ART. XXXIV.—*Protichnites and Climactichnites; A Critical Study of Some Cambrian Trails;** by LANCASTER D. BURLING.

JUDGING the nature of the maker of a trail by peculiarities in its composition may be difficult and the solution false—for example, the writer has watched the larvae of the common may-fly crawling along the mud on the tidal flats of the St. Lawrence and leaving a perfectly smooth sinuous trail or groove which would naturally be associated in the mind of almost anyone with the work of a worm, certainly nothing with the legs of a may-fly larva. That the Upper Cambrian sea was peopled by animals of large size is well known, but the trails upon which this inference is based have so far failed to indicate the true nature of their makers. Indeed they have been the subject of frequent and widely variant conjecture. A critical study of some of the trails in the Cambrian has yielded conclusions so substantial or so different from those in the literature that they appear to be worthy of record.

PROTICHNITES.

The trails to which this name has been applied were referred to the agency of a tortoise by Owen[1],† who later[2] assigned them to the work of a crustacean like *Limulus*. In this view he was followed by Dawson[3] and Dana.[4] Dawson later[5] assigns them indubitably to the work of crustaceans, but lessens the weight of this reference by suggesting that *Climactichnites* may have been made by the same animal. With the exception of Chapman,[6] who suggests that both *Protichnites* and *Climactichnites* are of fucoidal origin, succeeding authors, beginning with Billings in 1870,[7] have referred them to the work of trilobites. Packard[8] thinks they could "perhaps have been made by the extremities of the feet of a small shrimp-like creature." Later[9] he questions the ability of *Paradoxides* to make the trail, a question first raised by Dawson.[10] Walcott[11] unhesitatingly states that they "were made by trilobites of the genus *Dicellocephalus*."

Let us look at the trails themselves and see whether or not their critical study may not yield results of tangible value in the identification of their makers. *Protichnites* (see fig. 1) is characterized by two rows of footprints paralleling a median groove. They have been found on Upper Cambrian sandstones in Ontario and New York. The trails give us several clues as to the animal which made them, and these facts

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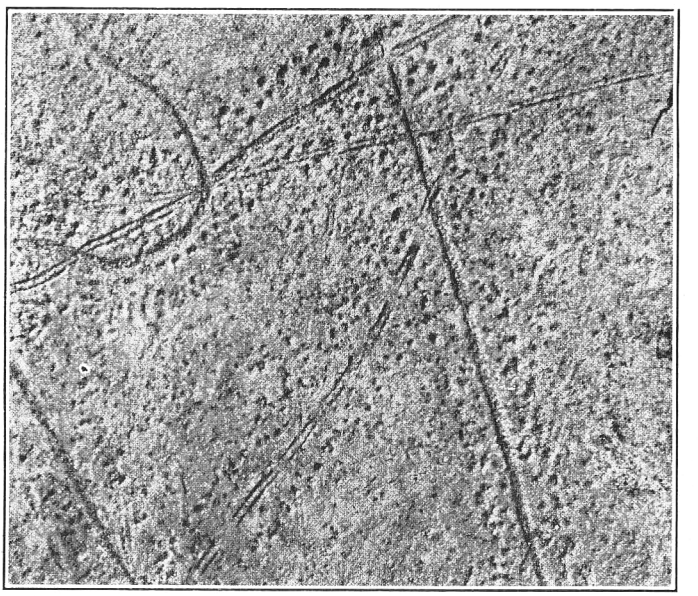
† For references, see the literature at end of article.

and the inferences they support follow, using the same notation in each case.

Facts: (*a*) the side tracks are frequently three-toed;[12] (*b*) these trifid tracks usually toe in; (*c*) the side tracks are usually 2 or 3 inches apart[13] though trails up to 5 or 6 inches across have been observed; (*d*) the trails are not straight, and a single trail has been observed to reverse its direction entirely so that the animal moved off in a direction parallel to but opposite to that of its previous track, all in a distance of less than three

FIG. 1.



Upper Cambrian Trails.

FIG. 1. *Protichnites logananus* Marsh ×1/6. (After Walcott.) Ausable Chasm, N. Y. U. S. Nat. Mus.

times the width of its track, the sharpest curve observed having a radius but little more than half the width of its track; (*e*) some of the median grooves are double and very sharply incised, others on the same slab betray no doubling, yet the width of the single groove closely approximates the distance between the double tracks; (*f*) the median groove does not swing to the side when the trail makes a turn, even on the sharpest curves the median groove lies midway between the

side leg tracks; (*g*) in one trail the median groove is only impressed at intervals, but these are regular and occur 26 times in a horizontal distance equal to 25 times the width between the tracks; (*h*) where the trail crosses a ripple marked surface all traces of ripple mark are obliterated for a distance a little wider than the extreme width of the trail, and the feet tracks are large and coarse with the median groove deeply incised; (*i*) on a surface adjacent to that showing *g* occurs a trail simulating *Protichnites*, but without the median groove and with the feet tracks small and sharply impressed; (*j*) the side rows of leg tracks are not arranged along a single straight line, but appear to be more or less double; (*k*) where the median groove is deep the side tracks are proportionately deep; (*l*) where the median groove is only marked at intervals, as in *g*, the impressions of the legs betray a tendency to be arranged in slightly curved lines concave toward the center, with the crests about as far apart as the intervals dividing the impressions of the median groove and more or less opposite to these impressions; (*m*) the number of leg impressions was counted in two places on the trail mentioned in *g*; in one where a group of 9 median groove impressions was available 65 leg impressions occurred on one side, 63 on the other; in another group of 6 the number of leg impressions was respectively 38 and 40; each of these groups was crossed by another trail, and the number of legs may be greater on this account.

Inferences: (*a*) Some of the appendages used by the animal in walking were three-toed; (*b*) the animal toed in, and toeing in is usually characteristic of heavy low-lying bodies whose feet touch the ground well toward if not beyond the sides of the body; (*c*) if the inference in *b* is correct, the animal was neither wider nor narrower than the track and individuals ranged in size from 2 to 6 inches in width; (*d*) its body was either extremely flexible or else short and more or less circular in outline; (*e*) the animal usually (see *i*) did not carry the entire weight of its body on its legs, but allowed a median portion to rest on the bottom and this portion was apparently forked in some, club-shaped in others—perhaps a sexual difference; (*f*) the part of the body which rested on the bottom was not the telson of a *Limulus*-like crustacean or trilobite, but was a process situated somewhere between or very close to the legs; (*g*) the animal was able to bear almost its whole weight (all, if *i* was made by the same animal) on its legs, but where its median portion did just graze the ground it did so once for every time it moved forward through a distance equal to its own width; this corroborates *d* in indicating the general correctness of making the animal round or oval in outline; (*h*) the animal was heavy, and its legs were comparatively short

and sank deeply into the bottom; (*i*) the ends of the legs were more or less pointed and could only support the entire animal when walking on a hard bottom (*i* may have been made by a different animal); (*j*) the legs were not all of the same length; (*k*) the question of whether the median portion touched the bottom or not was apparently one of whether or not the bottom was soft enough to allow the legs to sink in, though it must be recorded that the trail described in *i* is 6 inches or more across and may have been made by a very large and perhaps strong form; (*l*) the front and back legs were respectively shorter than those in the centre; (*m*) in making this trail, *g*, the animal was apparently skipping along with the body supported in the water, and the impressions of the feet are probably not confused. If this inference is correct, and remembering that the trails are crossed by others, the number of pairs of legs was in all probability 6, though it averages nearly 7.

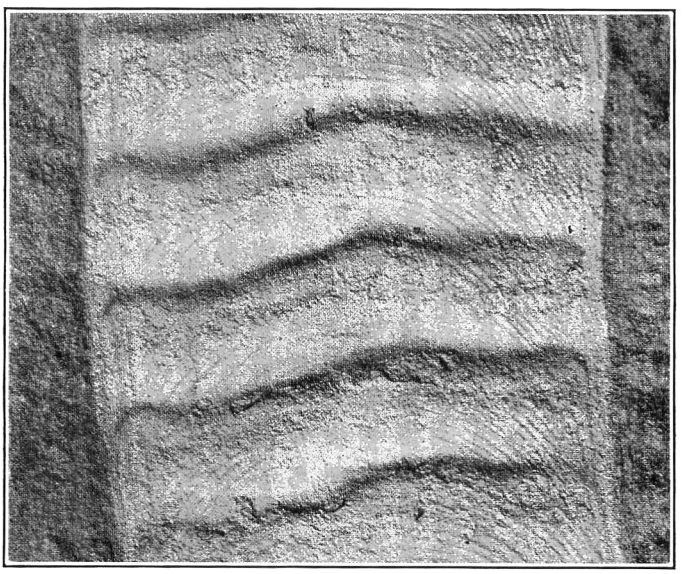
Climactichnites.

Logan, the first describer of these trails, believed them[14] to be the work of molluscs, a suggestion which received support as late as 1903 when Woodworth[15] published the first illustration of the peculiar oval bodies which have been found at one end of the trails at Mooers, New York. Walcott[16] has recently figured a similar oval body from the Upper Cambrian at New Lisbon, Wisconsin. He refers them to the work of annelids, a reference which was anticipated by Gratacap in 1901.[17] Curiously enough several of the earlier writers believed *Climactichnites* and *Protichnites* to be different expressions of the trail of the same animal, an observation which received experimental confirmation at the hands of Sir William Dawson[18] who discovered that when walking on the bottom the horse-shoe crab used its legs and made a trail like *Protichnites*, but that in shallow water just covering the body it propelled itself by moving its abdominal gill plates and left a trail resembling *Climactichnites*, (*a*) "except that the oblique furrows made by the legs between the median and lateral ridges are directed in the reverse direction";[19] (*b*) "except that in the track of *Limulus* the lateral and median lines are furrows instead of ridges."[20] Jones[21] believed them to be the flattened galleries of burrowing crustaceans, and Grabau[22] in 1913 suggests that the oval bodies of Woodworth may be collapsed burrows. Dana,[23] Billings,[24] and Packard[25] believed they were to be ascribed to trilobites. Todd[26] concludes that the animal was provided with a rigid caudal shield, with bristles or slender spines, and that the ambulatory organs leaving the last impressions were very perfectly flexible and must have been in pairs, each capable of motion independent of its fellow. Hall[27] says that "the

markings under consideration do not appear to have been made by an animal provided with free movable limbs, or otherwise with very short limbs, without the acute appendages belonging to *Limulus*." Patten[28] was the first to suggest an Eurypterid origin, "the abdominal gill plates making the rhythmic ridges in the sand." Grabau and Shimer[29] assign the trails to the work of "some unknown terrestrial or semi-terrestrial animal."

Authors are generally agreed that the oval bodies represent the end of the trail; thus Woodworth[30] has suggested that they

FIG. 2.



Upper Cambrian Trail.

FIG. 2. *Climactichnites youngi* (Chamberlin), 5/6 nat. size. (After Walcott.) New Lisbon, Wis. U. S. Nat. Mus.
(The front end of the trail is toward the bottom of the page.)

represent the end of the trail, and Eastman[31] states that "the animal, if an Eurypterid, moved toward the sedentary impression and not away from it." Todd,[32] who apparently did not have the opportunity of observing the oval bodies, records his belief that the apex of the V-shaped impressions points forward, and Walcott[33] speaks of the oval bodies as terminal and (p. 284) of the forward-curving transverse furrows made by pressing the beach-sand backward in creeping."[34] The observa-

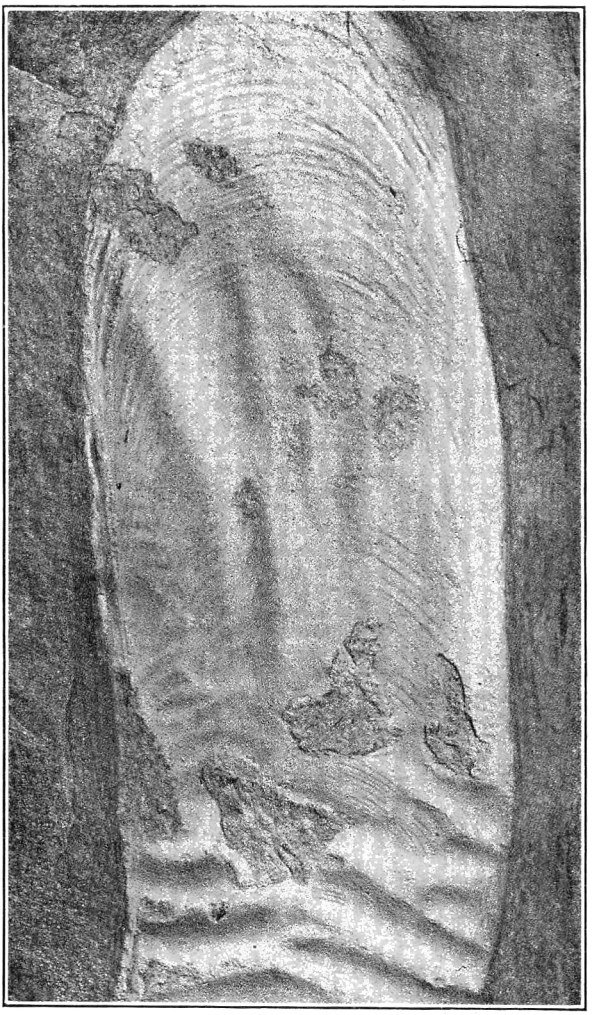
tions of Kishinouye[35] indicate that the apex of the V-shaped impressions in the somewhat similar track of *Limulus* points forward. As already mentioned, however, Packard records[36] the fact that the oblique furrows of *Limulus* are directed in a direction reverse to that of the ridges of *Climactichnites*, and Patten,[37] in comparing the tracks with those of *Limulus*, states that the tracks showed a beginning in a hollow in the sand, and thus corresponded to those of *Limulus* "which remains buried on recession of the tide and upon its first return crawls and then swims away."

Grabau[37a] mentions *Climactichnites*-like trails in the Silurian, which may have been produced by eurypterids with bilobed telsons, myriopodus types, or insecta.

Climactichnites may be characterized as consisting of a series of more or less transverse subparallel ridges bounded on either side by a lateral ridge. They have been found on Upper Cambrian sandstones in Ontario, New York, and Wisconsin. Let us examine the trails critically to see whether or not they speak for themselves, dividing fact from inference as we did in discussing *Protichnites*.

Facts: (*a*) the lateral ridges may be almost absent or may be very coarse, in which case they are regularly swollen at intervals equal to the distance between the transverse ridges, and each swollen portion appears to merge at one end into an adjacent cross ridge; (*b*) the lateral ridges vary from $1\frac{1}{4}$ to $4\frac{1}{2}$ inches apart in specimens from Wisconsin, but average 4 to 6 inches apart in specimens from New York and Canada; (*c*) the transverse ridges are usually arched or V-shaped but they are frequently very irregular, even sinuous or double bow-shaped, and the angle of the V varies within wide limits; the apex of the V is not always symmetrically spaced, betraying a general tendency to swerve to the outside on curves, but being irregularly disposed even on tangents; (*d*) there is more or less interruption of each ridge at the apex of the V, so much so that the line connecting the apices sometimes forms a slightly marked ridge; (*e*) the transverse ridges are usually equally spaced, but this again varies greatly and the ridges may be small and irregularly spaced; (*f*) lying upon the ridged trail in the specimen from New Lisbon, Wisconsin (see fig. 2), is a series of very closely spaced almost semicircular raised lines which cross the transverse ridges without interruption or deflection; (*g*) the convexity of the lines mentioned in *f* is directed in the same direction as the apex of the V-shaped arch in the transverse ridges; (*h*) Todd[38] mentions longitudinal lines which are sometimes wavy; (*i*) the trail completely reverses its direction in a distance almost equal to 5 times its width, the sharpest curve observed being one with a radius of little more than one-half

FIG. 3.



Upper Cambrian Trail, New Lisbon, Wisconsin.

FIG. 3. *Climactichnites youngi* (Chamberlin), 3/4 nat. size. (After Walcott.) U. S. Nat. Mus.
(As now interpreted the animal moved toward the bottom of the page.)

the width of the track; (*j*) at one end of several of the trails convex oval bodies as wide as, or slightly wider than, the trail and little more than $2\frac{1}{2}$ times as long are present (see figs. 3 and 4). Woodworth[39] figures these as symmetrically rounded at both ends, Walcott's specimen[40] shows the outline at only one

FIG. 4.

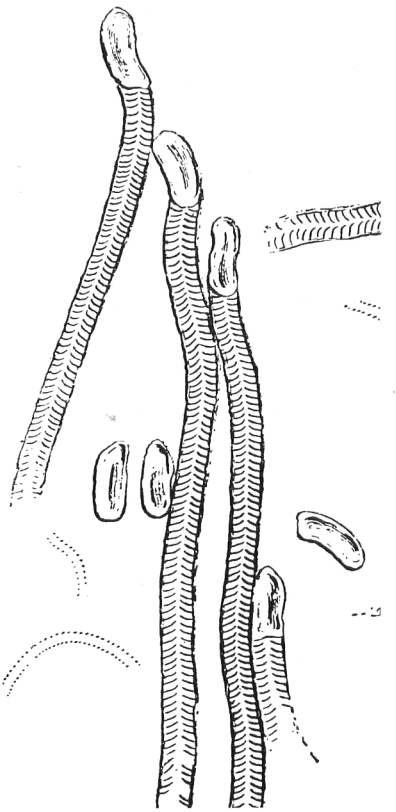
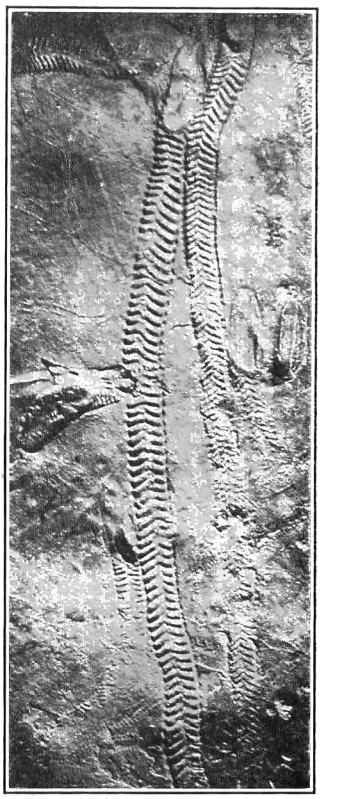


FIG. 5.



Upper Cambrian Trails, Mooers, N. Y.

FIG. 4. *Climactichnites wilsoni* (Logan), ×1/25. (After Clarke.) State Museum, Albany, N. Y.

FIG. 5. From a photograph of a cast of the slab shown in fig. 1, in the Brooklyn Museum. The animal that made the trail is now believed to have moved away from the oval body end.

end, but the slab in the Museum at Albany,[41] of which there is a partial replica in the Brooklyn Museum (see figure 5), shows specimens with one end rounded, the other (the end toward the trails) unsymmetrically arched outward, symmetrically

V-shaped outward, abruptly truncated at right angles to the longer diameter, and even arched inward; (*k*) the "oval bodies" are themselves frequently curved, even broadly S-shaped; (*l*) the apex of the V-shaped transverse ridges always points toward the "oval bodies"; (*m*) the V-shaped transverse ridges may often be seen to extend nearly half way beneath the oval-body; (*n*) the trails are nearly always faint and disappear at the end opposite to the one bearing the "oval body."

Inferences: (*a*) the side ridges were apparently made in the same push that made the transverse ridges, and that both are ridges instead of furrows indicates that the apex of the V-shaped ridges points backward with reference to the line of progress, for this is the only direction in which material could be shoved outward and heaped up along the edges of the trail; (*b*) in all probability these figures represent the entire width of the animal; (*c*, *d*, and *e*) the portion of the animal making the transverse ridges was very flexible and capable of making movements differing in amplitude, direction, and form; the interruptions in the center (*d*) are to be expected, and do not require a division of the ridge-forming portion, a view which is corroborated by the wide lateral shifting exhibited by this median ridge; (*f*) these semicircular raised lines must have been made last or they would have been obliterated or marred, and must indicate the conformation of the back end of the animal; their close spacing would indicate slowness of forward movement or creep; (*g*) the apex of the V-shaped ridges therefore points also toward the rear; (*h*) probably made, as Todd suggests, by bristles or other portions of the under surface as the animal moved along,—I have not observed them; (*i*) the animal, or its ambulatory organ, was very flexible, or else short and more or less elliptical in outline; (*j*) the evidence seems to warrant us in disagreeing with the concensus of previous opinion (see p. 391), and in supposing these oval bodies to represent the initial resting place of the animal that made the trails, the round ends, as indicated in *a* and *f*, being the rear and the V-shaped end the front. This front end was capable of being moved from V-shape forward (its position in repose) to V-shape backward, and this movement carried the animal along. The convexity of these oval bodies may be explained as follows: If an animal with a very flexible under surface or foot were stranded on the retreat of the tide, scour would obliterate the previous tracks and would reduce the general level of the beach wherever it was not protected from erosion by the disk-like foot, and the edges of this organ would naturally be depressed in an endeavor to prevent being washed away. The lens of sand thus enclosed would be left upon the departure of the animal at the approach of the next tide, its

preservation, and that of the tracks made in moving away, being due to fortuitous circumstances; (*k*) corroborates *i* in proving the animal or its foot to be extremely flexible; (*l*) therefore, if we are right in *a*, *f*, and *j*, the apex of the V always points in the direction from which the animal has been moving, not forward as nearly everyone has supposed, Patten[42] being the only one to suggest a possible difference; (*m*) unless the ambulatory organ or organs occupied nearly half of the under surface this fact alone would prove that the animal moved away from the oval-body end. The preservation of these marks in the portion of the trail where the body must have rested seems to the writer to be explained by supposing the edges of the disk-like foot to be sufficiently extended in repose to protect the last marks made by the animal previous to its rest—the oval body is frequently about one fifth wider than the immediately adjacent trail; (*n*) the progressive faintness and disappearance of the trails at the end opposite to that bearing the oval bodies is characteristic of nearly all of the trails; all of those, for example, which exhibit both ends in the specimen at Albany.[43] They certainly seem to corroborate *a*, *f*, *j*, and *m*, in indicating that the animal started from the oval-body end and rose into the water at the other end, as pointed out by Patten,[44] and that they could swim.

In some trails, notably the one running down the center of the slab in the museum at Albany, the disposition of the ridges is such as to suggest that the animal did move toward the oval body end of the trail. The impressions of the curved margin described under *f* on a previous page were unknown to geologists until the specimen from New Lisbon, Wisconsin, was figured by Walcott in 1912, and while Walcott adheres to the belief that the New Lisbon animal also moved toward the oval-body end we have endeavored to show that this specimen proves the oval body end to be the initial portion of the trail. The V-shaped ridges in both the Albany and New London specimens point toward the oval-body end, and it is somewhat improbable that the animal should have moved *toward* that end in the one case and *away* from it in the other. However, there are certain differences in the trails, and these may be due either to causes dependent on the physical conditions at the time the trails were made or to differences in the animals themselves. The New Lisbon specimen certainly started from the oval body end to crawl away; those in the Albany slab may have come to rest in the manner described by the early observers. Naturally, however, the conclusion that the oval-body end was made last has called forth attempts to explain the disappearance of the animal.

Conclusions.—The animals that inhabited the sea some thirty million years ago are known to us with a perfection that is a continual source of wonder, and the discoveries of the past few years in these ancient rocks are little short of marvellous, but that the Cambrian seas were peopled by a host of forms of which we know little or nothing is no less certain than that the waters of pre-Cambrian time were full of life. While certain of these unknown forms offer us nothing more substantial than the record of their reptant efforts, the desire to know is responsible for attempts at their deciphering. The facts are daily becoming more numerous and the inferences surer. That *Protichnites* was made by a short, low-lying, and more or less heavy set, approximately 12-legged crab-like animal, and that *Climactichnites* was made by the snail-like creep of a flexible slug-like animal which was frequently stranded at low tide, but was able to swim in the waters of the full tide, have passed the stage of guess-work and border on the real.

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34. It should be noted that these "forward-curving transverse furrows" are more or less sinuous and bend sharply backward (using the same terminology) at their union with the sides of the trail, which they join at a tangent. Consideration of this one trail alone (pl. 39, fig. 2 of Walcott) seems sufficient to prove that the animal must have progressed in a direction exactly opposite to that assumed by Walcott. Under the new interpretation the transverse furrows bend sharply forward at the sides and are bent backward in the center, and are closely covered by the series of curved raised lines left by the posterior margin of the animal (see *g* of text).
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41. See Bull. New York State Mus., No. 80, 1905, pl. 3.
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