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NEW FACTS CONCERNING BOTHRIOLEPIS.

WILLIAM PATTEN.

In the following paper, I shall present a preliminary account of my observations on a large collection of *Bothriolepis* recently obtained in New Brunswick. A more complete and fully illustrated account will be presented later.

This new material shows structural features heretofore unknown, and much that one could hardly hope to see preserved in any fossils, especially in ones so old as these.

The trunk, Fig. 1, was very slender and covered with a soft skin devoid of scales or of any other markings except those mentioned below. In spite of its delicate structure it is often only moderately compressed, or distorted. In the region of the posterior dorsal, it may present a somewhat triangular cross section, resembling that of *Cephalaspis* in a corresponding region, but without any traces of a lateral fold or of fringing processes.

A few small irregular plates, with the typical sculpture of the buckler, are imbedded in the skin along the dorsal surface, immediately in front of the anterior dorsal, and numerous minute ones are scattered irregularly over the flanks in the same region.

One specimen shows indications of a lateral groove, and, dorsal to it, a few oblong folds suggestive of segmentation.

The anterior dorsal fin is low and elongated, the posterior one very high and rounded. Both fins are often preserved with wonderful clearness, but show no other detail than a faint striation probably due to the presence of delicate subdermal rays.

The elongated tail, with its axis slightly curved, terminates in a narrow band. The dorsal margin consists of a delicate membrane, strengthened by a row of curved rods lying close together and arranged with great regularity. The basal ends of the rods are swollen, and one is turned a little to the left, and the adjacent one, to the right, of the median line. The rods extend on to the ventral margin of the terminal band, into the ventral lobe. The latter is faintly striated like the dorsal fins. Its anterior ventral margin appears to divide, as though it were continued forward

into the lateral folds, although no such folds have been detected in the trunk region.

There are no indications whatever, in either surface views or in sections of vertebral centra or arches, and the preservation of the specimens is so perfect, that there is every reason to believe such structures, even if formed of cartilage only, were absent. Neither have we found any indications of a notochord, although one may infer from the outline of the trunk that a notochord was present. It was probably surrounded by a membranous sheath of no more consistency, if as much, than that in *Amphioxus*.

Several specimens show a remarkable membranous frill protruding from the ventral and lateral margins of the posterior opening of the buckler. It extends completely across the ventral surface like a curtain, and is entirely separate from the overlying trunk. The lateral margins vary a good deal in different specimens, but, when clearly shown, they extend backwards in long lobes, which in one specimen are clearly thrown into regular folds like those indicated in the restoration. On the sides and toward the dorsal surface, the membrane appears to be reduced to a narrow fringe projecting from the inside margins of the opening of the shield, Fig. 2.

The ventral surface of the trunk extends without interruption or attachment over the frill and for about an inch over the visceral surface of the posterior ventrals. Here there is a prominent transverse ridge and a large scar on either side, probably the places of attachment of the trunk to the shield.

A large but very thin and nearly circular scale, or plate, marked with deep-lying radiating lines and with superficial concentric ridges is attached to the ventral surface of the trunk, between it and the inner surface of the posterior ventrals. The opening to the cloaca lies just above this plate, Fig. 2.

All the sectioned specimens showed the presence inside the buckler of a peculiar core, about an inch and a half long and half an inch in diameter, Fig. 2. It varies in shape in different individuals, but in all of them it has essentially the same characters and the same location in an antero-posterior direction. But its position shifts from side to side as though it were suspended in a rather large space and free to move laterally, or in a dorso-

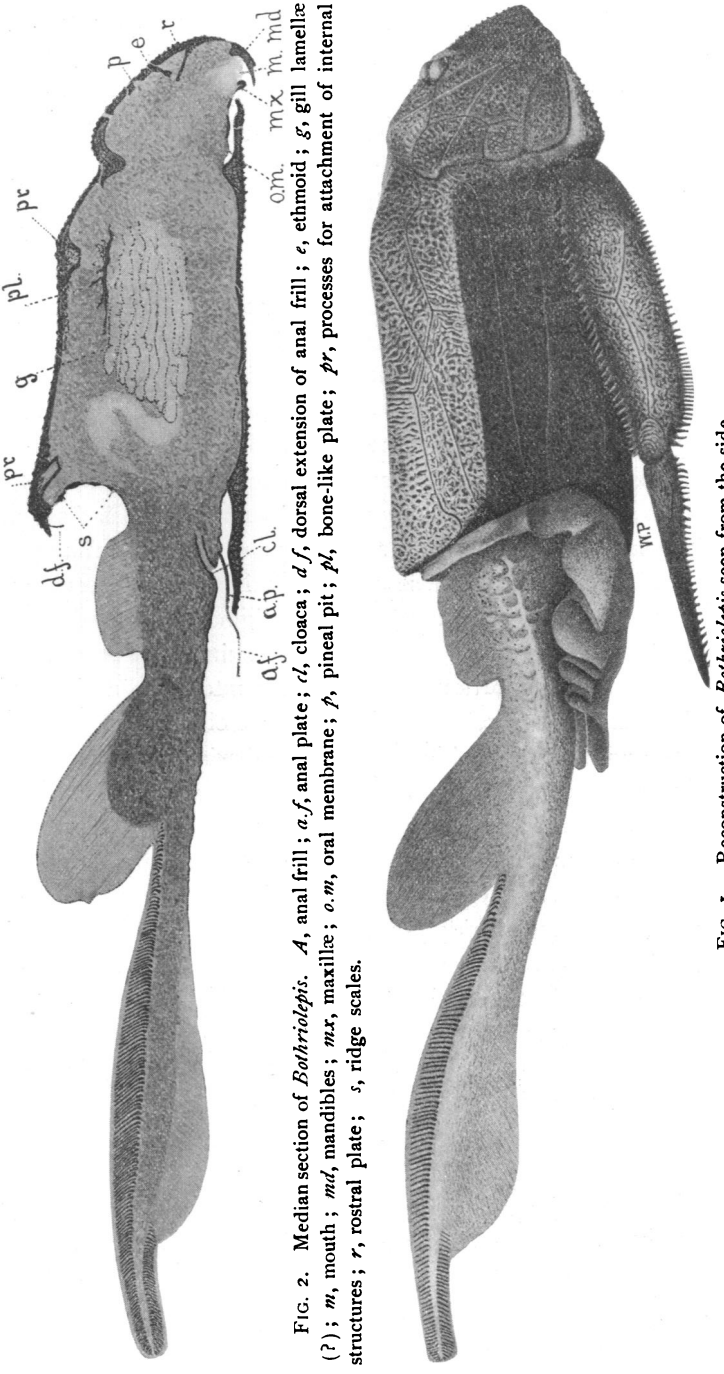

FIG. 2. Median section of *Bothriolepis*. *A*, anal frill; *a.f*, anal plate; *cl*, cloaca; *d.f*, dorsal extension of anal frill; *e*, ethmoid; *g*, gill lamellæ (?); *m*, mouth; *md*, mandibles; *mx*, maxillæ; *o.m*, oral membrane; *p*, pineal pit; *pl*, bone-like plate; *pr*, processes for attachment of internal structures; *r*, rostral plate; *s*, ridge scales.

FIG. 1. Reconstruction of *Bothriolepis* seen from the side.

ventral direction. Its anterior end lies back of the cervical suture and from there it extends backwards about two thirds the length of the post-cephalic portion of the buckler. It is readily recognized by its fine, soft matrix and the concentric black lines, each line clearly and sharply defined and separated from the adjacent ones by regular intervals. The lines are similar in color and thickness to those made by the skin when seen in section. The whole structure, while puzzling, is unquestionably produced by some organic structure, not by sedimentation within an irregular cavity, or by mud accumulated within the alimentary canal. The anterior boundaries of the black lines are ill defined, but the posterior ones often form distinct loops as though the whole structure consisted of a series of broad lamellæ wrapped around a central axis, and with free, more or less separated, posterior margins. In some cases the whole mass of lamellæ is much distorted, or they may protrude from some rupture in the walls of the crushed shield. Under these conditions they still preserve their essential characters, showing that while originally soft and flexible they had at least as much firmness as the skin of the trunk. Behind the laminated portion, the soft matrix extends in an irregular undefined and structureless mass toward the cloaca. The remaining space within the buckler may be filled with a coarser matrix similar to that in which the whole animal is imbedded.

On the dorsal side of the laminated body, there are usually scattered fibrous masses, and one or more irregular, undefined bony plates, apparently attached by vertical sheets of blackened tissue to a low median ridge on the inner surface of the anterior median dorsal. Anteriorly, this ridge deepens into a prominent hollow process directed downwards and forwards toward the thickest part of the covering on the laminated core, Fig. 2.

Several specimens have been found with the mouth parts in their natural position, held there by membranes, whose contours can be determined with considerable accuracy.

The oral region, Fig. 3, is covered by an undulating structureless membrane in which are imbedded the various oral plates. The membrane is attached to the lateral and anterior margins of the head, as far at least as the shoulder on the anterior border of the mandibles. It extends backwards, underneath the anterior

ventro-laterals, as far as the large transverse ridge on their inner surface, to which it seems to be attached. It extends across the median line without interruption except between the mandibles. It also appears to be absent between the mandibles and maxillæ, Figs. 2 and 3, *o.m.*

The mandibles are thin, concave plates of bone, continuous with the oral membrane on the sides and in front, but with free

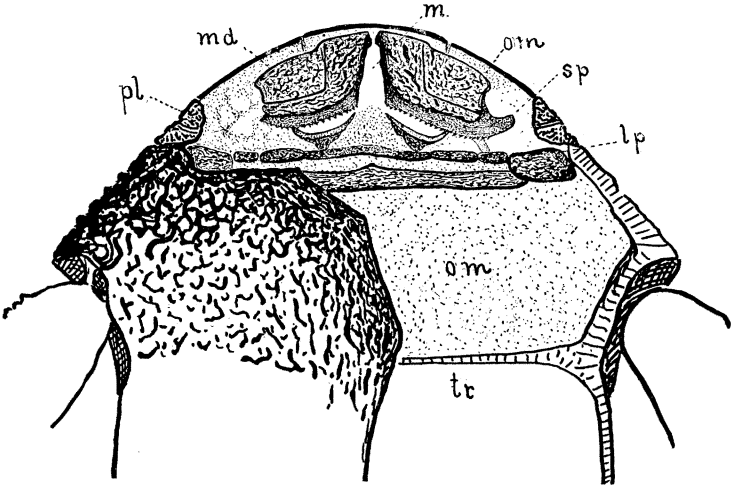

FIG. 3. Ventral side of head, with the anterior ventro-laterals removed on one side, to show extension backwards of oral membrane to the transverse ridge, *tc*; *l.p*, lateral plate attached to the two transverse bars; *m*, mouth; *md*, mandibles; *o.m*, oral membrane; *pl*, prelateral; *sp*, spur for attachment of muscles. × 1⅓.

median and posterior margins. The exposed surface presents the characteristic sculpture and the well known sensory groove. The posterior margin is nearly smooth and sharply bevelled, ending in an extremely thin edge nearly the whole length of which is broken into irregular serrations. The lateral and central serrations have more or less truncated points, the median ones are more regular in shape, sharply pointed and directed diagonally backward and inward toward the median line. The median margins of the mandibles are very thick and are provided with two horizontal edges, Fig. 4, *B*. Anteriorly the innermost edge becomes nearly vertical, forming a sharp-edged, tooth-like process, rounded in outline when seen from the side, Fig. 3. The plate

said by Woodward to unite the two mandibles does not exist. The plate seen by him was without doubt the displaced thin shelf of bone projecting backwards from the inner surface of the premedian or ant-orbital, Fig. 2.

The notched anterior margins of the mandibles are uniformly thin and rounded, and are continuous with the oral membrane, which unites them with the margin of the head, except possibly for a short space near the median line. The lateral margin is narrow and rounded where it becomes continuous with the oral membrane. A broad spur extends laterally on the visceral side of the membrane (Fig. 3) serving no doubt for the attachment of muscles.

The visceral aspect of the mandibles is nearly smooth, except for what appear to be some indistinct muscle scars and a very

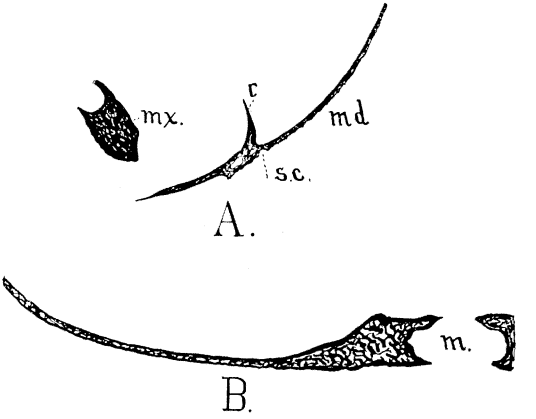

FIG. 4. *A*, sagittal section through mandibles and maxillæ, a little to one side of the median line of the head; *md*, mandibles; *mx*, maxillæ; *r*, internal muscular (?) ridge; *s.c*, sensory canal. *B*, transverse section of the mandibles to show heavy median margins. × 5⅓.

prominent sharp-edged ridge, which extends the whole length of the mandibles, Fig. 4, *A*, *n*.

The maxillæ are peculiar S-shaped plates lying behind, or more requently underneath, or dorsal to, the mandibles, Figs. 3 and 5. The median arm of each maxilla usually stands so as to expose a nearly smooth rounded ventral edge and a finely ornamented, somewhat triangular, strongly convex posterior surface. The median margin is undulating in outline and with a smooth border. In

sagittal sections it is seen to be deeply concave on its median posterior face, Fig. 4, *A*, *mx*.

The lateral arm of the maxilla is a narrow band, dull black and smooth. In the position shown in Fig. 3, it lies below the oral membrane with its concave surface directed upward and forward.

At the union of the two arms the band is twisted through an angle of about 45°, so that when seen directly from behind the ventral edge of the median arm forms a nearly straight line, while the lateral arm is concave on its ventral surface and on its posterior margin, Fig. 5, *A* and *B*.

The position and structure of the mandibles clearly indicates

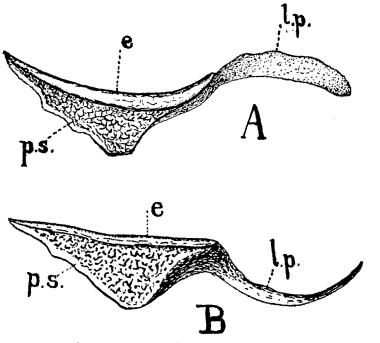

FIG. 5. *A*, maxillæ seen from ventral side and a little from behind. *B*, same seen directly from posterior surface. × 4.

that each mandible moved independently to and from the median line, so as to bring their stout crushing and cutting edges into apposition. They are frequently found with their posterior margins widely separated from the body, or even thrown forward in front of the head with their ventral surfaces facing upwards. Thus it is extremely probable that the mandibles, like two great lids or covers, could swing forwards and backwards on the membrane attached to their anterior margins, although it is improbable that they normally passed beyond the vertical position during life, Fig. 2.

The maxillæ are usually widely separate in the median line, and each was probably quite independent of the other. Their form indicates that their movements were complex. They appear to have had a rotary movement on their long (transverse)

axis, thus swinging their ventral edges forwards and backwards in a nearly horizontal plane. At the same time their median ends could be thrown forwards and medianly, thus bringing their diverging median margins more nearly parallel, and nearer together in the median line. The difference in curvature, density and rigidity between the mandibles and maxillæ, and the direction of the marginal spines on the mandibles and their absence on the maxillæ makes it very improbable that one pair acted directly against the other. It is more likely that the maxillæ merely pushed the food forward and inward, where it could be crushed, or cut, between the stout margins of the mandibles, in a manner similar to that which obtains in the mouth parts of arthropods.

I regard the paired upper and lower jaws of *Bothriolepis* as the homologues of separate right and left halves of the embryonic mandibular and maxillary arches of the higher vertebrates. As is well known these ridge-like lobes appear in all vertebrate embryos on the sides of the head, close to the nerve cord and then migrate toward the median ventral side. These embryonic mandibular and maxillary lobes I have for many years regarded as the vestiges of arthropod appendages which, owing to the special conditions under which the vertebrate head is developing, are carried toward the hæmal side of the head, instead of the neural side.

Bothriolepis is the only fish-like animal in which the halves of the jaws are separate, and functionally independent in the adult, and it thus supplies precisely the condition which the arthropod theory of the origin of vertebrates demands.

Back of the maxillæ, the oral membrane is strengthened by two bands of dermal armor. They are very thin and delicately ornamented, and when the head is in a normal position the posterior band is entirely, and the anterior one partly, overlapped by the anterior ventral plates. The narrow anterior band consists of five or six segments. The posterior one is unsegmented. Both bands are attached to a large lateral plate, the lateral end of which is bent at right angles, and attached to the lateral walls of the head, Fig. 3.

A small quadrilateral plate, that I shall call the *prc-lateral*, lies

just in front of the extra-lateral. It should be regarded as belonging to the anterior dorsal margin of the head, Fig. 1. But it is movable and is nearly always folded over on to the ventral surface, Fig. 3. It is marked with a sensory groove, probably a continuation of the anterior vertical one, although it does not appear to be exactly in line with it.

The median plate of the ocular opening is nearly perforated by a deep pineal foramen, often indicated by a low tubercle on

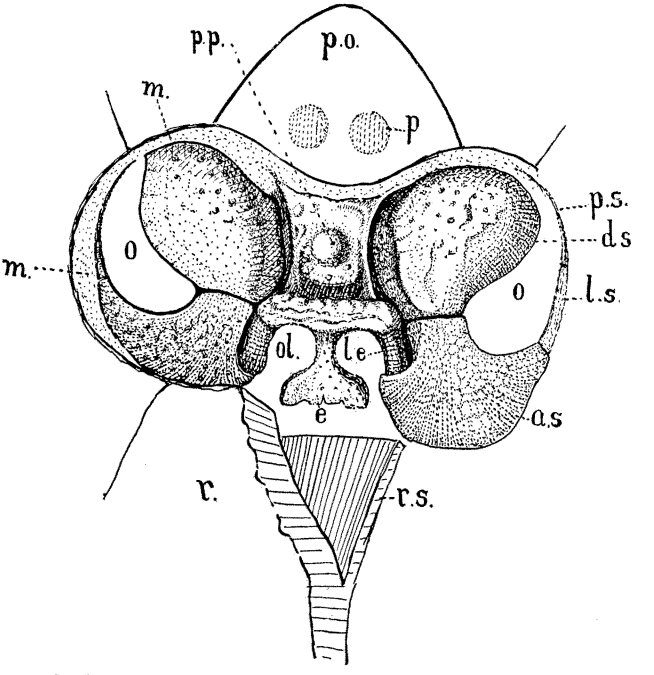

FIG. 6. Ocular and olfactory plates, in position with part of the rostral and lateral plates removed. *a.s*, anterior sclerotic; *d.s*, dorsal sclerotic; *e*, ethmoid; *l.e*, lateral arm of ethmoid; *l.s*, lateral sclerotics; *m*, membrane; *o*, corneal surface of eye; *ol*, olfactory opening; *p*, two pineal eye pits on under side of post-orbitals; *p.p*, pineal tubercle on outside of pineal plate; *p.s*, posterior sclerotics. × about 5½.

the outer surface, Fig. 6. A pair of similar pits, but not quite as deep and without any surface indications of their presence, are clearly shown on the inner surface of the small post-orbital. There is every reason to regard these three pits as similar in character and as indicating the presence of a tri-ocular median eye.

A broad thin shelf of bone extends inwards from the ant-orbital plate forming a wide chamber between the anterior surface of the T-shaped bone described by Whiteaves, or the ethmoid as I shall call it, and the two arms of the ant-orbital, Fig. 2. When the anterior face of the ethmoid is exposed, it is seen that its arms nearly enclose two circular openings, *ol*, in which the floor of the olfactory organ was probably situated, and which also served for the passage of the olfactory nerves.

These two pits clearly correspond to the antorbital fossæ of *Cephalaspis* and *Trematapis*, and thus a more satisfactory explanation of the location of the olfactory organs is furnished than the suggestion that they are situated on the margins of the mandibular plates, where there are no indications whatever of any infoldings of the oral membrane that might be regarded as olfactory organs.

Two large saucer-shaped sclerotic plates are attached by short movable arms to the lateral arms of the ethmoid, *a. s.*, and two much thinner and crescent-shaped plates, *l. s.* and *p. s.*, form the lateral and posterior walls of the orbits. The well known plate attached to the sides of the pineal plate, *ds*, completes the dorsal wall of the orbit.

All these plates are held together, and to the sides of the sensory opening, by tough but flexible membranes, leaving thus a relatively large space for the movements of the various parts. It is clear from the position of the plates in different specimens that the pineal plate could be pushed backward for several millimeters drawing the ethmoid backwards and upwards so as to open the olfactory chamber. This movement would also raise the anterior and lateral sclerotics which in turn would elevate the dorsal sclerotics and expose the eye openings, *o*, on the sides and front. The reverse movement would lower the ethmoid and draw the corneal surface of the eye into a pocket formed by the thick median margins of the adjacent cranial plates. Thus the eyes and olfactory pits could be opened and closed by the same set of movements.

The sensory canals that converge toward the median occipitals do not unite there as usually figured. Their posterior ends separate close to the median line and terminate in two small open-

ings, evidently comparable with the openings to the so called endolymphatic ducts of *Trematapis*.

In order to understand the morphology of the cephalic region of the Ostracoderms it is essential to know the location of the gills. Certain problematical structures found in the chamber in front of the ridge on the inner surface of the anterior ventro-laterals I formerly regarded as gills. I have not found any additional evidence in support of this conclusion. The presence of gills at this place would indicate that the extra-lateral was an operculum guarding the exit to the gill chamber, for it is the only cranial plate that could possibly act as such.[1] But its movements must have been very restricted and the place left for the passage of water extremely narrow, for both dorsal and ventral margins are articulated to the margins of the laterals and to the anterior ventrals respectively. The movement, such as it is, appears to be merely a tilting or partial rotation of the plate on its long axis in order to accommodate the slight dorso-ventral movement of the front part of the head, which would be impossible without some such arrangement.

On the other hand several facts indicate that the gills may have been situated in the post-cephalic portion of the buckler. These facts are (1): The presence of the superimposed lamellæ covered with what appears to be a continuation of the integument. These folds are more suggestive of gills than of any other known organs, and are almost invariably distinctly preserved, even where there is no trace of a notochord, showing that they must have had considerable power to resist decay, more, for example, than the folds in the mucous membranes of the viscera, the only other structures with which they might be compared. Moreover, if the walls of the viscera are as well preserved as this, then other internal organs should be visible in sections also, but as they are not, we are obliged to conclude that the folds in question are not produced by intestinal folds, or by any other structures of that

[1] The rather large opening in the sides of the anterior ventrals beneath the base of the pectoral spines, Fig. 1, could have hardly served any other purpose than for the passage of blood vessels and nerves to the pectoral spines.

The structure of the proximal end of the pectoral appendage indicates that some of the muscles moving the appendage were attached to the outer surface of the base of the appendage and to the outer surface of the anterior ventro-laterals.

nature. (2) The small size of the trunk at the posterior opening of the dorsal shield, and the presence of what appear to be dermal plates within the thoracic buckler, suggest that the trunk extends forwards within the buckler nearly to the head region, and that it is attached to it only along the low ridge and to the two large processes in the mid-dorsal line, to the posterior corner of the posterior ventro-laterals, where there are two large scars and a transverse ridge, and to the internal ridges near the junction of the cephalic and post-cephalic portions of the buckler. (3) The fact that the greater part of the buckler is usually filled with the same kind of matrix as that on the outside, while the part containing the finer matrix, and indicating the presence of organic material, forms a comparatively narrow band. (4) If the gills are located in this large chamber, the water must have passed out of the buckler at the posterior end, on either side of the trunk. Such a condition would harmonize with the fact that the cloaca is situated so far forward, for without such a current of water the excreta could not be easily discharged.

In conclusion, we may add that if the gills are located in the thoracic portion of the buckler, it becomes extremely probable that *Bothriolepis* possessed an atrial chamber similar to that of *Amphioxus*. The formation of such a chamber could have been brought about by the extension of the margins of the cephalic shield of such a form as *Cephalaspis* and their union on the ventral side, thus enclosing almost the whole ventral surface of the trunk from the anus nearly to the mouth, including the marginal appendages. The latter would then occupy about the same relative position as the lamellæ of *Bothriolepis*.

There has evidently been a forward extension of the ventral shield of *Bothriolepis* so as to partly cover the plates imbedded in the membrane of the oral region. The whole of this region, back to the ridge on the inner surface of the anterior ventro-laterals, with its four rows of plates, corresponds to the uncovered oral region of *Trematapis*, with its four rows of small plates surrounding the mouth.

HANOVER, N. H.,
June 21.