nivoræ, for example, have a curious hæmostatic or erectile apparatus in connection with the hair bulb, and around the neck of the bottle-shaped bulb is an annular arrange-

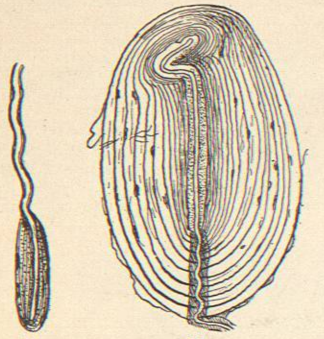

FIG. 1902.—*A*, Krause's End-Bulb. *B*, Pacini's body.

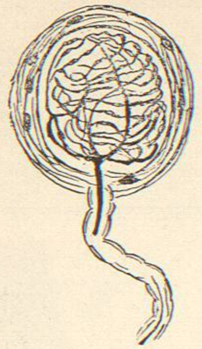

FIG. 1903.—Nerve Ending in Human Conjunctiva. (Dogiel.)

ment of fibres that seems to be intended to serve as a means of receiving tactile impressions arising from movements of the hair.

Terminal Corpuscles.—These differ from the free termini in the fact that the nerve ending is surrounded by a more or less complicated sheath of connective tissue, and it would appear as though the arrangement of parts was destined to apply external pressure or irritation more directly or powerfully to the nerve fibre.

The nerve bulbs of Krause are the simplest of these organs and are found in the conjunctiva, lips, tongue, and genitalia. They consist simply of a sac of connective tissue of round or oval form in which the end-fibre lies either as an axial thread or as a complicated coil. In the case of the genital corpuscles there seems to be, according to Dogiel, a complicated lateral anastomosis between the fibres of the different corpuscles affording an opportunity for excessive irradiation of the stimulus.

Tactile corpuscles proper are much more complicated structures. The neurilemma of the entering nerve fibre becomes continuous with the sheath of the corpuscle. Each corpuscle may receive from one to four fibres which enter with their sheaths for some distance. The fibre then becomes non-medullated and forms numerous coils or loops within the corpuscle. These corpuscles are especially numerous on the palms and soles, on the margins of the lips and in the genitalia, but are not confined to these organs.

Pacini's corpuscles, which are most numerous in the joints and in the mesentery, though also found in the

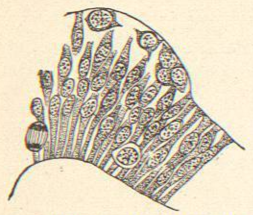

FIG. 1904.—An Early Stage in the Olfactory Epithelium. Neuroblasts proliferating and migrating to inner aspect of epithelium.

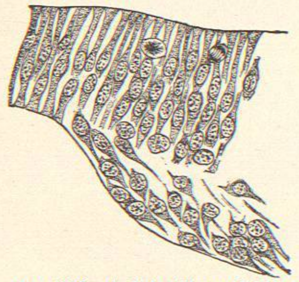

FIG. 1905.—A Later Stage of Olfactory Epithelium. Beginnings of olfactory nerve.

corium layer of the skin of the extremities, have something in common with the end-bulbs, being quite simple in structure, with a single straight or slightly curved axial nerve fibre. The simple bulb is, however, clothed with numerous concentric capsules and the whole covered with a connective-tissue pseudo-epithelium of polygonal cells.

Organs of Special Sense.—It is generally believed that the sensory elements in the organs of higher sense have been derived from the simple form of rod cell found in the lateral-line buds and taste buds. The latter have already been referred to as being obviously similar to the lateral-line organs, and we believe that whatever method of nerve connection shall be determined in one will also be found characteristic of the other, unless, indeed, the nervous connections in one or the other case prove to be secondary, as is not impossible. From a speculative point of view it is impossible to say whether the gustatory cells are derived from parts of the lateral sensory bands arising between the pituitary and the olfactory or whether they have entered the mouth in a secondary way viâ the gill clefts.

For both the olfactory and Jacobson's organ the direct connection of the specific cell with the nerve fibre has been demonstrated.* In these cases most writers agree also that the radix fibres are the product of moniliform series of neurocytes or neuroblasts. The writer is much inclined to regard this as the primitive method of nerve formation and one that prevails in the case of other peripheral nerves in a disguised form.

The first indication of the change of the ordinary to the sensory epithelium is seen in the thickening of a portion of the superficial layer from the morphological front of the head (the region of the future infundibular recess)

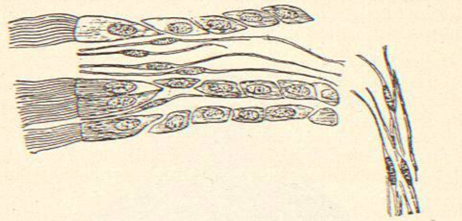

FIG. 1906.—Teased Preparation for Olfactory Epithelium of Salamander.

in relatively broad bands, one on either side of the head. As the head flexures increase, these areas are carried ventrad and come to occupy the roof of the mouth and adjacent parts of the buccal cavity. The development of the taste buds from this epithelium we have not traced in these subjects, though it is probable that they are formed from this proton, as the mucous parts of the hypophysis are. At the time the first olfactory rudiments appear, the curvature is such that the hemispheres are protuberant in front and so come nearly in contact with the prota of the olfactory in the two bands of germinative epithelium above mentioned. Still there is no difficulty in seeing that the original proliferations take place in the skin, and that the constant proliferation by division of the earlier cells spins the nerve fibre from the original

* Although there was for a long time considerable disagreement as to the actual connections of the olfactory nerve fibres, and the classical studies of Kölliker, Klein, and Piana left the matter open, it seems as though the later studies of Ehrlich, Arnstein, Cajal, Gehuchten, Retzius, Brunn, and Lenhossék, who employed the silver and methylene-blue methods, were sufficient to prove conclusively that the olfactory epithelium possesses rod cells whose proximal end is in actual continuity with the fibre of an olfactory nerve filament. The writer has frequently verified this in specimens of Amphibia double-stained with hæmatoxylin and picrocarmine, in which very unambiguous views can be secured. A few figures from these preparations were published by Mr. Bawden, then a student in the writer's laboratory (Jour. Comp. Neurol., iv.). Our studies in the development of the olfactory nerve show that the proton of the nerve is formed in or under the epithelium of the nasal area, and that the nerve grows by moniliform concrescence of cells which arise by mitosis from this proton. From this standpoint, then, it would be expected that the neurocytes of origin would be found in the epithelium. In all essential respects the relations in Jacobson's organ are the same as in the true nasal olfactory epithelium.

source to the point where the tuber subsequently arises. In fact, the tuber, which has frequently been compared to the ganglion of origin of a cranial nerve, does not seem to afford origin for any centrifugal fibres whatever. In preparations by the silver method it is easy to see that the neurite of the moniliform chain of the olfactory nerve comes into relations in the glomerules with dendrites of the mitral cells.

For a long time during the development of the brain an obvious ganglionic mass lies below the skin at the base of the point of origin of the olfactory. The gradual elaboration of the cavities of the nares only serves to redistribute the prota without materially disturbing the simplicity of the arrangement.

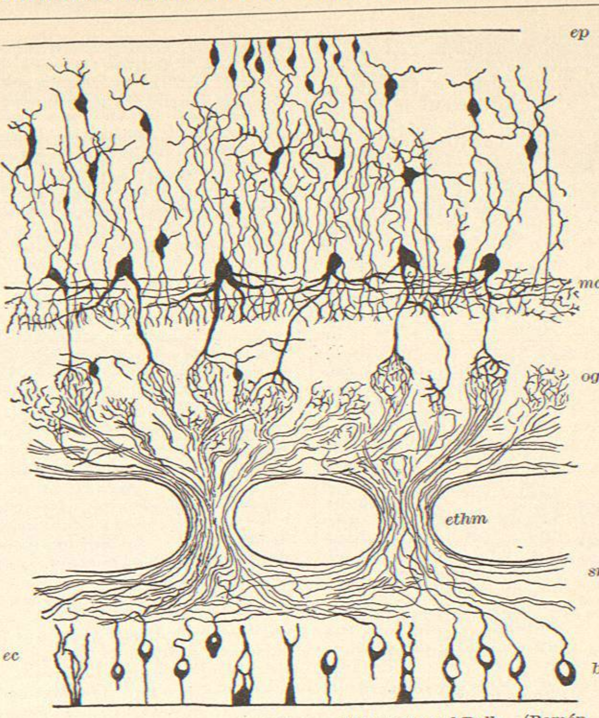

FIG. 1907.—Structure of the Olfactory Filaments and Bulb. (Ramón y Cajal.) *bc*, Bipolar cells of the olfactory mucous membrane; *sm*, submucosa; *ethm*, cribriform plate of the ethmoid; *og*, olfactory glomeruli; *mc*, mitral cells; *ep*, epithelium of the olfactory ventricle; *ec*, epithelial cells of the olfactory membrane.

The fact that the lens is essentially a sensory depression, homologous with the nasal sac, is one of the well-established generalizations of the last few years. In this case, however, neuroblasts are not developed, and the spongioblasts undergo very remarkable gelatinous transformation, though the nuclei may always be demonstrated by sufficient preparation.

The internal ear is the next organ of this lateral series, and its formation beautifully illustrates the uniformity in diversity characteristic of all morphological processes. The auditory sense organ, like the preceding, is an invagination of specialized sensory epithelium continuous with that which, in lower vertebrates, forms the "organs of the lateral line." It first appears as a saucer-like depression (Fig. 1908), from which is formed the capsule from the various transformations of which the "membranous labyrinth" with its sensory patches is formed.

The primitive sac divides into a cephalic and a caudal portion. Comparison of the methods of development of the lateral-line organs in the dogfish, for example (Ayers), shows great similarity with the early morphological changes in the ear by which the semicircular canals are formed. "Within the two chambers formed four canal sense organs develop. The two external organs are soon enclosed within the ampulla of the two complete and relatively large canals which are now formed about them." "Up to this time the organs have retained the primitive relations to each other, a serial arrangement along a line running in an antero-posterior direction. Now there begins a distortion of the structure as a whole, which continues ever after and reaches its greatest development in the mammals, viz., a process of sinking and drawing out ventrally of the posterior chamber of the ear, so that hereafter we might speak of a superior and an inferior portion or chamber" (Ayers). By progressive subdivisions the four patches give rise to the eight definitive auditory sensory organs of mammals. Meanwhile, the neuroblasts have migrated to the ectal surface and give rise to the two ganglia (vestibuli and cochleæ) from which the two branches of the auditory nerve are produced.

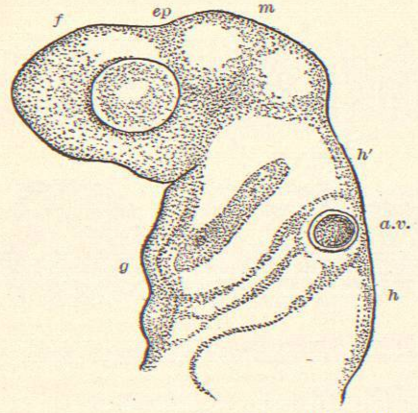

FIG. 1908.—Head of Embryonic Shark, *Acanthias vulgaris*, showing the saucer-like depression, corresponding to the insinking sense organ which is to be converted into the auditory sense organs of the shark. *a.v.*, Auditory vesicle; *ep*, position of epiphysis; *m*, mesencephalon; *f*, fore-brain; *g*, gill region; *h*, medulla. (After Ayers.)

The transformations of the epithelium in the formation of the organ of Corti are out of place here, but obey laws easily intelligible from our knowledge of the history of the spongioblasts elsewhere.

The retina is essentially a modification of a portion of the primitive neural tube. The pigment layer undergoes a change directly comparable with that which produces the velum cerebelli or the introductory stages of plexus formation. The original limits of the tube are represented in the retina by the membranæ limitantes.

The relations are at first exactly as in the brain proper (Fig. 1909). The neuroblasts are

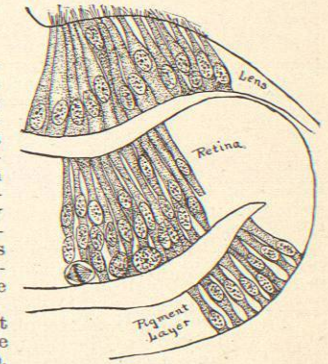

FIG. 1909.

formed adjacent to the ventricular surface and migrate to the ectal surface. A portion remains in the nuclear (granular) layers and corresponds to the granules which lie adjacent to the ventricles in the brain. The method of formation of the rods and cones is still a matter of dispute. Professor His thinks they are formed by protrusion of backward-growing processes of the neuroblasts. It is, perhaps, doubtful if we have not to do with the nuclei of the spongioblasts and the greatly modified homologues of the cilia characteristic of ventricular epithelium. In any case the true neurons collect in a single or double series on the vitreous surface of the retina, and give rise to an axis-cylinder process which passes through the chiasm to the tectum opticum, and to protoplasmic processes which subdivide in the "inner molecular layer" (equivalent to the marginal reticular zone of the brain). The direct connection between the ganglion cells and the rods and cones has not been observed, and probably the connection is through a reticulum or neuropilem as in all other cases. The nerve fibres develop in the human retina at about the fifth week. It is obvious, from the results of recent investigation, that fibres arising in the tectum opticum pass toward the retina as well as vice versa.

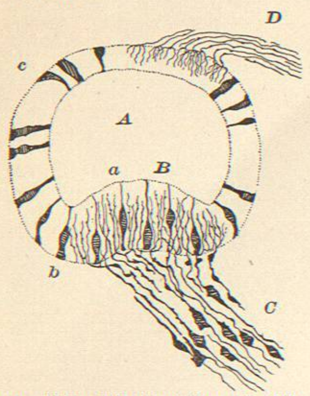

FIG. 1910.—Collecting Filaments of the Vestibular Branch of the Auditory Nerve. (Ramón y Cajal.) Transverse section of the semicircular canal of a mouse. *A*, Lumen of the canal; *B*, acoustic crest; *C*, bundle of nerve fibres containing bipolar cells; *D*, a similar bundle supplying the top of the canal; *a*, *b*, and *c*, varieties of bipolar epithelial cells.

Further discussion of the organs of special sense is rendered unnecessary by the fact that vision and audition are fully treated under these heads.

Muscle Spindles are problematical nervous organs which are supposed to supply the sensory stimuli on which are based the muscular sense and pressure sense. They were first described by Kölliker but were first proven to be sensory by Sherrington. The most complete account is that of Huber and DeWitt (*Journ. Comp. Neurol.*, vii., 3, 4) from which the following is taken.

"The capsule or perimysial sheath, has essentially the same structure in all vertebrates examined, although it varies much in thickness. It is made up of concentrically arranged layers of white fibrous tissue, the several layers being often in close apposition, or again more or less distinctly separated one from the other, leaving larger or smaller clefts between them. The number of these concentric layers varies; Sherrington places it at six to eight, which number holds good for many of the muscle spindles seen by us, especially those found in mammalian muscle. The fibrous tissue of the concentric lamellæ is white fibrous, practically devoid of yellow elastic tissue. At the beginning of the muscle spindle (proximal end), the capsule becomes continuous with a somewhat thickened perimysial sheath, which surrounds the muscle fibres about to enter the muscle spindle. The behavior of the capsule at the distal end of the muscle spindle depends somewhat on its relative position in the muscle. The spindle may be embedded in the muscle substance, in which case, as Sherrington correctly states, 'its long axis lies parallel to the muscle fibres amid which it is embedded'; here the distal end of the capsule seems again to become continuous with the internal perimysium.

"More immediately surrounding the enclosed muscle fibres, designated by Sherrington as '*intrafusal fibres*,' there is found a connective-tissue sheath which he has described as the '*axial sheath*,' consisting of thin bands or plates of white fibrous tissue in which nuclei are numerous.

"Between the capsule and the axial sheath is found a relatively large lymph space—Golgi and Sherrington—designated by the latter as the '*periaxial space*'; this, he correctly states, is 'bridged across and partially subdivided in many points by extremely tenuous membranes and filaments.' The periaxial lymph space is broadest near the middle of the muscle spindle, generally tapering off toward the ends. The intrafusal fibres are sometimes in the middle of this space and again eccentric. The space also shows buddings here and there, which seem, however, in a large measure due to foldings in the capsule, the result of contraction of the contiguous muscle fibres."

From one to four large medullated nerves end in the smaller spindles and from five to eight in the larger, compound spindles.

Single spindle nerves are surrounded by a thick sheath of Henle; small bundles of spindle nerves, by a connective-tissue sheath, which becomes in part continuous with the capsule, in part with the axial sheath. The spindle nerves remain medullated until they are within the axial sheath, the internodal segments becoming shorter as the muscle spindle is approached; but this is more especially noticeable after they have penetrated the capsule. After losing the medullary sheath (within the axial sheath), the non-medullated continuation of spindle nerves undergoes further subdivision, before the ultimate ending is reached.

Ruffini, whose account we may here follow, describes, for the cat, three types of ultimate endings of the spindle nerves—spiral, circular, and flower-like endings ("terminaisons à spirales, à anneaux, et à fleurs"). Of these, the spiral endings may be first considered, as they seem to us the most typical. The non-medullated terminal branch of the spindle nerve thus ending, flattens out into a ribbon-like ending, more or less irregular, which is spirally wound around the intrafusal fibre, this spiral extending for a longer or shorter distance along the intrafusal fibre; the spiral turns are sometimes so close together that they almost touch each other, or again, farther apart, so that they can be clearly made out. These spirals have also been described by Kerschner, who very correctly adds that from place to place offshoots proceed from the spiral, which may end on the intrafusal fibre surrounded by the spiral, or on some contiguous intrafusal fibre. The "ring-shaped" endings of Ruffini have, we believe, been correctly interpreted by Kerschner as lateral views of flat spirals. Such ring-shaped endings may, however, now and then be formed by short side branches of the non-medullated terminal branches, which almost completely, or completely, encircle an intrafusal fibre; several such endings may be side by side on an intrafusal fibre. The flower-like endings mentioned by Ruffini, are, no doubt, as suggested by Kerschner, the terminal endings

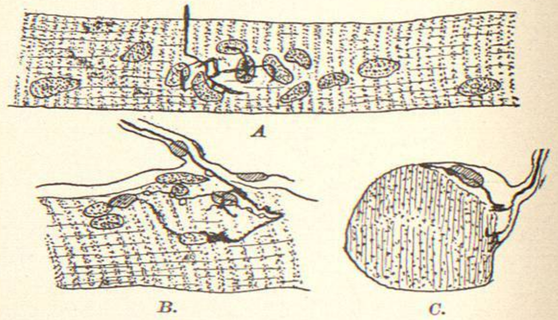

FIG. 1911.—*A* and *B*, Motor Plates from Muscle of Rabbit; *C*, cross section of muscle and motor plate of Frog. (After Huber and DeWitt.)

of the spirals, or of branches from the spirals; they may, however, now and then be seen as branches from the terminal, non-medullated continuation of the spindle nerves, which have a zigzag course on an intrafusal fibre without forming a spiral.

Batten shows that "in infantile paralysis the spindle remains absolutely normal, although the surrounding tissue undergoes complete atrophy. In tabes, he shows that certain changes take place in the termination of the nerve, the general structure of the spindle remaining normal. In progressive muscular atrophy the spindle remains unaltered, and the same is probably true with regard to peripheral neurites. Section or atrophy of the nerve trunk leads to atrophy of the muscle fibres within the spindle, though it is probable that it takes a considerable length of time for changes to take place in the muscle fibre within the spindle."

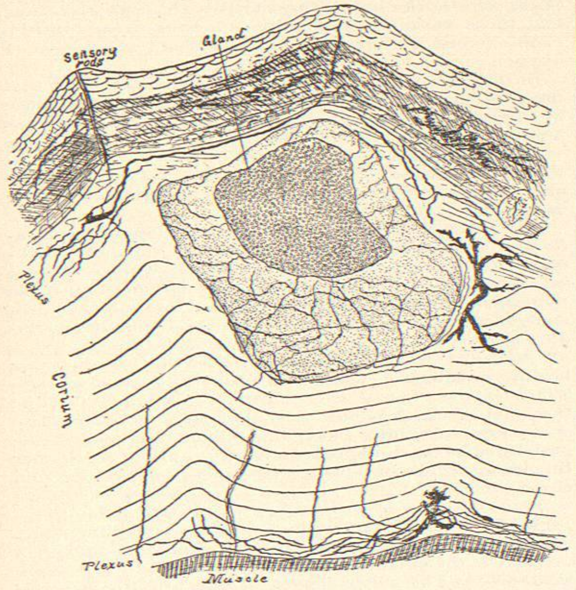

FIG. 1912.—Section of the Skin of the Head of a Toad (Bufo) after *intra-vitam* injection with methylene blue and fixation with Bethe's solution of molybdate of ammonia. Examined in glycerin. The section is somewhat oblique so that the duct and part of the body of the gland are absent. The delicate non-medullated fibres are seen generously distributed over the uncut surface of the gland. Coarser fibres are also seen in the lower and upper plexuses, also a bundle of sensory rods at the left.

KINESODIC END-ORGANS.—The most important termini of the centrifugal system are those upon muscles and glands. The motor end-plates are the points of attachment of the motor nerve fibres upon the muscles and are accordingly the receiving stations of the muscle and the points whence the stimulus is distributed to the fibre prior to its contraction. They were first observed by Doyère in 1840 and have been the subjects of much patient investigation since that time. The best work in this field is that of Kuehne, which has been ably supplemented by Huber and DeWitt. The fibre penetrates the sarcolemma and forms a very complicated arborescent figure by the ramifications of the axis cylinder, and this may be regarded as the end-brush of one or more motor neurites. The granular mass in which the nerve fibre terminates was at first supposed to be an expanded portion of the nerve fibre. It contains nuclei (the sole nuclei) which have been variously interpreted. The following summary from Huber probably expresses the present state of our knowledge:

"(1) The ramified terminations of the axis cylinder in the motorial endings of striped muscle are the end-brushes of the neuraxes of motor neurons, and are similar in structure to the end-brushes of other cerebro-spinal fibres.

"(2) This end-brush (*das Geweih*, Kühne) terminates in the sarcoplasma, therefore under the sarcolemma of the muscle fibres. At the place of ending of the nerve fibres, the sarcoplasma may be accumulated in a circumscribed mass, forming an elevation, more or less distinct, on the side of the muscle fibre, as in reptilia, birds, and mammalia, or spread out over a proportionately greater area of the muscle fibre, as in amphibia. In the mass of sarcoplasma, the muscle nuclei (sole nuclei of other writers) are relatively more numerous than in other parts of the muscle fibre.

"(3) The neurolemma of the nerve fibre terminating in the motorial ending becomes continuous with the sarcolemma at the point of entrance of the said nerve fibre into the sarcoplasma. Over the endings, sarcolemma or neurolemma nuclei—telolemma nuclei—are seen.

"(4) The neuraxis of the motor neuron loses its medullary sheath before piercing the sarcolemma."

With reference to the endings in glands and other visceral organs space need not be taken here as the discussion will naturally accompany the articles on these organs. The drawing in Fig. 1912 will sufficiently illustrate the complexity of the nerve supply to glands and the difference between these endings and those of a sensory nature.

C. L. Herrick.

ENDOTHELIOMA. See *Sarcoma.*

ENDOTHELIUM. See *Epithelium.*

ENEMATA. See *Enteroclysis* and *Alimentation, Rectal.*

ENGADINE (UPPER), SWITZERLAND.—The Upper Engadine valley extends from Maloja, at the summit of the pass, to a little beyond Samaden, in a direction from southwest to northeast. Through this valley runs the Inn, while high mountains belonging to the Bernina and Julier chains enclose it on either side. The Upper Engadine valley is wider than the lower and contains several lakes. It is about thirty miles in length, and varies from a half a mile to a mile in width; and its mean height above sea level is 5,500 feet. The whole Engadine is one of the highest inhabited valleys in Europe. In the Upper Engadine are situated the health resorts of Maloja, St. Moritz, and Samaden, where consumptives go in the winter for the "air cure"; and Pontresina and others which are visited in the summer only.

The Upper Engadine valley is again divided into an upper and a lower portion, quite different in the character of their scenery. In the upper portion, extending from Maloja to St. Moritz, where are situated the lakes beforementioned, the mountain boundaries on either side are grander and wilder and much loftier, and their summits are covered with extensive glaciers and snow fields. In the lower half, extending from St. Moritz to the termination of the valley, the picture is quite different. "Here there are no lakes, the floor of the valley is much wider, and is occupied by broad stretches of meadow-land through which the Inn quietly and tamely flows along." "The mountains on each side are of lower elevation; they all rise in gentle slopes from the floor of the valley, and present no bold or striking features of form or outline."

The upper or southern end of the valley is open and affords a ready ingress to storms of wind and rain approaching the valley from the southwest; the wind, however, blows most in spring and summer, while the winter is the calmest season of the year.

Climate.—The climate of the Upper Engadine is very similar to that of the neighboring valley of Davos, already described. (Cf. *Davos.*) In the first place, there is the striking variability of the temperature as in all high-lying stations. The diurnal variations are sudden and