

Static biting in lizards: functional morphology of the temporal ligaments

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Abstract

In lizards, the basic lepidosaurian bauplan of the skull is modified by the reduction of one or more skull elements such as the lower temporal bar (e.g. iguanids), the upper temporal bar (e.g. varanids) and the postorbital bar (e.g. geckos). Skull modifications in *Ploceoderma stellio*, *Uromastix acanthinurus*, *Corucia zebrata* and *Tiliqua scincoides* are restricted to the reduction of the lower temporal arcade (the plesiomorph condition for lizards; i.e. possessing a 'basic' skull). In spite of the potential mobility (streptostyly) of the quadrate, none of these species shows streptostylic movements during the static power phase of biting. It is assumed that the temporal ligaments fulfil the role of the lower temporal arcade in stabilizing the quadrate. This function is supported by the results of mathematical simulations, which demonstrate that static biting loads the ligament in tension. Apparently, these basic lizard skulls show a shift of the attachment site of the temporal ligament from the quadrate to the lower jaw. This does not affect its quadrate-stabilizing function. However, analyses of forces occurring in the quadratomandibular joint suggest that skull configurations with a jugomandibular ligament confine the possible orientations of the joint forces to a narrow range, more aligned with the quadrate. In this way, optimization of the joint morphology to resist loads imposed by biting might more easily be reached. This is assumed to be important for lizards with a robust skull built for forceful biting.

Key words: bite modelling, lizards, temporal ligaments, jaw system, functional morphology

INTRODUCTION

In their paper of 1981, Rieppel & Gronowski argue that the loss of the lower temporal arcade in diapsid reptiles was obviously not correlated with the development of streptostyly, but likely induced by the expansion of the jaw adductors. Yet, such a loss inevitably influences the stability of the jaw suspension. Reaction forces exerted by the food particle on the jaw during forceful biting must have caused considerable bending stresses at the quadratosquamosal junction, an effect that would have been amplified by the increase of the jaw musculature. It is thus conceivable that the development of a joint between the quadrate and squamosal bones was a consequence of the loss of the lower temporal arcade. According to Iordansky (1990), these were the first steps in the gradual transformation leading to the amphiki-netic lizard skull.

The moments at the quadratosquamosal joint can be

assessed by considering all forces acting directly on the quadrate. These are the quadratomandibular joint forces generated by biting and the forces produced by muscles attached to the quadrate. Cleuren, Aerts & De Vree (1995) showed that, in crocodylians, the joint forces are in all circumstances absorbed by the heavily ossified wedge formed by the quadrate and the lower temporal arcade. The observation that, in many lizard species, firm ligamentous connections (the jugomandibular or quadratojugal ligaments; see Iordansky, 1996) are found at the exact position where crocodylians have the lower temporal bar, made these authors postulate that, in lizards, joint forces during forceful biting must point caudally. These would then tend to rotate the quadrate backwards and thus load the ligaments in tension. Therefore, Cleuren *et al.* (1995) suggested that the temporal ligaments serve the same purpose as does the lower temporal arcade in crocodylians, namely the stabilization of the quadrate during the power phase of the bite cycle.

This assumption does not entirely fit the role of the temporal ligaments in cranial kinesis as put forward in a recent paper by Iordansky (1996). Hence, we want to

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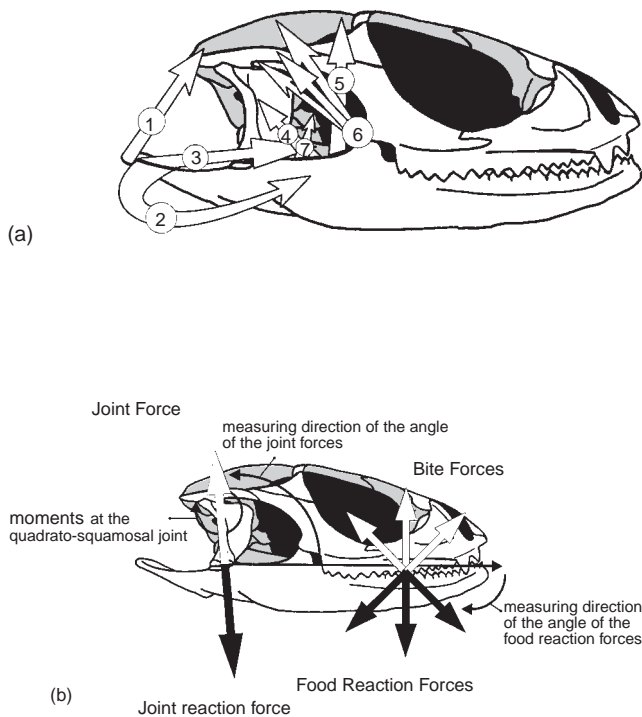


Fig. 1. (a) Schematic graphical representation of the predominant lines of action of the major groups of jaw muscles, demonstrated for *P. stellio*. 1: m. depressor mandibulae, 2: m. pterygoideus lateralis, 3: m. pterygoideus medialis, 4: m. adductor mandibulae posterior, 5: m. pseudotemporalis (superficial and profundus parts), 6: m. adductor mandibulae externus group (from top to bottom the medialis, the superficialis and the profundus parts), 7: constrictor dorsalis group (mainly mm. levator and protractor pterygoidei). (b) Action and reaction forces at the jaw joint and at the bite point. The direction of the joint force is measured relative to the line interconnecting the jaw joint and the anterior tip of the upper jaw. Bite forces are measured relative to the lower jaw. More medially situated bone structures are shaded.

evaluate their function by applying a static biting analysis to four lizard species (two acrodonts and two scincids) which all possess temporal ligaments (*in casu* jugomandibular ligaments) in spite of their largely akinetic skulls. Extant iguanians and scincids can be considered possessing a basic skull in a sense that, apart from the lower temporal bar, no further skull reductions and modifications necessary for amphikinesis have occurred. The only potential for cranial kinesis is thus streptostyly. Nevertheless, quadrate movements during the static power phase of biting do not occur in the species used for this study (evidenced by cineradiography). This means that, during static biting, all moments about the quadratosquamosal joint annul each other.

Yet, this is not a proof for the stabilizing function of the temporal ligaments. Forces of muscles bridging the quadratosquamosal joint might immobilize the quadrate. Moreover, to be useful, static biting must load the

temporal ligaments in tension and even then other stabilizing structures like joint ligaments can still play a role in preventing obvious displacements of the quadrate.

A mathematical model is used to simulate static biting. First, the moments about the quadratosquamosal joint induced by the reaction forces of the food particles on the jaw (see Fig. 1) are determined. This allows the contribution of the muscle action and the potential role of ligament tension in the stabilization of the quadrate to be assessed. Magnitude and orientation of joint forces at the quadratomandibular joint are determined. The effect of shifting the insertion of the temporal ligament from the jaw (i.e. jugomandibular ligament) to the quadrate (i.e. quadratojugal ligament) is discussed. To frame findings in a phylogenetic perspective, they are compared with the results found for the tuatara (*Sphenodon punctatus*) which still possesses a lower temporal bar.

MATERIAL AND METHODS

Ploceoderma stellio (Henle, 1995; formerly known as *Stellio stellio* or *Agama stellio*), *Uromastix acanthinurus* (acrodonts), *Corucia zebrata* and *Tiliqua scincoides* (scincids) were the species used for this study (see Table 1). Two adult *Corucia zebrata*, 2 *Ploceoderma stellio*, and 2 *Uromastix acanthinurus* specimens were used for the cineradiographic recordings. All animals were obtained from a commercial dealer. The animals were kept in a glass vivarium on a 12h light/dark cycle and were offered water and food consisting of a variety of fruits, and vegetables (*C. zebrata* and *U. acanthinurus*) or crickets, mealworms and grasshoppers (*P. stellio*) *ad libitum*. The environmental temperature varied from 26 °C during the daytime to 20 °C at night; an incandescent bulb provided the animals with a basking place at a higher temperature (35–40 °C).

For the first 3 species, cineradiographic recordings of feeding sequences were made by means of a Siemens Tridoros-Optomatic 880 X-ray apparatus equipped with a Sirecon-2 image intensifier. Feeding bouts were recorded laterally with an Arriflex 16 mm ST camera equipped with a 70 or 50 mm lens at a film speed of 50 frames per second. Potential cranial kinesis was rated by digitizing the radio-opaque markers inserted in the involved skeletal elements (for a more detailed description see Herrel, Cleuren & De Vree, 1996). During the implantation of the radio-opaque markers, animals were anaesthetized by an intramuscular injection of Ketalar (100 mg/kg bodyweight for *C. zebrata*; 125 mg/kg bodyweight for *U. acanthinurus* and 200 mg/kg bodyweight for *P. stellio*). Placement of the markers was checked on dorsoventral and lateral X-rays. Special attention was paid to the angular position of the quadrate. For *Tiliqua*, kinesis was tested on the skull from a preserved specimen stripped of integument and muscles (ligaments left intact).

For each species, one specimen (preserved specimens;

Table 1. Measurements of the specimens used for the dissection

	<i>Ploceoderma stellio</i>	<i>Uromastix acanthinurus</i>	<i>Corucia zebrata</i>	<i>Tiliqua scincoides</i>
Mass (g)	40	110	380	510
Snout-vent length (cm)	11	16	24	31
Tail length (cm)	15.5	10	33	19
Skull length (cm)	2.4	2.82	5.11	6.58
Skull width (cm)	1.89	2.66	4.08	3.67

Table 2. (a) Model input for *Ploceoderma stellio*

Muscle	Weight (g)	% weight	Fibre length (cm)	Phys. cross-section (1/cm ²)
MAMESA	0.11	8.8	0.74	0.14
MAMESP	0.09	7.2	0.59	0.15
MAMEM	0.14	11.2	0.56	0.24
MAMEPa	0.03	2.4	0.80	0.03
MAMEPb	0.06	4.8	0.74	0.08
MAMEPc	0.01	0.8	0.71	0.02
MPsTS	0.03	2.4	0.77	0.04
MPsTP	0.03	2.4	0.67	0.05
MAMP	0.08	6.4	0.37	0.22
MPt lat	0.35	28	0.67	0.52
MPt med	0.23	18.4	0.52	0.45
MPt dir	0.03	2.4	0.58	0.04
MPt dors	0.06	4.8	0.37	0.15
MPPt	0.01	0.8	0.29	0.05
MLPt	0.002	0.16	0.14	0.013
MDM	0.07	5.6	1.46	0.05

(b) Model input for *Uromastix acanthinurus*

Muscle	Weight (g)	% weight	Fibre length (cm)	Phys. cross-section (1/cm ²)
MAMESA	0.99	15	0.04	0.144
MAMESP	0.5	7.6	0.09	0.172
MAMEM	1.30	19.6	0.075	0.221
MAMEP	0.52	7.9	0.06	0.117
MPsTS	0.60	9.1	0.01	0.017
MPsTP	0.50	7.6	0.02	0.032
MAMP	0.48	7.3	0.10	0.199
MPt ext	0.64	9.7	0.22	0.333
MPt ant	0.68	10.3	0.04	0.058
MPt med	0.39	5.9	0.11	0.277
MDM	1.04	15.7	0.10	0.094

(c) Model input for *Tiliqua scincoides*

Muscle	Weight (g)	% weight	Fibre length (cm)	Phys. cross-section (1/cm ²)
MAMESA	1.25	12.3	0.748	0.75
MAMESP	0.60	5.9	1.49	0.40
MAMEM1	1.19	11.7	0.897	0.89
MAMEM2	1.02	10	0.624	0.62
MAMEP	0.46	4.5	0.344	0.34
MPsTS	0.38	3.7	0.190	0.19
MPsTP	0.89	8.8	0.553	0.55
MAMP	0.87	8.5	0.653	0.65
MPt	3.51	34.6	3.337	3.34
MPPt	0.09	0.9	0.43	0.20
MLPt	0.03	0.3	0.47	0.06
MDM	0.27	2.7	0.154	0.15

(d) Model input for *Corucia zebrata*

Muscle	Weight (g)	% weight	Fibre length (cm)	Phys. cross-section (1/cm ²)
MAMES	1.14	24.5	1.038	1.10
MAMEM	0.76	16.3	0.996	0.77
MAMEP	0.46	9.9	0.945	0.48
MPsTS	0.20	4.3	1.768	0.11
MPsTP	0.53	11.6	1.044	0.50
MAMP	0.23	4.9	1.037	0.22
MPt lat	1.30	27.9	1.06	1.23
MPt dors	0.03	0.6	0.344	0.10
MPPt	0.03	0.6	0.47	0.07
MLPt	0.02	0.4	0.49	0.05
MDM	0.15	3.2	1.28	0.11

% weight is the mass of the muscle concerned, expressed relative to the total adductor mass (excluding the constrictor dorsalis group: MPPt and MLPt, and the jaw opener: MDM). MDM: m. depressor mandibulae, MAMEM: m. adductor mandibulae externus medialis, MAMEP: m. adductor mandibulae externus profundus, MAMES: m. adductor mandibulae externus superficialis, MAMESA: m. adductor mandibulae externus superficialis anterior, MAMESP: m. adductor mandibulae externus superficialis posterior, MAMP: m. adductor mandibulae posterior, MLPt: m. levator pterygoideus, MPt: m. protractor pterygoidei, MPsTS: m. pseudotemporalis superficialis, MPsTP: m. pseudotemporalis profundus, MPt ant: m. pterygoideus anterior part, MPt dir: m. pterygoideus direct part, MPt dors: m. pterygoideus dorsal part, MPt ext: m. pterygoideus externus, MPt lat: m. pterygoideus lateralis, MPt med: m. pterygoideus medialis.

P. stellio, *C. zebrata* and *T. scincoides*: private collection; *U. acanthinurus*: Royal Belgian Museum of Central Africa, Tervuren, Belgium) was dissected (see Table 1). After the precise localization of the temporal ligaments, all distinct jaw muscle bundles of one body side (Table 2, Fig. 1a) were removed one by one and weighed accurately (0.001 g). Next, the muscle bundles were immersed in a HNO₃ 30% aqueous solution for 24 hours to separate the muscles fibres and then stored in a 50% aqueous glycerol solution. Twenty muscle fibres per bundle were selected at random and then drawn

using a Wild M5 dissecting microscope with a camera lucida. The average fibre length per bundle was determined. The physiological cross-section of each bundle was approximated by the ratio of the mass over the mean fibre length (i.e. a density for muscle tissue of 1000 kg m⁻³ was used).

The analysis of biting in the examined lizards relied on the computation of the static force equilibrium. The model used was an adopted version of the one applied by Cleuren *et al.* (1995). Muscle forces were simply scaled to their physiological cross-section (250 KPa;

Herzog, 1994), as it was shown that simulations with all muscles fully active give results (relative forces and force orientations) comparable to those of physiologically relevant mimics of crushing and holding bites (Cleuren *et al.*, 1995). Muscle orientation was defined by the 3D-coordinates of the centres of origin and insertion. Only the sagittal component, which depends upon the degree of jaw depression, was taken into account. This spatial information was gathered from prepared skulls, dissections and orthogonal X-rays (Siemens Tridoros Optomatic 800). As argued by Cleuren *et al.* (1995), this planar model can be regarded as 3-dimensional in cases of symmetrical biting (as during crushing and holding in reptiles). For practical reasons (i.e. high variability of the fibre orientation), pinnation angles were not taken into account. Muscle forces were entered for one body side only. They must be regarded as an estimate of the forces actually involved in biting.

Mean fibre lengths, muscle masses and coordinates of origin and insertion of jaw muscles for *Sphenodon punctatus* (snout-vent length: 22.1 cm, weight: 242 g) were obtained from Gorniak, Rosenberg & Gans, 1982.

For the simulations, 3 groups of muscles were considered (Fig. 1a): the bi-articular muscles crossing both the jaw and the quadratosquamosal joint (group A) and 2 groups of mono-articular muscles crossing either the jaw (group B) or the quadratosquamosal joint (group C). Calculation of the moment exerted by all jaw closers about the quadratomandibular 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° with respect to the lower jaw, see Fig. 1b) 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, etc. (cf. Cleuren *et al.*, 1995). Biting points (= point of application of the food-reaction forces) were selected on the basis of observational studies of feeding in unrestrained animals. These observations also showed small gape angles during static, forceful biting. To standardize the simulations, a fixed gape angle of 10° was used.

Each food reaction force also exerts a moment about the quadratosquamosal joint, which must be annulled to maintain the static equilibrium condition characteristic for the power phase of biting. The moment required to counteract the effect of the food reaction force at the quadratosquamosal joint was determined (i.e. the reverse of the moment induced by the food reaction force): this is called the 'required' moment. Bi-articular muscles used for biting (group A) inherently exert a moment about the quadratosquamosal joint too. This moment was calculated and expanded by the moment generated by mono-articular muscles (group C) when present. 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). For the 4 lizards, it was assumed that the jugomandibular ligament generates this remaining

required moment, on the premise that biting loads the ligament in tension (i.e. compressive loading excludes stabilization of the quadrate by the ligament). This assumption allowed the calculation of the tensile force occurring in the ligament. This force applies to the lower jaw, and must be included when framing the equations for static equilibrium of the jaw. As in all cases, the jugomandibular ligament inserts just next to the joint: it is assumed that ligament tension exerts no moment on the jaw. Taking account of: 1) a particular food reaction force; 2) all muscle forces participating in jaw closure; and 3) the ligament tension, the magnitude and orientation of the resulting joint reaction force (Fig. 1) exerted by the quadrate on the jaw was calculated (i.e. solving static equilibrium). The joint forces are thus those forces acting from the jaw on the quadrate with the opposite sign and direction of the joint reaction forces. Notice that these forces must be regarded as the actual forces seen across the articulating surfaces, including the effect of muscular activity (so called 'bone on bone forces'; see Winter, 1990; Nigg, 1995).

Joint forces were also calculated for the theoretical situation where the temporal ligaments do not attach to the jaw, but to the base of the quadrate (i.e. replacing jugomandibular by quadratojugal ligaments). This condition logically holds for the simulations of biting in the tuatara too, as in this species the ligament is absent.

Conventionally, counterclockwise moments in lizards facing to the right are regarded positive, clockwise moments as negative. Segmental weights were not considered in the simulations since they are negligible compared to the other forces involved (less than 1% of the biting forces).

RESULTS

Temporal ligaments

Detailed examination revealed two temporal ligaments in *Ploceoderma stellio*. They do not attach to the quadrate as described by Haas (1973), but insert on the jaw and consequently must be considered jugomandibular ligaments (cf. Iordansky, 1996). The exact attachment site is located 2 mm below the quadratomandibular joint on the lateral side of the articular bone. The first ligament (jml1, Fig. 2) is most pronounced and runs to the postorbital process of the jugal bone. The second ligament (jml2, Fig. 2) is much weaker and runs to the anterior part of the upper temporal arcade formed by the jugal bone. For the simulations, only the first massive ligament is considered.

The jugomandibular ligament (jml) in *Uromastix acanthinurus* is well developed and originates from the dorsolateral side of the surangular bone, just in front of the articulation surface between lower jaw and quadrate (Fig. 2). It broadens and extends upwards to attach along the posterior side of the ascending part of the jugal bone (Fig. 2). An intermediate ligament orientation is used in the simulations.

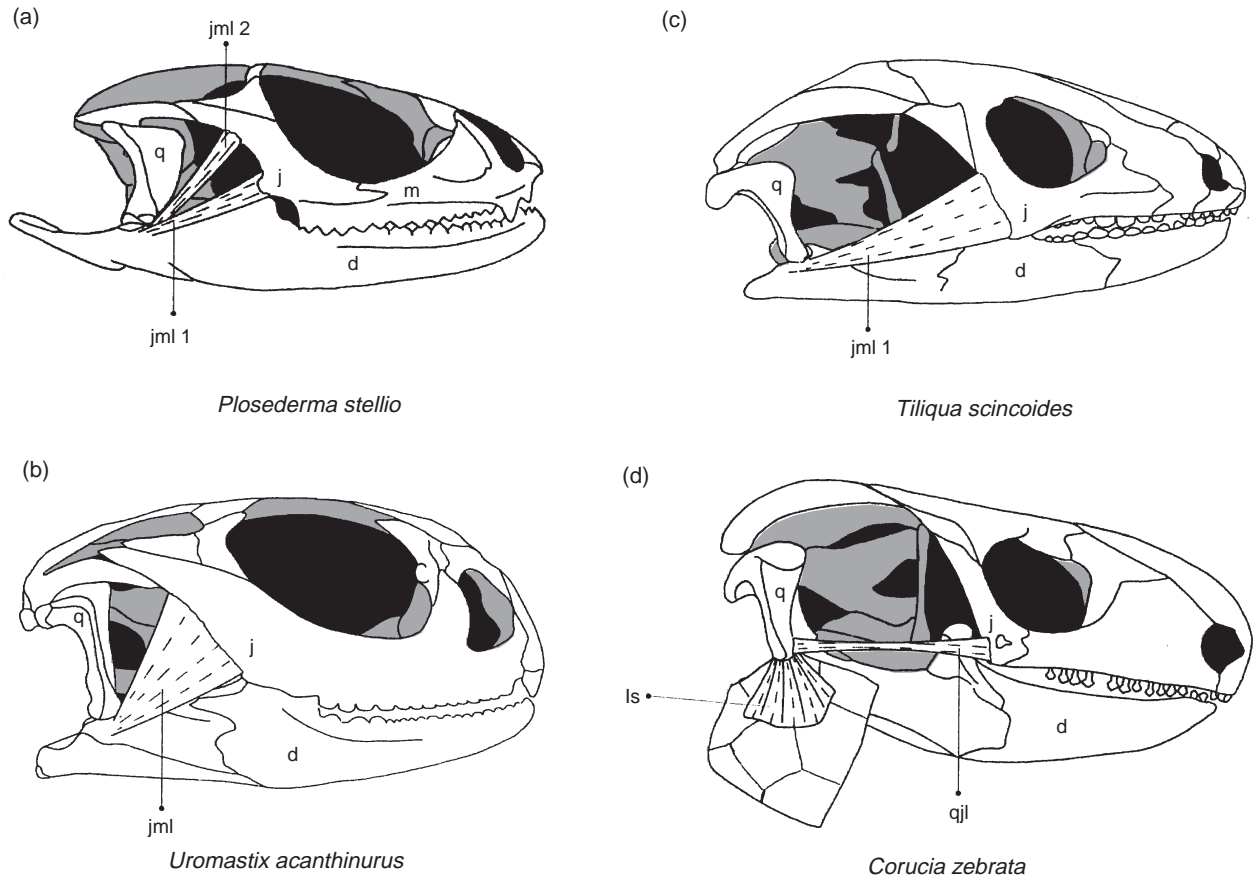


Fig. 2. Temporal ligaments. (a) Lateral view of the skull of *P. stellio*. Both the first (jml1) and second (jml2) jugomandibular ligaments are drawn to show exact attachment sites. (b) Lateral view of the skull and the jugomandibular ligament of *U. acanthinurus*. (c) Lateral view of the skull of *T. scincoides*. The second jugomandibular ligament has been removed to show the insertion site of the better developed first one (jml1). (d) Lateral view of the head of *C. zebrata*. At the base of the quadrate the skin is cut loose and lifted sideways to expose the strongly developed ligamentous sheet (ls) originating at the base of the quadrate and the dorsolateral aspect of the lower jaw. Also shown is the weakly developed quadratojugal ligament (qjl). d: dentale, j: jugale, jml: jugomandibular ligament, ls: ligamentous sheet, m: maxilla, q: quadratum.

Two temporal ligaments inserting on the lower jaw are found in *Tiliqua scincoides*. The ventral one (jml1, Fig. 2) is strongly developed and runs from the dorso-lateral side of the surangular and articular bones just in front of the articulation surface to the posterior edge of the jugal bone. The second, less developed ligament originates from the dorsolateral side of the surangular bone and lies external to the posterior part of the first ligament. It runs anterodorsally to attach to the jugal bone at the level of the upper temporal arcade. Only the first ligament is considered in the simulations.

Corucia zebrata seems to have a poorly developed quadratojugal ligament (qjl, Fig. 2). Additionally, a strong ligamentous sheet (ls, Fig. 2) originates from both the base of the quadrate and the dorsal side of the articular bone. This sheet extends anterodorsally to merge with the dermal layer of the skin at the level of the temporal region, which contains closely interconnected osteoderms. This rigid part of the skin is tightly attached to the posterodorsal edge of the jugal bone (Fig. 2). At least the ventral part of this sheet can be considered functionally as a jugomandibular ligament.

A similar construction was described for *Eumeces* (Iordansky, 1996).

Morphometrics

Masses, fibre lengths and physiological cross-sections of all muscles involved in the simulations are given for all animals in Tables 2a through 2d. Jaw muscles were subdivided into five major groups (see Fig. 1a): the external adductor complex (MAME), the pseudotemporal complex (MPsT), the posterior adductor (MAMP), the pterygoid group (MPt) and the constrictor dorsalis group (MPpt & MLPt) (See also Haas, 1973; Gomes, 1974; Herrel, Cleuren & De Vree, 1995).

Cranial kinesis

No cranial kinesis (*sensu* Frazzetta, 1962) was observed during feeding in *P. stellio* and *C. zebrata*. In spite of the absence of meso- and metakinesis in *U. acanthinurus*, distinct streptostyly was present during feeding (see also

Table 3. Model output at gape 10° and all jaw closers 100% active; for a given range of food reaction force orientations (Orientation FRF) the corresponding bite forces, the actual joint forces, the orientation of these joint forces, the required and remaining moment at the quadrate-squamosal joint and the tension in the jugo-mandibular ligament are given for the examined species. PS: *Ploceoderma stellio*; CZ: *Corucia zebrata*; SP: *Sphenodon punctatus*; TS: *Tiliqua scincoides*; UA: *Uromastix acanthinurus*

Orientation FRF (°)	Bite Force (N)					Joint Force (N)					Orientation of the Joint Forces (°)				
	SP	PS	UA	TS	CZ	SP	PS	UA	TS	CZ	SP	PS	UA	TS	CZ
-138	35.9	9.3	13.5	41.8	53.1	37.6	27.5	33.5	132.2	111.7	122.0	67.6	92.1	112.6	110.3
-126	30.0	7.8	11.2	34.5	44.7	32.0	26.4	30.8	121.7	100.9	110.3	67.2	90.9	112.0	109.7
-114	26.8	7.0	9.9	30.5	40.1	29.0	25.6	28.8	114.0	92.9	98.9	66.8	89.9	111.5	109.1
-102	25.2	6.6	9.3	28.5	37.8	27.5	24.9	27.2	107.7	86.0	87.8	66.5	89.0	111.0	108.5
-90	24.8	6.5	9.1	27.8	37.4	27.2	24.3	25.7	102.0	79.7	76.9	66.2	88.1	110.6	107.9
-78	25.5	6.7	9.3	28.4	38.6	27.8	23.6	24.3	96.3	73.2	65.9	65.8	87.0	111.0	107.2
-66	27.5	7.3	10.0	30.4	41.8	29.6	22.9	22.7	90.1	65.9	54.7	65.4	85.6	109.4	106.2
-54	31.3	8.3	11.3	34.2	47.8	33.2	22.1	20.7	82.6	57.0	43.2	64.9	83.7	108.4	104.6
-42	38.3	10.2	13.7	41.3	58.9	39.8	20.8	18.2	74.5	44.5	31.3	64.1	80.5	106.8	101.3

Orientation FRF (°)	Required Moment (Nm)					Remaining Moment (Nm)					Ligament tension (N)				
	SP	PS	UA	TS	CZ	SP	PS	UA	TS	CZ	SP	PS	UA	TS	CZ
-138	0.80	0.18	0.35	1.87	1.67	0.40	0.14	0.18	1.35	0.92	22.3	17.1	99.4	75.2	
-126	0.74	0.16	0.32	1.75	1.54	0.34	0.12	0.15	1.23	0.79	19.7	13.7	90.2	64.6	
-114	0.68	0.15	0.29	1.66	1.44	0.28	0.11	0.12	1.14	0.69	17.8	11.3	83.5	56.6	
-102	0.64	0.14	0.27	1.58	1.36	0.24	0.10	0.10	1.06	0.61	16.2	9.2	78.0	49.8	
-90	0.60	0.13	0.25	1.51	1.28	0.20	0.09	0.08	0.99	0.53	14.7	7.3	73.0	43.5	
-78	0.56	0.12	0.23	1.44	1.20	0.16	0.08	0.06	0.92	0.45	13.2	5.4	68.0	37.0	
-66	0.51	0.11	0.21	1.37	1.12	0.11	0.07	0.04	0.85	0.37	11.4	3.4	62.5	29.8	
-54	0.46	0.10	0.18	1.28	1.01	0.06	0.06	0.01	0.76	0.26	9.3	0.9	55.9	20.9	
-42	0.38	0.08	0.15	1.16	0.85	-0.02	0.04	-0.02	0.64	0.10	6.3	-2.6	50.0	8.3	

Throckmorton, 1976). During the slow opening of the mouth, the quadrate slowly swings forward ($\pm 8^\circ$) with respect to the neurocranium. At the beginning of the fast opening phase, the angular velocity of the quadrate increases and the antieriad rotation of the quadrate continues for another 10° . At the time of maximal gape, the quadrate movement reverses until the beginning of the slow closing/power stroke phase. During this last phase, the quadrate remains immobile.

Although no direct measure of intracranial movements could be performed on *T. scincoides*, manipulations using wet, cleared skulls did not indicate streptostyly, meso- and metakinesis. This observation is supported by the absence of cranial kinesis in the related scincid lizard *Trachydosaurus rugosus* which has a similar feeding ecology (De Vree & Gans, 1987, 1989).

Simulations

The results of the bite simulations are summarized in Table 3. For a varying orientation of the food reaction forces (from -42° = antieriad to -138° = posteriad; see Fig. 1b), the bite forces, the joint forces, the orientation of these joint forces, the required and remaining moments at the quadrate-squamosal joint and the tension in the jugomandibular ligament are given. For comparison, results for *Sphenodon punctatus* are provided as well (Table 3, SP).

DISCUSSION

In the lizards used for this study, no intracranial kinesis could be observed during the power phase of biting, which means that the skull is in a static equilibrium. Thus, at the jaw joint, the moments of the active jaw closers are countered by the moment of the food reaction force. At the quadrate-squamosal joint, the net result of all forces exerting a moment must equal zero too. Directly obvious in this are: (1) the forces exerted by the jaw on the quadrate: these are the joint forces caused by the activity of the jaw closers (groups A & B; see Table 2) and the food reaction force; and (2) the force of all muscles inserting on the quadrate. Alternatively, one could also consider the moments about the quadrate-squamosal joint induced by: (1) the food reaction forces; by (2) the contraction of the biarticular jaw closers (group A, see Table 2); and by (3) the muscles between quadrate and neurocranium (group C). If the net moment obtained by either of the two entirely equivalent options differs from zero, additional stabilizing mechanisms are required to maintain the observed static equilibrium at the level of the quadrate-squamosal joint. We applied the second option, because then joint forces need not be known in advance.

To assess the feasibility of the jugomandibular ligament as a stabilizer, the effect of muscle action on the quadrate must be rated first. The required moments about the quadrate-squamosal joint, as presented in

Table 3 (see also Fig. 1b), are the moments needed to fix the quadrate if only the food reaction forces are considered (i.e. as if no muscles bridge the quadratosquamosal joint). The remaining required moment is what remains from this when muscle forces are entered. Required moments are in all cases positive, indicating that the food reaction forces (irrespective of their orientation) tend to rotate the quadrate backwards. Since the remaining required moments are consistently smaller than the required ones, muscles always oppose this tendency, but to a variable degree, depending upon species and orientation of the food reaction force.

As mentioned earlier, remaining required moments must be delivered by structures other than muscles in order to stabilize the quadrate. For the lizards studied, in all cases except for the extremely forward pointing food reaction forces in *Uromastix* (see Table 3; -42°), these moments still have a positive sign. This means that a jugomandibular ligament is definitely useful as quadrate stabilizer in virtually all biting conditions, since the needed counterclockwise moment can perfectly be delivered by ligament tension. Only if the exceptional forward orientation of the food reaction forces truly occurs in *Uromastix* is a ligament ineffective. In that case, the quadrate should rotate forward during forceful biting, shifting the jaw anteriorly until the consequent decrease in orientation of the food reaction force balances the moments about the quadratosquamosal joint. However, such biting orientations undoubtedly are very rare.

The loss of the lower temporal arcades obviously removes constraints upon the architecture and size of the jaw musculature and may have been an important factor in the emergence of the squamate reptiles (Rieppel & Gronowski, 1981). However, the charge of this loss is a potential instability of the skull, especially during forceful biting. The above conclusions strongly suggest that jugomandibular ligaments (and possibly quadratojugal ligaments too) are correlates of the constructional release of the jaw adductors. A ligament provides the necessary strength to act as a quadrate stabilizer, yet allowing for a substantial expansion of the jaw musculature owing to its compliant nature. On average, tensile strength of ligaments and tendons equals about 100 MPa (Currey, 1984; Herzog & Loitz, 1994). This rounded figure allows a simple translation of the ligament tension given in Table 3 into the minimally required ligamentous cross-section (i.e. divide the given values by 100; cross-section in mm^2). Reliable measurements of cross-sectional area are difficult to obtain because only preserved material was available.

However, based on rough measurements taken on the dissected specimens, jugomandibular ligaments seem to be about five times thicker than strictly required; which nicely accords with the range of biological safety factors found for tendon and ligament (Bennett, 1992). This conclusion is an additional argument in favour of the premised stabilizing function of the jugomandibular ligaments. However, the loss of the lower temporal

arcade limits in turn the possible muscular arrangement in the lizard head: the remaining required moment at the quadratosquamosal joint must be counterclockwise to make the jugomandibular ligament useful as quadrate stabilizer. This prerequisite is determined in a very complex way by the orientation, relative size and activation level of all the muscle bundles involved in the power phase of biting. For instance, Cleuren *et al.* (1995) showed that an hypothetical lizard with a crocodile-like muscle system should show, for all biting conditions, a forward rotation of the quadrate as it is described for the extreme bite force orientation in *Uromastix*. In most lizards, the volume in front of the quadrate is packed with muscles and a frontal shift of the quadrate would readily interact with proper muscle function. The need for counterclockwise remaining required moments seems to be met in *Sphenodon* too (with its lower temporal arcade; see Table 3: remaining required moments). This suggests that constructional alterations in the musculo-skeletal system of the skull of primitive Lepidosauromorpha led already to the achievement of the requirement for counterclockwise remaining required moments. This may be regarded as an exaptation which paved the way for the sequence of changes that occurred in the primitive lizard skull: replacement of the lower temporal arcade by a ligament, a shift of the ligament to the lower jaw, and expansion of the jaw musculature.

If the ligament is indeed a replacement of the lower temporal arcade, one might expect it to attach to the base of the quadrate rather than to the mandible (i.e. a quadratojugal ligament). Indeed, Iordansky (1996) mentioned that the quadratojugal ligament is sometimes homologized with the reduced quadratojugal bone (Lakjer, 1926). Definitely, from the point of view of stabilization of the quadrate, both constructions are in fact equivalent. Nevertheless, the four examined species and most other lizards in which skull modifications remain restricted to the loss of the lower temporal arcade, show the temporal ligament inserting on the lower jaw (see Iordansky, 1996; Herrel, pers. obs.). This consistency points at a functional clue. Ligament tension will affect the force equilibrium of the lower jaw when the ligament inserts on the mandibula. This of course influences magnitude and orientation of the joint forces. The results presented in Table 3 took account of this. As the jugomandibular ligaments insert nearly in the joint, the effect of ligament tension on the moment about the joint is negligible and is not considered in the simulations. Table 4, however, summarizes joint forces and their orientation for the four lizard species, for a theoretical situation in which the jugomandibular ligament is replaced by a ligament attached to the base of the quadrate (i.e. a quadratojugal ligament). These results must be compared to the equivalent sections of Table 3. Generally, joint forces are lower (up to 20%) when the ligament inserts on the quadrate, which seems to be an argument in favour of the 'quadrate connection'. But, looking at ligament orientation, two important conclusions can be drawn: (1) the range of

Table 4. Model output at gape 10° and all jaw closers 100% active; for a given range of food reaction force orientations (Orientation FRF), the corresponding theoretical joint forces (no jugomandibular ligament) and their orientation are given for the examined species

Orientation FRF (°)	Theoretical Joint Force (N)				Orientation of the theoretical Joint Forces (°)			
	PS	UA	TS	CZ	PS	UA	TS	CZ
-138	23.4	27.5	117.3	111.8	118.9	122.7	159.1	149.6
-126	21.9	25.2	106.8	99.3	114.3	116.9	158.0	147.3
-114	20.9	23.8	99.1	90.0	110.5	112.1	157.0	145.1
-102	20.1	22.7	92.8	82.3	106.9	107.6	156.1	142.9
-90	19.5	21.9	87.1	75.2	103.4	103.1	155.1	140.4
-78	18.9	21.2	81.4	68.1	99.6	98.3	154.0	137.3
-66	18.4	20.6	75.2	60.5	95.0	92.7	152.6	133.1
-54	17.9	20.2	67.8	51.7	89.1	85.5	150.6	126.1
-42	17.6	20.1	58.0	41.2	80.4	75.4	147.1	111.6

possible orientations related to the different biting conditions increases substantially (up to 10-fold); and (2) joint forces diverge considerably from the long-axis of the quadrate. By confining joint force orientations to a narrow range, optimization of the joint morphology to resist all possible loading conditions during biting can more easily be reached. This reduces the risk of injuries or dislocations considerably. The impact of joint force alignment with the quadrate must be seen in the light of the orientation of the surfaces of the quadratosquamosal joint. Joint forces are “bone to bone” forces (cf. Winter, 1990), which can be resolved in normal (compression) and tangential (shear) components. The latter require additional stabilization (unless the joint is built for sliding). Therefore, it might be advantageous to reduce the shear components. It is remarkable that in the four examined species, the joint surface of the quadrate is perpendicular to its long axis.

Based on these conclusions, it can be argued that the ligament shift from the quadrate to the lower jaw in lizards with a basic skull must have occurred before, or at least simultaneously with, the expansion of the musculature (cf. Rieppel & Gronowski, 1981). It is, indeed, conceivable that otherwise the increased biting and muscle forces would have readily resulted in excess loadings of the joint structures, making the construction less viable. If the quadratojugal ligament represents the plesiomorph condition, this shift must have emerged several times during lizard evolution. As mentioned, the effect of the precise location of the insertion site of the temporal ligaments (i.e. a quadratojugal or jugomandibular ligament) on the quadrate (bending moments, moments about the quadrato-squamosal joint) is negligible, on condition that in both situations the ligament inserts close to the quadrato-mandibular joint. Therefore, it is intriguing that the survey presented by Iordansky (1996) and our results hint at a link between ligament insertion site and degree of skull modification. Jugomandibular ligaments appear to be confined to robust skulls in which only the lower temporal arcade is reduced (plesiomorph construction), whereas quadratojugal ligaments seem to be allied to skulls with further skeletal modifications (loss of the upper temporal and/

or postorbital arches, mobile construction). According to Iordansky (1996), temporal ligaments transfer quadrato-mandibular retraction to the upper jaw, causing the depression of the muzzle. This function must be rejected for at least the species examined in this study, and in all likelihood for all lizards with a basic skull construction, as neither kinematic analysis of feeding nor manipulation revealed any mesokinesis. In lizards with amphikinetic skulls, this function of the temporal ligaments might be present, although several other mechanical couplings between the quadratomandibular system and the muzzle exist (see also Iordansky, 1996). However, this does not explain why amphikinetic skulls seem to ‘prefer’ quadratojugal ligaments, as jugomandibular connections could perform equally well in this respect. Iordansky (1996) also suggested that jugomandibular ligaments couple jaw depression to quadratomandibular protraction, in a way comparable to the action of the postorbital ligament in birds (Bock, 1964; Weishampel, 1993). However, since jugomandibular ligaments always insert just near the joint, this effect is very small and remains restricted to a quadrate protraction of maximally a few degrees. In *Uromastix*, the only species studied here which showed quadrate movements during jaw opening, protraction mounts up to 20°.

Based on all these arguments, we postulate that temporal ligaments primarily function to stabilize the quadrate when the jaw system is loaded during feeding. The jugomandibular morph is likely to be the derived one. It emerged in forms built for strenuous biting which are further characterized by robust, largely akinetic skulls. The shift of the ligament’s insertion to the lower jaw can then help to protect the joint against the consequently higher joint forces in the way described above. However, further analyses of joint forces in lizards with amphikinetic skulls are needed to support this hypothesis.

Gingerich (1971) suggested that, in lizards, during static biting the lower jaw could act as a link instead of a lever, which implies that no joint forces emerge and that bite forces and (resultant) muscle forces are aligned. This author argues that the mobility of the

quadrate serves to fulfil the latter condition. However, he only considers the adductor mandibulae and represents it by only a single force vector. Our simulations show that, for more realistic force input, none of the orientations of the food reaction forces coincides with zero joint forces and that quadrate rotation as a result of muscle action is prevented by the ligament tension. Therefore, it is very doubtful whether the lower jaw in lizards can indeed act as a link instead of a lever.

It must be obvious that the plausibility of all conclusions depend upon the reliability of the biting model. In the simulations, co-contraction of all jaw closers during the power phase of biting is assumed. This premise is supported by recordings of muscle activity in biting reptiles. During the power phase, where a firm contact between the food particle and the jaws is established, a high level co-contraction between the jaw closing muscles of both body sides is always observed (Gans De Vree & Carrier, 1985; Herrel, Cleuren & De Vree, 1997; J. Cleuren, pers. comm.). It is further assumed that all fibres in a muscle participate in the force generation (i.e. input forces scaled to the physiological cross-section). Cleuren *et al.* (1995) performed a quantitative analysis on their electromyograms in order to scale muscle input to the activation level too. These authors were able to show that the orientation and the relative magnitude of the joint forces do not differ between simulations of actual bites (scaled on EMG-intensity) and a bite where all muscles were maximally active. These two facts support the biological relevance of the simulations.

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