

Morphology of the Feeding System in Agamid Lizards: Ecological Correlates

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ABSTRACT

The interaction of organismal design with ecology, and its evolutionary development are the subject of many functional and ecomorphological studies. Many studies have shown that the morphology and mechanics of the masticatory apparatus in mammals are adapted to diet. To investigate the relations between diet and the morphological and physiological properties of the lizard jaw system, a detailed analysis of the structure of the jaw apparatus was undertaken in the insectivorous lizard *Ploceoderma stellio* and in closely related herbivorous lizards of the genus *Uromastix*. The morphological and physiological properties of the jaw system in *P. stellio* and *U. aegyptius* were studied by means of dissections, light microscopy, histochemical characterisations, and in vivo stimulation experiments. The skull of *Uromastix* seems to be built for forceful biting (high, short snout). Additionally, the pterygoid muscle is modified in *P. stellio*, resulting in an additional force component during static biting. Stimulation experiments indicate that jaw muscles in both species are fast, which is supported by histochemical stainings. However, the oxidative capacity of the jaw muscles is larger in *Uromastix*. Contraction characteristics and performance of the feeding system (force output) are clearly thermally dependent. We conclude that several characteristics of the jaw system (presence of extra portion of the pterygoid muscle, large oxidative capacity of jaw muscles) in *Uromastix* may be attributed to its herbivorous diet. Jaw muscles, however, are still faster than expected. This is presumably the result of trade-offs between the thermal characteristics of the jaw adductors and the herbivorous lifestyle of these animals. Anat Rec 254:496–507, 1999. © 1999 Wiley-Liss, Inc.

Key words: lizards; herbivory; jaw apparatus; morphology; stimulations; histochemical characteristics; trade offs

Understanding the basic structure and function of organisms has always fascinated biologists. More recently, a shift of interest from purely structural or functional analyses to a more complete, broader understanding of animal form and function in an evolutionary and ecological context has taken place (Wainwright and Reilly, 1994). Such studies focus on questions concerning the current design of organisms, the interaction of design with ecology, and the evolution of the design to its present form. The locomotor apparatus has been the showcase in many such ecomorphological studies, because effects of design on performance can easily be measured (Garland, 1985; Van Berkum and Tsuji, 1987; Losos, 1990; Garland and Losos, 1994). However, the feeding apparatus may provide an equally fascinating and fruitful area for ecomorphological study (Kiltie, 1982; Wainwright, 1987, 1988; Osenberg and Mittelbach, 1989), given that performance can be measured (Arnold, 1983).

In mammals, many studies have shown that the morphology and mechanics of the masticatory apparatus are adapted to diet (De Vree and Gans, 1976; De Gueldre and De Vree, 1988, 1990; Offermans and De Vree, 1993; see Hiiemae, 1978; Weijs, 1994 for overviews). Similarly, for a number of lizards it has been demonstrated that a clear relation between the feeding ecology and bite force characteristics exists (Herrel et al., 1998b). Modeling of the jaw system shows that animals with a different feeding ecology

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differ in the performance of their feeding system, i.e., herbivorous species apparently bite harder than insectivorous ones. However, because the physiological properties of the jaw muscles are not taken into account in these models, questions concerning the physiological basis of this difference in bite performance remain.

Complex and integrated structures such as the feeding apparatus cannot be optimized for a single function without compromising other functions performed by the same apparatus (Arnold, 1989; Lauder, 1989). Functional trade-offs are thus expected for structures that seem to be optimized, or at least perform well within a very limited scope (Losos et al., 1993). However, such trade-offs predicted on the basis of biomechanical principles are not always easily detectable, and may even be absent (Van Damme et al., 1997). When considering the feeding apparatus of lizards, it can be expected that the ability to bite hard (as required for feeding on hard or tough food objects) has its drawback on other design criteria (e.g., speed). Animals such as shingleback lizards are capable of crushing snail shells by activating their massive and complexly pinnate jaw-closer muscles in an unfused tetanus, with the pulses of several motor units occurring in synchrony (Gans and De Vree, 1986). However, although these lizards possess a very powerful bite, they are also slow and hardly capable of catching agile food items. On the other hand, lizards that need fast jaw closing to capture fast prey will need fast jaw muscles. Because the maximal contraction speed of white (fast-twitch glycolytic: FG) muscles is significantly higher than that of red (slow oxidative: SO) muscles, animals needing fast jaw closing are expected to show, predominantly, such muscles. However, one major drawback of such fast muscles is that they use more metabolic energy, causing them to fatigue sooner (see Aerts and De Vree, 1993 for a good example).

To investigate the possibility of such trade-offs, and to examine the morphological basis of the difference in bite performance in animals with a different feeding ecology, a detailed analysis of the structure of the jaw apparatus (osteology, myology) was undertaken, and the histochemical properties and contraction characteristics of the most important jaw closers were determined in the insectivorous lizard *Ploceoderma stellio* (Böhme, 1981) and closely related herbivorous lizards of the genus *Uromastix* (Dickson, 1965; Dubuis et al., 1971; Kevork and Al-Uthman, 1972; Grenot, 1976; Al-Ogily and Hussain, 1983; Bouskila, 1986; Bouskila, 1987). Because herbivorous lizards do not need fast jaw muscles but do need to chew their food repeatedly during longer periods, it can be expected that differences in fiber composition, and thus in contraction characteristics, exist between species.

MATERIALS AND METHODS

Morphology

Four adult specimens of *P. stellio* [snout-vent length (SVL): 85 ± 5 mm, mass: 41.5 ± 3.5 g], two adult specimens of *U. acanthinurus* (SVL: 180 ± 20 mm, mass: 160 ± 50 g), and one adult *U. aegyptius* were dissected and stained to characterize all jaw muscles (Bock and Shear, 1972). Drawings were made of all stages of the dissection using a Wild M5 dissecting microscope, provided with a camera lucida. For light microscopy, the heads of one specimen of each species were prepared for paraffin histology using standard techniques (Humason, 1979) and seri-

ally sectioned at 8–10 μ m. Sections were stained with Masson's trichrome.

Histochemistry

Muscle samples were obtained from one freshly killed adult specimen of *P. stellio* and one juvenile *U. aegyptius*. Small bundles were excised bilaterally from the jaw opener (both species), the external adductor (*P. stellio*, posterior superficial, medial, and deep parts; *U. aegyptius*, anterior and posterior superficial, medial, and deep parts), the posterior adductor (both species), the pseudotemporal (*P. stellio*, superficial and deep parts; *U. aegyptius*: superficial part), and the pterygoid muscle (*P. stellio*, medial and lateral parts; *U. aegyptius*, medial and external parts). The bundles were rapidly frozen in isopentane, precooled with liquid nitrogen, and subsequently stored at -70°C until required.

From each muscle, series of transverse sections were cut in a cryostat (-22°C), mounted on dry slides, and air dried. Subsequent sections of each series were stained for one of the following enzymes: alkaline-stable myofibrillar adenosine triphosphatase (mATPase) by preincubation for 15 min at pH 9.4 and incubation for 35 min (37°C), acid stable mATPase by preincubation for 5 min at pH 4.6, 4.3, or 4.2 and incubation for 35 min, reduced nicotinamide adenine dinucleotide tetrazolium reductase (NADH-TR) with an incubation time of 60 min at 37°C , and menadione-linked α -glycerophosphate dehydrogenase (α -GPD) with an incubation time of 60 min at 37°C .

Muscle fibers were classified as belonging to one of three types (Tables 1 and 2) based on histochemical staining intensities. Whereas type I shows characteristics of slow fibers (most likely tonic), type II can be classified as fast-twitch oxidative glycolytic (FOG) and type III as FG (Peter et al., 1972; Throckmorton and Saubert, 1982; Morgan and Proske, 1984).

Contraction Characteristics

In vivo stimulation of the external adductor [m. adductor mandibulae externus (MAME), medial part in *Uromastix*, and medial and deep parts in *Ploceoderma*], the posterior adductor [m. adductor mandibulae posterior (MAMP), in both species], the pseudotemporal muscle (MPsT [m. pseudotemporalis], superficial part in both species), and the pterygoid muscle (MPt [m. pterygoideus], medial and externus parts in *U. aegyptius*; the externus part in *U. acanthinurus*, and the medial part in *Ploceoderma*) was performed on three similarly sized adult *P. stellio* (mass: 39.3 ± 5 g), two adult *U. acanthinurus* (mass: 223.5 ± 110 g), and one juvenile *U. aegyptius* (131.63 g). The animals were anesthetized by an intramuscular injection of Ketalar (ketamine hydrochloride, Parke-Davis, Dublin) (*P. stellio*: 200 mg/kg; *U. aegyptius*: 100 mg/kg). Deep anesthesia was maintained by further administration of Ketalar during the experiment, when required. Bipolar stainless steel electrodes were inserted percutaneously into the muscles of both sides. Electrode placement was confirmed by dissection. The free ends of the electrodes were connected to a stimulator (Grass S48). Subsequently, the animals were fixed with the occlusal plane of the upper teeth horizontally. The teeth enclosed a custom-made bite force registration apparatus based on a Kistler force transducer (type 9203; range -500 to 500 N) connected to a Kistler (type 5058A) charge amplifier.

TABLE 1. Histochemical characteristics of muscle fibers identified in the jaw muscles of *Plocederma stellio* and *Uromastix aegyptius*

Type	mATPase pH 9.4	mATPase pH 4.6	mATPase pH 4.3	mATPase pH 4.2	NADH-TR	α-GPD
I	–	0, –	0	0, –	++	+
II	+	+, ++	–, ++	–, ++	++	+
III	+, ++	0, +	0, +	0, +	–, +	+, ++

0 = no or extremely weak activity, – = weak activity, + = moderate activity, ++ = strong activity. mATPase, myofibrillar adenosine triphosphatase; NADH-TR, reduced nicotinamide dinucleotide tetrazolium reductase; α-GPD, menadione linked α-glycerophosphate dehydrogenase.

TABLE 2. Histochemical properties of the jaw muscles in *Plocederma stellio* (PS) and *Uromastix aegyptius* (UA). For an explanation of fiber types (+ = present; – = absent), see Table 1 and text; see Fig. 2 for definitions of muscle abbreviations

Muscle	Type 1	Type 2	Type 3
MDM			
PS	–	–	+
UA	+	+	–
MAMESA			
UA	+	+	–
MAMESP			
PS	+	+	–
UA	–	+	–
MAMEM			
PS	–	+	+
UA	–	+	–
MAMEP			
PS	–	+	+
UA	+	+	–
MPsTS			
PS	–	+	–
UA	–	+	–
MPsTP			
PS	–	+	+
MAMP			
PS	–	–	+
UA	+	+	–
MPtlat			
PS	+	+	–
MPtmed			
PS	+	+	–
UA	+	+	–
MPtext			
UA	+	+	–

In a preliminary experiment, the stimulation voltage was varied from 1 V to 15 V to determine the required stimulation voltage (lowest voltage still producing maximal force output). Next, supramaximal (10 V) single square-wave stimuli (pulse length: 2 msec) or stimulus trains (train duration: 500 or 250 msec) were applied to each muscle bilaterally. The stimulation circuit was charge-balanced by a coupling capacitor and bleed resistor (Loeb and Gans, 1986) to avoid muscle damage and undue fatigue. The mechanical response (twitch or tetanus) was recorded by means of the isometric force transducer. The signal was displayed on a Tektronix (R5103N) storage oscilloscope and a Gould (Brush 481) multichannel chart recorder. The output of the stimulator and the force transducer were recorded simultaneously on a Honeywell 96 FM 14-channel tape recorder at a speed of 0.095 m/sec. In general, relative isometric tension will be reported as

absolute values might be modified by changes in electrode position, and caution should be taken in comparisons between specimens and/or species (Gans and De Vree, 1986).

To determine the tetanic fusion frequency, the stimulation frequency was varied from 10 to 90 Hz (steps of 10 Hz; 5 near fusion) until the effect of the individual stimulation pulses was no longer visible on the force output curves.

RESULTS

Morphology

The structure of some elements of the cranium and the mandibula will be discussed briefly in accordance with Jollie (1960) and Avery and Tanner (1971). The musculature of the jaws is discussed using the nomenclature of Lakjer (1926), Oelrich (1956), and Haas (1973).

Osteology

The skull of agamid lizards is relatively wide in comparison to that of other lizards. Characteristic of the agamid skull is the fusion of almost all dorsomedial bones. Thus, premaxillae, frontalia, and parietalia are fused at the median without clear sutures between the two sides. The bauplan of the skull is rather similar in both species and has been described previously (El Toubi, 1945, 1947). Here, only the quadrate and its articulation will be described.

The proximal part of the quadrate, which is rather solid in both species, contacts the squamosum, the parietal, and the paraoccipital process. The caudal edge of the squamosum lies in a small depression in the dorsal surface of the quadrate. Ventrally, the quadrate articulates with the lower jaw (Fig. 1A–C). The pterygoid is medially attached to the distal, smaller head of the quadrate by means of connective tissue. Clear interspecific differences in this attachment, related to differences in quadrate mobility during jaw opening, are observed. Although the connection is rather tight in *P. stellio*, considerable movement at the pterygoid–quadrate junction is possible in *Uromastix*.

In the lower jaw, the articular bone (an ossification of Meckel's cartilage) forms the articulation of the mandibula with the skull (Fig. 1A and 1D). Posteriorly, the articular forms a retroarticular process (Fig. 1A). The species differ markedly in the importance of the retroarticular process; it is short in *Uromastix*, whereas it is long and slender in *Plocederma*.

Myology (Figs. 2, 3)

Jaw adductors are described as consisting of three major groups (Figs. 2, 3). The first group is that of the MAME, which is further subdivided into four major subgroups

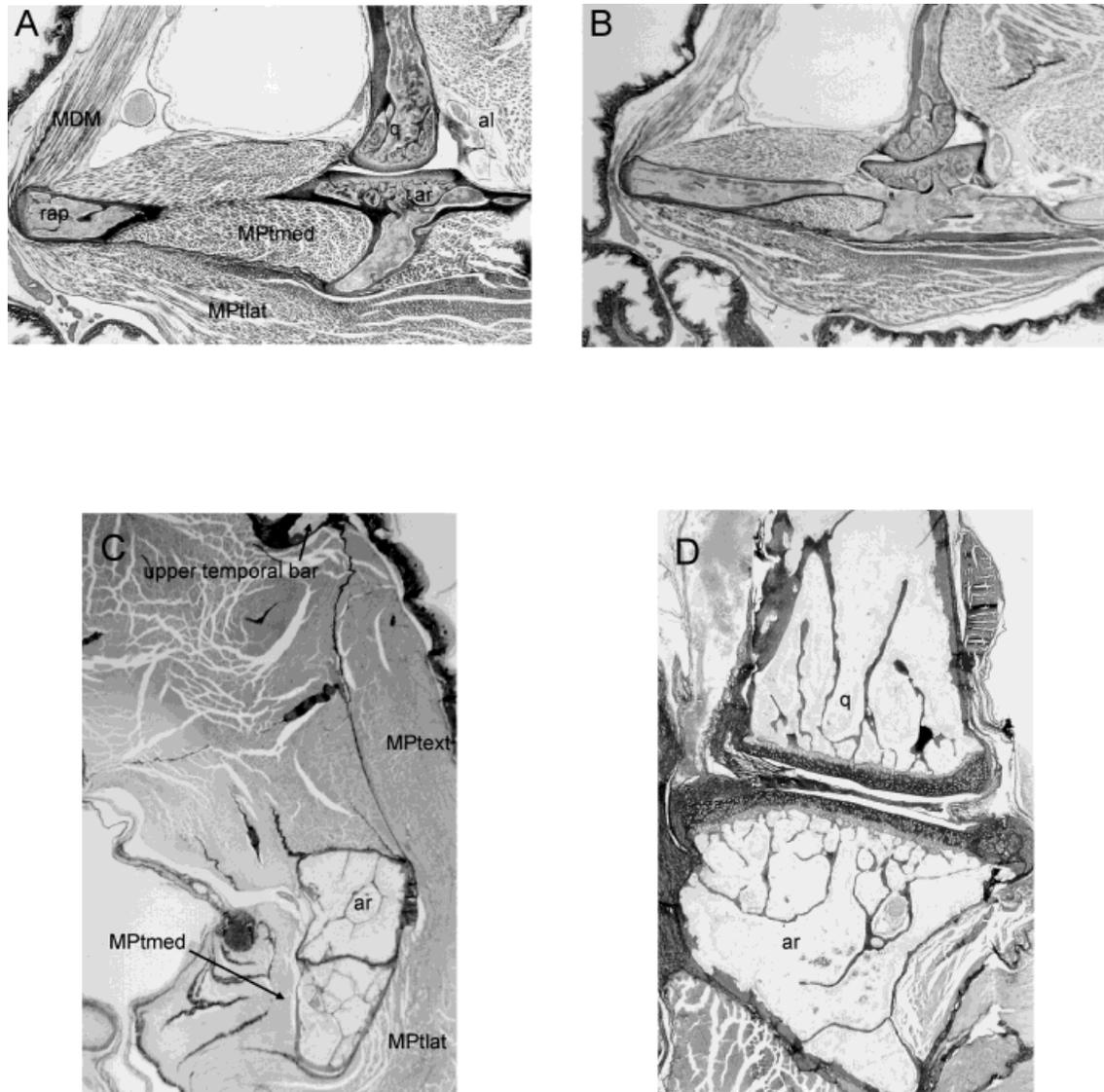


Fig. 1. Light microscopic views of sections through the jaw articulation in *Ploceoderma stellio* and *Uromastix acanthinurus*. **A:** Medial sagittal section ($\times 20$) through the jaw articulation in *P. stellio*. **B:** Somewhat more laterally situated sagittal section ($\times 16$) in *P. stellio*. Note the difference in the articulating surfaces, indicating a typical saddle-shaped joint. Note also the anterior ligament stabilizing the quadrate with respect to the lower jaw. **C:** Transverse section ($\times 16$) through the anterior jaw articulation in *U. acanthinurus*. Note the MPtext originating at the connective tissue sheet

attached to the upper temporal bar and curving ventrally around the lower jaw. The superficial and medial parts of the pterygoid muscle can also be observed. **D:** Somewhat more posterior transverse section at higher magnification ($\times 32$) through the lower jaw articulation in *U. acanthinurus*. al, anterior ligament; ar, articular; MDM, m. depressor mandibulae; MPtext, m. pterygoideus externus; MPtlat, m. pterygoideus lateralis; MPtmed, m. pterygoideus medialis; q, quadrate; rap, retroarticular process.

according to the position of the muscles relative to one another and to the basal aponeurosis.

The complex external adductor musculature is composed of a superficial part that can be subdivided into an anterior and a posterior portion [mm. adductor mandibulae externus superficialis anterior and posterior (MAMESA, MAMESP)], and a levator (*Ploceoderma* and *Uromastix*) and retractor (*Uromastix*) anguli oris muscle. The anterior superficial part originates at the inner aspect of the temporal arch and inserts on the dorsolateral side of the lower jaw. The posterior superficial part, on the other

hand, originates on the dorsal aspect of the quadrate by means of an aponeurosis and inserts on the posterolateral side of the dentary, anterior to the insertion of the anterior part. Both levator and retractor anguli oris muscles originate at the ventrolateral aspect of the temporal arch and insert on the rictal plate (= mundplatte; Oelrich, 1956).

The medial and deep (mm. adductor mandibulae externus medialis and profundus, respectively) parts of the external adductor both insert on the basal aponeurosis that extends upwards from the coronoid process, and

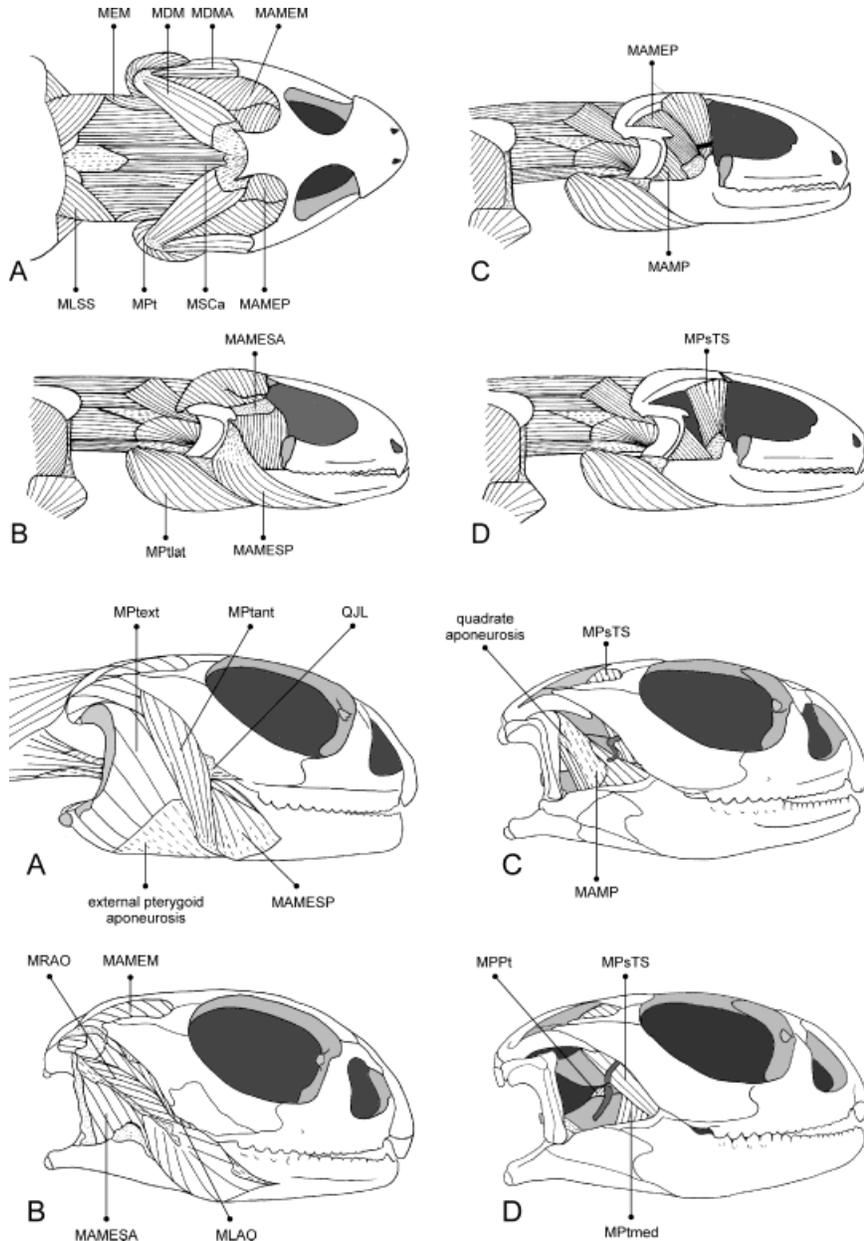


Fig. 2. *Ploceoderma stellio*: jaw musculature. **A**: Dorsal view after removal of the skin. **B**: Lateral view after removal of the skin, the QJL, parts of the jugal, squamosal, and postorbital bones, the MDM, the MDMA, the MLAO, and some superficial cervical muscles. **C**: Deeper view after removal of the MAMESA, the MAMESP, and the MAMEM. **D**: Still deeper view after removal of the MAMEP. MAMEM, m. adductor mandibulae externus medialis; MAMEP, m. adductor mandibulae externus profundus; MAMESA, MAMESP, mm. adductor mandibulae externus superficialis anterior and posterior; MAMP, m. adductor mandibulae posterior; MDM, m. depressor mandibulae; MDMA, m. depressor mandibulae accessorius; MEM, m. episternocleidomastoideus; MLAO, m. levator anguli oris; MLSS, m. levator scapula superficialis; MPt, m. protractor pterygoideus; MPstS, m. pseudotemporalis superficialis; MPtlat, m. pterygoideus lateralis; MSCa, m. spinalis capitis; QJL, quadratojugal ligament.

Fig. 3. *Uromastix acanthinurus*: jaw musculature. **A**: Lateral view after removal of the skin. **B**: Deeper view after removal of the MPttext, the MPtlat, and the QJL. **C**: Lateral view after additional removal of the MLAO, the MRAO, the MAMESA, the MAMESP, the MAMEM, and the MAMEP. **D**: Deeper view after removal of the MAMP. MPtlat, m. pterygoideus anterior; MPttext, m. pterygoideus externus; MPtmed, m. pterygoideus medialis; MRAO, m. retractor anguli oris. For an explanation of other abbreviations, see legend to Fig. 1.

originate on the medial side of the squamosal, jugal, and postorbital bones on the one hand (MAMEM), and on the parietal and the prootic bones on the other hand (MAMEP).

The internal adductor consists of two major parts: the musculus pseudotemporalis and the musculus pterygoideus. The pseudotemporal muscle (MPsT), which is situated anteriorly in the temporal fossa, can be subdivided into a superficial and a deep part. The superficial part originates on the anterolateral side of the parietal bone. The deep part originates on the epipterygoid bone and the dorsal aspect of the membranous wall of the brain case. Both parts insert at the medial side of the lower jaw, just posterior to the coronoid. The pterygoid muscle (MPt) can be divided into a medial and a superficial, lateral part in both lizards; in *Uromastix*, an extra portion is also present

(Lakjer, 1926). The deep part (MPtmed, Fig. 1A and 1C) of the pterygoid muscle runs from the ventral side of the pterygoid to the medioventral side of the articular. The superficial part (MPtlat, Fig. 1A) originates on the lateral aspect of the articular bone and runs anteroventrally, curves around the lower jaw, and inserts by means of a well-developed aponeurosis at the ectopterygoid–pterygoid junction. The extra portion in *Uromastix* (Fig. 1C) originates on the lateral side of the squamosal, the anterior side of the quadrate, and on the superficial aponeurosis overlying the external adductor and attaching to the upper temporal bar, and inserts on the superficial pterygoid aponeurosis that curves around the lower jaw and attaches to the ventral side of the pterygoid bone.

The posterior adductor (MAMP) originates on the quadrate and runs directly to its insertion on the medial side of

the lower jaw, posterior to the coronoid process. Near its origin, it is covered by the clearly distinguishable quadratus aponeurosis.

The musculus levator pterygoidei (MLPt) is a very small and slender muscle that originates partially on the membranous wall of the braincase and partially on the epipterygoid. Its fibers run lateroventrad and insert on the anterodorsal aspect of the pterygoid bone. The musculus protractor pterygoidei (MPPt) is also a small muscle, originating on the processus basiptyergoideus, the ventral part of the prooticum and the membranous wall of the braincase. Its fibers run posteroventrad and insert behind the insertion of the MLPt on the posterodorsal aspect of the pterygoid bone.

The musculus depressor mandibulae (MDM, see also Fig. 1A and 1B), consists of two parts in *P. stellio* but only one in *U. acanthinurus*. The main part originates in both species on the posterior edge of the parietal; in *P. stellio* it covers the accessory part (MDMA) near its insertion on the retroarticular process.

HISTOCHEMISTRY

Three distinct fiber types are identified on the basis of histochemical staining intensities (Table 1). Type I fibers are characterized by a strong reduced nicotinamide dinucleotide tetrazolium reductase (NADH-TR), moderate α -GDP, and weak or no m-ATPase activity. This type most probably corresponds to a tonic (T) fiber (Gleeson et al., 1980). Type II fibers, on the other hand, stain darkly for alkaline, and moderately to strongly for acid-stable m-ATPase. Nevertheless, the NADH-TR reaction for all these fibers is strong and α -GDP staining is moderate. These fibers thus show typical FOG characteristics. The last fiber type (type III, see Fig. 4) stains lightly for NADH-TR and moderately to strongly for α -GDP. The m-ATPase activity is rather variable (varying from little or no to moderate staining), but always moderate to strong for alkaline stable m-ATPase. These fibers thus show characteristics consistent with a FG fiber typing (Peter et al., 1972).

In *P. stellio*, all three fiber types are observed (Table 2). Most muscles are composed of several fiber types. Only the jaw opener, the posterior adductor, and the superficial part of the pseudotemporal muscle are completely homogeneous. Although the former two consist exclusively of type III fibers, and can thus be considered as FG, the superficial part of the m. pseudotemporalis is composed of type II fibers. Other muscles contain maximally two fiber types and may be compartmentalized or mixed. The three fiber types are never observed together, and muscles contain either types I and II or types II and III (Table 2). Compartmentalized muscles usually consist of an inner oxidative (type II) and outer glycolytic (type III) region. Although the medial (Fig. 4) and deep parts of the external adductor are composed of type II and III fibers, the posterior superficial part of this muscle in *Plocoderma* is composed of types I and II. The MPSTP [m. pseudotemporalis profundus], the MPtlat, and the MPtmed are composed of types II and III.

Remarkably, in *U. aegyptius*, type III fibers are not observed. Muscles consist of either type II fibers or a mixture of types I and II (Table 2). The MAMESP, the MAMEM, and the MPST are strictly FOG muscles. The other muscles examined (MDM, MAMESA, MAMEP, MAMP, and MPt) contain a mixture of both slow oxidative

and FOG fibers. Muscles are usually of the mixed type, but may show some compartmentalization (e.g., MPt).

STIMULATIONS

Contraction characteristics were obtained for individual muscles in all species examined (Table 3). Additionally, the effects of stimulation frequency and temperature on physiologically relevant cocontractions of these jaw closers (in an effort to simulate biting) were examined.

In *P. stellio*, individual differences were minor and thus the results are averaged over the three specimens tested (Table 3). The time to peak tension is short in all muscles examined (between 10 and 20 msec; Table 3). Twitch duration, on the other hand, is longest in the MPtmed (about 5 msec), shortest in the MAMEP (about 32 msec), and intermediate in the other muscles examined (Table 3). In all muscles, train frequencies between 60 Hz and 70 Hz produced fusion. Lower frequencies, between 30 Hz and 50 Hz, produced summation and caused an unfused tetanus. Still lower frequencies (between 10 Hz and 30 Hz) showed no staircase effect. Twitch tension expressed as percentage of maximal tetanic tension is highly variable and lies between one-tenth (MAMEM) and about one-third (MPST) of maximal tetanic tension.

Because two species of *Uromastix* were used, and because size differences are considerable between the two *U. acanthinurus* specimen tested, the results for each individual are represented in Table 3. Clear interspecific and size-dependent differences are observed. Jaw muscles in *U. aegyptius* are somewhat slower, but are still fast. The time to peak tension is lowest in the MAMP (24.38 msec), highest in the MAMEM (31.46 msec), and intermediate in other muscles (Table 3). The twitch duration is again somewhat longer in *U. aegyptius* for all muscles examined (Table 3). In the small *U. acanthinurus* specimen, jaw muscles are as fast as in *P. stellio*. Still, in the larger specimen, jaw muscles are considerably slower (Table 3). Remarkably, the twitch duration is considerably longer in both *U. acanthinurus* specimens, when compared with the data for *P. stellio* and *U. aegyptius* (Table 3). Fusion frequencies between 60 Hz and 65 Hz generally produce fusion in most muscles of both *Uromastix* species, but are considerably higher in the MPST and the MAMP in *U. acanthinurus*. Summation begins at frequencies of about 20–30 Hz and causes a three- to fivefold increase in tension near fusion frequencies (e.g., from 1.25 N to 3.95 N in the MAMP in *U. acanthinurus*; see Fig. 5). Twitch tension values in *Uromastix* are somewhat less variable and are about one-fifth of maximal tetanic tension in most muscles (Table 3).

Changes in stimulation frequency had a clear effect on maximal tetanic tension of cocontractions in both species. A stimulation frequency of 15 Hz produced only about half the tension generated when stimulating at 35 Hz or 50 Hz in *P. stellio*. In *Uromastix*, a 3- (*U. acanthinurus*) to 10-fold (*U. aegyptius*) increase in maximal tension occurred when increasing the stimulation frequency from 10 Hz to 60 Hz. Maximal tetanic tension is usually reached after the third or fourth stimulus pulse when stimulating at 30 Hz or higher.

The effect of temperature on twitch characteristics, fusion frequency, and maximal tetanic tension was examined on a physiologically relevant cocontraction of several jaw closers (the MAMEM, MPST, and MPtmed in *P. stellio* and *U. aegyptius*, and the MAMEM, MPST, and MPt in

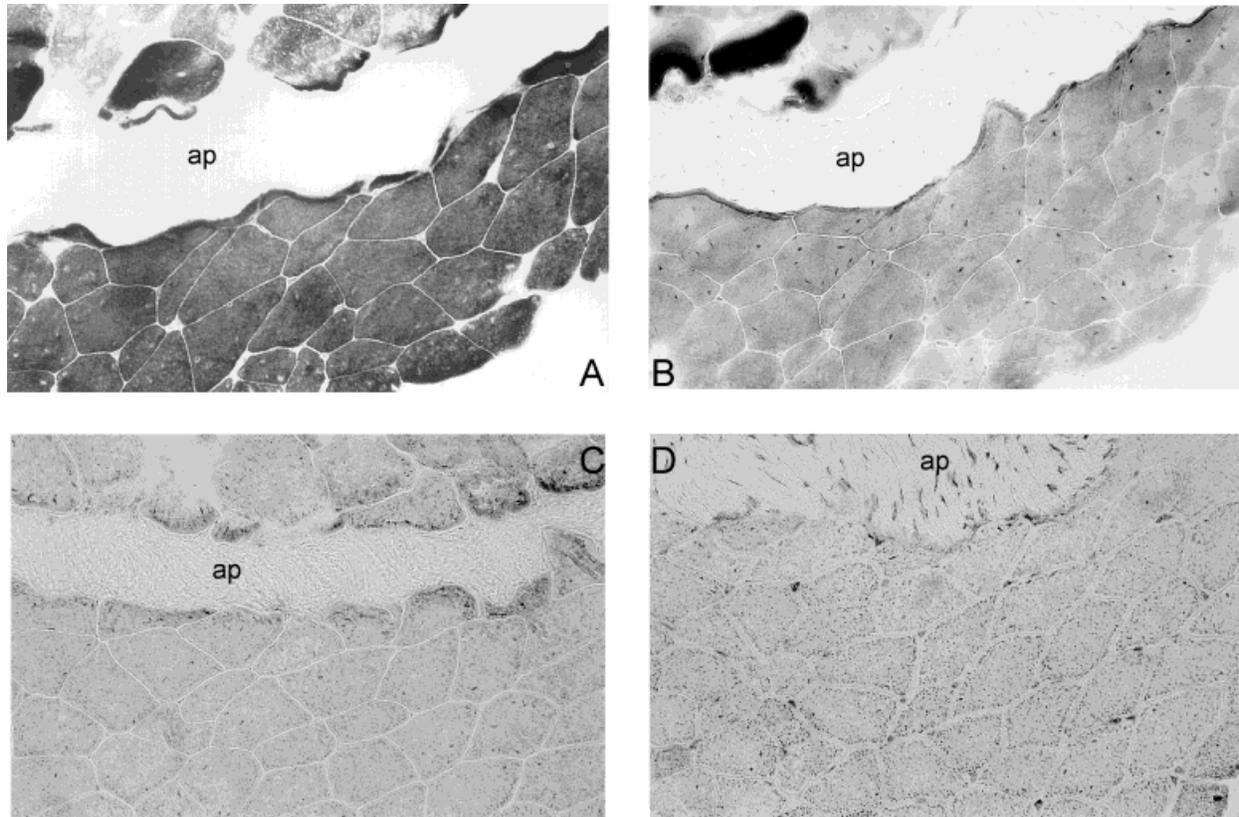


Fig. 4. Histochemical stainings of transverse sections ($\times 200$) through fast glycolytic (FG) fibers in the m. adductor mandibulae externus medialis in *Ploceoderma stellio*. **A:** Alkaline stable mATPase reactivity (pH 9.4). **B:** Acid stable mATPase reactivity (pH 4.2). **C:** Menadione-linked α -glyc-

erophosphate dehydrogenase reactivity. **D:** Reduced nicotinamide adenine dinucleotide tetrazolium reductase reactivity. ap, medial sheet of coronoid aponeurosis.

U. acanthinurus). A decrease of temperature with 10°C (from 40°C to 30°C) decreases the fusion frequency (FF) to about 30 Hz in all species. A further decrease of temperature to 20°C in *Uromastix* decreased the fusion frequency to 10 Hz. Both the time to peak tension and twitch duration (Table 3) increase significantly with a decrease in temperature in all species. Maximal tetanic tension decreases almost 30%, and maximal twitch tension at 30°C is only about 25%, and at 20°C only about 19% of maximal twitch tension at 40°C in *Uromastix*. The decrease of temperature had little effect on the intrinsic muscle properties, because after rewarming, twitch and fusion characteristics were similar to the original values (at 37°C , time to peak tension: 27.50 ms; twitch duration: 62.56 ms; twitch tension expressed as percentage of maximal tetanic tension: 80% of the original tension at 41°C ; FF: 60 Hz).

DISCUSSION

Morphology

Based on observations in herbivorous dinosaurs and tortoises (King, 1996) some predictions can be made regarding the skull structure in herbivorous lizards. As for overall skull shape, a high, short, and solid akinetic skull is expected. The reason for this is simple: a high skull allows the jaw muscles to insert more perpendicularly at the lower jaw, which increases the moment they deliver at

the quadrato-articular joint. Bluntness of the head leads to a shorter snout length, which again increases the mechanical advantage because the effect of the force of the jaw closers is larger at the front of the jaw because of the reduction of the lever arm of the bite forces. Finally, a solid akinetic skull is expected, because powerful jaw muscles are present. These impose high loads and stresses on the skull, especially at the intracranial joints. Such stresses can become fairly high (Herrel et al., 1998a, b) and might deform or even damage the skull.

In both of the species examined in this study, the gross morphology is rather similar (El Toubi, 1945, 1947). Both *Uromastix* and *Ploceoderma* possess the rather broad skull, and acrodont dentition typical for agamine and uromastixine lizards. However, the skull of *Uromastix* is markedly higher and the animals possess a shorter snout. The skull of *Uromastix* thus seems to fit the predicted type. However, although the skull of *Ploceoderma* is akinetic, *Uromastix* shows a loose, ligamentous pterygoid-quadrato connection and potential quadrato mobility. However, no quadrato movements are observed during the power stroke (Herrel et al., 1998a); therefore, the skull in *Uromastix* can be considered functionally akinetic during forceful biting. Additionally, the skulls of both species are very solid because of fusion of most dorsal elements.

TABLE 3. Jaw muscle twitch and tetanus characteristics

		<i>Ploceoderma stellio</i>		
MAMEM	20.00 ± 1.09	49.50 ± 7.45	±65	10
MAMEP	12.63 ± 2.53	32.13 ± 5.63	±65	17
MPsT	12.83 ± 1.00	36.25 ± 9.15	±65	35
MAMP	10.80 ± 1.06	33.58 ± 6.32	±70	25
MPtmed	15.50 ± 2.97	56.67 ± 8.00	±70	30
Cocontraction				
40°C	20.83 ± 1.89	52.83 ± 11.24	±65	18
30°C	46.5 ± 6.35	85.33 ± 6.45	±30	9
		<i>Uromastix aegyptius</i>		
MAMEM	31.46 ± 0.36	53.75 ± 43.02	±60	23
MPsT	27.50 ± 1.25	75.83 ± 3.21	±65	24
MAMP	24.38 ± 1.08	35.42 ± 1.57	±65	15
MPtmed	30.21 ± 0.18	65.32 ± 6.90	±60	26
MPttext	24.75 ± 0.36	46.67 ± 4.52	±65	22
Cocontraction				
40°C	26.30 ± 0.00	47.81 ± 1.33	±60	10
30°C	35.42 ± 0.95	80.63 ± 2.86	±30	14
20°C	185.63 ± 16.79	610.63 ± 152.91	±10	22
		<i>Uromastix acanthinurus</i> (small)		
MAMEM	20.00 ± 0.00	126.00 ± 4.36	±60	26
MPsT	8.00 ± 2.00	86.67 ± 2.31	±80	33
MAMP	11.67 ± 1.15	88.67 ± 4.16	±90	24
MPttext	18.00 ± 4.58	111.33 ± 13.61	±60	24
Cocontraction				
40°C	13.00 ± 1.73	113.33 ± 9.45	±60	38
		<i>Uromastix acanthinurus</i> (large)		
MAMEM	45.33 ± 1.04	109.83 ± 11.25	±60	15
MPsT	15.83 ± 2.02	73.70 ± 20.49	±70	11
MAMP	11.67 ± 1.53	93.67 ± 5.69	±90	12
MPttext	49.50 ± 2.60	154.33 ± 3.75	±50	21
Cocontraction				
42°C	18.83 ± 1.53	90.50 ± 6.26	±70	27
30°C	53.00 ± 2.65	143.00 ± 29.51	±40	18

TD, twitch duration; TF, tetanic frequency; TTP, time to peak tension; % maxTT, twitch tension expressed as percentage of maximal tetanic tension. For *Uromastix*: $N = 5$ (5 replications) for all muscles within 1 individual; for *P. stellio* $N = 3$ (3 different individuals; each five replications) for all muscles; $N = 5$ in 1 individual for cocontractions. See Fig. 2 for definitions of muscle abbreviations.

As stated earlier, the high skull of *Uromastix* theoretically allows the jaw closers to insert more perpendicularly at the lower jaw. However, the orientation of most jaw closers is rather similar in both species because of the high degree of pinnation of the external adductor caused by packing constraints (Rieppel and Gronowski, 1981; Herrel et al., 1998a). However, in *Uromastix* the constructional limitations set on the jaw adductors by the presence of postorbital and temporal bars (Herrel et al., 1998a, b) have been overcome. In this species, the lateral part of the pterygoid muscle extends from the pterygoid, curves around the lower jaw and attaches, not as in *Ploceoderma* at the lateral side of the lower jaw, but at the ventrolateral side of the temporal bar (Fig. 2). By doing so, an additional muscle volume, lying external of the postorbital space, is created.

Additionally, because of its highly vertical orientation, the externus part of the pterygoid muscle has a very favorable lever arm and thus contributes substantially to the total bite force (Herrel et al., 1998a, b). As a result, total bite forces are thus considerably higher in *Uromastix*.

Histochemistry

The fiber types histochemically identified in the lizards examined in this study fit the pattern of fiber type composition observed in other squamates (Talesara, 1972; Gleeson et al., 1980; Guthe, 1981; Guppy and Davison, 1982; Throckmorton and Saubert, 1982; Gleeson, 1983; Gleeson and Harrison, 1986; Abu-Ghalyun, 1995). Fibers were classified as corresponding to tonic (type I), FOG (type II), or FG (type III) categories, based on their histochemical staining intensities. Although the characterization of types II and III is rather straightforward (i.e., FOG, FG), the characterization of type I fibers is not so straightforward (Throckmorton and Saubert, 1982). Although they show the histochemical properties of typically slow fibers, the difference between tonic and slow-twitch oxidative fibers is hard to make based solely on histochemical stainings. Although most authors consider slow muscle fibers in lizards as tonic (e.g., Gleeson et al., 1980; Guthe, 1981; Throckmorton and Saubert, 1982; Gleeson and Harrison, 1986) there seem to be some indications that slow-twitch oxidative fibers might be present in some lizards (Morgan and Proske, 1984). Although none of the muscles examined here consists solely of type I fibers, the contraction characteristics of the MPt in *Uromastix* (containing a large area consisting solely of type I fibers) are typically those of slow-twitch fibres in both species, *U. aegyptius* and *U. acanthinurus*, examined (see also Morgan and Proske, 1984). Clearly, the innervation pattern (plate versus grape-like motor endings), and in vitro contraction characteristics should be examined to be able to classify and determine the exact physiological properties of these type I fibers.

In *Ploceoderma*, all three fiber types are observed. However, in contrast to what is observed in *Tupinambis* (Throckmorton and Saubert, 1982), no muscle contained more than two types, and types I and III never occurred together in any one muscle. Remarkably, in *Uromastix*, no type III (FG) fibers are observed. Although clear interspecific differences occur, in both species the pterygoid muscle contains predominantly slow, oxidative fibers, whereas the external adductor and pseudotemporal muscles contain more fast fibers. One major difference between species is the fiber type observed in the posterior adductor; although this muscle is composed of predominantly slow and oxidative muscle fibers in *Uromastix* (types I and II), it is characterized as FG in *Ploceoderma*. Similarly, in *Tupinambis* (Throckmorton and Saubert, 1982), this last muscle is composed of only FG fibers.

This observation is rather surprising because based on electromyographic (EMG) recordings of the jaw muscles during feeding, it was predicted that in *P. stellio*, MAMP, MAMEP, and MPt would be composed of oxidative fibers (Herrel et al., 1997). Clearly this prediction does not hold true for the MAMP and partially also for the MAMEP in *P. stellio*. Although these muscles remain active throughout a feeding sequence (large number of bites), they do not show the expected oxidative capacity. In *Uromastix*, on the

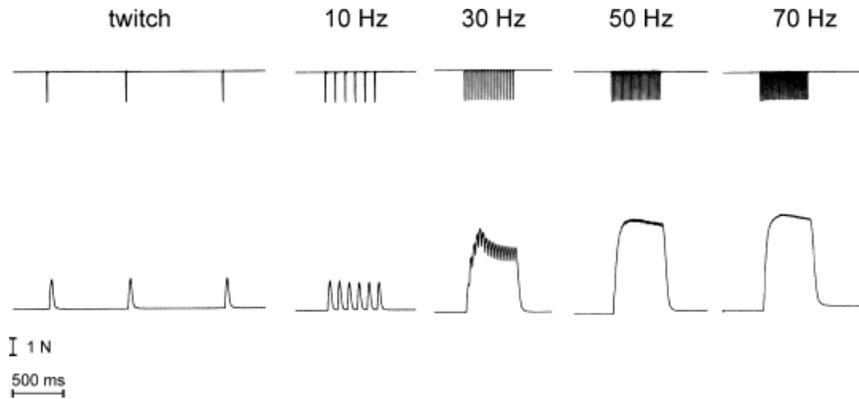


Fig. 5. Representative tracings of a stimulation of the m. pterygoideus medial in *Uromastix aegyptius*. **Top:** Supramaximal stimulus (10 V); three twitches, followed by stimulations of 500 msec at frequencies of 10, 30, 50, and 70 Hz. **Bottom:** Isometric tension exerted at the front of the jaws on a force transducer as a result of the corresponding stimulation regimen. The scale is equal for all tension tracings.

other hand, both of these muscles are composed of both SO and FOG fibers and thus show a larger oxidative capacity. In *Uromastix*, as in *Ploceoderma*, these muscles typically show prolonged activity together with the pterygoid muscle throughout a feeding sequence (personal observation) in correspondence with their physiological properties. One possible explanation for the unexpected result in *Ploceoderma* for the MAMP might be related to the size and position of this muscle. In this lizard, the MAMP is a small muscle crossing the jaw articulation from the anterior side of the quadrate to the medial side of the lower jaw just in front of it. Presumably this muscle counteracts the joint forces tending to rotate the quadrate backwards (Herrel et al., 1998) and thus plays an important role in the stabilization of the quadrate during jaw closing, and plays only a minor role in biting.

Stimulations

Although based on in vivo stimulations of whole muscles, jaw muscle twitch kinetics are comparable to results obtained for in vitro studies on lizard (Marsh and Bennett, 1986a, b; Swoap et al., 1993), and frog (Peplowski and Marsh, 1997) limb muscles. Nevertheless, for muscles with a high degree of pennation such as the external adductor or the lateral and externus parts of the pterygoid muscle, whole muscle kinetics are presumably not representative for isolated fiber contractions, but still give biologically relevant results. Other muscles such as the MAMP, the MPST, and the MPtmed are parallel fibered, show no or few aponeuroses, and can thus be compared with in vitro studies. For example, at 42°C, fast-twitch iliofibularis muscle fibers in *Dipsosaurus* show a time to peak tension of 11.1 msec (Swoap et al., 1993); time to peak tension in the MAMP in *P. stellio* (which is entirely composed of fast-twitch fibers) at 42°C is 10.8 msec. Clearly, results are comparable, and the experimental setup used in this study, based on whole muscle stimulations, thus gives reliable results. Additionally, because experimental conditions for both species were identical, comparisons between species can safely be done (e.g., maximal tetanic tension in both *Uromastix* species are very similar for similarly sized animals; *U. aegyptius*: 5.09 N; small *U. acanthinurus*: 6.86 N; large *U. acanthinurus*: 11.65 N).

The results from these stimulations are generally in accordance with the results of the histochemical analysis. Muscles in *Uromastix* tend to be somewhat slower and

show a fused tetanus at slightly lower frequencies. Tetanic fusion starts at about 60 Hz or 65 Hz, depending on the muscle and species examined, and is much higher than that reported for jaw muscles in *Trachydosaurus rugosus* (15 Hz; Gans and De Vree, 1986; personal observations), but is similar to those for jaw muscles in *Gekko gekko* and *Anolis equestris* (personal observations; Cleuren J., personal communication).

Clearly, there are interspecific and size-dependent differences in the contraction characteristics of the *Uromastix* specimens tested. As expected, the size of the animals has a clear effect on the contraction data, with larger animals having slower muscles than smaller ones. Nevertheless, the relative data (i.e., differences among muscles) are comparable between individuals, and the overall pattern of contraction characteristics is stable within species. Interspecific differences are also obvious; not only are jaw muscles faster in *U. acanthinurus* (compare data for the small individual with those for the *U. aegyptius*), but twitch duration is also markedly longer. Most likely, in *U. acanthinurus*, less tonic, and more FOG and probably also FG (as indicated by the extremely low TTP data for the MPST) fibers are present. Nevertheless, this needs to be confirmed by examining the histochemical properties of the jaw muscles in this species.

An explanation for the longer twitch duration in *U. acanthinurus* is less obvious, but because the results for the two specimens are very consistent, this phenomenon is most likely not caused by experimental error. One possible explanation is that interspecific differences exist on a biochemical level; i.e., it could be possible that the rate at which calcium is pumped out of the cell is lower in *U. acanthinurus*, thus causing slower muscle relaxation in these animals. However, if this would be true, the fusion frequency in *U. acanthinurus* should be lower too. Because this is not the case, this hypothesis seems improbable. Another explanation could be that interspecific differences exist in the mechanical properties (e.g., viscoelastic properties) of the muscle-tendon system considered. As the twitch duration is mainly longer in highly pennate muscles (e.g., MPt, MAME) this hypothesis seems plausible.

The effect of temperature was tested on cocontractions of several jaw muscles. This seemed biologically relevant as EMG studies for all species have shown that jaw closers are always used in bilateral temporal synchrony during the intraoral transport stage (Herrel et al., 1997; unpub-

lished data). Data thus gathered are a useful measure of the effect of temperature on whole animal performance. Temperature had a marked effect on the contractile properties of the jaw muscles in all species examined. A drop of 10°C in temperature markedly increased both the time to peak tension, and the twitch duration in all animals examined. As a result of the increase in relaxation time, fusion tetanus frequencies dropped to about 30 Hz. These results correspond to data gathered for in vitro studies on lizard, turtle, and frog limb muscle (Marsh and Bennett, 1986a, b; Mutungi and Johnston, 1987; Peplowski and Marsh, 1997). However, our results contradict the statement that maximal force generation in vivo should be temperature independent (Bennett, 1985). Stimulations at 10°C below the optimal temperature decreased tetanic force output considerably in all three species (*P. stellio*: from 0.6 to 0.2 N; *U. aegyptius*: from 5 to 3 N; *U. acanthinurus*: from 12 to 5 N). This apparent discrepancy might be because previously only the thermal dependence of FG fibers in vitro was studied (Bennett, 1985), whereas here the effects of temperature on whole muscle performance is based on the contraction characteristics of several fiber types in several cocontracting muscles. This observation illustrates that conclusions drawn from in vitro studies on single fibers should be interpreted cautiously when considering whole animal performance.

Ecological Correlates

Are there clear correlates between the morphological and physiological characteristics of the jaw closers in the animals examined and their dietary preferences? On the one hand some interspecific differences might indeed be related to differences in diet between both species. For example the presence of the extra portion of the pterygoid muscle, the absence of FG muscle fibres in at least one of the two species examined of *Uromastix*, and the presence of more muscles showing SO fibers (indicating a large oxidative capacity) seem to indicate that the jaw system in this lizard genus is optimized for hard and prolonged biting. This is very useful for herbivorous lizards that generally need more bites to adequately reduce their food before swallowing (personal observation). Additionally, herbivorous lizards such as *Uromastix* have to eat more, and during longer periods of the day (e.g., the average duration of a feeding bout in wild *U. aegyptius* is 9 min, and up to six bouts per day were observed; see Bouskila, 1986) to supply their energy needs.

On the other hand, why do herbivorous lizards still show such fast jaw muscles? One could have expected that, for an animal not having to hunt for an active, elusive prey, fast jaw muscles are unnecessary. For example, in the shingleback lizard, jaw muscles are extremely slow (Gans and De Vree, 1986), which corresponds well with its omnivorous diet of fruits, plants, snails, and carrion (Dubas and Bull, 1991). At least two scenarios are possible to explain the presence of fast jaw muscles in *Uromastix*. First, because insectivory is plesiomorphic within Chamaeleonidae (sensu Frost and Etheridge, 1989), we cannot exclude simple phylogenetic inertia. If no selection pressures ever arose, herbivorous species such as *Uromastix* would retain the ancestral state as observed in chameleons and generalized lizards such *P. stellio* (Joger, 1991).

As an other alternative, we would like to advocate the existence of a possible trade-off occurring between the need to feed for prolonged periods (as a result of their herbivorous diet) and the presence of extremely slow muscles. Given the effects of a decrease in temperature on 1) maximal tetanic force output (decrease), 2) twitch characteristics (slower), and 3) fusion frequencies (much lower), animals with muscles composed of predominantly slow oxidative fibers functioning optimally at high temperatures (as observed in *T. rugosa* where the fusion frequency is less than 20 Hz; Gans and De Vree, 1986) would be unable to feed efficiently once temperatures dropped by even 10°C. Nevertheless, for lizards such as *Uromastix*, which have a preferred activity temperature around 40°C (Grenot and Loirat, 1973), such temperature drops occur regularly during the activity season. For example, in spring the average body temperature of these lizards is markedly lower ($\pm 35^\circ\text{C}$; Grenot, 1976). Nevertheless, because during this period large amounts of fresh plant material are present, the animals feed frequently, eat large quantities of food, and replenish their tail fat reserves (Grenot, 1976). This clearly puts a limitation on the minimal temperature by which the jaw adductors have to be able to function. Clearly, the conflicting demands of herbivory (i.e., the need to bite hard during prolonged periods) and muscle physiology put a constraint on the evolution of slow jaw muscles in *Uromastix*.

Nevertheless, even when possessing fast muscles (as observed in *Uromastix*), these will be working suboptimally during certain periods. However, animals not needing a fast bite, such as herbivorous or omnivorous lizards, will be able to take up the required daily amounts of energy at these lower temperatures despite the suboptimal performance of the jaw muscles. Somewhat similarly, it has been demonstrated that maximal power output limits limb cycling frequencies at lower temperatures in lizards (Marsh and Bennett, 1986a, b; Johnson et al., 1993; Swoap et al., 1993). Relations between ecology, morphology, performance, and function are thus not always clear-cut, and might be obscured by trade-offs.

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