THE PLANE OF FRACTURE OF THE CAUDAL VERTEBRAE
OF CERTAIN LACERTILIANS

By C. W. M. PRATT, *From the Department of Anatomy, Manchester University*

Certain lizards have the power of producing self-mutilation by severance of the tail; this autotomy is followed in the course of time by regeneration. The phenomenon is a well-known one, but a thorough scientific examination of the actual anatomical conditions that make it possible has not been carried out. Its occurrence in *Sphenodon* was first described by Günther (1867), and later by Howes & Swinnerton (1901). Its general presence among the Lacertae and Geckones has attracted the attention of investigators such as Leydig, Gegenbaur, Hyrtl, Müller and many others. In spite of the natural interest that this phenomenon has excited, the literature on the subject is full of misleading and confusing statements, and it is with the object of clearing up this confusion that the present investigation has been undertaken.

It is generally agreed that this highly specialized protective mechanism on the part of the lizard is a result of adaptation to prevailing environmental conditions (Morgan, 1901). It is of interest that it does not occur in any species in which the tail possesses a definite and specialized function, such as swimming or grasping, since under these conditions it would prove to be a distinct disadvantage by causing mechanical instability. Associated with the development of the power of autotomy there is a corresponding increase in length of the tail. Boulenger (1920) states that the more primitive members of a genus possess a relatively shorter tail in relation to the length of the body than do the more specialized species.

In order that autotomy may occur, a predetermined fracture plane is developed across the tail. Usually this takes the form of a series of such planes, resulting in a segmented condition. The actual relation of such planes to the vertebra has caused a certain amount of confusion. Most investigators, such as Gadow (1901, 1933), Cope (1892, 1900) and Woodland (1920), state that the plane passes through the centrum of the vertebra, dividing it in some cases into equal and in others into unequal portions. Leighton (1903) claims that in *Lacerta viridis* and *Anguis fragilis*, at least, there is an intervertebral fracture plane. His evidence for this statement, however, is not very convincing.

Those morphologists who believe in the intracentral fracture plane are further divided in their views as to the exact relationship of the fracture plane to the constitution of the vertebra itself. A fracture plane passing approximately through the middle of a vertebral body would suggest an intersegmental condition in the true morphological sense. Goodrich (1930) accepts this, by explaining that it is due to the failure of fusion of the caudal and cephalic halves of adjacent sclerotomes. Gadow (1933), with his views on vertebral constitution, considers it not to be truly intersegmental, since if it were, it would occur between the basiventral and interventral elements, that is, between the centrum and the intervertebral disc. This would support Leighton's intervertebral fracture-plane theory.

The origin of the vertebral fracture plane, as given by Gadow (1933), is that a cartilaginous septum develops in the middle of the vertebra, destroying the notochord. This is often known as the 'chordal cartilage'. Gegenbaur (1862) and Hyrtl have both shown that the split which is often present in the vertebra develops only after ossification has taken place. It commences on the outside, becomes deeper, and then extends to the neuro-central suture and even to the neural arch. This split, though rendering autotomy more simple, is not essential, since, according to Cope (1892, 1900), it is not present in *Ophisaurus* (the glass snake), which shows the phenomenon in a high state of perfection.

The septum, which appears to represent an intersegmental structure, is almost certainly secondary in nature. Goodrich (1930) points out that it is not seen in any of the primitive reptiles, while Gadow (1933) and Willeston (1925) state that it is a post-embryonic or at least a late embryonic development.

Having considered the general morphological interpretation of the fracture plane, the structural details associated with the occurrence of autotomy will be described. The present investigation has been confined to two indigenous species, *Lacerta vivipara* and *Anguis fragilis*. A careful description has been made by Woodland (1920) of the Indian Gecko (*Hemidactylus flaviviridis* Rüp.), which makes a useful comparison.

The most anterior caudal vertebrae possess no split in their centra and form the basal unsegmented region of the tail. Such a condition is essential for the protection of the cloaca. The first vertebra to show the presence of a split is either the seventh or the eighth and, in *Sphenodon* at least, it is not
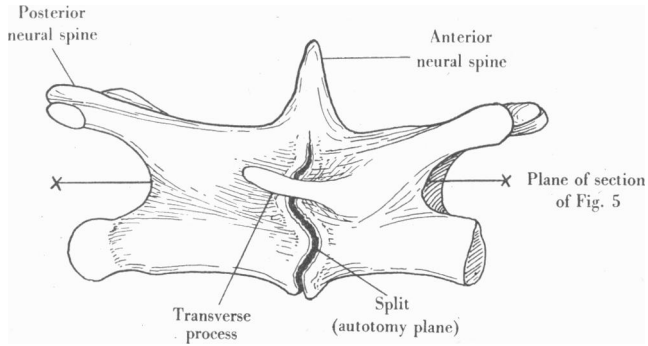
Fig. 1. *Lacerta vivipara*. Mid-caudal vertebra, lateral aspect. ×22·5.

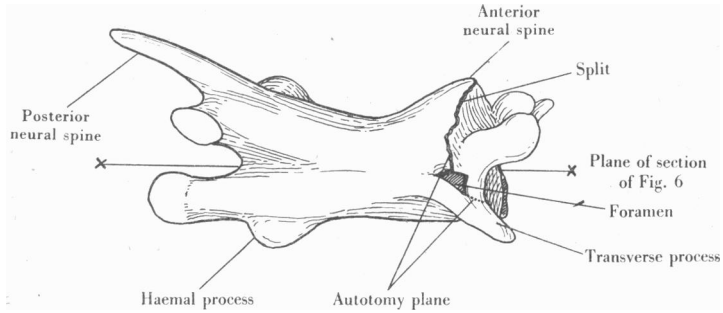Fig. 2. *Anguis fragilis*. Mid-caudal vertebra, lateral aspect. ×10.
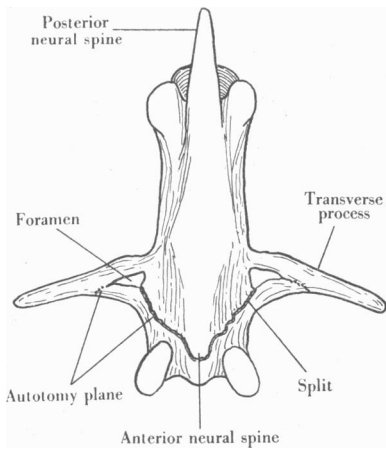
Fig. 3. *Anguis fragilis*. Mid-caudal vertebra, dorsal aspect. ×10.

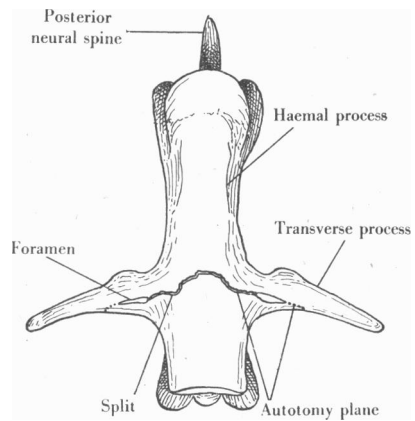Fig. 4. *Anguis fragilis*. Mid-caudal vertebra, ventral aspect. ×10.

constant for a species, occurring from the sixth to the eighth vertebra (Howes & Swinnerton 1901).

In *Lacerta vivipara*, the split divides the centrum and extends into the neural arch almost to the neural spine (Fig. 1). Here it ceases and if autotomy occurs, it causes direct fracture of the bone. The split divides the vertebra approximately into halves in the mid-caudal region, though cephalad it may occur between the anterior and middle thirds of the vertebra, but it always passes posterior to the transverse process. The split is bordered by well-marked lips which may be due to the growth of the vertebra

spine (the 'anterior neural spine' of Cope, 1900). Laterally, it reaches the anterior border of the foramen which partly divides the transverse process at its base. Thus when autotomy occurs, the only part actually fractured is the anterior part of the divided base of the transverse process, resulting in a short transverse process retained by the animal and a long process attached to the lost tail. Unlike the condition present in *Lacerta*, the split occurs very near the anterior end of the vertebra; approximately a quarter of the vertebra is divided from the rest in autotomy, and this occurs both in the anterior and mid-caudal
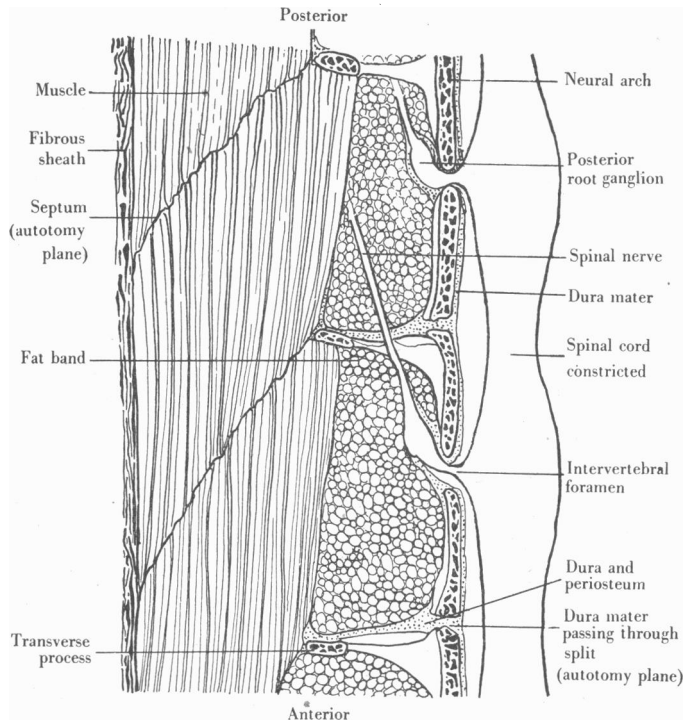

Fig. 5. *Lacerta vivipara*. Horizontal section of mid-dorsal region, through plane of transverse process (only one side shown). × 22·5.

after formation of the split. Howes & Swinnerton (1901) claim that in *Sphenodon*, on the ventral surface, these lips provide additional protection to the haemal canal. The lips are bound together by means of the dura mater which issues from the vertebral canal, passes through the split, blends with the periosteum and, outside the vertebra, becomes continuous with the tissue of the autotomy plane (Fig. 5). Thus when autotomy occurs, this tissue is torn away from the bone.

In *Anguis fragilis* (Figs. 2–4) the conditions are somewhat different. The split extends across the centrum and across the neural arch, including the neural spine (the 'anterior neural spine' of Cope, 1900).

regions. The split is not quite as wide as in *Lacerta* either in the centrum or in the neural arch or spine, but is more like a crack in the bone. Its constant presence and the fact that the periosteal covering is intact show that it is not solely a result of mechanical strain, though probably it is brought about in this way early in life and long before autotomy occurs. There is no continuance of tissue from within the vertebra as in the case of *L. vivipara*, even in the more marked region of the split, though if the split is not very wide there is a continuance of periosteum across it (Fig. 6).

It is interesting to note that in both species the

spinal cord itself shows marked constriction at the fracture plane (Figs. 5, 6), a possible means of ensuring minimal damage. The relation of the spinal nerve is essentially the same in both species. On leaving the intervertebral foramen, the anterior and posterior roots join to form the spinal nerve, which passes backwards above the transverse process and across the fracture plane where, at least in the case of *L. vivipara*, its sheath of dura mater is continuous with the septal tissue (Fig. 5). The nerve passes within the 'fat band' to the next segment which it supplies. Woodland (1920) states that the regene-

attachment is to the vertebra and to the septa covering the fat bands, while the anterior attachment is largely into the next segment via the septal tissue. Thus when autotomy occurs, the proximal end of the lost tail has eight pointed muscle bands protruding.

In *L. vivipara*, the anterior attachments of the lateral muscle bands are made to the transverse process by means of a mass of septal tissue (Fig. 5), while in *A. fragilis* there is a direct attachment to the transverse process of the next segment (Fig. 6) which results in the division of the process on fracture.
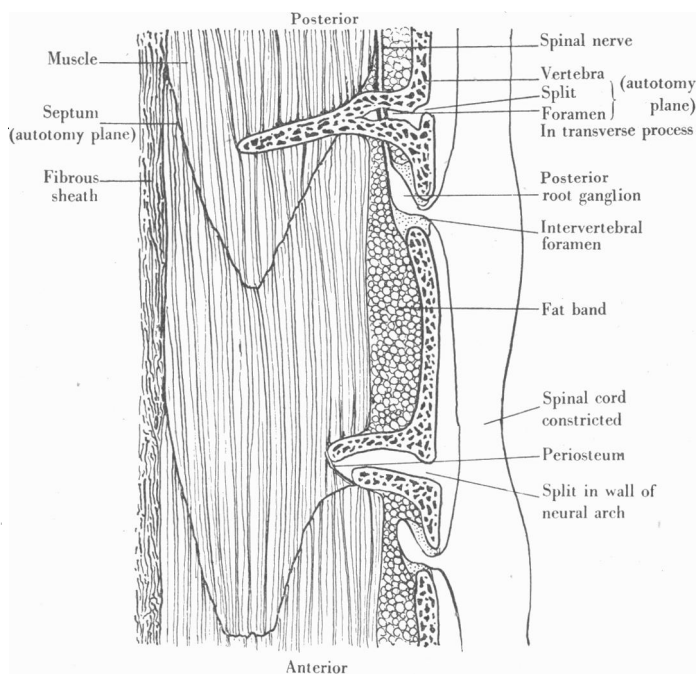

Fig. 6. *Anguis fragilis*. Horizontal section of mid-dorsal region, through plane of transverse process (only one side shown). × 10.

rated tail may be supplied by the last two or three spinal nerves, which suggests that one nerve may supply several segments.

The importance of the special arrangement of the muscles is emphasized by Woodland (1920) and others, for without this, autotomy could not occur. This is really the most important part of the mechanism of autotomy, for if the bone is fragile, it will readily fracture without any preformed split and this undoubtedly often occurs.

In each species the arrangement is similar. Due to the presence of fibrous septa, the muscles are arranged into eight bands, two ventrally, four laterally and two dorsally, and these all interdigitate with those of the next segment. The posterior

The apparently unstable attachment of the anterior ends of the muscle bands into septal tissue can be understood when it is realized that, in ordinary movement of the tail, the tension produced by the muscular contractions is equally distributed throughout all the segments. However, when one part of the tail is fixed, as occurs when it is caught by a bird, the undue strain produced by the movement of the rest of the tail in front of the fixed part results in fracture.

The relation of the fracture plane to the scales is well known, occurring in most cases between every two rows of scales, a fact that can be made use of in determining possible planes of fracture, as in the basal region where scaling is irregular, no fracture

plane exists. Beneath the scales is a subcutaneous fibrous sheet which is continuous with the septal tissue and shows no indication of segmentation. It is somewhat thicker and far stronger in *A. fragilis* (Fig. 6) than in *L. vivipara* (Fig. 5).

The integrity of the tail can now be considered, for though at times it may be a great advantage to undergo autotomy, it must be possible to sustain certain mechanical strains without fracturing. In *L. vivipara* a protection against excessive autotomy is present in the integument, but much more important is the fibrous tissue binding the lips of the vertebral split together and the dura mater which blends with the periosteum. The strong subcutaneous fibrous sheet seen in *A. fragilis* affords great protection to the tail, in fact, it is very difficult to break the tail by simple mechanical strain, while in *L. vivipara* the tail appears by comparison very fragile. It is interesting to note that there is not the strong fibrous sheet binding the split as there is in *L. vivipara*, for any strain the well-protected

vertebra might undergo would be met by the thin periosteal covering and the undivided transverse process.

In conclusion, it is found that certain lizards have developed a special caudal fracture plane and that morphologically this plane is almost certainly intersegmental. Those species which show the development of this plane exhibit the phenomenon of autotomy. The nature of the plane is not as stated by Woodland (1920), a hyaline septum, making a continuous cleavage plane, save for blood vessels, nerves and spinal cord; but rather is a partial cleavage (or fracture) plane of most of the tissues of the tail which is compensated for by the strengthening of other tissues in order to prevent excessive autotomy. The amount and position of the strengthening material, however, vary considerably with different species.

REFERENCES

BOULENGER, G. A. (1920). *Monograph of the Lacertidae*, 1, 33. Brit. Mus. (Nat. Hist.).

COPE, E. D. (1892). *Proc. Amer. phil. Soc.* 30, 185.

COPE, E. D. (1900). *The Crocodiles, Lizards and Snakes of North America*, p. 190. New York.

GADOW, H. F. (1901). *Amphibia and Reptiles*. Camb. Nat. Hist. 8, 297, 495, 503.

GADOW, H. F. (1933). *Evolution of the Vertebral Column*. Ed. by Gaskell and Green, pp. 261, 268, 274. Cambridge.

GEGENBAUR, C. (1862). *Vergl. Anat. der Wirbelsäule bei Amphibien u. Reptilien*. Leipzig.

GOODRICH, E. S. (1930). *The Structure and Development of Vertebrates*, p. 62. London: Macmillan and Co.

GÜNTHER, A. C. (1867). *Philos. Trans.* 157, 606.

HOWES, G. B. & SWINNERTON, H. H. (1901). *Trans. zool. Soc. Lond.* 16, 23.

LEIGHTON, G. A. (1903). *The Life History of British Lizards*, p. 113. London.

MORGAN, T. H. (1901). *Regeneration*, pp. 155–8. New York.

WILLESTON, S. W. (1925). *The Osteology of the Reptiles*, p. 109. Harvard Univ. Press.

WOODLAND, W. F. N. (1920). *Quart. J. micr. Sci.* 65, 63.