

Functional morphology of a highly specialised pivot joint in the cranio-cervical complex of the minute lizard *Ablepharus kitaibelii* in relation to feeding ecology and behaviour

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Abstract

The snake-eyed skink *Ablepharus kitaibelii* is one of the smallest European lizards, but despite its minute size it is able to feed on comparatively large prey. Here we investigate the diet of *A. kitaibelii* and the mechanisms that allow the skink to overpower relatively large and even noxious prey. High-speed cinematography showed that *A. kitaibelii* uses a series of shaking and battering movements to immobilise and kill prey prior to swallowing. During this process, the skink rises up on the hind limbs and then whacks the prey sideways on the substrate by twisting the trunk, neck and head laterally. Our analysis showed that the shaking kinematics is very uniform among the investigated specimens. The morphological investigation of the cranio-cervical system revealed that *A. kitaibelii* possesses a well-developed synovial joint between the odontoid process of the axis, the atlas, and the basioccipital. The odontoid process is cylindrical and slim and together with the atlas and the basioccipital it forms a highly specialised pivot joint for lateral head rotation. We propose that the occipito-atlanto-axial complex of *A. kitaibelii* represents a functional adaptation for additional stabilisation of the cranio-cervical complex during prey shaking. Digital data from morphological databases showed that specialised joints of this type are very rare, but do also occur in other squamate groups. Thus we hypothesise that specialised cranio-cervical joints have evolved parallel as functional adaptations to different feeding and locomotion patterns. Future studies that link feeding kinematics and locomotion to cranio-cervical morphology might elucidate the function of various specialised occipito-atlanto-axial systems of squamates.

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Introduction

Feeding behaviour and performance during food uptake, intraoral transport (including chewing and puncture crushing) and deglutition have been thoroughly investigated in lizards (Schwenk, 2000; Herrel *et al.*, 2001a, 2007; Ross *et al.*, 2007). Besides the ongoing debate on the utilisation of venom in lizards (Herrel *et al.*, 1997; Fry *et al.*, 2006, 2009, 2010; Fry and Scheib, 2007; Weinstein *et al.*, 2009), several strategies for mechanical killing and immobilising of prey are described to date for this group. Nonophidian lepidosaurs kill prey by biting, suffocating, shaking or crushing, and dragging it against the substrate (Schwenk, 2000). *Varanus exanthematicus* (Bosc, 1792) utilises a number of bites to kill a mouse, but it also shakes and hits the prey against the substrate or against objects (Smith, 1982). A very similar behaviour was reported for *Varanus salvator* (Laurenti, 1768) (Honegger and Heusser, 1969; Dauth, 1983). The leopard lizard, *Gambelia wislizenii* (Baird and Girard, 1852), processes noxious prey by increasing gape cycle frequencies (Lappin and German, 2005).

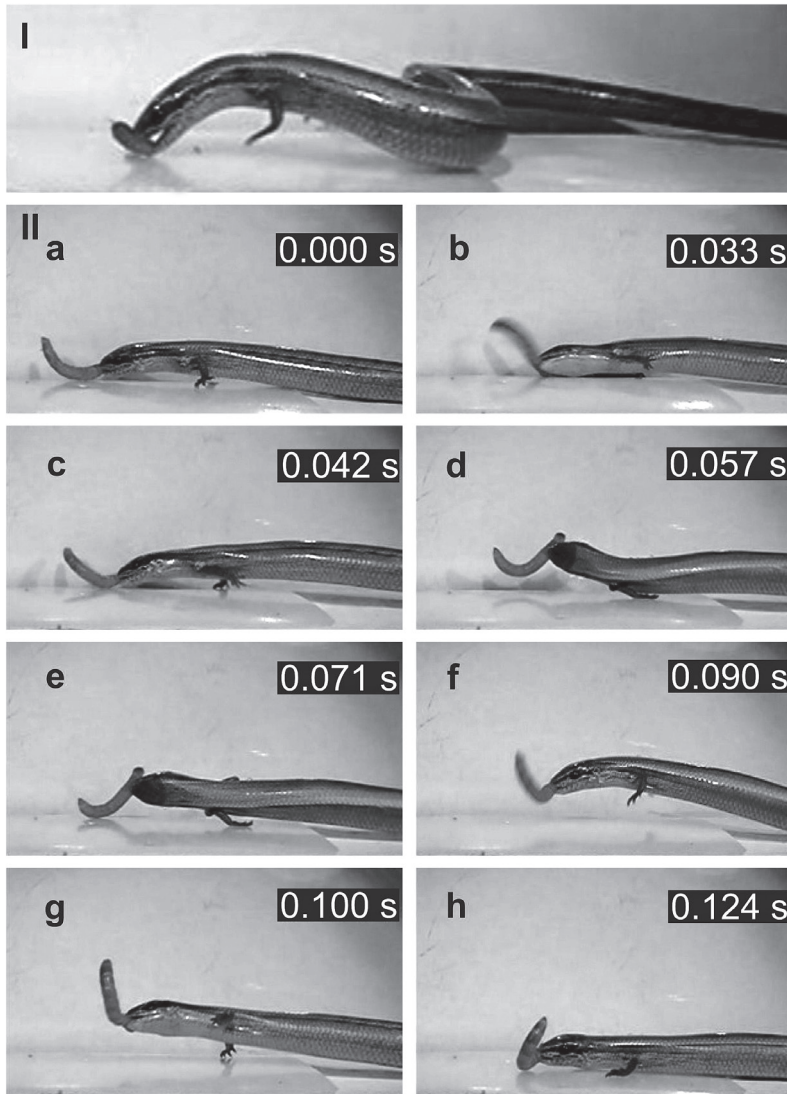


Fig. 1. Kinematics of prey capture and immobilization in *Ablepharus kitaibelii*. (I) Selected frame from a prey capture sequence in *A. kitaibelii*. (II) Selected sequence representing a prey shaking cluster (a-h). Time in seconds (s).

Some lizards rely on hard bites for killing. The teiid *Tupinambis teguixin* (Linnaeus, 1758) smashes its prey by crushing bites with a maximum bite force over 100N (McBrayer and White, 2002). Similarly, molluscivorous lizards use repetitive crushing bites to break the shell of snails, applying even higher bite forces of more than 400N (Schaerlaeken *et al.*, 2012). The scincid *Tiliqua rugosa* (Gray, 1825) crushes snails and mice by prolonged bursts of all jaw-closing muscles (Herrel *et al.*, 1999b).

Another behaviour of nonophidian lepidosaurs to immobilise prey is 'prey-shaking' or 'death-shaking' (Dauth, 1983, 1986). The tokay gecko *Gekko gekko* (Linnaeus, 1758) shakes and hits pray against the substrate until it becomes completely motionless (Rolloff,

1957). The much smaller five-lined skink *Plestiodon fasciatus* (Linnaeus, 1758), was observed to catch large prey by biting and to immobilise it by lateral shaking and by battering it against a rock ledge (Fitch, 1954).

The species investigated here, the European snake-eyed skink *Ablepharus kitaibelii* (Bibron and Bory de Saint-Vincent, 1833), is even smaller than *P. fasciatus*, but feeds on relative large butterflies, cicadas and even on noxious spiders (Herczeg *et al.*, 2007) and chilopods (see results). The present study addresses the strategies, which allow *A. kitaibelii* to subdue large prey. In lizards, bite force is strongly correlated with overall body size (da Silva *et al.*, 2014) and the size and shape of the head (for an overview see Anderson *et al.* (2008)). Lizards with larger heads possess more voluminous ad-

Table 1. Diet of the snake-eyed skink. Food spectrum of *Ablepharus kitaibelii* according to the three methods of research, *n– number of studied excrements, n – number of studied individuals.

| Orders | This study | | Angelov <i>et al.</i> (1966) | | Herczeg <i>et al.</i> (2007) | |
|------------------|------------|-----------|------------------------------|-----------|------------------------------|-----------|
| | *n | % (total) | n | % (total) | n | % (total) |
| Araneae | 7 | 23.3 | 6 | 25 | 25 | 18.5 |
| Lithobiomorpha | 2 | 6.7 | – | – | – | – |
| Hymenoptera | 3 | 10 | 2 | 8.3 | 20 | 14.8 |
| Coleoptera | 2 | 6.7 | 6 | 25 | 23 | 17 |
| Hemiptera | 12 | 40 | 5 | 20.9 | 50 | 37 |
| Diptera | 1 | 3.3 | 1 | 4.2 | 5 | 3.7 |
| Pseudoscorpiones | – | – | 2 | 8.3 | 3 | 2.2 |
| Lepidoptera | – | – | 2 | 8.3 | 9 | 6.6 |
| Other | 3 | 10 | – | – | – | – |

ductor muscles and are capable of applying harder bites (Herrel *et al.*, 1996, 1999a, 2007; Huyghe *et al.*, 2009). Bite force across lizard species can be predicted on the base of the shape of the head. Width and height of the head are the most important indicators of the ability of a lizard to bite hard (Herrel *et al.*, 1999a, 2001a, b, 2004; Vanhooydonck *et al.*, 2011), but also the length of the head impacts bite performance, at least in genus *Chamaeleolis* Duméril & Bibron, 1837 (Herrel and Holanova, 2008). Considering the very small overall size of *A. kitaibelii* and the shape of its head, it is likely that its main strategy to immobilise prey is not based on hard biting (Anderson *et al.*, 2008), and it was mentioned briefly that that *Ablepharus* Fitzinger, 1823 shakes its prey after uptake (Dauth, 1983). In this work we use high-speed video cinematography to analyse this behaviour in detail. In such shaking movements, forces generated post-cranially have to be transmitted to the head of the predator and on the prey, therefore we additionally studied the morphology of the joints between the elements of the cranio-cervical system (sensu Weisgram and Zweers, 1987). We compare the bauplan of the cranio-cervical joint of *A. kitaibelii* to other lepidosaurs from different taxa and discuss possible relations between the morphology of the occipital-atlas-axis complex and species ecology.

Material and methods

The object in this study *A. kitaibelii* is a very small lizard with snout-vent length up to 55.5 mm in females (Ljubisavljević *et al.*, 2002) and 47.5 mm in males (VV and NT, unpubl. data). The species inhabits dry bushy meadows, and oak forests in South-east Europe and Western and Central Asia Minor (Schmidtler, 1997; Stojanov *et al.*, 2011). In Bulgaria *A. kitaibelii* is distrib-

uted sporadically on the territory of the country up to 1550 m altitude but is absent in the low valleys and deforested terrains (Tzankov, 2007). Data on the diet of the species are scarce and partly controversial. It was reported that *A. kitaibelii* feeds on small insects and their larvae (Fejervary, 1912) and more generally on members of seven different arthropod orders (Herczeg *et al.*, 2007). It was also reported that *A. kitaibelii* does not feed on big and hard prey (Angelov *et al.*, 1966).

In order to fill the gap of information concerning the diet of the species we investigated the food spectrum in *A. kitaibelii* by analysing excrements from a total of 25 wild individuals inhabiting three Bulgarian localities. Preliminary data for the food spectrum of the species were taken by examination of the excrements of live individuals. For the purpose, live specimens were caught and kept a few days in boxes and after that they were released back into the wild. Specimens were caught in Zemen (14.09.10, relative coordinates N42.47 E22.72, 20 faeces from 7 specimens); Belovets (29.07.10, relative coordinates N43.80 E26.43, 8 faeces from 8 specimens); and Pancharevo (15.09.10, relative coordinates N42.58 E23.43, 2 faeces from 2 specimens). The chitin rests in the faeces were identified to order level by using a dissection microscope.

In indoor experiments, three adult wild skinks (body length 35, 46 and 53 mm) were filmed in a glass terrarium (40×20×03 cm). Six shaking clusters (groups of prey shakes) were filmed per individual in lateral view, using a Casio EX-FH20 high-speed camera (210 frames per second). As food items we used *Tenebrio* larvae with a total length of 18 (± 3) mm (over twice the length of the lizard's skull). Kinematic analysis was performed by using SIMI MatchiX © SRM software. Kinematic data was tested with Shapiro–Wilk test for normal distribution. The p-value was less than the chosen alpha level (p<0.05) for one individual, then the null hypothesis

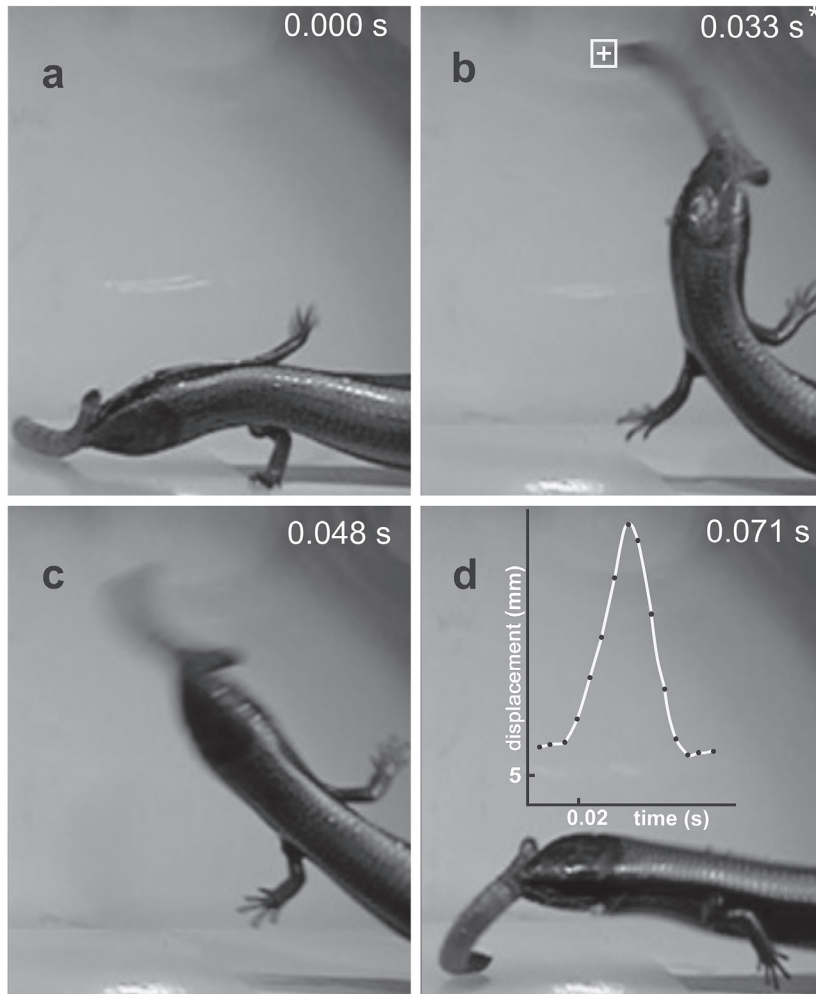


Fig. 2. Prey battering against the substrate. *Ablepharus kitaibelii* is able to hit its prey against the substrate with an average speed of more than 2m/s. (a, b) The prey is lifted. (c, d) The prey is hit against the substrate. (d) shows the kinematic profile of the marker displayed in (b).

was rejected and Kruskal-Wallis test with a Bonferroni correction was later performed for a whole dataset. As no statistically significant difference between individuals was found, results from the three specimens were pooled and standard descriptive statistics including mean, range and standard deviation was performed.

We investigated the skull morphology using both high-resolution microscopic computed tomography (μ CT) and histology. For μ CT, an adult specimen was fixed in 4% formaldehyde and then washed and preserved in 70% ethanol. It was mounted in a plastic tube in 70% ethanol and scanned using a SCANCO μ CT35 with 70keV source voltage and 114 μ A intensity. Projections were recorded with an angular increment of 0.18°, and reconstructed slices measured 2048×2048 at a voxel resolution of 3.5 μ m. The reconstructed image was visualised via volume rendering using Drishti (Lima, 2012).

For histology, one adult specimen was fixed in Bouins fluid. For decalcification it was preserved in the fixative for 20 days. After dehydration it was embedded in paraffin and sagittally sectioned (section thickness 3 μ m) with a Thermo Scientific™ HM355S-2 microtome. Sections were stained with haematoxylin and eosin in order to get good overall contrast for bones, articular cartilages and the articular capsule and to analyse the cranio-cervical-joint on tissue level. Colour micrographs were taken with a Zeiss AxioImager Z2 microscope.

In order to assess the differences in cranio-cervical morphology in major squamate groups, we juxtaposed a recent molecular phylogeny of squamates (Pyron *et al.*, 2013) to a recent morphological tree (Gauthier *et al.*, 2012), and plotted the abundance of different states of cranio-cervical morphology for each group on these trees. Data for most squamate groups was available

Table 2. Kinematic analysis of the shake clusters. This table shows average durations of prey shaking clusters and single prey shakes as well as the number of shakes per shaking cluster for three specimens.

| Variables | Specimen 1 | Specimen 2 | Specimen 3 |
|----------------------------------|---------------|---------------|---------------|
| Duration of a shake cluster (s) | 0.182 ± 0.041 | 0.162 ± 0.039 | 0.190 ± 0.031 |
| Minimal–maximal duration (s) | 0.124–0.233 | 0.114–0.214 | 0.143–0.228 |
| Number of analysed clusters | n=6 | n=6 | n=6 |
| Number of shakes in a cluster | 3.333 ± 0.516 | 3.000 ± 0.624 | 3.500 ± 0.548 |
| Minimal–maximal number of shakes | 3–4 | 2–4 | 3–4 |
| Number of analysed clusters | n=6 | n=6 | n=6 |
| Duration of single shakes (s) | 0.053 ± 0.015 | 0.051 ± 0.011 | 0.052 ± 0.008 |
| Minimal - maximal duration (s) | 0.033–0.095 | 0.038–0.080 | 0.038–0.067 |
| Total number of analysed shakes | n=20 | n=18 | n=21 |

from the digital database Digimorph (www.digimorph.org; Humphries, 2004). In total we analysed the cranio-cervical morphology of 110 squamate species based on Digimorph datasets. Data on cranio-cervical morphology of Rhynchocephalia (*Sphenodon punctatus*) was taken from Jones *et al.* (2009).

Results

Analysis of diet

Analysis of the diet of wild populations showed that *A. kitaibelii* feeds on various arthropod taxa (Araneae, Lithobiomorpha, Hymenoptera, Coleoptera, Hemiptera, Diptera, Pseudoscorpiones and Lepidoptera) including noxious spiders and chilopods (Table 1).

Feeding kinematics

Feeding experiments showed that *A. kitaibelii* uses jaw prehension to catch its prey. Initially, the anterior part of the body is lifted and the head is bent ventrally (Fig. 1I). Food uptake is immediately followed by prey shaking. Single prey shakes were very fast in all three investigated specimens (durations in average 0.052 ± 0.01 s) and relatively uniform in their kinematics (Table 2). The number and the duration of the shakes within shaking clusters did not differ significantly among the individuals ($p > 0.05$ for all pairs). At the beginning of each shaking cluster, *A. kitaibelii* rises up its chest and the fore limbs, while the hind limbs and the tail stay in contact to the substrate. Next it stretches the fore limbs laterally and twists the neck and the head sidewise. Afterwards *A. kitaibelii* hits the prey against the substrate or shakes it in the air. Subsequently the body is twisted

in the alternative direction (see Fig. 1II, Supplementary video 1). The maximal number of shakes grouped in a shaking cluster was 4 and the minimal number was 2 (3.28 ± 0.54). In two prey shaking film sequences, the prey was lifted and then ‘battered’ laterally against the substrate (Fig. 2, Supplementary video 2). On the base of the kinematical profile of prey movement measured at the most distant part of the prey item (Fig. 2) we calculated that the lizard is able to accelerate the larvae and hit it against the substrate with an average speed of over 2 m/s in less than 25 milliseconds (see Fig. 2d, Supplementary video 2).

Morphology of the cranio-cervical-joint

Ablepharus kitaibelii possesses a well-developed synovial joint formed by three bones: the basioccipital, the atlas, and the cylindrically elongated odontoid process of the axis (Fig. 3d). The basioccipital is a thin bone, but it is markedly thickened at the occipital condyle (Fig. 3a, c) that has a ventrally curved groove in which the odontoid process lies. The atlas articulates anteriorly with the single occipital condylus and posteriorly with the axis (Figs 3b, d, 4), and its neural arches do not fuse dorsally (Figs 3a, c, 4). Altogether the occipito-atlanto-axial complex forms a well-developed pivot joint (Fig. 3b).

Discussion

Analysis of diet

Our analysis of *A. kitaibelii* excrements from three different Bulgarian populations showed that 63.3% of found food items belonged to either Araneae or

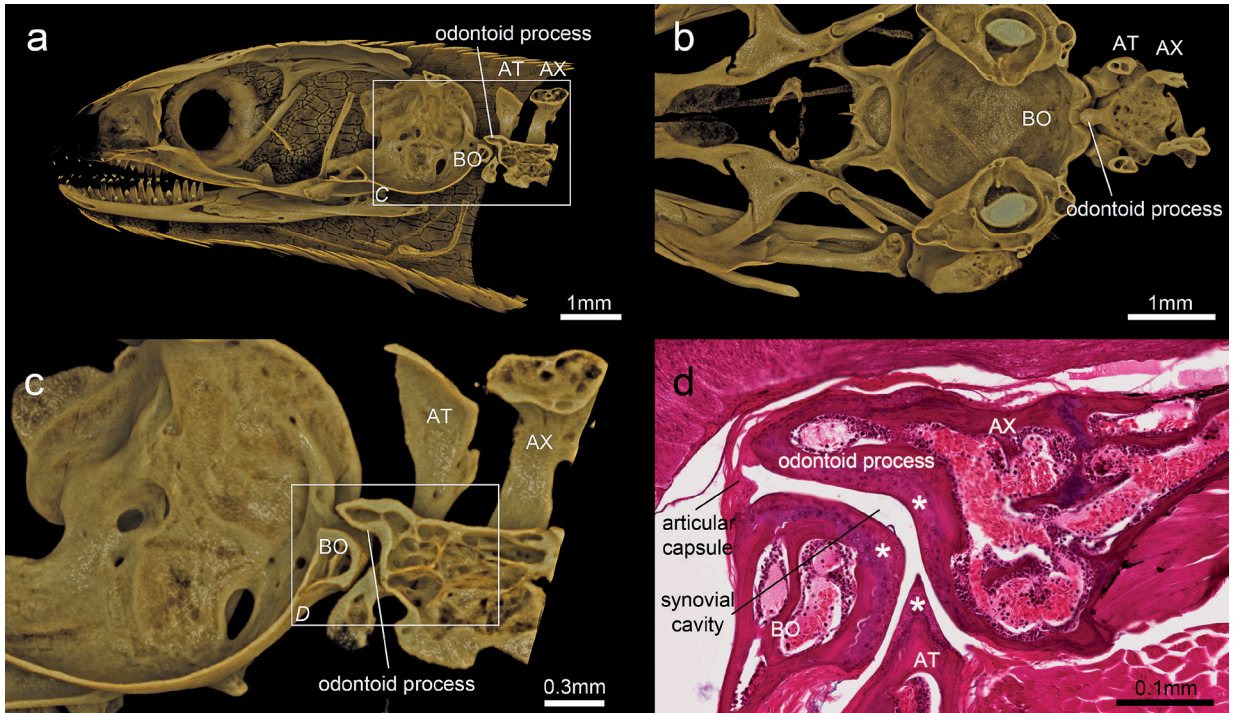


Fig. 3. Morphology of the occipito-atlanto-axial complex in *Ablepharus kitaibelii*. (a) Sagittal section of the skull based on microCT scan. (b) Detailed dorsal view of the occipito-atlanto-axial based on microCT scan. (c) Lateral section through the occipito-atlanto-axial joint based on microCT. (d) Histological section representing the sagittal plane of the occipito-atlanto-axial joint. AT, atlas; AX, axis; BO, basioccipital; * articular cartilage.

Hemiptera. The found food spectrum was similar to previous data (Angelov *et al.*, 1966; Herczeg *et al.*, 2007) on *A. kitaibelii* diet (Table 1). Angelov *et al.* (1966) dissected the stomachs from individuals of two localities of Bulgaria, collected in May. Herczeg *et al.* (2007) studied the food spectrum of *A. kitaibelii* populations in Hungary at different seasons (spring and summer) by flushing the stomach content. A comparison of the three datasets shows on the one hand that two groups of arthropods reported in earlier studies, Pseudoscorpiones and Lepidoptera, were not found in the present study. On the other hand, the present study for the first time reports Lithobiomorpha as part of the diet of *A. kitaibelii*. Interestingly, the smallest of all skink species, *Menetia greyi* Gray, 1845, also feeds on noxious prey (Pianka, 2011).

Feeding kinematics and morphology of the cranio-cervical-joint

Ablepharus kitaibelii is able to feed on relatively large and even harmful prey, despite its minute body size and its fragile skull. High-speed video sequences showed

that the prey is immobilised by vigorous shaking and battering movements (Fig. III and Supplementary videos), thus confirming previous observations (Dauth, 1983). The position of the body and the head of the lizards during these fast movements suggested that forces created by twisting of the trunk are transmitted to the prey via the predators head. The morphology of the cranio-cervical joint shows that the occipito-atlanto-axial complex of *A. kitaibelii* functionally represents a well-developed pivot joint.

In amniotes, the first two cervical vertebrae (atlas and axis) are typically modified to support the movements of the skull. In most extant amniote groups, the atlas is ring-shaped and lacks a pleurocentrum, thus consisting of the neural arches and the first intercentrum, while the first pleurocentrum is attached to the axis and forms the odontoid process. Such a situation is found in lepidosauria, crocodiles, birds, and mammals, while chelonians show a more plesiomorphic condition (Romer, 1956; Hoffstetter and Gasc, 1969; Wake, 1992).

Plesiomorphic for amniotes, a single convex occipital condyle forms a ball-and-socket joint with the first

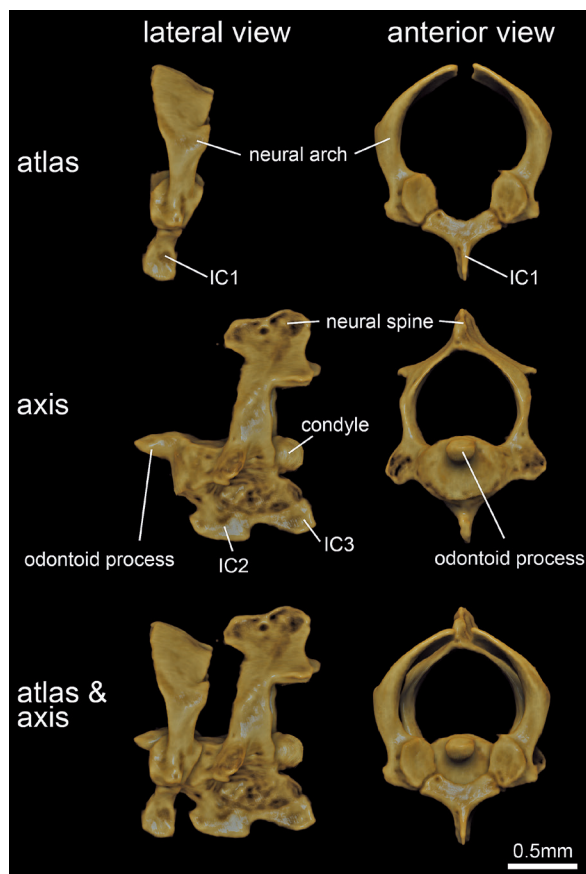


Fig. 4. Atlas and axis of *Ablepharus kitaibelii*. The atlas is a slender ring formed by the first intercentrum (IC1) and the two neural arches, which do not fuse dorsally. The first pleurocentrum (odontoid process) is fused to the stout axis, which also contains the second and third intercentrum (IC2 and IC3).

two cervical vertebrae, which allows for rotation in basically all directions. Such ball-and-socket joints can still be found in various amniote groups (Kasper, 1903; Hoffstetter and Gasc, 1969; Weisgram and Zweers, 1987). Additionally in some groups, most markedly in mammals, the odontoid process is elongated and acts as a pivot in turning the head (Wake, 1992). In the following we call this a ‘functional odontoid process’, and a functional odontoid process evolved homoplastically in different amniote lineages (Schaeffer *et al.*, 1972). The functionality and morphology of the odontoid process is most specialized in mammals, where it allows a lateral movement between atlas and axis, while the joint between the double occipital condyles and the atlas only allows a vertical movement (Romer, 1956). No reptile has evolved precisely the mammalian type of

atlas and axis, still various specializations have evolved within squamates (Romer, 1956). In many lizards the odontoid process comes to lie within a trough on the dorsal surface of the occipital condyle (Rieppel, 1980), while the atlas articulates via a concave facet to the occipital condyle.

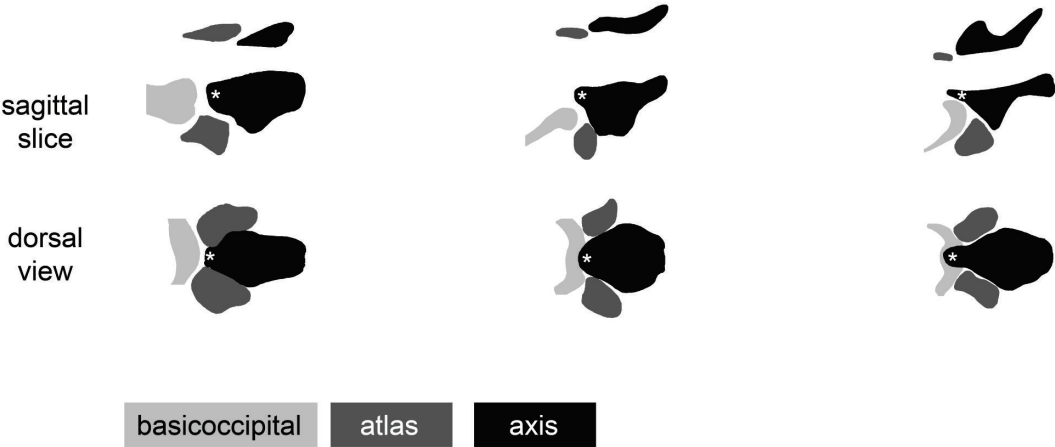
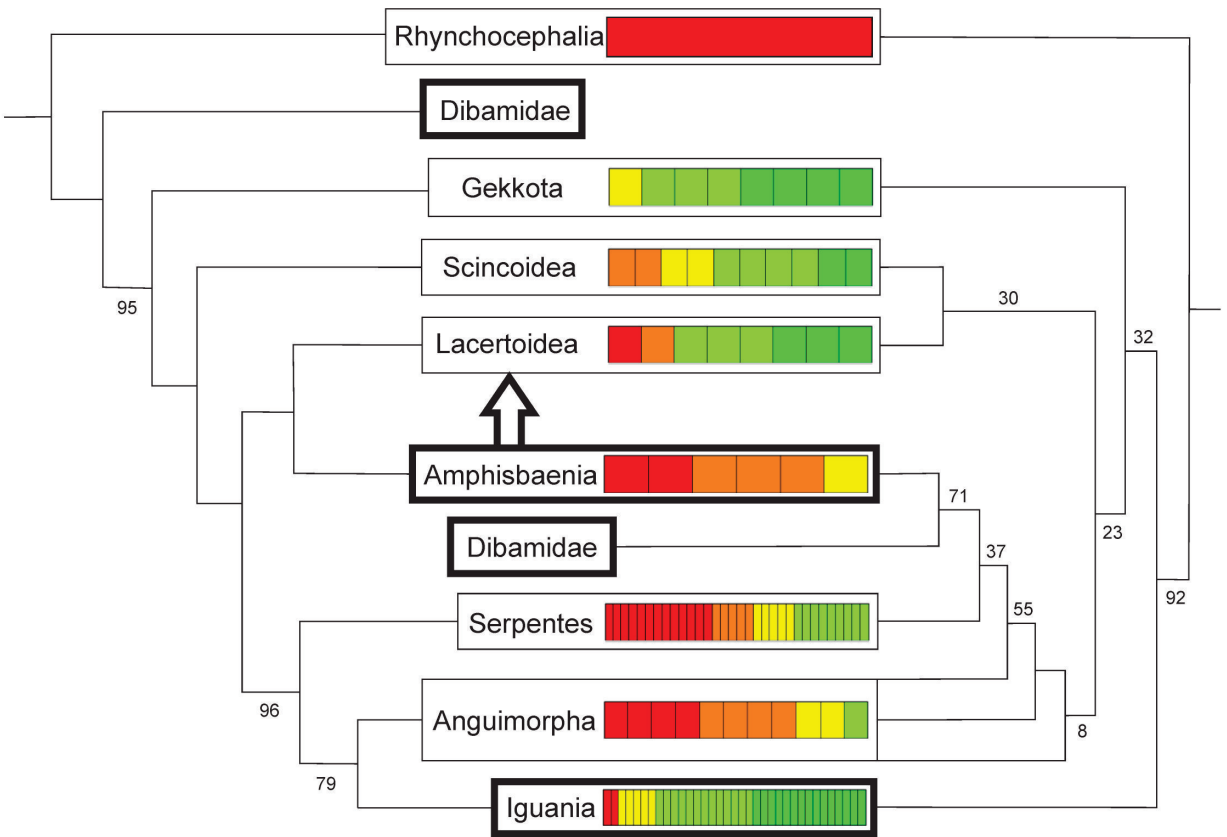
In *A. kitaibelii*, the morphology of the odontoid process is highly distinct. In its slim cylindrical appearance (Fig. 3b) it acts as a highly efficient pivot for lateral head rotation. Since in reptiles the atlas is more or less locked to the axis (Hoffstetter and Gasc, 1969), rotation occurs between the odontoid process and the skull, while in mammals rotation is between the odontoid process and the atlas. Considering the fast and vigorous head rotation during prey shaking, we hypothesise that the cylindrical odontoid process stabilises the cranio-cervical complex during prey shaking and improves the transmission of post-cranially created muscle forces onto the head. While the occipito-atlanto-axial joint stabilises the cranio-cervical joint during lateral rotation, it likely restricts the ability of the species to flex the cranium ventrally against the atlanto-axial complex (Fig. 11).

Differences in cranio-cervical morphology between major squamate groups

To our knowledge this is the first study that correlates feeding kinematics to cranio-cervical morphology in lizards. Considering the high variability in morphology of the odontoid process and the fact that some species totally lack an odontoid process *e.g.* the snake *Uropeltis* Cuvier, 1829 (Hoffstetter and Gasc, 1969), we think that linking feeding kinematics and locomotion to cranio-cervical morphology across various squamate groups should be a fruitful endeavour. In order to estimate the variability in cranio-cervical joints we screened μ CT datasets from 110 representatives of squamata (S3 Table) from the digital database Digi-morph (www.digimorph.org, Humphries, 2004). This screening revealed the presence of a functional odontoid process in 90 of these species. The analysis also showed that highly specialised pivot joints with a slim cylindrical or conoid odontoid process as described here for *A. kitaibelii* are very rare, but can be found in some iguanians (*e.g.* *Uma scoparia* Cope, 1894), some gekkotans (*e.g.* *Lialis burtonis* Gray, 1835), or in some teiids (*e.g.* *Aspidoscelis tigris* (Baird and Girard, 1852)). In most of the investigated squamate species the odontoid process is stout and blunt, and either pyramidal-shaped or round. Such joints can be found in some

Molecular tree modified from
Pyron et al. 2013

Morphological tree modified from
Gauthier et al. 2012



iguanians (e.g. *Anolis carolinensis* Voigt, 1832), scincoids (e.g. *Amphiglossus splendidus* (Grandidier, 1872)), or serpents (e.g. *Lachesis muta* (Linnaeus, 1766)). Blunt odontoid processes are limited in acting as pivot, thus such joints likely function as an intermediate between a ball-and socket and a specialised pivot joint. Other squamates entirely lack a functional odontoid process, such as some chameleons (e.g. *Brookesia brygooi* Raxworthy and Nussbaum, 1995), some amphisbaenians (e.g. *Amphisbaena fuliginosa* Linnaeus, 1758), or some serpents (e.g. *Boa constrictor* Linnaeus, 1758). Altogether the analysis of the digital datasets showed that the cranio-cervical joint of squamates is extremely variable even within taxa, a fact that warrants thorough functional investigation (see also Cernansky *et al.*, 2014; in chameleons, members of the genus *Rhampholeon* Werner, 1902 show totally different axis morphology). Although variability is large within major squamate groups, some general trends can be observed. Well-developed joints between occipital and odontoid process are common in iguanians, gekkotans, scincoids, and lacertoids, while they are rather rare in anguimorphs and totally lacking in amphisbaenians (Fig. 5, S3 Table). Therefore, the rareness of well-developed functional pivots in fossorial and legless species may be linked to species ecology e.g. in terms of locomotion.

Conclusions

Within squamates, highly specialised cranio-cervical joints such as the pivot joint described here evolved in parallel in various groups, and we hypothesise that such joints often represent functional adaptations to specific feeding and locomotion patterns. Linking feeding kinematics and locomotion to cranio-cervical

morphology in future studies might further elucidate the function of specialised occipito-atlanto-axial systems. The distribution of cranio-cervical joints in squamate groups shows that functional odontoid processes are rare in fossorial and legless groups.

Recent studies on higher-level squamate phylogeny still show major disagreements between molecular and morphological data (Fig. 5) (Gauthier *et al.*, 2012; Pyron *et al.*, 2013). Based on the high degree of parallel evolution, we think that the analysing of the morphology of the occipito-atlanto-axial complex will not help to resolve these disagreements.

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◀ Fig. 5. Variability of the occipito-atlanto-axial complex in major squamate groups. The variability of the occipito-atlanto-axial complex is plotted on two recent trees of higher-level squamate phylogeny. Left side: generalized tree (numbers at nodes are SHL values greater than 50%) presented by Pyron *et al.* (2013). Right side: generalized maximum parsimony strict consensus tree (numbers at nodes are BS values) presented by Gauthier *et al.* (2012). Bold frames indicate current disagreements between molecular and morphological data. In total we screened 110 digimorph (Humphries, 2004) microCT datasets for the presence and the morphology of a functional odontoid process (an odontoid process that acts as pivot in turning the head). By looking at sagittal and horizontal microCT slices we classified species into five groups according to the degree of overlap between the odontoid process and the basioccipital (1 (red) = no overlap, no functional odontoid process; 2-4 intermediate forms of overlap and odontoid process morphology; 5 (green) = perfect overlap, elongated odontoid process). Functional odontoid processes are common in e.g. iguanians and gekkotans (where they occur in more than 50% of the analysed species), but they are rare in e.g. amphisbaenians and serpents. Number of species analysed: Iguania n=35; Gekkota n=8; Lacertoidea n=8; Scincoidea n=10; Amphisbaenia n=6; Serpentes n=32; Anguimorpha n=11. Data on Rhynchocephalia was taken from Jones *et al.* (2009). * odontoid process.

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Online supplementary material

- S1. Video: This movie shows a prey shaking cluster typical for *Ablepharus kitaibelii* when feeding on *Tenebrio* larvae.
- S2. Video: In some sequences, prey immobilization behaviour included battering of prey items against the substrate.
- S3. Table: Variability of the occipito-atlanto-axial complex in major squamate groups.