plates of opposing layer. Short blunt spine projects backward from each of three posterior-most infermarginals. Mouth probably located above and between anterior processes of anterocentral infermarginals (suborals). Feeding apparatus includes grill-like series of movable (ctenoid) plates that surround anterior thecal margin. Vertical blade-like process on lower side of anterocentral supermarginal (suroral) separates two lateral series of nine ctenoids. Upper part of each ctenoid articulates either with suroral or one of two thin, flat, narrow (lateral) plates that extend outward from suroral across superior surface. Anal pyramid composed of elongate, radially arranged, small plates located between layers of marginal frame near posterior midline. Apparent overlapping of infermarginals beneath anal pyramid probably allowed thecal expansion. Inner surface of right anterolateral supermarginal has prominent sulcus that may have partly enclosed a hydropore or other body opening. Plates of superior and inferior central surfaces (centralia) flexibly arranged and distinctly smaller in size than marginals. Superior centralia cover slightly larger area than inferior centralia, and are composed of tiny polygonal plates. Inferior centralia are roughly aligned elongate plates of slightly larger size than superior centralia.

Etymology: From Greek ktenos, a comb, and kystis, a sac.

Ctenocystis utahensis, new species

Holotype: (Fig. 1B) USNM 163252 (6). Description: Because Ctenocystis is monotypic at present, characteristics of the species are the same as those given in the generic diagnosis. The species is named for the state of Utah where it was discovered.

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- 6. Holotype and illustrated paratypes are depos-ited with paleontological collections of U. S. National Museum (catalog Nos. USNM 163252–163257). Remainder of specimens are deposited with paleontological collections of Department of Geological and Geophysical Sciences, University of Utah (UU 100-102), and Museum of Commention Teology, Han and Museum of Comparative Zoology, Har-vard University (MCZ 605).
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1514

logical and Mineralogical Survey. J.S. was supported by NSF graduate fellowship program and the Department of Geological Sciences, Harvard University. We thank L. Gunther, V. Gunther, R. L. Randolph, R. E. Peterson, and G. Planansky for several ctenocystoids that were contributed.

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Choroid Plexus and Cerebrospinal Fluid Production

Abstract. Acute progressive hydrocephalus occurred in 76 rhesus monkeys undergoing ventricular obstruction 2 to 6 months after choroid plexectomy and was only slightly less pronounced than in 73 nonplexectomized animals with similar ventricular obstructions. The composition of cerebrospinal fluid after choroid plexectomy was essentially normal. Experiments with ventricular perfusion techniques indicate only a slight reduction in cerebrospinal fluid production after choroid plexectomy. Thus, the choroid plexus is probably not the sole or even the major source of cerebrospinal fluid within the primate ventricular system.

Since the experiments of Dandy and Blackfan (1, 2) it has been generally accepted that cerebrospinal fluid is secreted or otherwise formed within the cerebral ventricles by the choroid plexuses. Recent reports tend to support this view (3), but there is enough conflicting data (4, 5) to justify a review. Among the facts most difficult to reconcile with this theory is that, in the treatment of hydrocephalus, removal of the choroid plexus (choroid plexectomy) is rarely curative and is far less effective than might be anticipated.

In this report the consequences of ventricular obstruction in normal and choroid-plexectomized rhesus monkeys are examined, and composition and rates of production of cerebrospinal fluid in these two groups are reported. Because the validity of any study of the choroid plexus depends on the refinement of the experimental model, the technique of choroid plexectomy that was used is described.

The choroid plexus was removed from either one or both lateral ventricles of 76 rhesus monkeys through a small occipital burr hole. The ventricles were entered through a 0.5-cm cortical incision (Fig. 1A) with fine surgical instruments. After the ventricle was entered at the level of the trigone, the plexus was grasped with forceps just in

front of the glomus and was stripped back gradually from the foramen of Monro. Similarly, the choroid plexus of the temporal horn was gently stripped back toward the glomus, where the entire structure was carefully removed in one piece (Fig. 1B). Retractors or other instruments were not used within the ventricular cavity, and bleeding was controlled with frequent saline irrigations rather than by electrocauterization or other hemostatic devices. Nevertheless, many failures occurred, and it was necessary to exclude a number of cases. In some instances, although it was believed that complete plexectomy had been performed, subsequent study revealed excessive scar formation in the operative area, unsatisfactory healing of the cortical incision, or residual tags of choroid plexus. Eventually, 35 animals with unilateral plexectomies and 41 animals with bilateral plexectomies were accumulated in which the operation was accomplished with what was believed to be a minimum of surgical trauma.

After choroid plexectomy, the animals were returned to their cages for 2 to 6 months. Thereafter, these animals and a group of normal rhesus monkeys were operated upon as follows. (i) In 6 unilaterally plexectomized animals, 35 bilaterally plexectomized animals, and 73 normal rhesus monkeys, the fourth ventricle was obstructed with an inflatable balloon (6). (ii) In ten cases of unilateral plexectomy and in six cases of bilateral plexectomy, the third ventricle (including both foramina of Monro) was obstructed by inserting cotton through a small opening in the corpus callosum. (iii) In 19 cases of unilateral plexectomy, the foramen of Monro on the same side was obstructed by simple scarification of the foraminal orifice (Fig. 1E). At selected intervals from 3 hours to 3 months after ventricular obstruction, the animals were killed and perfused with either glutaral-

Table	1.	Cisternal	cereb	rospi	inal	flu	id. Data
given	in	milligrams	per	100	ml	of	cerebro-
spinal	flu	uid.					

Ion	Content in 14 normal animals	Content in 16 plexecto- mized animals
Na ⁺	158	156
K+	2.8	2.7
Cl	132	129
Ca^{2+}	4.9	5.0
PO_4^{2-}	1.4	1.6
Mg^{2+}	3.5	3.8
Protein	18.1	18.2

SCIENCE, VOL. 166

dehyde or formalin through the heart.

All animals developed hydrocephalus after ventricular obstruction. Ventricular enlargement was acute and progressive, and within 3 to 6 hours the changes were readily recognized. In many cases, no difference in either the rate or degree of ventricular enlargement could be distinguished between the normal and plexectomized groups (compare C and D, Fig. 1). Considering all animals, however, it was apparent that the hydrocephalic changes were slightly less advanced among plexectomized animals. This was confirmed by cases of unilateral plexectomy undergoing third ventricular block; in many of these, the plexectomized ventricle was slightly less dilated than the ventricle containing a choroid plexus, although in some brains ventricular enlargement was symmetrical. In contrast to the findings of others (1, 5), the plexectomized ventricle did not collapse after obstruction of the foramen of Monro (Fig. 1E). And, if significant time elapsed between the time of obstruction and the time of death, ventricular enlargement was dramatic (Fig. 1F).

In a number of cases excluded from this series because of excessive surgical manipulation of the ventricular cavity or its ependymal lining, a substantial fibro-glial scar developed which resulted in obliteration of the ventricular cavity. The degree of this obliteration varied with the degree of trauma, and in earlier cases in which a retractor had been used to elevate the roof of the ventricle, the entire chamber was frequently obliterated by a scar binding the roof and floor along the line of the stripped plexus. In less severe cases, the scar was limited to the area of the occipital incision and resulted in a trapped temporal horn which dilated behind the scar. So effective was scarification in obstructing ventricles that it was used to seal the foramen of Monro in 19 cases (Fig. 1E). It is possible that the "ventricular collapse" reported (1, 5) after choroid plexectomy was the result of simple scarring of the ventricular cavity. In one report (5), the illustrated cases show large cortical lesions with considerable distortion of the ventricles by apparent scar formation. In another report (1), the experiment was performed on a single dog and there was no pathological study reported. Regardless, the current findings indicate that hydrocephalus can occur rapidly and progressively in the plexectomized

19 DECEMBER 1969

ventricular system and that the choroid plexus is not essential either as a source of ventricular fluid as claimed by Dandy (l) or as a pulsatile mechanism for expanding the ventricle as suggested by Bering (5). Such a conclusion is in keeping with the clinical findings in many hydrocephalic patients with choroid plexectomies.

In 21 plexectomized and 15 normal

sized ventricles. The plexuses from the

left and right lateral ventricles are

shown below the brain specimen. (C)

rhesus monkeys, cerebrospinal fluid was collected from the cisterna magna by percutaneous puncture and analyzed. There were no significant differences between the two groups (Table 1). Electrophoresis of cerebrospinal fluid from these two groups also failed to show any differences. The animal lacking the choroid plexuses from both lateral ventricles is capable of elaborat-



Ventricular enlargement occurring 5 days after complete fourth ventricular obstruction in a nonplexectomized animal. Transverse measurement of lateral ventricle at junction of frontal horns and body was 0.8 cm. Scale line is 1 cm. (D) Ventricular enlargement occurring 5 days after complete fourth ventricular obstruction in a plexectomized animal. Plexuses removed from the right and left lateral ventricles 10 weeks before second operation are shown below specimen. Transverse measurement of lateral ventricle at junction of frontal horns and body was 0.9 cm. (E) Obstruction of the right foramen of Monro (arrow) in an animal with prior right choroid plexectomy. Note ispsilateral ventricular enlargement. Hydrocephalus is of 3 weeks' duration. (F) Bilateral obstruction of the foramina of Monro in an animal with prior bilateral choroid plexectomy. Arrows point to well-healed cortical incisions. Hydrocephalus is of 3 months' duration. ing a fluid which is similar, if not identical, to cerebrospinal fluid produced by the nonplexectomized animal.

Ventricular perfusion studies were performed on five bilaterally plexectomized animals and nine normal rhesus monkeys with C14-labeled inulin according to the technique of Pappenheimer et al. (7). Production of cerebrospinal fluid by both lateral ventricles, third ventricle, and aqueduct of Sylvius (determined by ventriculo-aqueductal perfusion) averaged $15.6 \pm 4.5 \,\mu l/min$ in normal animals (8) and $11.6\pm3.2 \ \mu l/$ min in plexectomized animals (9). This represented an overall decrease in production of cerebrospinal fluid of only 26 percent after removal of the choroid plexuses from both lateral ventricles. Even if the choroid plexus of the third ventricle produces fluid in proportion to its size and weight (10), the total contribution of the combined plexuses was less than one-third of the newly formed cerebrospinal fluid rostral to the fourth ventricle.

It seems reasonable to conclude that the plexus contributes to the formation of cerebrospinal fluid, but there is even stronger evidence to indicate that it is not the sole or even major source within the primate ventricular system. It is possible, of course, that some functions of the plexus are assumed by other structures after choroid plexectomy.

Bering and Sato (11) have concluded that considerable cerebrospinal fluid is produced outside the ventricular system (in the subarachnoid space). However, the consensus view is that, within the ventricular system, cerebrospinal fluid is elaborated primarily by the choroid plexuses. Current data indicate that this is not the case and that most of the cerebrospinal fluid formed within the ventricles is either a specific secretion of the ependymal epithelium or represents a product of cerebral metabolism which enters the ventricular system across the ependymal lining, or both. THOMAS H. MILHORAT

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Spherical Urine in Birds: Petrography

Abstract. The white part of bird droppings (the urine) consists of microscopically uniform spheres 2 to 8 micrometers in diameter. Strange behavior of the spheres in polarized light indicates that they are often made of a spiraling arrangement of crystals that are particularly well revealed by the electron microscope. Bird urine has a varied composition, and x-ray analysis shows that it does not consist largely of uric acid, as has frequently been parroted.

During an investigation of the geology of Recent sediments, I accidentally discovered that the white part of bird droppings (the urine) consits of minute spheres with extraordinary optical behavior. At the same time, a student was working on Arctic muds and



Fig. 1. Pigeon droppings as seen under a light microscope. Largest spheres measure about 5 µm. [Swallow Hall, University of Missouri; C. M. Hoskin, collector]

found abundant quartz spheres of similar size. The present investigation was begun in order to study a possible link between the two occurrences. A few simple experiments showed that statements on the composition of bird urine in standard texts are erroneous, and I report these findings in the hope that further investigations may be made by others in the fields concerned.

It is not customary for biologists to use high-powered polarizing microscopes on excrement; hence in reading more than 50 references on excretion, I found only two that say anything more specific than that bird urine is a whitish, pasty, semisolid mass of microcrystalline uric acid crystals. Kaupp (1) showed a poor photograph of hen urine with rhombs, which were said to be uric acid, and exceedingly minute dots, said to be sodium urate. Steel (2) described the white part of fowl excrement as consisting "almost entirely of minute crystalline spheroids of ammonium urate and uric acid. constituting the urinary secretion of the fowl," and said the same applies to other birds. Steel apparently did not look at the material in polarized light, and his is the only published microscopic description I have encountered; even Hutchinson's (3) massive volume on guano mentions no microscopic study of modern bird droppings.

In America, I examined the white part of the droppings of chicken, goose, turkey, pigeon, sea gull, sparrow, starling, and parakeet, in addition to many "unknowns" scraped up from various sidewalks, fence posts, or automobiles. In Australia, I examined urine of pigeons, sparrows, magpies, galahs (a type of parrot), parakeets, white and black cockatoos, ravens, eagles, emus, and sea gulls. Without exception, the white part of the excretion consists almost entirely of spheres (or aggregates of spheres) with identical optical behavior and general appearance, and there appears to be only one solid phase present (Fig. 1). In any one specimen, the spheres appear to be of rather uniform size, although the average size of the spheres varies from about 2 to 8 μ m in various droppings. Under highest magnification, some of the larger spheres show an apparent radial-fibrous structure, and rare broken ones divide along radial fractures as if they also had a similar structure.

When the Nicol prisms were crossed (without any interference-figure apparatus in use), the spheres showed pseudointerference figures and appeared to