THE MECHANISM OF AUTOTOMY IN *LACERTA*

By

LESLEY SHEPPARD AND A. D'A. BELLAIRS
Department of Anatomy, St. Mary's Hospital Medical School,
London, W.2.

(*Received* 27/2/72)

Introduction

Many lizards have a special mechanism for breaking off their tails as a means of escape from enemies, the process being known as autotomy (self-mutilation). As a rule the break occurs at one of a series of predetermined planes of weakness which are distributed along the greater part of the tail, one of these fracture planes passing through each of the caudal vertebrae and surrounding tissues. Fracture planes are absent in the base of the tail which contain the first six or more vertebrae; this region is close to the reproductive organ so that autotomy here would not be desirable.

The structure of the fracture planes has been described by various authors; among the most important accounts are those by Woodland (1920) of the gecko *Hemidactylus*, and by Pratt (1946) and Quattrini (1952a, b; 1953, 1954) of lacertids. Etheridge (1967) has described variations in the arrangement of the bony fracture planes in a wide range of saurian groups. Nevertheless, certain points, in particular of the muscular system, still require clarification and interpretation along functional lines.

Except when stated otherwise, our anatomical observations refer to the mid-caudal region of *Lacerta vivipara*, of which skeletal preparations and serial sections stained with Masson's trichrome, Van Gieson, and haematoxylin and eosin were available. We have also filmed 24 induced autotomies in 6 specimens of the Madeira wall lizard (*Lacerta dugesii*) at ambient temperatures of 30-35°C.

FRACTURE PLANES AND CAUDAL ANATOMY OF *LACERTA VIVIPARA*

1. THE VERTEBRAE

The vertebral fracture planes have been well described by Pratt. Each plane is represented by a split which divides the vertebrae into anterior and posterior portions, the anterior being slightly shorter (Figs. 1, 2). The split divides the centrum, where its edges are bordered by conspicuous bony ridges or " lips ", and continues dorsally through the neural arch on each side; it then extends up into the anterior neural spine but stops just short of the tip. The split passes mainly behind the single transverse process on each side, but passes obliquely through the posterior part of the base of the process. In some sections periosteal connective tissue can be seen within the margins of the split. A few cartilage cells can sometimes be seen embedded in the bony lips of the split, but we can find no distinct septum or ring of cartilage (or of other material) within the split as some workers have described.

2. THE AUTOTOMY SEPTUM, SKIN, AND SEGMENTATION OF THE TAIL

The vertebrae of the tail are surrounded by a layer of fat, and outside this again are the muscles and the skin Both fat and muscles are subdivided by a number of septa or sheets of connective tissue (Fig. 3D). The autotomy septum will be described first; the other septa are more conveniently dealt with along with the muscles and fat.

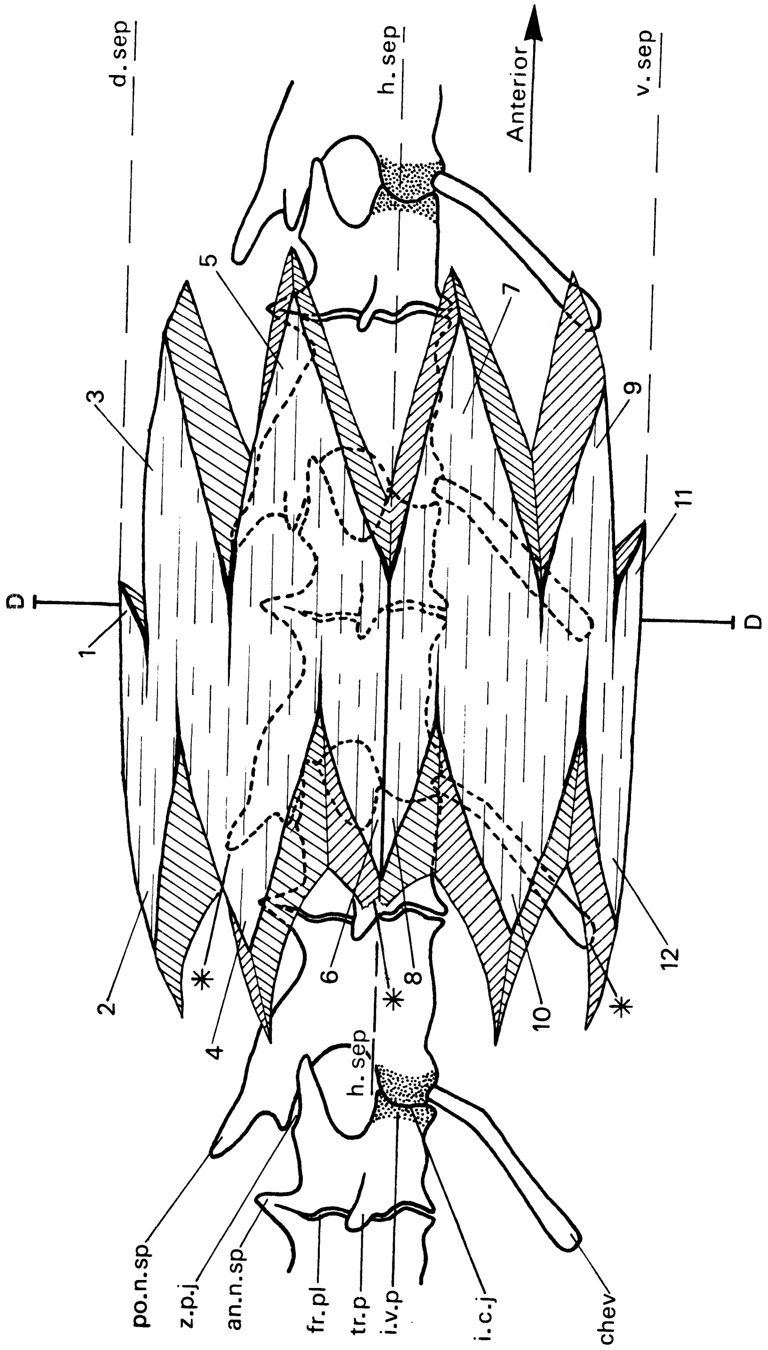

Fig. 1

The autotomy septum arises from the margins of the vertebral split, where it blends with the periosteum, and continues the plane of fracture outwards across the soft tissues towards the skin. It is perforated in the midline beneath the vertebra by the caudal artery and vein and does not cross the vertebral canal.

Although the outline of the autotomy septum conforms with the complex interlocking arrangement of the muscles, it lies essentially in the transverse plane of the tail. Consequently these septa demarcate a series of autotomy segments throughout the tail, except for the basal region. Each autotomy segment includes a muscle segment or myomere, a segment of fat, and the rear part of one vertebra together with the front part of the vertebra behind it. This arrangement corresponds with the segmental pattern of embryonic development. Each vertebra is derived from parts of two adjacent segments, and the autotomy septum and split in the vertebra represent the site of the primitive intersegmental boundary (*see* Werner, 1971).

The caudal scales are segmentally arranged, there being two transverse scale rows to each autotomy segment. The scales of the front row of each segment are shorter in antero-posterior length than those of the back row, and at autotomy the split in the skin occurs through the scale hinges at the front of a short row and behind a long row (Quattrini, 1952a). This point corresponds approximately with the split in the vertebra and is a useful guide in experiments which involve amputation of the tail.

The autotomy septum appears to end by blending with the deep layer of the dermis. Previous authors have described modifications for autotomy in the dermis of various lizards, including *Lacerta sicula* (Quattrini, 1954). In some of our material of *L. vivipara* the middle layer of the dermis beneath the appropriate scale hinges shows a localised condensation of connective tissue (Fig. 2). The junction between this and the looser adjacent tissue may provide a plane of cleavage.

3. THE MUSCLES, FAT AND LONGITUDINAL SEPTA

The muscles of the autotomous part of the tail have a complicated arrangement which is not easy to describe. Each muscle segment, together with the segment of fat which it surrounds, is divided into four portions, easily recognisable in transverse section (Fig. 3D). Thus, on each side of the tail there is one epaxial muscle and fat band, and similar hypaxial structures; these are separated by a horizontal longitudinal septum. This septum is attached along its inner edge to the length of the vertebra in the region where centrum and neural arch merge, and to the transverse process. Like the median septa it ends at the deep aspect of the dermis.

Each epaxial and each hypaxial muscle and fat band is separated from its fellow of the opposite side by a part of the longitudinal median septum. The dorsal part of this, between the epaxial tissues, arises from the dorsal midline of the vertebra, including the anterior and posterior neural spines.

The ventral median septum which separates the hypaxial structures is bilaminar, each layer arising from the centrum and intervertebral pad slightly to one side of the midline (Fig. 3D). The two layers of this septum enclose the caudal artery and vein and are attached to the two limbs of the V-shaped chevron bone. Where this septum lies between the ventral fat bands it encloses a smaller band of fat between its layers.

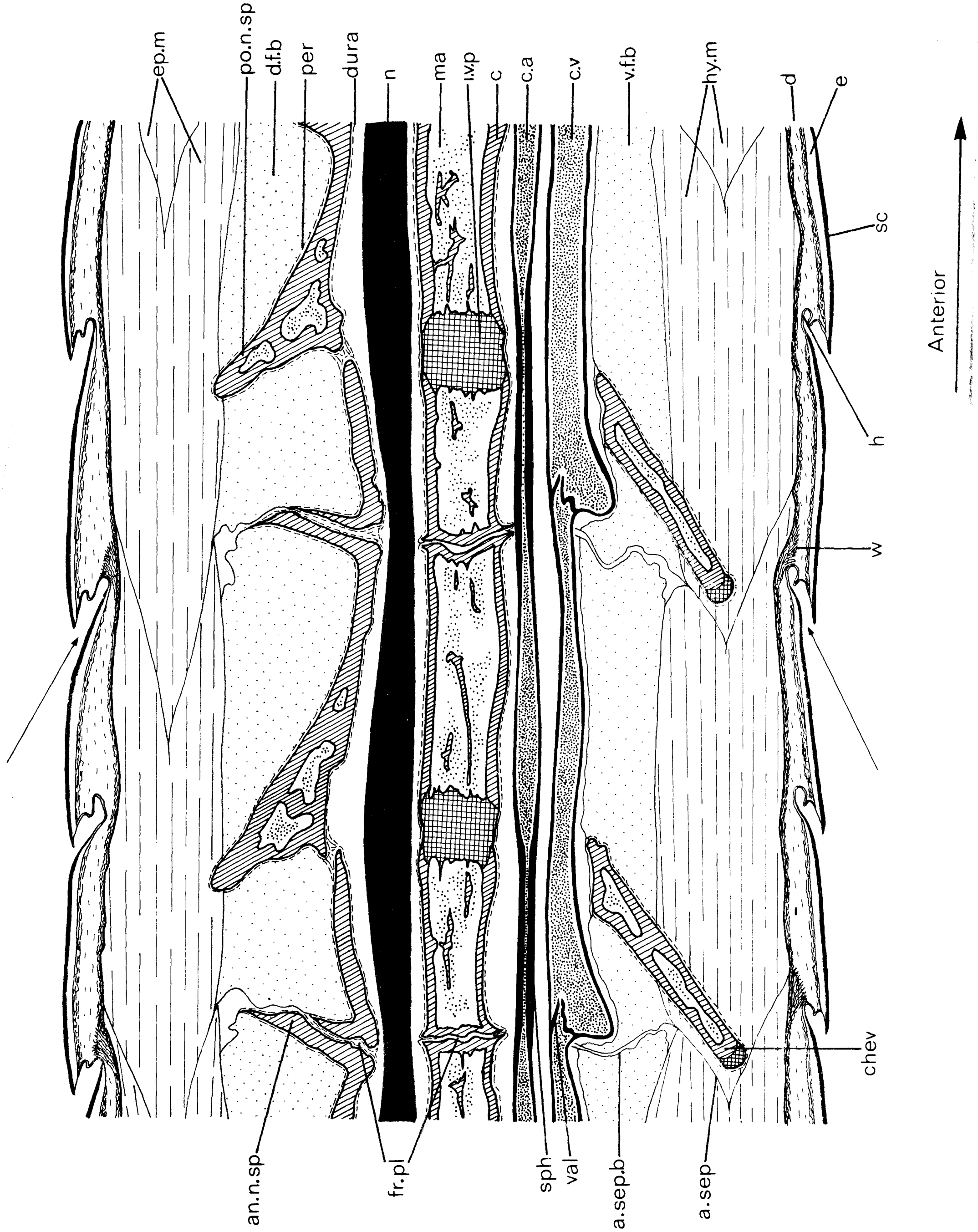
ep.m
po.n.sp
d.f.b
per
dura
n
ma
i.v.p
c
c.a
c.v
v.f.b
hy.m
d
e
sc
h
w
chev
Anterior
an.n.sp
fr.pl
sph
val
a.sep.b
a.sep

Fig. 2

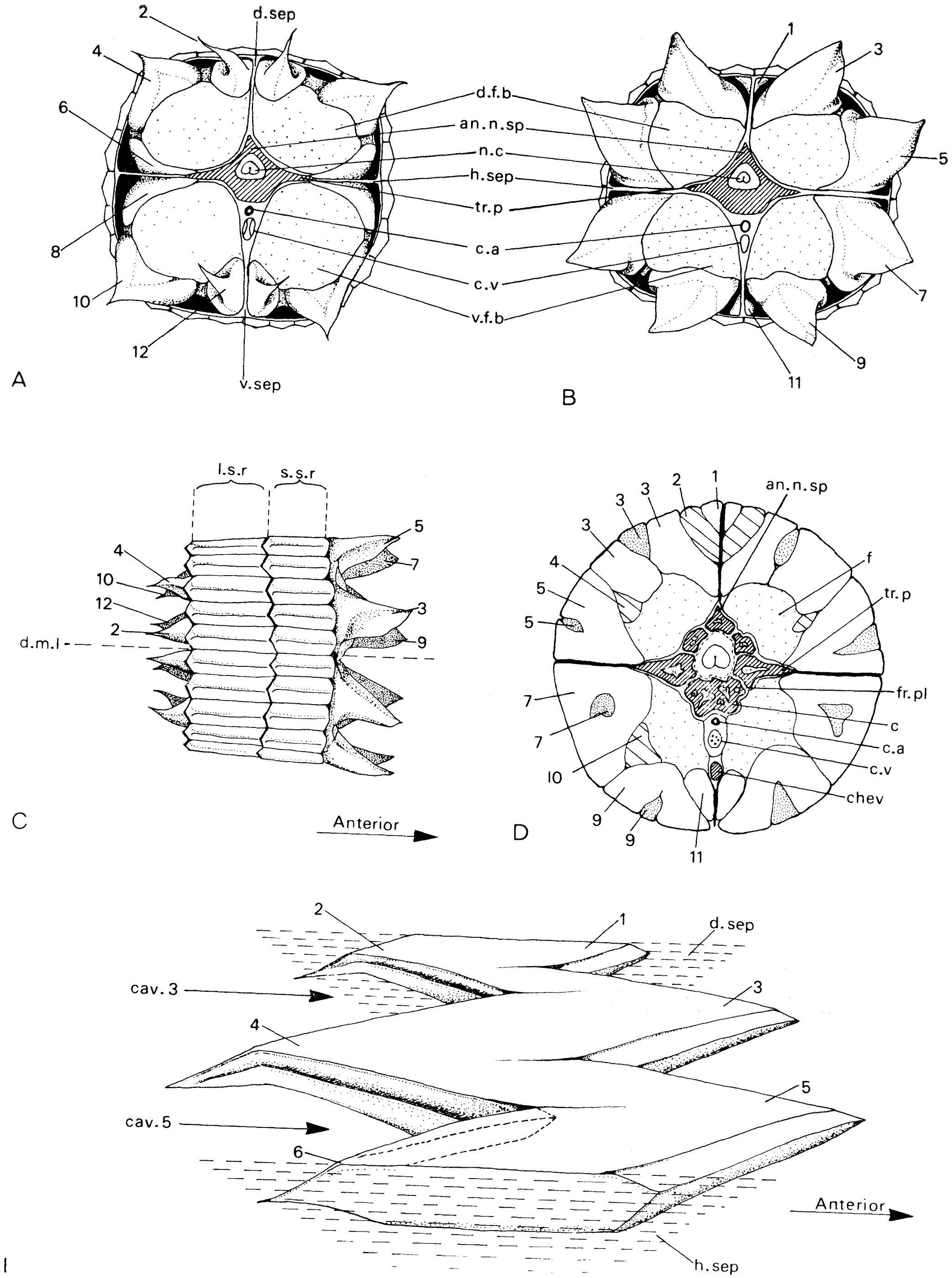
2
d.sep
4
1
3
6
d.f.b
an.n.sp
n.c
h.sep
tr.p
c.a
c.v
v.f.b
5
8
10
12
v.sep
7
9
11
A
B
l.s.r
s.s.r
d.m.l
C
Anterior
an.n.sp
f
tr.p
fr.pl
c
c.a
c.v
chev
D
cav. 3
cav. 5
d. sep
h.sep
Anterior

Fig 3

Each epaxial and each hypaxial muscle has three (dorsal, middle and ventral) pointed processes in front (designated by odd numbers in Fig. 1), and three behind (even numbers). These interlock with the corresponding processes of adjacent muscles and enclose recesses in which the tips of the latter are lodged (Fig 3C, 3E). The processes of each muscle are partly separated from each other by bands of connective tissue, and are separated from those of the muscles of adjacent segments by the autotomy septum. The anterior dorsal processes of each epaxial muscle (1) and the anterior ventral processes of each hypaxial muscle (11) are smaller than the rest.

Because of the interlocking arrangement the muscle blocks seen in transverse section may be derived from two or more segments (Fig. 3D).

Superficially the muscles are attached to the dermis. Their deep surfaces are mainly in contact with the fat bands, but are attached to the vertebrae in certain places, either directly or through the medium of septa. These attachments are as follows:

(a) The dorsal parts of the epaxial muscles (2) on each side are attached to the posterior neural spine, both directly and via the dorsal median septum.

(b) A small slip of muscle fibres arises from the deep aspect of the posterior middle epaxial process (4) and is attached to the capsule of the zygapophysial joint by means of a fibrous band.

(c) The posterior ventral epaxial process (6) is directly attached to the front of the transverse process of the vertebra.

(d) The posterior dorsal hypaxial process (8) is also attached to the front of the transverse process.

(e) The posterior ventral hypaxial process (12) is attached to the tip of the chevron.

As Woodland (1920) and Quattrini (1952b) have pointed out, only the posterior processes of the muscles have firm bony attachments. Each anterior process extends into the recess between the posterior processes of the muscle in front and is attached only to the autotomy septum. At autotomy separation will therefore take place only at this anterior and weaker attachment.

Immediately after autotomy has occurred, four pairs of anterior muscle processes can be seen projecting conspicuously from the front of the detached portion of tail (3, 5, 7, 9 in Figs. 1 and 3B, 3C). The processes 1 and 11 in Fig. 1. do not project from the tail fragment.

The broken surface of the stump shows four pairs of recesses which, before autotomy, accomodated the anterior processes of the tail fragment. These recesses lie between the posterior processes of the muscles in front (Figs. 3A, 3E). The latter project beyond the broken skin of the stump to some extent, though they are less prominent than the anterior processes on the fragment and seem to have been overlooked by most workers. Soon after autotomy they appear to shrink and become hidden by the contraction of the skin around the stump surface. We confirm Quattrini's observation (1954) that after breakage the autotomy septum adheres to the posterior processes. The septum may therefore protect the muscles of the stump from injury; this helps to explain the finding that muscle cells make no substantial contribution to the blastema from which the regenerating tail is formed (*see* Bryant, 1970).

4. THE SPINAL CORD AND BLOOD VESSELS

The spinal cord is slightly constricted in the region of each vertebral fracture plane, the constriction being more marked in the lateral plane than dorsi-ventrally.

Quattrini (1954) was unable to find sphincters in the wall of the caudal artery of *Lacerta sicula*. In *L. vivipara*, however, the walls of this artery show a series of elongated regional thickenings. Each of these starts just behind the level of the vertebral split and extends forwards as far as the front of the

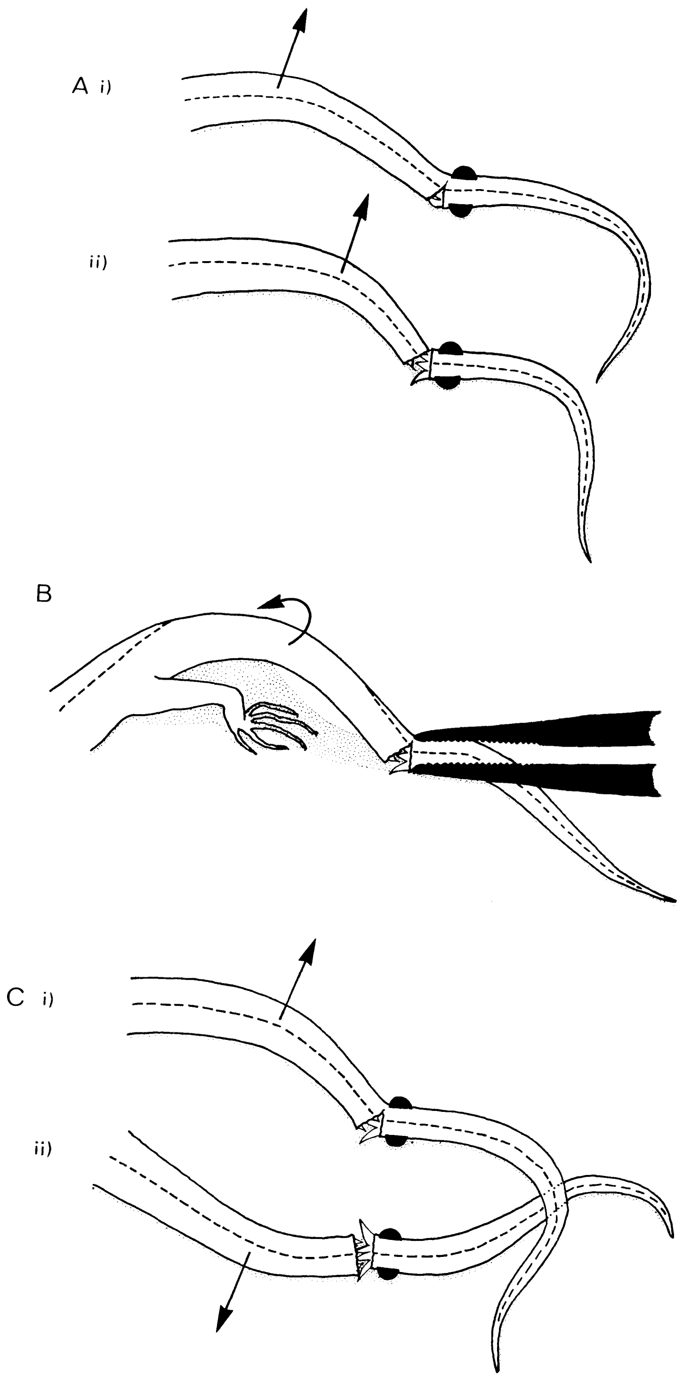

Fig. 4

same vertebra, therefore occupying nearly half of the autotomy segment. As in *L. sicula* the caudal vein contains a series of valves, each lying slightly in front of the corresponding vertebral split (Fig. 2). The effect of these valves, like that of the arterial "sphincters" would be to prevent undue loss of blood after autotomy.

DISCUSSION

1. SIGNIFICANCE OF THE FAT LAYER

Most, if not all of the autotomous lizards described, and a few non-autotomous ones such as the Gila monster (*Heloderma suspectum*) possess a submuscular fat layer. This caudal fat is thought to provide a reserve of food. In *Lacerta vivipara* it is utilised during or just after hibernation (Avery, 1970), while in certain geckos and in the Gila monster it is drawn upon when the animal shelters from the rigours of a semi-arid habitat (Bogert and Del Campo, 1956).

The adaptive value of autotomy, as Etheridge points out, is very high and seems to be more important in many lizards than the benefit of storing fat in the tail. The fact that a caudal fat layer, divided by septa into transverse segments and longitudinal bands, appears to be characteristic of autotomous lizards even suggests that the fat may play some part in the mechanism of autotomy, quite divorced from its nutritive function. This idea is strengthened by the absence of caudal fat in non-autotomous forms such as the monitors (*Varanus*) and agamids such as *Calotes* (Woodland, 1920; Ali, 1949), but further work on biomechanical lines is needed to clarify this problem.

2. MECHANISM OF AUTOTOMY

Although autotomy may be facilitated by the mechanical strain exerted by a predator, it normally seems to involve active contraction of the tail muscles to a greater or lesser extent. These muscles have two distinct functions; to produce normal flexion of the tail, and to bring about autotomy. Their precise actions during the latter process can perhaps only be elucidated by electrophysiological methods; we were able, however, to draw certain inferences from the present study.

Our film shows that when the tail is grasped by forceps, the regions in front of and behind the point of seizure frequently contract strongly; sometimes the distal part of the tail writhes violently. Flexion of the tail in front of the forceps often takes place in both the lateral and vertical (dorsi-ventral) planes; the two movements are often combined to produce a rotatory effect. Here our observations differ from those of Woodland who found that in geckos only lateral flexion was important. By fixing the tail at one point the forceps act as a fulcrum for leverage; in some cases the tail was actually twisted around the forceps. The fixation of the tail probably helps to concentrate the stress at one particular fracture plane. Under natural conditions a comparable fixed point would be provided by the jaws or paw of a predator.

In most cases the fracture occurred at the front of the autotomy segment which was being held; it never took place more than three segments anterior to this. The economical character of autotomy, in which only a minimal portion of tail is usually shed, has been noted by previous workers.

Both Woodland (1920) and Boring *et al.* (1948) suggested that in geckos successive contraction of the muscles on two opposite sides of the tail is necessary to complete autotomy. Similar to-and-fro movement seemed to occur in a few of the autotomies observed by us in *Lacerta dugesii* (Fig. 4C). In the majority of cases filmed, however, the autotomising region of the tail seemed to be bent in one main direction only; to one side (Fig. 4A), or up or down, or in a rotatory fashion. (Fig. 4B).

The skin is first split on the stretched, convex aspect of the tail and then the muscles on this aspect separate from their weak anterior attachments. The split then appears to travel right across the remaining tissues of the tail. Separation of the two halves of the vertebra would require little force because of the presence of the fracture plane; separation of the fat segments on both sides would also be easy because the intra-adipose part of the autotomy septum consists of two layers with a potential plane of cleavage between them. It is perhaps more surprising that the skin and full thickness of the muscles on the concave, flexed aspect of the tail should also readily be divided by unidirectional bending without to-and-fro movement. It is possible either that such movement does occur but that the amplitude of the second contraction is so slight as not to be easily discernible in our film (except in a few cases); or else that the final rupture of the more superficial tissues on the concave aspect is effected by direct or rotational stress rather than by contralateral flexion.

Woodland and Boring *et al.* believed that the muscular contraction involved in autotomy is limited to a single segment only. This seems improbable, especially if to-and-fro movement is postulated. If the muscles on the stretched convex side of one segment are initially pulled away from their attachments they would be unable to contract effectively to produce a second flexion in the opposite direction. It is possible to envisage an alternative and more complicated mechanism in which the muscles are separated, not by stretching but by the force of their own contraction. We think it more likely, however, that several muscle segments are involved on one or both sides, and that if to-and-fro movement is necessary the intact segments adjacent to the ruptured one bring about the second contraction.

Woodland found that autotomy only occurred if part of the tail was fixed in some way. Nevertheless, it has occasionally been recorded in some species without the tail actually being touched; we have observed this once in *Lacerta dugesii*. It is possible that in such cases some irregularity of the ground or some feature of the surroundings would offer the necessary resistance to serve as a fixed point of leverage. Whether autotomy can ever occur if the tail is completely free remains uncertain.

SUMMARY

1. The anatomy of the mid-caudal fracture planes of *Lacerta vivipara* is described, with special reference to the muscles and connective tissue septa. The presence of valves along the caudal vein is a feature of interest.

2. The role of the muscles in producing autotomy is discussed, partly on the basis of a film of induced autotomies in *Lacerta dugesii*.

We are grateful to Mr. David Rodgers of the Photographic Department, St. Mary's Hospital Medical School, for his great assistance in preparing the film, and to Mr. Barry Martin for skeletal preparations. This work was assisted by a grant from the Science Research Council.

REFERENCES

ALI, S. M. (1949). Studies on the anatomy of the tail in Sauria and Rhynchocephalia. Part III. *Varanus monitor* (Linné). *Proc. Ind. Acad. Sci.* **30, 155-67**.

AVERY, R. A. (1970). Utilization of caudal fat by hibernating Common Lizards, *Lacerta vivipara. Comp. Biochem. Physiol.* **37,** 119-21.

BOGERT, C. M. and DEL CAMPO, R. M. (1956). The Gila monster and its allies . . . *Bull. Am. Mus. nat. Hist.* **109,** 1-238.

BORING, A. M., CHANG, L.-F. and CHANG, W.-H. (1948). Autotomy and regeneration in the tails of lizards. *Peking Nat. Hist. Bull.* **17,** 85-108.

BRYANT, S. V. (1970). Regeneration in amphibians and reptiles. *Endeavour*, **29, 12-17**.

ETHERIDGE, R. (1967). Lizard caudal vertebrae. *Copeia*, 699-721.

PRATT, C. W. M. (1946). The plane of fracture of the caudal vertebrae of certain lacertilians. *J. Anat.* **80,** 184-88.

QUATTRINI, D. (1952a). Richerche anatomiche e sperementali sulla autotomia della coda lucertole . . . *[Lacerta sicula]. Archo. zool. ital.* **37,** 131-70. (1952b): *Ibid.*, 465-515.

QUATTRINI, D. (1953). Autotomia e struttura anatomica della coda dei Rettili . . . *[Lacerta vivipara; L. viridis]. Mon. zool. ital.* **61,** 36-48.

QUATTRINI, D. (1954). Piano di autotomia e rigenerazione della coda nei Sauri . . . *[Lacerta sicula]. Archo. ital. Anat. Embriol.* **59,** 225-82.

WERNER, Y. L. (1971). The ontogenetic development of the vertebrae in some gekkonoid lizards. *J. Morph.* **133**, 41-92.
WOODLAND, W. N. F. (1920). Some observations on caudal autotomy and regeneration in the gecko (*Hemidactylus flaviviridis* Rüppel) . . . *Q. Jl. Microsc. Sci.* **65**, 63-100.

ABBREVIATIONS

an.n.sp, anterior neural spine
a.sep, autotomy septum between muscles (one-layered)
a.sep.b, autotomy septum through fat (two-layered)
c, centrum
c.a, caudal artery
cav, cavity into which muscle process fits
chev, chevron bone
c.v, caudal vein
d, dermis
d.f.b, dorsal fat band
d.m.l, dorsal midline
d.sep, dorsal part of median longitudinal septum
dura, dura mater
e, epidermis
ep.m, epaxial muscle
f, fat band
fr.pl, vertebral fracture plane
h, hinge of scale
h.sep, horizontal longitudinal septum
hy.m, hypaxial muscle
i.c.j, intercentral joint
i.v.p, cartilaginous intervertebral pad
l.s.r, long scale row
ma, marrow cavity of vertebra
n, n.c, nerve cord
per, periosteum
po.n.sp, posterior neural spine
sc, scale
sph, " sphincter " of caudal artery
s.s.r, short scale row
tr.p, transverse process
val, valve in caudal vein
v.f.b, ventral fat band
v. sep, ventral part of median longitudinal septum
w, plane of weakness in dermis
z.p.j, zygapophysial joint
1,3,5, anterior processes of epaxial muscle
7,9,11, anterior processes of hypaxial muscle
2,4,6, posterior processes of epaxial muscle
8,10,12, posterior processes of hypaxial muscle.

FIGURE 1.

Diagram showing relationships of muscles and vertebrae in mid-caudal region of *Lacerta vivipara,* seen from right side after removal of skin (*c.* x^{15}). The muscles of a single autotomy segment are shown. Attachments of muscles to vertebrae indicated by *. The line DD shows plane of transverse section in Fig. 2D.

Long broken lines: outer surface of muscle, normally in contact with dermis. *Short broken lines*: outline of vertebrae, concealed by muscles. *Slanting lines*: Interlocking surfaces of muscle processes; these are covered by the autotomy septum.

Abbreviations on p. 285.

FIGURE 2.

Diagrammatic vertical longitudinal section through middle part of tail of *Lacerta vivipara,* slightly to one side of midline. (*c.* x^{25}). Arrows indicate points where skin breaks at autotomy.

Abbreviations on p. 285.

FIGURE 3.

A, B, C; *Lacerta dugesii.* A, tail stump after autotomy. B, proximal end of tail fragment after autotomy. C, one autotomy segment seen from above, showing scales, and muscle processes projecting behind and in front of the segment, after autotomy (All *c.* x^{10}).

D, E; *Lacerta vivipara.* D, transverse section through middle of tail in region of the autotomy plane (*c.* x^{10}). Interlocking muscle processes of segment in front in slanting lines; of segment behind in stipple. E, single epaxial muscle segment seen in oblique lateral view after removal of skin: diagrammatic. Outline of concavity between muscle processes in short broken lines. Longitudinal septa shown in long broken lines. Cav. 3 and cav. 5; cavities for processes 3 and 5 of muscle segment behind.

Abbreviations on p. 285.

FIGURE 4.

Diagrams illustrating methods of autotomy when tail is fixed. A, by lateral flexion in one direction (i and ii show successive phases). B, by flexion and rotation. C, by successive flexions (i and ii) in opposite directions (to-and-fro movement). Dorsal midline shown in broken lines. Forceps (tips only in A and C) are in black. Arrows show directions of bending.

SITE TENURE AND SELECTION IN THE AFRICAN GECKO *TARENTOLA ANNULARIS* (GEOFFROY).

by

J. L. Cloudsley-Thompson
Department of Zoology, University of Khartoum, Sudan*

(*Received* 13/12/71)

In an artificial " room ", geckos sheltered most often behind " pictures " providing the greatest security. Despite an abnormally high population density, there was a significant tendency for each " picture " to be occupied only by a single gecko, indicating a degree of spacing. Individual geckos tended to occupy the same sites in many successive observations. " Pictures " lying horizontally on the floor were preferred to " pictures " hanging on the " walls ". The attraction of the pictures was apparently due to the concealment they provided and not to the reduction in light intensity afforded. A " field " experiment confirmed the existence of site tenure and indicated a very slow rate of recolonisation in nature.

---

*Present address, Department of Zoology, Birkbeck College, University of London, England.