1 We wish to thank Dr Ned Porter for both his generous donation of a supply of hydroperoxide and for his suggestions regarding possible reaction mechanisms. This research was supported by U.S.P.H.S. N.I.H. Grants ES00798, HL16264 and T32 GM07105.
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Streptostyly and muscle function in lizards

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Summary. Retraction of the quadrate during jaw closure in lizards increases the moment arm and thereby the mechanical advantage at which the jaw adductors work on the lower jaw.

Cranial kinesis in lizards has attracted the attention of many workers already, the classic contributions being those of Bradley[2] and Versluys[3]. More recently, Frazzetta[4] reviewed the problems involved and found that most Lacertilia of present times are characterized by amphikinesis. Not only is the braincase movably suspended within the dermatocranium, but also the upper jaw and with it the whole muzzle unit can be rotated upwards and downwards around the mesokinetic joint dorsally and the hypokinetic joint ventrally (figure). Upwards rotation of the muzzle unit involves a protraction of the basal unit (pterygoid); the lower end of the movably suspended (streptostylic) quadrate swings forwards. Depression of the upper jaw results from a retraction of the basal unit; the lower end of the quadrate swings backwards. Frazzetta[4] and Iordansky[5] discussed previous theories and put forward new ones concerning the adaptive significance of amphikinesis. These will be critically evaluated elsewhere.

During the transition from fossil amphibians (or rhipidistians) to reptiles, a reorientation of the jaw musculature took place leading to the change from a 'kinetic inertial system' to the 'static pressure system' of captorhinomorphs[6,7]. Jaw adductors no longer exerted maximal force on the lower jaw ramus with the jaws maximally depressed, as in rhipidistians or anthracosaurs, which resulted in a snapping bite. Instead, maximal force is exerted on the lower jaws near to closure, an important adaptation of the early reptiles to an insectivorous habit[7].

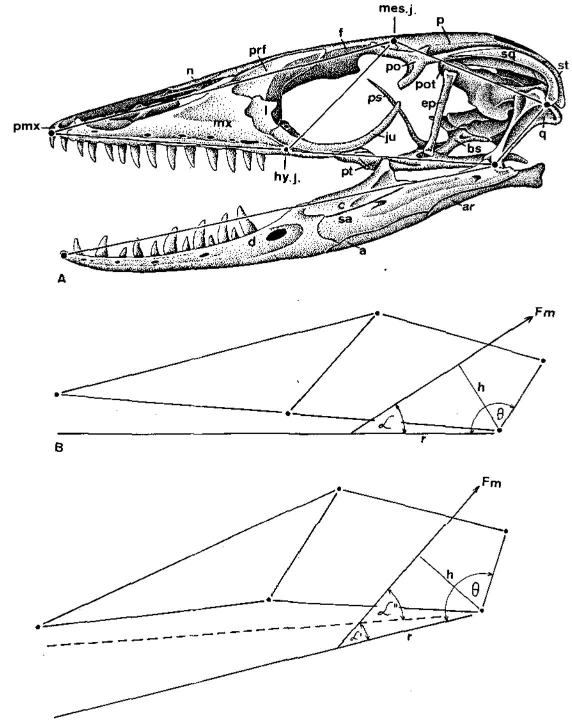
The first lizards evolving during the Triassic, the Eolacertilia, showed a streptostylic quadrate but no hinge-joint between the frontals and the parietals. They lacked mesokinesis[8].

During the Jurassic and Early Cretaceous, modern lacertilian infraorders became established. Amphikinesis appears as a characteristic feature of modern lizards[4].

Recent X-ray cinematography on a feeding *Varanus bengalensis* showed quadrate protraction and corresponding upwards rotation of the muzzle unit to occur during jaw opening. Assuming a constant angle θ between the lower jaw ramus and quadrate, protraction of the lower end of the quadrate will decrease the gape during mouth opening, as has been pointed out by Frazzetta[4] and Throckmorton[9]. Cranial kinesis therefore does not increase the gape.

Retraction of the lower end of the quadrate and corresponding depression of the muzzle unit occurs during jaw closure, as it has also been reported for *Gerrhonotus*[4] and *Uromastyx*[9]. It will be noted from the figure, C, that, assuming a constant angle θ between the lower jaw ramus and the quadrate, the latter's retraction will cause an increase in gape.

The most massive jaw adductor muscle in *Varanus* is the posterodorsally sloping m. adductor mandibulae externus, the greatest bulk of which originates from the parietal unit, e.g. from the upper temporal arch and from the parietal.



The application of the quadric crank model[4] to the skull of *Varanus salvator* to illustrate quadrate retraction during jaw closure. The main muscle force Fm is assumed to work along the direction indicated by the bodenaponeurosis and associated tendons. For further explanation see text. Abbreviations: a, angular; ar, articular; bs, basisphenoid; c, coronoid; d, dentary; ep, epipterygoid; f, frontal; h, moment arm; hy.j, hypokinetic joint; ju, jugal; l, lacrimal; mes.j, mesokinetic joint; mx, maxilla; n, nasal; p, parietal; pmx, premaxilla; po, postorbitofrontal; pot, prootic; prf, prefrontal; ps, parasphenoid; pt, pterygoid; q, quadrate; sq, squamosal; st, supratemporal; Fm, main muscle force exerted by the external adductor.

The moment this muscle will exert on the lower jaw depends on its absolute force Fm and on the moment arm h, whereby $h = r \cdot \sin \alpha$. The figure, B and C, demonstrates that assuming a constant angle θ, retraction of the quadrate will cause a reorientation of the external adductor increasing its insertional angle α (α') and therewith increasing h, thus leading to a greater mechanical advantage of the muscle.

Assuming a constant size of the prey, the widening of the gape which results from quadrate retraction will necessitate further jaw elevation to hold the prey. This jaw adduction will further increase the insertional angle α (α'') and thereby maximize the mechanical advantage at which the external adductor works.

The above argument can be extended to all other jaw adductors inserting into the mandible except for the m. pterygoideus.

This muscle, however, is critical during initial phases of jaw closure[7] and hence does not interfere with the system described above.

In conclusion, the acquirement of a streptostylic quadrate early during the evolution of primarily insectivorous lizards (Eolacertilia[8]) can be understood as a perfection of the static pressure system which first evolved in the earliest reptiles, the captorhinomorphs.

1 Acknowledgments. I am greatly indebted to Prof. Dr med. M. Elke who made the X-ray cinematography possible at the Röntgeninstitut, Kantonsspital Basel. I thank Dr R.L. Carroll, Montreal, Canada, Dr G.S. Throckmorton, Dallas, USA, and Dr D.G. Senn, Basel, for critically reading the manuscript.
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Nuclear lamellae in the germ-line cells of gall midges (Cecidomyiidae, Diptera)[1]

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28 November 1977

Summary. Lamellar structures in oogonial and spermatogonial cells of gall midges were found to form a complicated system of intranuclear compartments inside which all heteropycnotic chromosomes present in the germ-line cells of these insects are located. In this way, the heteropycnotic S-chromosomes are separated by the nuclear lamellae from the remaining, decondensed chromosomes (E-chromosomes) of the interphase germ-line nucleus.

The part of the nucleus, in the oocytes of different groups of animals, in which chromosomes are grouped, is often separated from the remaining part of the karyoplasm by structures collectively termed the chromosome or karyosphere capsule[2-7]. The structure of the capsules may differ in various animals but in most of the known cases they are transient differentiations of the nucleus which occur in a particular species in the course of oogenesis. The role of these structures remains to be elucidated.

The intranuclear chromosome capsules in the Cecidomyiids differ from similar structures in the oocytes of other animals in that they occur not only in the course of oogenesis but also in other developmental stages of the germ cells. Moreover, there is reason to presume that their occurrence in the Cecidomyiidae is connected with the functioning of a singular cytogenetic system, particular to this family of the Dipterous flies. One of the main features of this system is the presence in the germ-line nuclei of both males and females of 2 sets of chromosomes: S-chromosomes found in both the generative and somatic cells and E-chromosomes which are limited to the germ-line nuclei only.

The chromosome capsule in the oocytes of the Cecidomyiidae was first described in *Mikiola fagi* as a vesicular element composed of concentric lamellae[8]. In the diplotene, these lamellar structures envelope the S-chromosomes exclusively which, contrary to the E-chromosomes, pair to form chiasmatic bivalents. In this stage of oogenesis, the E-chromosomes are found in the form of univalents on the outside of the system of lamellar vesicles. These observations, made in light microscope, have been confirmed by electron microscope studies of the oocytes of a different gall midge[9,10]. For some time there have also been clues that the chromosome capsules in gall midges occur even in the primordial germ cells[11]. Recent electron microscope studies have confirmed the presence of a chromosome capsule in the polar cells of Miastor and have revealed its lamellar structure[12].

In the light of these observations, it seemed interesting to discover whether lamellar chromosome capsules are present in the gonial cells of larval gonads in the Cecidomyiidae.

Material and methods. The studies were made on the larval ovary of 2 non-paedogenetic species of gall midges, *Rhabdophaga rosaria* and *Mayetiola poae*, and on the testes of larvae of the latter species. The gonads were fixed in 5% glutaraldehyde buffered at pH 7.4 with 0.1 M phosphate for 60 min, washed in 0.1 M phosphate buffer, postfixed with 2% osmium tetroxide, and embedded in a mixture of epon and araldit. Ultrathin sections were stained with uranyl and lead salts[13].

Results and discussion. In the early stages of embryonic development, a certain number of chromosomes in the germ-line cells of the Cecidomyiids are subjected to heterochromatinization[11,14-16]. In many species the number of chromosomes subjected to this process is the same in male and female[17-21], and there is evidence for assuming that it is the set of S-chromosomes that becomes heteropycnotic in the germ cells of both sexes[19,22].

In both species examined, the S-chromosomes of the interphase germ-line nuclei show strong positive heteropycnosis and, as in most gall midge species, form a compact group on one side of the nucleus. The E-chromosomes, which take up the remaining part of the nucleus are represented by diffuse chromatin and a certain number of relatively small and irregularly shaped heterochromatin blocks (figures 1, 3 and 4). Moreover, it is seen from these figures that the part of the interphase nucleus, in which the S-chromosomes are grouped, is occupied by a system of interconnected electron dense sheets or lamellae, which form an irregular network with honey-comb-like structure