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ON THE

HEAD KIDNEY OF BDELLOSTOMA,

WITH A

SUGGESTION AS TO THE ORIGIN OF THE SUPRARENAL BODIES.

BY

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On the Head Kidney of Bdellostoma, with a Suggestion as to the Origin of the Suprarenal Bodies.

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With Plate XV.

The structure of the greater part of the kidney of Bdellostoma and the Myxinoids generally has been known since the time of Johannes Müller. It consists of a simple segmental duct on each side, which represents both the Wolffian and Müllerian ducts of the higher Vertebrates, giving off in its course a series of short tubules, each of which ends in a large glomerulus. These tubules are segmentally arranged, a single pair being present in every segment of the body in the anterior three fourths of the region lying between the anus and the hinder border of the pericardium. The relations of this system of simple segmental tubules, opening into a segmental duct, were described with perfect accuracy by Johannes Müller;[1] and no important additions have since been made to the account which he gave.

The whole system obviously represents the Wolffian body of the higher Vertebrates before the splitting of the segmental duct into Wolffian and Müllerian ducts.

In front of the kidney proper, however, there is on each

[1] 'Vergleichende Anatomie d. Myxinoiden,' Berlin, 1836—1845.

side a small, lobulated, apparently glandular body, whose structure is not so well known.

Each of these bodies is, in Bdellostoma Forsteri, from 20 to 25 millimètres long, and from 5 to 7 mm. broad; looked at with a simple lens, or with the naked eye, it is seen to consist of several small lobuli, which project into the cavity of the pericardium on the one hand, the whole gland being connected on the other with the connective-tissue adventitia of a great vein—the gland of the right side with the adventitia of the portal vein, that of the left with the anterior cardinal. In Pl. XV, fig. 1, an attempt has been made to represent the appearances seen on looking at the gland from the interior of the pericardium.

Johannes Müller[1] described these organs as consisting of "very small elongated lobuli, which are attached to blood-vessels, and are united with one another by loose connective-tissue. Each lobulus or cylinder consists . . . . of a double row of cylindrical nucleated cells, like those of a columnar epithelium, the two rows of cells fusing with one another at the base of each lobulus. Between them run blood-vessels."

No further statements on the subject were published till 1875, when Prof. Wilhelm Müller[2] gave an account of some observations made on Myxine glutinosa. In this animal Prof. Müller found that the bodies in question were connected each with the segmental duct of its own side, while the "double rows of cells" of Johannes Müller he found to be segmental tubules of a perfectly normal character, communicating by ciliated funnel-shaped openings with the pericardium, and provided with glomeruli.

The obvious inference was that these organs represented that anterior part of the kidney which is so well developed in many larval Icthyopsida, and which is known as the "pronephros," or "head kidney."

Professor Müller, however, expressly states in his paper that his investigations were made upon very young animals.

[1] Loc. cit., part iii, pp. 7, 8.

[2] 'Jenaische Zeitschrift,' ix, 1875, pp. 111—113.

During the summer of last year, Mr. Sedgwick, while visiting the Cape of Good Hope, collected amongst other things a large number of very fine specimens of Bdellostoma Forsteri, var. hexatrema; and on his return to Cambridge he very kindly obtained permission from the Royal Society, for whom the specimens were collected, to allow me to examine their renal organs. On making a superficial examination of the so-called head kidneys, it was evident, as shown in fig. 1, that they were separated by a considerable distance from the anterior end of the segmental duct (*s. d.*), the only structures passing from one organ to the other being apparently blood-vessels. The subsequent preparation of a complete series of sections, the first of which passed through the anterior extremity of the "head kidney," the last through the beginning of the segmental duct, proved conclusively that with the exception of a rudiment to be spoken of presently, no trace of connection existed between the two organs.

Transverse sections showed the presence of a number of branched ducts, evidently the "pronephric tubules" of Wilhelm Müller, which opened on the one hand into the pericardium, and on the other into a central duct (figs. 3, 7).

These tubules (Pl. XV, fig. 7) had an average diameter of 6 mm.; there was no increase, but rather a diminution in diameter at the openings into the pericardium (figs. 2, 3, 7, *f.*). Each tubule was lined by cubical or columnar cells, the protoplasm of which was finely granular; each cell contained a large, elliptical, highly refracting nucleus, containing numerous coarse dark granules (fig. 7). At the mouth of each tube the columnar lining epithelium was continued into the flat pericardial epithelium (fig. 7, *p. c.*). No traces of cilia were found on the cells bounding the openings into the pericardium. Outside the lining epithelium was a well-marked basement membrane (fig. 7, *b. m.*); and outside this, in the spaces between the tubules, was a small quantity of connective tissue, and an exceedingly rich plexus of blood-capillaries (fig. 7, *b. c.*); so that during life a very considerable quantity of blood must be constantly passing between the tubules of the gland.

The tubules are for the most part aggregated into considerable lobuli; but here and there these lobuli become smaller, and in some sections tubules are seen which project separately into the pericardium; several such were cut transversely in the section from which fig. 3 was drawn, and they are seen to be separately invested by pericardium.

Passing inwards towards the centre of the gland, the tubules unite with one another, still maintaining the same characters, and not showing any appreciable change in diameter, till they finally open into a large central duct (fig. 3, C. D.).

The central duct is elliptical in cross section, its long diameter being about 0·2 mm., its short diameter 0·5 mm.; it may be single, as represented in the diagrammatic longitudinal section (fig. 2), or it may be divided into two or three anastomosing branches. It is lined by a single layer of very long and slender columnar cells, each about 0·07 mm. long by about 0·009 mm. broad, and having a large oval nucleus, with a dark outline and granular contents towards its outer end. The protoplasm of these cells is crowded with granules (fig. 4), and the free extremity of each is produced into a number of fine pseudopodia, round which are collected numerous granules (fig. 4). It is difficult to avoid the belief that the appearances described are due to the fact of the epithelium cells being actively amœboid during life, and of their pouring into the lumen of the central duct a quantity of secretion granules.

Outside this epithelium is a strong basement membrane (figs. 4, 6, *m*), which is connected with a tolerably compact coating of connective tissue, investing the whole duct.

The lumen of the duct was filled, in all my preparations, with a larger or smaller amount of material resembling a blood-clot, and consisting of a finely granular matrix (fig. 5), in which were contained oval nucleated cells, identical, so far as I was able to see, with the red blood-corpuscles found in blood-clots from the surrounding vessels. After a careful comparison, both with sections and with teased-out preparations of the blood-clots of the great veins, I have been unable to come to any other conclusion than that the central duct does actually contain in preserved specimens a blood-clot, and, therefore, in the living animal blood.

The above description applies to the main body of the duct; anteriorly it gives off a bunch of tubules, similar in all respects to those given off from its sides (see diagram, fig. 2), while posteriorly it ends in a mass of tissue (figs. 2 and 6 and 7), resembling the trabecular supporting tissue of a lymphatic gland. Fig 6 shows a portion of the periphery of a section through this tissue. It is seen to consist of a network of nucleated, branched connective-tissue cells, with elongated meshes, in which are several scattered blood-corpuscles (*b. c.*).

This lymphatic tissue is covered by a well-marked epithelium (B), forming the capsule of a large glomerulus (figs. 2 and 6, *gl.*), which lies close to it. From this glomerulus strands of blood-vessels pass off at frequent intervals into the lymphatic tissue. Such a strand is figured at *x* in fig. 6.

Owing to the impossibility of injecting a capillary plexus in an animal which has been preserved in chromic acid, I have not been able to obtain any very definite proof that blood can pass by these strands of vessels into the lymphatic tissue of the duct, and so into its lumen; but I am strongly inclined to believe that this is the case.

I have occasionally seen capillaries leading directly from the lumen of the central duct, though I have been unable to follow them for any distance.

Until, however, further observations on fresh specimens can be made, I venture to think that I have shown tolerably good reason for assuming that the blood enters the lumen of the central duct of the "head kidney" through the glomerulus at its posterior extremity.

In some of my series of sections there is a considerable interval between the glomerulus just described and the segmental duct, which is occupied by nothing but connective tissue. In other, presumably younger specimens, I find traces of a continuation of the renal duct into the head kidney; though in no case have I seen a continuous lumen in the connecting piece.

It therefore seems to me that the organ, whose anatomy I have just described, may very probably have resembled, in its earlier stages, the head kidney described by Wilhelm Müller, in which case it would have to be regarded as a part of the embryonic kidney, modified, in connection with the needs of the animal, to perform some unknown function in the elaboration or purification of the blood.

Such a modification of a part of the embryonic kidney is by no means unique amongst vertebrates. In the last paper which he wrote for this Journal, the late Professor Balfour[1] showed that, at all events, in a considerable number of Teleostei the head kidney becomes in the adult transformed into a mass of tissue resembling a lymphatic; and he subsequently discovered the same modification in the head kidney of Lepidosteus.[2]

This being the case, the question arises whether there may not exist, in all vertebrate animals, similarly modified portions of the primitive kidney. I believe that such structures are, as a matter of fact, to be found in the suprarenal bodies.

Though this view of the nature of the suprarenals is by no means in accordance with that generally held, none of the facts at present known concerning either their adult relations or their mode of development seem to me to disprove it.

First, as to their relations in the adult.

In Elasmobranchs there are, as Balfour has shown,[3] two distinct sets of structures to which the name "suprarenal bodies" has been applied; first, a series of paired, apparently glandular bodies, arranged segmentally, and each connected with a sympathetic ganglion; these bodies, first accurately described by Leydig,[4] are attached on each side to the dorsal wall

[1] Balfour, on the Structure of the Organ known as the Head Kidney in Teleostei, this Jour., 1882.

[2] "On the Structure and Development of Lepidosteus osseus," by F. M. Balfour and W. N. Parker, 'Phil. Trans.,' 1882.

[3] 'Elasmobranch Fishes.'

[4] Rochen und Haie, Leipzig, 1852, 'Untersuchungen über Fische und Reptilien, 1853.

of the cardinal vein on each side, projecting into its lumen. They are best developed in the region of the mesonephros. In the region of the hind kidney, these bodies are replaced by a median, impaired structure, the lobuli composing it being closely connected on each side with the adjacent parts of the kidneys.

In Teleostei suprarenals are at all events frequently absent; or, as I would rather suggest, they are represented by the greatly metamorphosed head kidney described by Balfour.[1] In other cases, where suprarenals have been detected, they have always been attached to the surface of the kidney.[2]

In Amphibia, they are embedded in the substance of the kidney, either on its ventral surface (frog), or on its internal border (Triton); and they, like the kidneys, receive blood from the renal portal vein.[3]

In Reptiles[4] the adult structure of the suprarenals strongly supports the view that they are modified portions of the mesonephros. In the male lizard, for example, they lie suspended in the mesorchium, between the testis and the seminiferous Wolffian tubules, with which latter they are closely connected.

In snakes the relations are very similar, while there is a remarkably well developed "adrenal portal" circulation.

In Birds and Mammals the highly specialised suprarenals retain, as might be expected, fewer traces of their mode of origin than is the case in lower forms.

It is evident, from the above sketch of their relations, that the only case among lower Vertebrates, in which any well-marked separation between kidneys and suprarenals occurs, is among Elasmobranchs, where the anterior paired portion of the suprarenal system is very distinctly separated from the mesonephros. This fact, however, is probably due simply to the extreme degree of specialisation undergone by the meso-

[1] Loc. cit.

[2] Ecker, 'Der feinere Bau der Nebennieren,' 1846.

[3] Owen, 'Anatomy of Vertebrates,' vol. i, p. 543.

[4] Braun, "Bau u. Entwick. d. Nebennieren d. Reptilien," 'Arb. Zool. Inst.,' Würzb., 1872.

nephros in the male, where it forms the complicated network of the epididymis, while in the female it by no means retains its primitive characters.

In Amphibians and Reptiles the intimate connection of the two sets of organs, and the great similarity between their means of blood supply—each receiving a portion of venous blood from the trunk or hind limbs, which passes through the organ (kidney or suprarenal as the case may be), to go to the vena cava—are surely most easily explained by supposing both organs to be parts of a single primitive structure, which are undergoing specialisation in different directions.

The very general absence of suprarenals, as separate structures, in Teleosteans, together with the existence of a peculiarly modified head kidney, has already been mentioned as leading to the same conclusion. The connection between the suprarenals and more or fewer of the sympathetic ganglion, which exists in so many forms (Elasmobranchs, Reptiles, Birds, Mammals) can hardly be other than secondary.

The development of the bodies in question has been worked out in Elasmobranchs by Balfour,[1] in Reptiles by Braun,[2] and in Mammals by Mitsukuri[3] and Janosik.[4] In all these forms the first recognisable rudiment of a suprarenal is in the form of a compact mass of mesoblastic tissue, lying dorsal to the Wolffian body, between it and the aorta; and therefore just at the base of the ridge of the commencing generative epithelium. The cells composing this mass envelope a certain number of sympathetic ganglia; forming the cortical part of the adult suprarenal, while the cells of the ganglia form its central part. The question of the homologies of the cortical part of the suprarenals must, if it is to be settled by embryological evidence at all, be decided by observations on the mode of origin of the primitive cell-mass from which the cortical substance of the adult organ arises. On this point there is, however,

[1] 'Elasmobranch Fishes.'

[2] Loc. cit.

[3] This Journal, Jan., 1882.

[4] 'Archiv für Mikroscopische Anatomie,' xxii Band, 1883.

very little evidence. Balfour and Mitsukuri give no definite account of the mode of origin of the cell mass, their observations beginning at a time when it is already formed. Braun considers that in Reptiles it commences by the formation of aggregations of cells round branches of the vena cava, while admitting[1] that "the rudiment . . . . is often so close to the segmental tubules at their point of exit from the Malpighian capsules, that one is easily led to believe in the existence of a connection between the two." But the most striking observations on this point are those of Janosik, who finds that in Mammals there is, immediately in front of the Müllerian duct—that is, in the position of the head kidney—a number of solid cords of cells, connected at intervals with the peritoneal epithelium, and resembling exactly, so far as one can judge from the account given, a series of solid rudimentary segmental tubules. These strings of cells have no connection with the renal duct, but pass directly into the cortical substance of the suprarenals.[2]

Such fragmentary observations as I have hitherto been able to make lead me to hope that I may be able at no very distant date to show that, at all events in Reptiles and Mammals, the connection between the Wolffian body and the suprarenal is much more intimate than has generally been supposed. But should this hope prove unfounded, and should subsequent observations prove that the primitive mesoblastic rudiment arises simply as a mass of cells lying dorsal to the Wolffian body, this would by no means afford sufficient reason for asserting that the one structure had never been connected with the other, for we know that precisely the same kind of separation of two primitively continuous parts of the kidney has taken

[1] Loc. cit., p. 23.

[2] A short time before the appearance of Dr. Janosik's paper, Dr. Renson published in the 'Archiv für Mikroskopische Anatomie' (Bd. 22, p. 600), an account of some observations which tend to prove the presence, in earlier mammalian embryos, of functional segmental tubules in the position of the solid cords of Janosik. As neither of these authors figure the structures described, it is impossible to judge how far the one set may prove identical with the other.

place in the case of the metanephros, which, originally continuous with the hind end of the Wolffian body, now develops from a separate blastema which bears much the same relation to the hinder end of that structure as the suprarenal blastema does to its anterior end—both modes of origin being probably equally due to the delay which always takes place in the histological differentiation of an organ which is only functional comparatively late in life, and to the need of separating as soon as possible all such temporarily useless structures from the actively functional Wolffian body.

In the present state of our knowledge as to the function of the suprarenals, it may seem unjustifiable to assume that they have any essential connection with the blood system. At present, the only piece of direct evidence of their possessing any function at all is derived from the phenomena of Addison's disease, which seems, so far as I can learn, to be essentially due to alterations in the blood supply. The constant alterations in the behaviour of the red corpuscles, their refusal to form rouleaux, and the frequent difficulty in obtaining a good clot from the blood of patients suffering from this disease, are very suggestive.

An important indication of the probable need for some set of glandular structures in connection with the vascular system is found in the very general presence of such glands among the Invertebrates. It is not too much to say that in every group of Invertebrates in which the vascular system has been at all carefully investigated, glandular appendages to the vessels have been found, which can, from their anatomical relations, have no other function than that of elaborating some of the constituents of the blood. Thus, in Chætopods[1] there are very frequently present small cæcal diverticula of the great vascular trunks, which are coated with large, nucleated cells, loaded with granules; these cæca may simply lie loosely along the sides of the vessels, or may be collected into definite glandular masses lying on the floor of the body-cavity. In leeches,

[1] See Claparède, "Organisation des Annélides Sédentaires," and Cosmovici, "Les Annélides Polychètes," 'Arch. Zool. Exp.,' viii.

some glandular function may possibly be attributed to the large chains of "botryoidal connective tissue" in which many of the blood-vessels end.[1] In Echinoderms, the abundance of glandular cells in the cardiac plexus is probably a principal cause of the whole organ being regarded by many observers as an excretory apparatus. Among Molluscs, glandular structures, connected with the auricles, have long been known among Cephalopods, while the glands of the pericardium of Lamellibranchs, associated as they generally are with the auricles and afferent vessels, are probably of the same nature.[2] Among Arthropods, the "coxal glands," recently described by Professor Lankester,[3] may perhaps prove to be connected with the vascular system, though the small blood supply at present recognised is certainly against such a view.

An investigation of the functions of these various structures in Invertebrates can hardly fail to afford an important clue to the real nature of the Vertebrate suprarenals.

EXPLANATION OF PLATE XV,

Illustrating Mr. W. F. R. Weldon's Paper "On the Head Kidney of Bdellostoma, with a Suggestion as to the Origin of the Suprarenal Bodies."

Complete List of Reference Letters.

B. Lining epithelium of a glomerulus. *b.-c.* Blood-corpuscles. *b. m.* Basement membrane. *c.* Blood capillaries. *cl.* Blood-clot in ventral duct of head kidney. *D. ep.* Epithelium of central duct. *gl.* Glomerulus at posterior extremity of head kidney. g^1. First glomerulus of functional kidney. g^2.

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[1] Lankester, "On the Vasifactive and Connective Tissues of the Medicinal Leech," This Journal, vol. xx, 1880.

[2] See Grobben, "Morphologische Studien über die Harnund Geschlechts-apparat, &c., der Cephalopoden," 'Arb. Zool. Inst. Wien,' v Bd., 1883.

[3] "On the Skeletotrophic Tissues and Coxal Glands of Limulus, Scorpio, and Mygale," This Journal, Jan., 1884.

Granules attached to epithelium of central duct. *f.* Opening of head kidney tubules to pericardium. *Ly.* Lymphatic tissue at posterior end of central duct. *pc.* Pericardial epithelium. *S. D.* Segmental duct. *s. d.* Atrophied portion of segmental duct. *v. c.* Great vein. *x.* Strands of blood-vessels passing from glomerulus to lymphatic tissue of head kidney.

Fig. 1.—View of head kidney of Bdellostoma, from within the pericardium. The segmental duct is seen through the wall of the pericardium. × 4 diam.

Fig. 2.—Diagrammatic longitudinal section through head kidney of Bdellostoma.

Fig. 3.—Transverse section through the middle of the head kidney. The tubules and the central duct are drawn, but the capillaries surrounding the tubules are omitted. Zeiss, obj. A, oc. 2.

Fig. 4.—Epithelium of central duct, showing granules thrown into its lumen. Zeiss, Obj. F, oc. 2.

Fig. 5.—Clot from central duct. Obj. F, oc. 2.

Fig. 6.—Transverse section through the lymphatic tissue at the posterior end of the central duct, showing strands of blood-vessels passing into it from the adjacent glomerulus. Obj. D, oc. 2.

Fig. 7.—Portion of periphery of a section similar to that shown in Fig. 3, showing the characters of the head kidney tubules and the surrounding blood-vessels. Obj. D, oc. 2.

Figs. 3 to 7 drawn with the camera lucida.

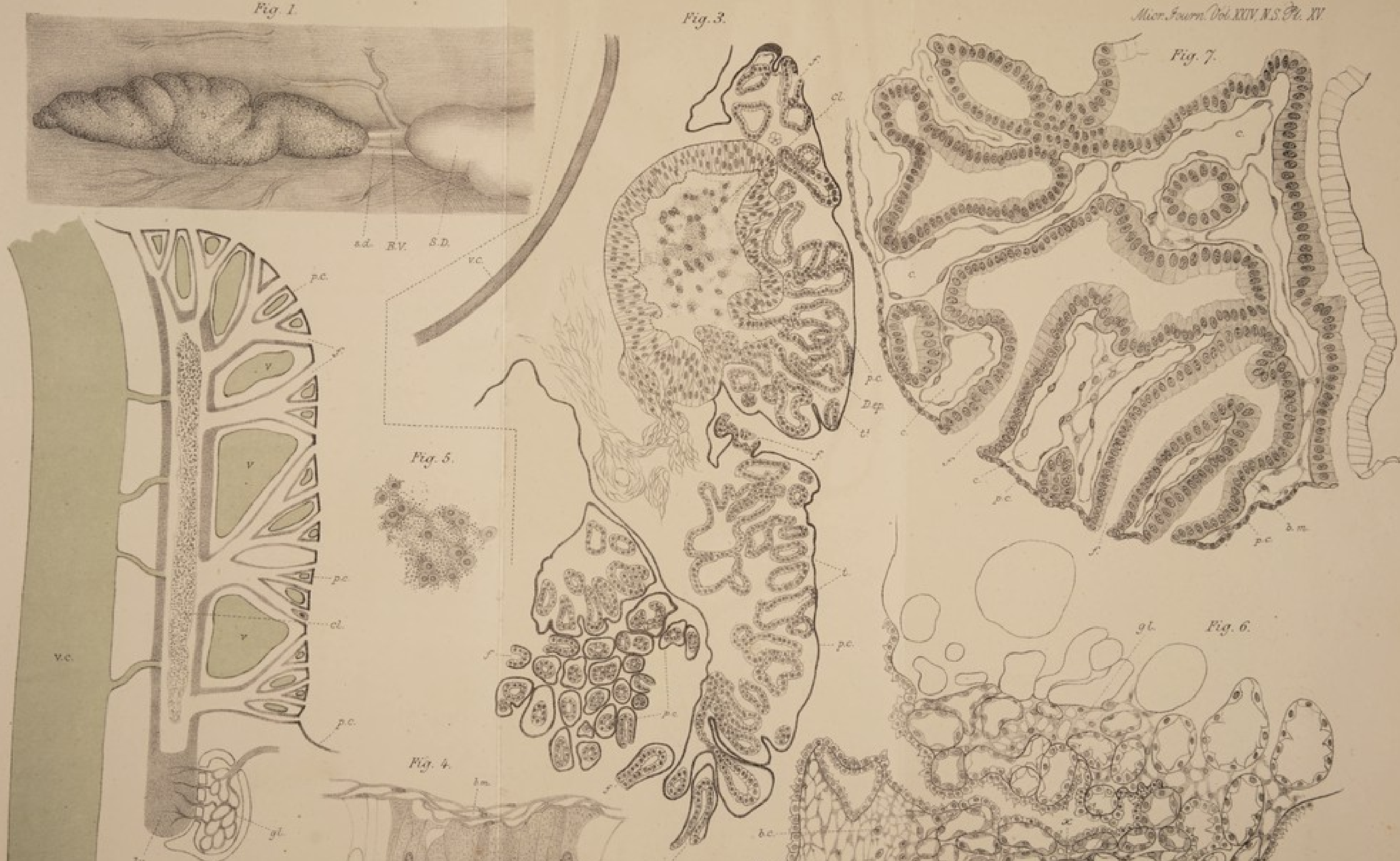
Fig. 1.
s.d.
B.V.
S.D.
Fig. 2.
V.C.
p.c.
f.
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s.d.
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