adductor is smaller in *S. punctatus* as predicted by Rieppel and Gronowski (Rieppel and Gronowski, 1981). Moreover, juvenile *S. punctatus* bite less hard than lizards of similar size. Although it is hard to extrapolate such data to other taxa, one piece of evidence suggests that this may

be a more general phenomenon. Crocodylians, characterized by the presence of a lower temporal bar also bite less hard on average than lizards of similar head lengths (Herrel and Aerts, 2003) (A.H., unpublished data). The reduced bite force capacity in animals with a complete lower arcade may have important implications for their efficiency in terms of number of transport cycles and duration of a transport cycle while processing food items. Indeed, in lizards, individuals with higher bite forces need fewer cycles to crush and transport prey (Verwajen et al., 2002). To determine whether high bite forces improve feeding efficiency in lizards relative to *S. punctatus*, transport and swallowing kinematic data were compared with data for *P. stellio*, an agamid lizard of similar size, feeding on the same prey (Herrel et al., 1996). Agamid lizards were considered to be an appropriate comparison given their overall similarity in cranial and hyolingual morphology (Schwenk, 2000).

Our data show that *S. punctatus* uses more transport cycles to process arthropod prey, which also last longer on average. As they spend more time on feeding (prey transport), less time is available for other behaviors (e.g. defending territories, mating, etc.) suggesting a less ‘efficient’ feeding cycle in *S. punctatus*. However, despite being slower and having lower bite forces, their unique propalinal jaw movement may allow these animals to effectively shear and reduce relatively large food items prior to swallowing. Our data support the hypothesis proposed by Rieppel and Gronowski (Rieppel and Gronowski, 1981) that the loss of the lower temporal bar was associated with an increase in bite force (i.e. lizards compared with *S. punctatus*), and demonstrate how differences in skull structure like the loss of the lower temporal bar may have considerable functional implications (increased bite force, reduced feeding time). However, as an alternative to losing the lower temporal arcade, a general bowing out of the arcade is observed in some groups, thus providing additional space for the jaw adductor musculature in a manner similar to the rounded zygomatic arches observed in mammals (Turnbull, 1970). Whereas this does provide additional space for jaw adductor muscles, the degree of bending of the arch may be limited given that it is loaded in compression (see below), which could result in too high stresses induced by biting. Clearly this needs to be tested by finite element models and *in vivo* measurements of strains in the lower temporal bar in *S. punctatus*.

The reduced bite force and feeding efficiency in animals with a complete lower temporal bar may help explain the early loss of this trait in the fossil record (Müller, 2003) and the paucity of extant organisms showing this morphology. Indeed, the presence of an intact lower temporal bar in the lepidosaur *S. punctatus* is interpreted as derived due to the existence of many Triassic rhynchocephalians with an incomplete bar (Carroll, 1985; Müller, 2003). Moreover, loss of the lower temporal bar may induce mobility of the quadrate and may lead to complex intracranial movements as observed in some lizards [e.g. geckoes (Herrel et al., 1999b; Herrel et al., 2000)]. However, this increased intracranial mobility in lizards is also

Table 4. Significant differences in the relative participation (Frac. part. jaw) of the different muscles groups in generating moments around the jaw joint in *Sphenodon punctatus* (SP) and *Ploceoderma stellio* (PS)

Muscle	Frac. part. jaw SP (G)	Frac. part. jaw SP (P)	Frac. part. jaw PS
MAME	0.546	0.580	0.699
MPsT	0.253	0.253	0.081
MPt	0.191	0.157	0.098
MPtat	0.010	0.010	—
Total	1.000	1.000	0.878

G, data from Gorniak et al. (Gorniak et al., 1982); P, data obtained by dissection of a specimen from the Prague Natural History Museum. MAME, m. adductor mandibulae externus; MPsT, m. pseudotemporalis; MPt, m. pterygoideus; MPtat, m. pterygoideus atypicus

Table 5. Model output at gape 10 deg. and all jaw closers 100% active

Orientation FRF (°)	Joint force (N)			Orientation of the joint forces (deg.)		
	SP (G)	SP (P)	PS	SP (G)	SP (P)	PS
–138	37.6	43.7	23.4	102.1	100.3	118.9
–90	27.2	41.0	19.5	77.7	78.0	103.4
–42	39.8	44.7	17.6	53.9	56.2	80.4

For a given range of food reaction force orientations (FRF) the corresponding joint forces and orientation of the joint forces are given. Note that the angle of the joint forces in *Sphenodon punctatus* (SP) tends to be slanted more anteriorly than in *Ploceoderma stellio* (PS). G, data from Gorniak et al. (Gorniak et al., 1982); P, data obtained by dissection of a specimen from the Prague Natural History Museum.

Table 6. Model output at gape 10 deg. and all jaw closers 100% active

Orientation FRF (°)	SP (G)		SP (P)		PS	
	ReqMQS	RemMQS	ReqMQS	RemMQS	ReqMQS	RemMQS
–138	0.694	0.017	0.695	–0.006	0.163	0.125
–90	0.565	–0.112	0.566	–0.135	0.129	0.091
–42	0.435	–0.242	0.436	–0.266	0.093	0.056

For a given range of food reaction force orientations (FRF) the corresponding required (Req) and remaining (Rem) moments around the quadrato–squamosal joint (QS) in *Sphenodon punctatus* (SP) and *Ploceoderma stellio* (PS) are given. G, data from Gorniak et al. (Gorniak et al., 1982); P, data obtained by dissection of a specimen from the Prague Natural History Museum.

associated with the loss of additional cranial elements, thus making it unlikely to be the driving force behind the loss of the lower temporal bar (Herrel et al., 2007).

Rynchocephalia are characterized by an enlarged lateral palatine tooth row, a feature not found in lizards. In the basal taxa, typically without a complete lower temporal bar, this tooth row is oblique to the marginal dentition but in the more derived spenodontines (also in eilenodontines), the tooth row runs parallel (Jones, 2008). Consequently, the skull of *S. punctatus* differs from that of all lizards in having two fixed rows of teeth on each side of the upper jaw and one row of teeth on each side of the lower jaw (Gorniak et al., 1982). This special dentition pattern allows an interdigitation of tooth rows, rather than interdigitation of teeth as observed in crocodilians for instance (Cleuren and De Vree, 2000). Additionally, *S. punctatus* uses a unique form of mandibular translation to shear food rather than the typical puncture-crushing of lizards (Gorniak et al., 1982; Schwenk, 2000). This has been suggested to date back to the pre-Triassic separation between spenodontid rhynchocephalians and carnivorous prolacertilians (Robinson, 1973). The presence of a lower temporal bar has been suggested to be associated with a shearing bite and could, thus, be functionally related to this behavior and may function to stabilize the quadrate (Lu et al., 2008).

With respect to this hypothesis, our modelling data show that biting in *S. punctatus* is typically associated with counter-clockwise moment acting around the quadrato–squamosal junction. This tendency to rotate the quadrate forwards upon contraction of the jaw adductors would be resisted by the presence of a rigid lower temporal bar as observed in *S. punctatus* and suggests that the lower temporal bar may indeed be linked to the presence of the translational power stroke. This does, however, raise the question as to why remaining moments in *S. punctatus* are always counter-clockwise. One obvious difference in the jaw closing muscles between *S. punctatus* and lizards is the presence of the m. pterygoideus atypicus (Gorniak et al., 1982; Wu, 2003). Indeed, this muscle is positioned such that it would cause a tendency to generate a counter-clockwise moment around the quadrato–squamosal joint if the lower jaw were not allowed to slide forward. However, a simulation where the m. pterygoideus atypicus is excluded from the static bite model in *S. punctatus*, does not show marked differences in the orientation of the joint forces and remaining

moments. Thus, rather than being due solely to the presence of the m. pterygoideus atypicus, the existence of a counter-clockwise moment indicates a substantial rearrangement of the entire jaw adductor complex.

Our model simulations also suggest that the orientation of the joint forces in *S. punctatus* is variable and shows a tendency to be oriented in front of the quadrate. The variability of the joint forces becomes especially apparent when comparing our model output with a simulation for a lizard (*P. stellio*) that does not take into account the jugomandibular ligament (see Herrel et al., 1998a). Indeed, for a similar range of food reaction force orientations, the angles of the joint forces in *P. stellio* are orientated more posteriorly (between 80 and 120 deg.) (see Table 5). Although speculative, we suggest that the variable orientation of the joint forces in *S. punctatus* could have resulted in the need for a broad and wide quadrate base, which secondarily may have allowed the development of the unique sliding joint of *S. punctatus*. In summary, our results suggest that the role of the lower temporal bar may be tightly linked to the translational movement of the lower jaw during the power stroke. Further analyses including finite element models may prove especially insightful to further elucidate the functional role of the lower temporal bar in *S. punctatus*.

This research was conducted under permit number WK-18692-RES from the Department of Conservation, Te Papa Atawhai, New Zealand. The authors would like to thank Jiří Moravec for allowing us to dissect a *S. punctatus* specimen from the collection at the Prague Natural History Museum, Dr Z. Roček for facilitating our stay in Prague, the staff at the Otorohanga Kiwi house for help and support with this project. Supported by a PhD grant of the Institute for the Promotion of Innovation through Science and Technology in Flanders (IWT-Vlaanderen) to V.S.

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