THE DEVELOPMENT AND MYELINATION OF THE POSTERIOR LONGITUDINAL BUNDLE IN THE HUMAN

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THE posterior (or medial) longitudinal bundle owes its interest partly to its early phylogenetic and ontogenetic development, and partly to the varied and numerous connections that indicate the importance of its functions. This bundle must not be confused with the dorsal longitudinal bundle of Schütz which runs through the central grey matter of the entire brain stem close to the floor and connects with the nuclei of all the cerebral nerves(1): it must also be distinguished from the faisceau longitudinalis medialis of Winkler(2), also called the faisceau fronto-occipitalis, that lies lateral to the head of the caudate nucleus.

The tract is present in all Vertebrates, and in Fishes, Amphibians and Reptiles it represents one of the largest bundles of the brain stem(3). In the human embryo it is said to develop in the 12 mm. stage(4), when it can be traced forwards to make a connection with the fibres of the posterior commissure which is already well developed. It is also stated (5) that as early as the end of the first month descending fibres from the nucleus of Darkschewitsch can be traced into the posterior longitudinal bundle.

The bundle contains various ascending and descending fibres, and their origin and course is stated somewhat variously by different writers. The most complete summary is that given by Cajal(6). He divides the fibres into an ascending and a descending group with the following components:

(1) Ascending fibres:

Arising from (a) Deiters' nucleus, many fibres crossed.

- (b) Substantia gelatinosa Rolando (sensory nucleus of nerve 5).
- (c) Anterior horn cells of spinal cord.
- (d) Cells of formatio reticularis.

Ending in

- (a) Nuclei of nerves 6, 4, 3.
 - (b) Interstitial nucleus of Cajal.
 - (c) Posterior commissure.
 - (d) Corpora mammillaria by passing in front of Gudden's tegmental bundle.

(2) Descending fibres:

Arising from (a) Interstitial nucleus of Cajal.

(b) Deiters' nucleus.

Ending in (a) Nuclei of nerves 4 and 6.

(b) Spinal cord, by anterior ground bundle.

In addition to these fibres, other workers describe the following connections:

- (1) Ascending fibres:
 - (a) Arising from the superior olive(7).
 - (b) Ending in the nucleus of Darkschewitsch (8, 9, 10).
 - (c) Passing to the optic thalamus(11), the infundibulum and the internal capsule(12).
- (2) Descending fibres:
 - (a) Arising from the superior olive(7).
 - (b) From the tectobulbar tract at the level of the red nucleus (13).
 - (c) Arising from the ganglion of Gudden (the termination of Gudden's dorsal tegmental bundle at the level of the nucleus of nerve 4)(8).
 - (d) Arising from the nucleus of Darkschewitsch (8, 14, 15).
 - (e) From the posterior commissure, crossed fibres (16).
 - (f) From Gudden's tegmental bundle (faisceau de la calotte de Gudden) (17, 18).
 - (g) Joining emerging fibres of nerves 7 and 12(19).
 - (h) From the paraventricular (or posterior hypothalamic) nuclei (20).

METHOD

The material on which this paper is based includes serial sections of brain stem from eighteen specimens of the following ages:

*10 mm.	One		22–24 weeks	One
*12 mm.	One		24-26 weeks	One
*17 mm.	One		26–28 weeks	One
20 mm.	One		36 weeks	One
8 weeks	One (unmeasured)		Full time	Two
37 mm.	One	*(One)	3-month infant	Two
10 weeks	One	、	8-month infant	One
*14-16 weeks	One		9-month infant	One
	* Serial, even	ry section.		

The younger embryos up to and including the 10-week specimen were fixed whole in formol-saline, cut serially, and the sections stained by Scott's haematoxylin and Biebrich scarlet. The brain stem and in most cases the spinal cord of the older specimens were dissected out, fixed in formalin, and subsequently treated by the Weigert-Pal method. All sections were mounted serially.

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The series stained by the Weigert-Pal method is particularly favourable for the study of the development and connections of those tracts that myelinate early, as their paths are not obscured by the general heavy myelination that is present even by 8 months after birth.

OBSERVATIONS

(a) 10-mm. embryo. The posterior longitudinal bundle was not identified.

(b) 12-mm. embryo. A clearly defined bundle of fibres is present in the floor of the fourth ventricle, on each side of the mid-line, occupying the position in which the posterior longitudinal bundle is found in later stages of development. This group of fibres runs close to the mid-line and parallel with the long axis of the brain stem. It could not be traced higher than the level of the superficial attachment of the fifth cranial nerve.

(c) 17-mm. embryo. A bundle of fibres similar to that seen in the 12-mm. embryo was identified, and found extending up to the same level. When traced downwards it was found as a large group of fibres running longitudinally between the olive and the mid-line on each side, and passing anteriorly to take part in the anterior ground bundle in the spinal cord.

(d) 20-mm. embryo. Sections through the level of the upper part of the fourth ventricle show well-defined bilateral bundles of fibres just below the floor close to the mid-line. Lower down in the middle pons region the definite bundles are lost, but in the lower pons and medulla regions the fibres are again seen in two discrete fasciculi lying more ventrally.

(e) 8-week embryo. The bundle is clearly defined at the level of the nucleus of the fourth nerve. Traced inferiorly the fibres become diffuse, but in the medulla they again make definite fasciculi.

(f) $8\frac{1}{2}$ -week embryo (37 mm.). In this embryo the posterior longitudinal bundle appears as a clearly defined group of fibres extending from about the level of the fourth nerve to the anterior ground bundle in the spinal cord. In the preparations the fasciculus could not be identified at higher levels, but in contradistinction from the younger embryos it formed discrete bundles throughout the pons levels.

(g) 10-week embryo. The bundle is considerably larger in size than in the younger embryo. Furthermore it can be traced up into the mid-brain region where it lies in close association with the nuclei of the third nerve and with the red nucleus. At this stage none of the fibres of the tract are myelinated.

(h) 14-16-week foetus. This is the youngest specimen stained by the Weigert-Pal method. It shows very slight myelination in the fibres of the bundle, and it may be assumed that no myelination occurs earlier because even at this age the myelin is very scanty and only present in a few of the fibres. Very finely myelinated fibres were traced as far up as the lower end of the third nerve nucleus and as far down as the anterior ground bundle of

the spinal cord. They were most numerous in the medulla, were almost lost in the lower levels of the pons, and again picked up at the upper part of the pons.

The origin of the fibres, although at first difficult to find owing to their small number, was nevertheless quite clear because the fibres of so few tracts show myelination at this age (21). In the medulla myelinated descending fibres arise from Deiters' nucleus and the superior olive in relatively considerable numbers, while ascending fibres arise in the reticular formation cells, but whether any of the fibres arising in Deiters' nucleus and the superior olive were ascending could not be determined. Myelinated connections with the sixth and the fourth nerve nuclei were seen (see diagram 1).

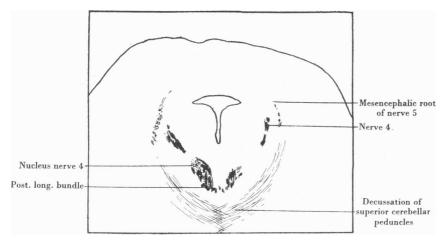


Diagram 1. Foetus 26-28 weeks.

A well-developed nucleus is seen sending a few myelinated fibres towards the posterior commissure, but the posterior longitudinal bundle is not myelinated at this level, so that any possible connection with this nucleus or with the nuclei of the third nerve could not be established. This nucleus is referred to in the remainder of this paper as the nucleus of the posterior commissure or "nucleus 1". In addition a small group of cells was found lying dorso-medial to this nucleus, which is described later as "nucleus 3".

(i) 24-26-week foetus. As in the 14-16-week foetus myelination in this bundle is most marked in the medulla. In the lower region of the pons the myelination is less but increases again in the upper pons levels; the whole tract, however, is very much better myelinated than in the younger foetus.

In addition to the connections previously established, myelinated fibres can be seen connecting the bundle with the nucleus of the third nerve, and with the nucleus of the posterior commissure and also connecting this nucleus with the posterior commissure. Myelinated fibres comparable to those which are definitely posterior longitudinal bundle fibres better seen in older specimens

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are present running in an oblique direction medial to the red nucleus and connecting at least in part with a small nucleus situated in the floor of the third ventricle in its posterior part (see "nucleus 4" later; see diagram 2). In addition another nucleus composed of large cells (referred to later as "nucleus 2") was found having some myelinated connections with the posterior longitudinal bundle. It is situated ventro-medial to the upper part of the nucleus of the posterior commissure, and rests on the capsule of the red nucleus.

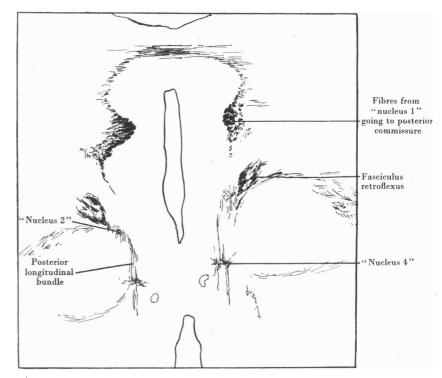


Diagram 2. Full-time foetus. Note "nucleus 4".

(j) 26-28-week foetus. The only difference noted from specimen (i) was the presence of a few fine myelinated fibres of the posterior longitudinal bundle crossing the middle line (see diagram 3) just medial to the point where the fasciculus retroflexus begins to impinge on the capsule of the red nucleus.

(k) 36-week foetus. No differences were observed from the previous specimen beyond an increase in the number of myelinated fibres in the bundle, and the appearance of myelinated fibres in connection with nucleus 3.

(1) Full-time foetuses (2 specimens). One specimen was better prepared than the other. The crossing fibres of the posterior longitudinal bundle were well marked lying considerably dorsal to the myelinating commissure of Forel,

and in sections showing these commissural fibres other myelinated fibres are seen some connecting probably with the nucleus previously noted in the floor of the third ventricle ("nucleus 4"), and others passing still more ventrally towards the lateral mammillary region. Although no definite connection can be established with the various mammillary nuclei, it is to be noted that fine myelinated fibres are seen in close connection with the cells of the accessory mammillary nucleus.

(m) Three-month infants (2 specimens). The bundle in the upper pons levels, divides into definite fasciculi. The greater degree of general myelination, especially in the higher regions, makes it more difficult to distinguish this bundle from other adjacent fibres. As in the full-time specimens, the fasciculus was traced up to the level of the mammillary region, the myelinated fibres becoming fewer in number and directed obliquely toward the mammillary bodies (see diagram 4). It is very doubtful, however, whether there is any connection with these bodies, and the bundle disappears at the upper level of the red nucleus. The nucleus of the posterior commissure and "nuclei 3 and 4" are well defined, but "nucleus 2" is difficult to identify as it is obscured by the myelinated fibres among which it lies.

(n) Eight-month and nine-month infants. The observations made on the younger specimens were confirmed in all levels below the nucleus of the posterior commissure. Unfortunately above this level the series of sections is too incomplete to admit of accurate deduction.

It is well known that the appearance of the bundle in section varies considerably at different levels of the brain stem, but as this has been fully described by others (22) it is unnecessary to repeat it here.

DISCUSSION

Examination of this series of specimens confirms the observations of others that the posterior longitudinal bundle appears first in the 12-mm. stage of development.

The fasciculus appears first in the medulla and lower pons levels, and rapidly extends downwards to the cord. The next group of fibres appears in the upper pons level and is not at first connected with the lower fibres, leaving a gap about and above the level of the entry of the fifth nerve. These upper fibres in the 8-week stage extend up to the level of the fourth nerve nucleus, and about the same time or a little later the gap between the first and the second groups of fibres is bridged across, the tract now appearing continuous between the spinal cord and the level of the fourth nerve nucleus. By 10 weeks' development the bundle has almost reached the level of the red nucleus and third nerve nuclei.

Myelination begins in the 14–16-week stage in a few fibres of the bundle. These myelinated fibres are most obvious in the medulla and lowest pons and cord, but almost lost in the lower and middle pons (the region corresponding

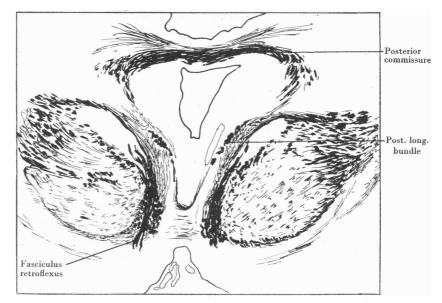


Diagram 3. Infant, 9 months. Note crossing fibres of posterior longitudinal bundle.

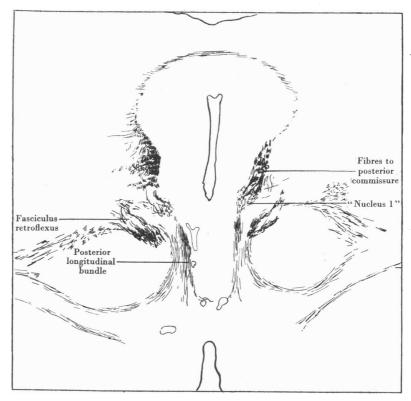


Diagram 4. Full-time foetus.

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to the gap that existed during the development of the fibres), and found again through the upper pons up to the lower end of the third nerve nuclei. Myelinated connections with the nuclei of Deiters' and of nerves 6 and 4 are present. Thus myelination occurs first in those fibres that have developed by 8 weeks, and in general myelination in the groups of fibres of the bundle follows in the same order as their development. [It is not suggested that there is any correlation between early development and early myelination; for example, the fasciculus retroflexus and the bundle of Vic D'Azyr are easily distinguished in an 8-week embryo, the former begins to myelinate about 26 weeks, the latter about full-time. The fornix is seen in a 10-week foetus, and myelinates 3 months after birth.]

By 24-26 weeks a myelinated connection is established with the nuclei of the third nerve, the nucleus of the posterior commissure and with "nucleus 2", and about the same time a few myelinated fibres cross near the upper end of the red nucleus just dorsal to the unmyelinated commissure of Forel, and connect with a small ventrally placed nucleus ("nucleus 4"). In the later weeks of foetal life the myelination is increased throughout the bundle, and at full time some fibres can be traced toward the lateral mammillary region.

Thus the component fibres and connections identified in this series correspond with those described by Cajal with the following reservations:

(a) Substantia gelatinosa of Rolando. This connection was impossible to identify in the older foetuses owing to the numerous myelinated fibres in the region, but in the 24–26-week specimen it was thought that such a connection existed.

(b) Anterior horn cells of spinal cord.

(c) Posterior commissure.

(d) Corpora mammillaria. No definite connection with these bodies was established.

In respect of connections other than those given by Cajal, the following were established:

(a) With the superior olive.

(b) With the nucleus of the posterior commissure.

(c) With a small ventrally placed nucleus ("nucleus 4").

Furthermore it is suggested that the fibres of the posterior longitudinal bundle crossing in the region of the red nucleus may possibly be those described by Beattie⁽²⁰⁾ as arising from paraventricular nuclei in connection with the central control of the sympathetic system.

The interstitial nucleus of Cajal and the nucleus of Darkschewitsch

During the study of the connections of the upper end of the posterior longitudinal bundle the authors found that this fasciculus freely connected with a large well-defined nucleus (see diagram 5) which also made abundant connections with the posterior commissure, and has been called, in the earlier

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part of the paper (on account of what appeared to be its chief connection), the nucleus of the posterior commissure or "nucleus 1". Judging from its position, and its relation to the posterior commissure, this nucleus should have been the nucleus of Darkschewitsch, for in certain references the terms "nucleus of Darkschewitsch" and "nucleus of posterior commissure" are used synonymously. On the other hand Cajal's diagram shows that his interstitial nucleus (lying nearer the red nucleus) makes more abundant connections with the posterior commissure, than does the nucleus labelled Darkschewitsch; in fact his interstitial nucleus may be said from his diagram to be furnishing the

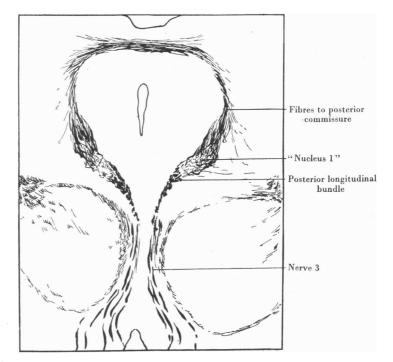


Diagram 5. Infant, 3 months.

bulk of the fibres to the ventral part of the posterior commissure. Search in the older material under investigation for the nucleus lying almost in the capsule of the red nucleus resulted in the establishment of a nucleus consisting of scattered cell groups, intimately related to the posterior longitudinal bundle but with no very apparent connection with the posterior commissure. This nucleus consisting in the older specimens of scattered cells was identified with a much more definite and discrete nucleus in the 24–26-week foetus and was called "nucleus 2" (see diagram 6). Two other nuclei had also been observed having connections with the posterior longitudinal bundle. The difficulty then arose as to which of these nuclei corresponded to the interstitial nucleus of

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Cajal, and to the nucleus of Darkschewitsch. A careful review of the literature on the subject of these nuclei was accordingly made. It was found that the descriptions by the various authors showed great discrepancies, not to say confusion (see Cajal(6), Gray(19,24), Foix(25,27), Ranson(23), Poirier and Charpey (28), van Gehuchten (26) and Winkler (14)).

A further careful study of the cells of this region was accordingly made in the material under investigation: the following account summarises the cell masses found in connection with the posterior longitudinal bundle, and the four nuclei which were found are carefully described as to position and connections, but in order to avoid further confusion in nomenclature they are referred to by numbers and the names used by Darkschewitsch and Cajal have been omitted.

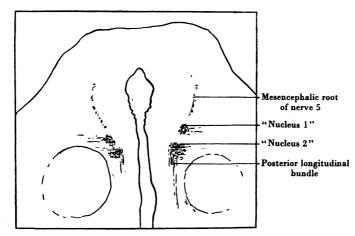


Diagram 6. Foetus of 24-26 weeks. [The red nucleus has been outlined, but no myelinated fibres are present in its capsule.]

Nucleus 1 (diagram 5), referred to in the previous part of this paper as the nucleus of the posterior commissure. This nucleus has its most bulky connection with the ventral part of the posterior commissure, and these fibres begin to myelinate as early as 14–16 weeks (i.e. before myelination of the posterior longitudinal bundle in this region). Myelinated connections between this nucleus and the posterior longitudinal bundle occur later, and furthermore myelinated fibres pass out laterally from this nucleus towards the thalamus (external nucleus) and also in the radiations of the calotte towards the globus pallidus. This nucleus is situated on the edge of the central grey matter surrounding the Sylvian aqueduct, and extends from the middle part of the third nerve nuclei up to the opening of the aqueduct into the third ventricle, that is to the level at which the fasciculus retroflexus is entering the capsule of the red nucleus.

Nucleus 2 (diagram 6). This nucleus appears in the higher sections of midbrain in which "nucleus 1" is disappearing. It lies slightly medial and ventral to "nucleus 1", resting on the capsule of the red nucleus, and between this nucleus and the myelinated fibres of the posterior longitudinal bundle, with which it appears to be connected. It consists of cells scattered in groups, and in older specimens it tends to become obscured by the increase of myelinated fibres in this region. It extends upwards to the upper limit of the posterior longitudinal bundle, that is to the upper end of the red nucleus. The nucleus was identified in the 14–16-week foetus, but not looked for earlier. Connections with the posterior commissure, if present, were difficult to establish.

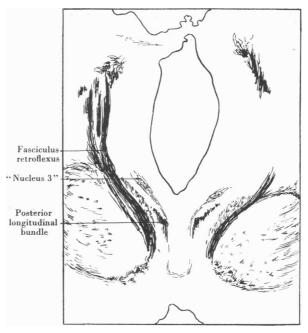


Diagram 7. Infant, 3 months. Note fine fibres passing ventrally from "nucleus 3".

Nucleus 3. This nucleus in the 3-month infant is well defined, and lies just within the lateral margin of the central grey matter of the floor of the Sylvian aqueduct (see diagram 7). Caudally it is found dorso-medial to "nucleus 1", and maintaining the same situation in the mid-brain it extends upwards to near the upper extremity of the red nucleus. A group of cells in a corresponding position was seen in the 14–16-week foetus but was not identified in sections of foetuses between this age and 36 weeks, by which stage a definite nucleus was seen with a few fine myelinated connections running in the direction of the posterior commissure. At birth this nucleus was definitely connected with fine myelinated fibres which pass ventrally medial to the posterior longitudinal bundle, some of these fibres crossing in the dorsal part of the commissure of Forel. Nucleus 4 (diagram 2). This is a very small nucleus present in all specimens older than 26 weeks lying in the floor of the third ventricle, medial to the red nucleus. It connects at least in part with the fibres of the posterior longitudinal bundle which in these sections are seen running in an oblique direction medial to the red nucleus. The myelinated fibres connected with this nucleus present a very characteristic appearance, because in addition to the fibres of the posterior longitudinal bundle running in a dorsi-ventral plane, there are other fibres (of unidentified destination) in connection with the nucleus which run medially and horizontally.

Cajal's description of the interstitial nucleus agrees with regard to its position with "nucleus 2" of this paper, but in the human foetus we did not find it abundantly connected with the posterior commissure as his diagrams of the nuclei in the cat suggest.

"Nucleus 1" in our material was the one most profusely connected with the posterior commissure: many writers speak of Darkschewitsch's nucleus as synonymous with that of the posterior commissure, and we feel that this name best describes it.

"Nucleus 3" on account of its position might be called the nucleus of Darkschewitsch because it lies just within the central grey matter, and though its earliest myelinated connections are with the posterior commissure, they are very scanty. Its later and more profuse connections are in a ventromedial direction. Its fibres differ from those of "nucleus 1" in that they are much finer, and throughout our series it appears as a definite and discrete nucleus; furthermore it was seen in the highest sections that also show "nucleus 1", and when "nucleus 1" disappears it was present in sections showing "nucleus 2".

"Nucleus 4" does not seem to have been described previously unless it is the "interstitial nucleus" described in Gray's text-book of *Anatomy* (19) as "a small collection of cells situated in the lateral wall of the third ventricle immediately above the upper end of the cerebral aqueduct." It is in any case very small in comparison with the other nuclei of the posterior longitudinal bundle.

The authors feel that "nucleus 1" may well be described as the nucleus of the posterior commissure, and "nucleus 2", since it lies among the fibres of the posterior longitudinal bundle, as the interstitial nucleus of the posterior longitudinal bundle.

SUMMARY

1. The posterior longitudinal bundle appears first in the 12-mm. embryo.

2. This bundle is one of the earliest to myelinate, the process beginning at about 14 weeks.

3. In the early weeks of development (previous to $8\frac{1}{2}$ weeks) there are two unconnected groups of fibres:

(a) A group connected with Deiters' nucleus which extends up into the lower pons, and downwards into the medulla and spinal cord.

(b) A group found in the upper pons region extending up to the fourth nerve nucleus.

4. At 14 weeks myelinated connections of the bundle are seen with the nuclei of Deiters' and of the sixth and the fourth nerves.

5. At 24 weeks myelinated connections occur with the nuclei of the third nerve and of the posterior commissure ("nucleus 1").

6. The various groups of fibres of the bundle myelinate in the same order as that in which they developed.

7. Myelinated fibres are seen within "nucleus 2" about 24-26 weeks: these may or may not at this age connect with the posterior longitudinal bundle.

8. Definite myelinated connections between the posterior longitudinal bundle and "nucleus 4" are seen at 26–28 weeks.

9. Myelinated connections of "nucleus 3" are seen at 36 weeks.

10. About 28 weeks a few myelinated fibres are seen crossing the mid-line in the supra-mammillary region their destination (or origin) is uncertain and they continue to increase in numbers in the older specimens, though all do not cross.

11. The nucleus of the posterior commissure ("nucleus 1") makes a definite connection with the posterior longitudinal bundle, and furnishes a large contingent of fibres to the ventral part of the posterior commissure.

12. In the region of the nuclei described by Darkschewitsch and Cajal four nuclei have been identified and described.

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* When this paper was ready for the press we received a note from Professor S. W. Ranson (Chicago) saying that he also has been investigating the nucleus of Darkschewitsch and the interstitial nucleus of Cajal, and was shortly publishing a note on their topography.

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