Committee on Publication

PROCEEDINGS

OF THE

Washington Academy of Sciences

VOL. VIII

1906

WASHINGTON
MAY, 1906–MARCH, 1907

AFFILIATED SOCIETIES.

Anthropological Society of Washington.
Biological Society of Washington.
Botanical Society of Washington.
Chemical Society of Washington.
Columbia Historical Society.
Entomological Society of Washington.
Geological Society of Washington.
Medical Society of the District of Columbia.
National Geographic Society.
Philosophical Society of Washington.
Society of American Foresters.
Washington Society of the Archæological Institute of America.
Washington Society of Engineers.

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NINTH ANNUAL REPORT OF THE SECRETARY, 1906.

TO THE WASHINGTON ACADEMY OF SCIENCES:

Mr. President and Members of the Academy: During the period from January 18, 1906, to January 17, 1907, the Academy has held the following meetings:

January 18, 1906 — Annual meeting for the election of officers, etc.

February 6, 1906 — Meeting to hear an address by Prof. Harry Fielding Reid on "The Various Methods of Estimating the Age of the Earth." This was discussed by Prof. Henry F. Osborn, Prof. Simon Newcomb and Mr. Bailey Willis.

February 23, 1906 — Meeting to hear a paper on "Old Age, Its Nature and Cause," by Prof. Chas. Sedgwick Minot. Discussed by Prof. A. F. A. King, Marshall A. Price and Dr. Harvey W. Wiley.

February 27, 1906 — Meeting to hear the annual address of the President of the Anthropological Society, Dr. Geo. M. Kober, on "The Health of the City of Washington."

April 14, 1906 — Meeting to hear a paper by Mr. John F. Hayford, on "The Recent Geodetic Evidence of Isostasy and its bearing upon the greater Geologic Problems." Introduced by Mr. O. H. Tittmann and dircussed by Major C. E. Dutton, Dr. C. Willard Hayes and others.

May 17, 1906 — Meeting to hear an address by Prof. Francis Gano Benedict on "The Respiration Calorimeter and the Factors of Human Nutrition." Discussed by Dr. J. B. Nichols, Dr. E. B. Rosa, and Dr. C. F. Langworthy.

November 27, 1906 — Meeting to hear an address by Prof. Chas. Hubbard Judd on "Visual Perception." Discussed by Prof. G. M. Stratton.

December 13, 1906 — Meeting to hear an address by Dr. Alexander Graham Bell on "Aerial Locomotion." Discussed by Mr. C. F. Manly and Prof. A. F. Zahm.

At the meeting of November 27, amendments to the By-Laws were adopted providing for a class of life members.

The Board of Managers has held eight meetings for the transaction of business.

Mr. Alexander Graham Bell having resigned the office of Vice-President, the National Geographic Society nominated in his place Mr. Willis L. Moore, who was duly elected by the Board.

Delegates were sent to represent the Academy at the celebration of the 200th anniversary of Franklin's birth held by the American Philosophical Society, April 17–20, 1906.

A Committee of Arrangements has been appointed to prepare for the reception of the International Zoological Congress which is to visit Washington in August, 1907.

At the time of the passage by Congress of the bill establishing a Board of Education in the District of Columbia the Managers sent to each Justice of the Supreme Court of the District of Columbia a resolution recommending the appointment on the Board of one or more members of recognized ability and attainment in some of the natural sciences and who are thoroughly familiar with modern methods of scientific teaching. Dr. Barton W. Evermann was subsequently appointed.

Vol. VII of the PROCEEDINGS has been completed and issued during the year and Vol. VIII is well advanced toward completion. A new catalogue of the members of the Academy and Affiliated Societies has been projected and is now in course of preparation.

Application having been made by the Washington Society of Engineers for admission to the group of Affiliated Societies it was favorably considered by the Board. A vote of the Academy is now being taken by correspondence, as provided by Art. VI, Sec. 2, of the By-Laws.

The Academy has suffered the following losses by death during the year:

H. G. Ogden died February 26, 1906.

S. P. Langley died February 27, 1906.

The statistics of membership at this date are as follows:

Patrons:		
At date of last report	8	
Elected during the year	0	8
Honorary Members:		
At date of last report	0	
Elected during the year	1	1
Life Members:		
At date of last report	0	
Elected during the year	1	1

Resident Members:			
At date of last report	167		
Elected and qualified during the year	10		
Transferred from non-resident list	1	178	
Deceased	2		
Resigned	4		
Transferred to honorary list	1	7	171
Non-resident Members:			
At date of last report	173		
Elected and qualified during the year	13	186	
Resigned	9		
Transferred to life list	1		
Transferred to resident list	1	11	175
			356
Counted twice			1
Total membership January 17, 1907			355

Respectfully submitted,

Frank Baker,
Secretary.

January 17, 1907.

NINTH ANNUAL REPORT OF THE TREASURER, 1906.

To the Washington Academy of Sciences:

The Treasurer has the honor to submit the following annual report of receipts, disbursements, and funds in his hands for the year from January 1, 1906, to December 31, 1906, when the account was closed and balanced:

The receipts during the year have been as follows:

Dues of resident members, 1903	$ 5.00	
Dues of resident members, 1904	10.00	
Dues of resident members, 1905	65.00	
Dues of resident members, 1906	710.00	$ 790.00
Dues of non-resident members, 1904	5.00	
Dues of non-resident-members, 1905	30.00	
Dues of non-resident members, 1906	775.20	
Dues of non-resident members, 1907	5.00	815.20

Sales of Publications and refunds from authors for reprints, etc	164.56
Interest on bank deposits and investments	622.97
Cash returned by Committee on Meetings, balance not used expenses meetings of November 27 and December 13, 1906	9.84
Total receipts	$2,402.57

The amounts and objects of the expenditures were as follows:

Paid on account of expenses incurred in previous year, 1905:

Secretary's office	$ 6.40	
Meetings	17.70	
Publishing Vol. VII of Proceedings	441.00	
Editor's office, 1905	500.00	965.10

Paid on account of expenses of the past year, 1906:

Secretary's office	$ 33.71	
Treasurer's office	101.39	
Meetings	291.09	
Publishing Vol. VIII of Proceedings	632.07	
Greeting to American Philosophical Society of Philadelphia	15.00	$1,073.26
Total disbursements		$2,038.36

Statement of Account.

Balance from last annual statement	$ 810.53
Receipts during the year	2,402.57
To be accounted for	$3,213.10
Disbursements during the year	2,038.36
Cash balance on hand	$1,174.74

Of this balance $195.09 belongs to the permanent fund, leaving $979.65 available for general expenses.

These funds are on deposit with the American Security and Trust Company, drawing 2 per cent. interest.

The only outstanding bills within the knowledge of the Treasurer are:

Editor's office, 1906	$500.00
Expenses of meetings	8.75
Expenses of Secretary's office	27.00

and the completion and binding of Vol. VIII of the PROCEEDINGS, which, it is understood, will not exceed the balance of funds on hand.

Dues remain unpaid as follows:

For 1902,	$ 10
1903,	15
1904,	35
1905,	60
1906,	250
	$370

The investments are the same as stated in the last annual report, namely:

Cash on hand belonging to permanent fund	$ 195.09
809 shares stock of Washington Sanitary Improvement Co.	8,090.00
1 share stock of Colonial Fire Insurance Co...............	100.00
2 shares stock Scheutzen Park Land & Building Association, par value $100, actual value doubtful, say $44.00	88.00
2 first trust notes of Laura R. Green, 3 years, 5 per cent. interest, for $2,000, and $1,500	3,500.00
1 first trust note of Aurelius R. Shands, 3 years, 4½ per cent. interest.......	444.44
	$12,417.53

The two notes of Laura R. Green are deposited with Thos. J. Fisher & Co., Washington, D. C., for collection of interest, and the remainder of the investments are in the Academy's safe deposit box at the Union Trust Company.

Respectfully submitted,

BERNARD R. GREEN,
Treasurer.

JANUARY 5, 1907.

PROCEEDINGS

OF THE

WASHINGTON ACADEMY OF SCIENCES

VOL. VIII, PP. 1–24. MAY 3, 1906.

MEXICAN, CENTRAL AMERICAN, AND CUBAN CAMBARI.

BY A. E. ORTMANN,

CARNEGIE MUSEUM, PITTSBURG, PA.

THE larger part of the material, upon which the following notes are based, was loaned to the writer by the Museum of Natural History of Paris through the kindness of Professor E. L. Bouvier, for which I wish to express my most sincere thanks. I am also under obligations to the Academy of Natural Sciences of Philadelphia, where I was granted the privilege of examining the crawfish-collections; some of this material has also been used for the following notes.

I. Subgenus **PARACAMBARUS**, new subgenus.

Paracambarus, new subgenus of Potamobiidæ (*Cambarus paradoxus*).

Sexual organs of male with the two parts in close apposition to their tips; in the male of the first form, both tips are shortly pointed and horny; in addition there is, on the posterior margin of the inner part, at a short distance from the tip, a long and strong, horny spine. Anterior margin of sexual organs without shoulder. Male with hooks on the ischiopodite of fourth pereiopods only. Female with a spiniform process on the sternum between the fifth pereiopods.

The presence of hooks only on the fourth pereiopods of the male, and the peculiar spine of the sternum of the female distinguish this subgenus at once from all other *Cambari*.[1] The male copulatory organs are also different from those of any other species of the genus, but they approach, to a certain degree, those of the subgenera *Procambarus* and *Cambarus*.

This is the sixth subgenus distinguished by the writer within the genus *Cambarus*.[2] It may be well to point out here the most important characters of these six subgenera by arranging them into a key.

KEY FOR THE SUBGENERA OF CAMBARUS.

a. Outer and inner part of male sexual organs in close apposition up to their tips; tips in the male of the first form horny or soft, with accessory horny spines.

- *b*. Both tips of male organs horny; inner part with a strong accessory spine on posterior margin. Female with a spine on sternum between fifth pereiopods. Male with hooks on ischiopodite of fourth pereiopods....... ....*Paracambarus*.
- *bb*. Both tips of male organs soft, with accessory horny spines on one of them. Female without spine on sternum between fifth pereiopods. Male with hooks on ischiopodite of third, or of third and fourth pereiopods.
  - *c*. Male organs with a small accessory spine, belonging to the inner part; anterior margin with a shoulder near the tips; male with hooks on third pereiopods..........*Procambarus*.
  - *cc*. Male organs with one to three horny accessory spines (often tuberculiform or plate-like), belonging to the outer part; shoulder generally absent, if present, remote from the tips; male with hooks on third, or on third and fourth pereiopods. *Cambarus*.

aa. Outer and inner part of male sexual organs distinctly separated for a more or less considerable distance at the tips; outer part, in the male of the first form, entirely transformed into a horny spine, rarely with a soft secondary spine.

- *d*. Outer part of male organs consisting of two rather long spines, one horny, the other soft, bristle-like; male with hooks on second and third pereiopods........................*Cambarellus*.
- *dd*. Outer part of male organs formed by one single horny spine;

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[1] Except *Cambarus montezumæ* (subgenus *Cambarellus*).

[2] See Proc. Amer. Philos. Soc., XLIV, 1905, 96 and 97, and Ann. Carnegie Mus., III, 1905, 437.

male generally with hooks on third pereiopods, rarely on third and fourth pereiopods.

e. The two parts of the male organs shorter or longer, often very long, straight, divergent, or gently curved......... *Faxonius.*

ee. The two parts of the male organs with rather short, sharply recurved tips, forming about a right angle with the basal part. .... *Bartonius.*

Paracambarus stands very isolated within the genus. We have regarded *Procambarus* as representing to a degree the old original stock of the genus. *Paracambarus* is more closely related to *Procambarus* than to any other subgenus, but there is no direct genetic connection imaginable. Although probably derived from common ancestors, each has apparently gone its own way of development, *Paracambarus* being rather extreme and one-sided in certain characters.

The only species, upon which this subgenus is founded, is new, and the description is as follows:

CAMBARUS (PARACAMBARUS) PARADOXUS,

new species.

Diagnosis: Rostrum subovate, slightly concave above, margins converging, without marginal spines, contracted into a short, triangular acumen; carapace without lateral spines; areola wide, slightly longer than half of the anterior section of the carapace; first pereiopods with the chela subovate, swollen; palm subcompressed, covered with strong, subsquamose tubercles, which form, near the inner margin, two to three irregular, longitudinal rows; fingers longer than the palm, with tubercles at the bases, and a longitudinal rib on the outer faces; cutting edges with strong, irregular tubercles. Carpopodite granulated and tuberculated, spinose on inner and lower side. Only fourth pereiopods hooked in the male. First abdominal appendages of male with both parts in close apposition to the tips; tips horny in the male of the first form, both with a slight outward and backward curve; inner part on posterior side, a short distance from the tip, with a strong and long, spiniform process. Annulus ventralis, of the female forming an almost semicircular, transverse elevation, convex anteriorly, depressed and concave posteriorly. Sternum between fifth pereiopods with a strong, triangular, anteriorly directed, spiniform process.

Description of adult male of first form:

Rostrum subovate, upper face slightly concave, margins elevated, converging, without marginal spines, contracted into a short, triangular acumen, which is shorter than the width of the rostrum at the base. *Postorbital ridges* subparallel, anteriorly without spines. *Carapace* rather compressed, covered with punctations, which are rather large on gastrical region and base of rostrum; sides of carapace finely granulated, granules more distinct on hepatical region. Suborbital angle blunt. Branchiostegal spine short, tuberculiform; cervical groove slightly sinuate; no lateral spines on the sides of the carapace; *areola* wide, with four to five irregular rows of punctations, slightly longer than half of the anterior section of the carapace (including rostrum).

Abdomen as wide as, and longer than, carapace; basal segment of telson with three or four spines on each side; posterior segment semicircular.

Epistoma with anterior part broadly triangular, sharply pointed in the median line; lateral margins concave anteriorly, convex posteriorly; *antennal scale* broad, greatest width anterior to the middle; flagellum rather short, reaching to the second or third abdominal segment.

First pereiopods rather stout; hand elongated-ovate, slightly compressed; surface with strong, subsquamiform tubercles, differing in color from the surface of the hand, being, in alcoholic specimens, bluish black, while the rest of the hand is brownish yellow; tubercles irregularly distributed, but with the tendency to form two or three rows near the inner margin, and slightly more crowded on the rounded outer margin of the hand; on under surface of hand, the tubercles are more remote from each other, and not colored differently from the surface. Fingers distinctly longer than the palm, slightly gaping at the bases, each with a smooth longitudinal rib on outer and inner face, included by rows of punctations; tubercles of palm extending upon bases of both fingers, and forming a short row upon proximal part of outer margin of movable finger; cutting edges with irregular, strong tubercles; tips horny, and generally another horny tooth a short distance from tip on cutting edge of the immovable finger.

Carpopodite short, with a longitudinal sulcus above, granulated and tuberculated; tubercles forming one or two spines on distal end of inner margin, and two other spines on lower surface, one on anterior margin, the other at the lower articulation with the hand. Meropodite granulated, but almost smooth on the larger portion of outer and inner face; several strong tubercles at distal end of upper margin; inner and outer lower margins each with a row of strong, spiniform tubercles, the outer row shorter. All the tubercles of the chelipeds appear squamiform on account of a fringe of short, stiff hairs at their anterior edges.

Ischiopodite of fourth pereiopods with a strong hook; this hook has a subcompressed, broad base, and is subcompressed, but narrower at the tip, and is slightly twisted. The ischiopodite of the third pereiopods is without hook, and there is only a slight, almost imperceptible elevation at its inferior margin.

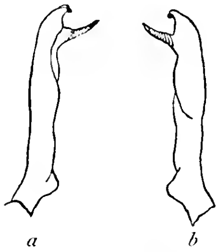

FIG. 1. *Cambarus paradoxus*, sp. n. First pleopod (right side) of male (I). *a*, outer view; *b*, inner view. Enlarged about four times.

First pleopods (see Fig. 1) reaching to the middle of the bases of the third pereiopods, stout, slightly curved backward; inner and outer parts subequal, in close apposition to the tips. Both tips curved gently backward, and slightly outward, horny; inner part, on posterior margin, at a short distance from the tip, with a strong, spiniform process, going off at an acute angle, and being longer than the two tips of this organ.

Male of the second form: Tips of inner and outer parts of sexual organs, as well as the spiniform process, not horny; hook of fourth pereiopods smaller and weaker.

Female: Similar to the male, but chelæ not so strong. Annulus ventralis transversely semicircular, anterior margin convex, elevated, with a curved longitudinal fissure; posterior margin with a subtriangular depression. Sternum between the fifth pereiopods with a triangular, spiniform process, directed forward, which fits into the depression of the annulus.

Aside from the peculiarities offered by the subgeneric characters, this species is also remarkable for its chelæ, which differ in a number of features from the types of chelæ usually seen in the genus *Cambarus*.

Measurements:

The following are the dimensions of the three type-specimens: ♂ (I): total length 48 mm.; carapace 23; anterior part 15, posterior part 8; abdomen 25; hand 17, palm 7, fingers 10; width of hand 7. — ♂ (II): total length 48.5 mm.; carapace 23.5, anterior part 15.5, posterior part 8; abdomen 25; hand 16, palm 6.5, fingers 9.5; width of hand 6. — ♀: total length 48 mm.; carapace 23, anterior part 15, posterior part 8; abdomen 25; hand 15, palm 6.5, fingers 8.5; width of hand 6.

The largest ♂ (I) measures 51 mm., and the largest ♀ 54.5 mm.

Locality: Sierra de Zacapoaxtla, State of Puebla, Mexico.— L. Diguet coll. 1904 ("ruisseaux torrentueux des montagnes, a le cañada de Tetela de Ocampo"). (Mus. Paris, numerous specimens.)

II. CAMBARUS (PROCAMBARUS) PILOSIMANUS,

new species.

Diagnosis: Rostrum subplane, with a marginal spine on each side; carapace with two lateral spines on each side; areola narrow, as long as, or longer than, half of the anterior section of the carapace; first pereiopods with the chela long, subcylindrical, slightly compressed, covered with tubercle-like granules; fingers about as long as the palm, each with a smooth longitudinal ridge on the outer side, for the rest densely pilose on outer and inner sides, the hairs extending upon the distal part of the palm. (In young individuals, the pilosity is less marked or even absent.) Carpopodite and meropodite granulated, and with a few granules developed into sharp spines on the inner and lower sides (indistinct in old individuals); third pereiopods hooked in the male; first abdominal appendages of male with inner part pointed and straight, longer and much thinner than the broad and blunt outer part; shoulder of anterior margin only slightly developed; inner face flattened and only slightly dilated. Annulus ventralis of the female conically elevated.

Description of adult male of the first form:

Rostrum subplane, margins elevated, gradually convergent, slightly convex, chiefly so anteriorly, with a distinct marginal spine on each side a short distance from the tip; acumen triangular, rather short, shorter than width of rostrum at base; margins of acumen hairy; *postorbital ridges* subparallel, ending in a spine anteriorly; *carapace* compressed, thickly and finely punctate, and finely granulated on the sides; suborbital angle blunt; branchiostegal spine small; cervical groove sinuate, two lateral spines on each side behind the cervical groove; *areola* very narrow, but not obliterated, with one irregular row of punctations, longer than half of the anterior section of the carapace (including rostrum).

Abdomen about as long and as wide as the carapace; basal segment of telson with two (rarely three) spines on each side; posterior segment broadly rounded, short.

Epistoma with anterior part triangular, obtuse; *antennal scale* broad, broadest in the middle; flagellum longer than the carapace, but shorter than the whole body.

First pereiopods elongated, subcylindrical; hand elongated, slightly compressed, with subparallel margins, widest at the base of the fingers; surface thickly granulate, granules tuberculiform, rounded, very distinct, subequal; fingers about as long as the palm, both on outer faces with a smooth longitudinal ridge; for the rest, the fingers are thickly pilose on outer and inner side, the pilosity extending a short distance upon the palm on both faces; carpopodite subcylindrical, with an indistinct, longitudinal sulcus on upper side; granulated everywhere, granules largest on inner side: a granule each at the distal end of inner margin, on the anterior margin of inner side, and at distal end of lower margin, more strongly developed and subspiniform (often only indistinctly so); meropodite granulated, granules indistinct on outer and inner faces; a subspiniform one near distal end of upper margin, and several subspiniform ones on lower side (often indistinct).

Ischiopodite of third pair of pereiopods with a strong hook.

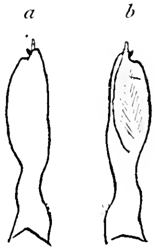

FIG. 2. *Cambarus pilosimanus*, sp. n. First pleopod (right side) of male (I). *a*, outer view; *b*, inner view. Enlarged about four times.

First pleopods (see fig. 2) rather short, straight; anterior margin with an indistinct, blunt shoulder near the tips; outer and inner part in close apposition to their tips; tip of outer part very blunt and rounded, slightly compressed in the anteroposterior direction; tip of inner part straight, thin and pointed, distinctly longer than outer part; at its base, on the anterior side, in front of the shoulder, there is a short, procurved, horny spine; inner part flattened on inner face, slightly dilated, with hairs radiating from an indistinct oblique rib.

Male of second form: The horny spine of the copulatory organs is replaced by a small, soft, blunt tubercle.

Young males (of first or second form), less than 50 mm. total length, differ in the areola, which is about as long as the anterior section of the carapace; chelipeds shorter and weaker, their granulations indistinct; they have short, scanty hairs, and the fingers are *not pilose;* carpopodite with well developed spines; meropodite also with sharp spines; one near distal end of upper margin, one at distal end of outer lower margin, and one or two at distal end of inner lower margin; besides, there are one to three more, forming an irregular row in the middle of the lower side.

Female: Young females are like young males, older individuals have the pilosity of the fingers well developed, but the chelipeds are less elongated than in old males, and consequently comparatively broader. The spines of meropodite and carpopodite of the chelipeds also have the tendency to disappear in very old individuals. Annulus ventralis a blunt, low, subconical tubercle, with an S-shaped longitudinal fissure.

Measurements:

The following are the measurements of the two type-specimens: ♂ (I): total length 72 mm.; carapace 36, anterior section 23, posterior section 13; abdomen 36; length of hand 30, width of hand 8. ♀: total length 62 mm.; carapace 31, anterior section 20, posterior section 11; abdomen 31; length of hand 19, width of hand 6.

The largest females measure 68 mm.; the largest male is the above type.

Localities:

Types and Cotypes: Coche, près de la rivière de Coban, Guatemala.—Exped. du Mexique. Bocourt (Mus. Paris, 10 ♂ (I), 3 ♂ (II), 9 ♀).[1]

Belize, British Honduras. —Exped. du Mexique (Mus. Paris, 1 ♂ (I)).

Remarks: There is quite a difference in the features of old and young individuals. Generally, in specimens less than 45 mm. long, the pilosity of the fingers is not developed, and meropodite and carpopodite of the chelipeds possess sharp spines. There is a ♀, 45 mm. long, which shows traces of pilosity, while two males of the first form, of 49 and 50 mm. respectively, do not show it. The smallest male of the first form that has it, is 58 mm. long. Upward of this size all specimens have the fingers densely pilose. The spines of the chelipeds disappear entirely only in the oldest individuals; the smallest male (first

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[1] I have not been able to locate this place, nor a river "Coban"; but Coban is the well-known capital of the province of Alta Vera Paz. The river at Coban is called Rio Cahabon. Coban, Alta Vera Paz, is the locality for a species of *Cambarus* mentioned by Huxley (1878).

form), in which they have disappeared, is 58 mm. long, but in another, 62 mm. long, they are still recognizable. Three other males of the first form, 69, 71, 72 mm., have no spines. In the females, the spines generally persist up to a size of 60 and 62 mm., but they are missing in two females of 62 and 68 mm. length.

Cambarus pilosimanus is closely allied to *C. williamsoni* Ortmann[1] from Los Amates, near Izabal, Guatemala. Indeed, it may be identical with it. The difference of the pilosity of the chelæ in old individuals of *C. pilosimanus* is very marked however, but we are to bear in mind that the largest individual of *C. williamsoni* was rather small (51.5 mm.). Aside from the pilosity of the chelæ, the only important difference noted is in the male copulatory organs, *C. pilosimanus* having the shoulder less developed, and the tips of the inner and outer part more strongly contrasted. But this difference is not necessarily specific, since for the rest the copulatory organs of both species are built according to the same plan. Other differences are only slight and apparently unimportant. In the young of *C. pilosimanus*, where the pilosity of the chelæ is not developed, the carpopodite and meropodite always possess a number of sharp spines, while in *C. williamsoni* only in the very young are traces of such spines visible on the meropodite. In specimens of about the same size, the granulations of the hand are more distinct in *C. williamsoni*, although in old individuals of *C. pilosimanus* the granules are much stronger than in any specimens of *C. williamsoni* that are known. Further, the hand of *C. pilosimanus* is comparatively less slender, and is broader than in *C. williamsoni*.

The close affinity, if not identity, of these two species is also borne out by the geographical distribution, but the two known localities of *C. pilosimanus* are farther north than that of *C. williamsoni*. It is quite possible that additional material will demonstrate their identity, but for the present I separate them, since there is no individual among the material from the province of Izabal that shows any trace of the pilosity of the chelæ.

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[1] Ann. Carnegie Mus., III, 1905, 439.

III. CAMBARUS (PROCAMBARUS) MEXICANUS
Erichson.

Literature: see Faxon, Mem. Mus. Harvard, 10, 1885, 50, and:

Camb. mex. Ortmann, Zoöl. Jahrb. Syst., 6, 1891, 12; — Faxon, Proc. U. S. Nat. Mus., XX, 1898, 649; — Hay, Amer. Natural., XXXIII, 1899, 959 and 964.

Camb. (*Cambarus*) *mex.* Ortmann, Proc. Amer. Philos. Soc., XLIV, 1905, 101.

Camb. (*Procambarus*) *mex.* Ortmann, Ann. Carnegie Mus., III, 1905, 438.

I have examined the male of the first form of this species preserved in the Philadelphia Academy, from Mirador, Mexico (already mentioned by Faxon). The copulatory organ belongs to the type of the subgenus *Procambarus* and is allied to that of *C. williamsoni* and *pilosimanus*. It differs in the very strongly developed shoulder, and the position of the horny, procurved spine, which is almost terminal on the inner part. The tips of inner and outer part resemble those of *C. williamsoni.*

An *additional locality* for this species is represented in the collections of the Philadelphia Academy:

Texolo, State of Vera Cruz, Mexico. — S. N. Rhoads coll. 1899. — 3 ♂ (II), 2 ♀. (Texolo is near Xico, on the branch road from Jalapa, distant about 15 miles from Jalapa.)

In the males of the second form of this set, the shoulder of the sexual organs is not quite so sharp, and the inner part is more pointed.

IV. CAMBARUS (PROCAMBARUS) CUBENSIS
Saussure.

Literature: see Faxon, Mem. Mus. Harvard, X, 1885, 51, pl. 2, f. 1; pl. 8, f. 5, and:

Camb. cub. Faxon, Proc. U. S. Nat. Mus. 1885, 358; Hay, Amer. Natural., XXXIII, 1899, 959-963.

Camb. (*Cambarus*) *cub.* Ortmann, Proc. Amer. Philos. Soc., XLIV, 1905, 101.

Camb. (*Procambarus*) *cub.* Ortmann, Ann. Carnegie Mus., III, 1905, 438.

Among the material from the Paris Museum, sent to me by Professor Bouvier, the following specimens were present:

1. 1 ♂ (II), 2 ♀. Cuba; Peters.

2. 4 ♂ (II), 1 ♀. Cuba; Peters. (Nos. 1 and 2 apparently from the Berlin Mus.)

3. 2 ♂ (I), 2 ♂ (II), 4 ♀. "Amerique"; Morelet. (All badly damaged, but copulatory organs well preserved.)

4. 1 ♂ (I), type of Saussure's *C. consobrinus.* (Dry specimen, mounted upon a piece of pith; badly damaged, and copulatory organs not visible.)

The following remarks are to be made:

1. *C. consobrinus* Saussure[1] is undoubtedly identical with *C. cubensis.* Although in the present type-specimen the male organs are not visible, it agrees with *C. cubensis* in all other respects. It has a very small lateral spine on the carapace. But such a spine is also present in two specimens (♂ and ♀) in our first set, while the third (♀) has only a trace of it. In the five specimens of the second set, which are all very young, two males (II) have a small granule in its place; the others are apparently smooth. Of the eight specimens of the third set, one (a male of the first form) shows a small tubercle, and two females have none. The rest is too poorly preserved.

2. The *male copulatory organs* (Fig. 3, *a–c*) need some discussion. The description given by v. Martens (Arch. f. Naturg., 38, 1872, p. 129) is quite correct, disregarding a lapsus calami or misprint, that renders a certain passage unintelligible. V. Martens says (translated): They consist of two parts "an outer one, which ends in a blunt point, and has the anterior margin near this point considerably swollen; and an inner one, which extends beyond the former posteriorly, and forms on the inner side a plane, ovate face, *which is adjacent to that of the appendage of the* ANTERIOR *side* ('*welche sich an die des Anhanges der* VORDEREN *Seite anlegt*'). At its end there are two lobes, one in close apposition to the end of the outer part, the second one shorter, projecting separately forward, and more rounded."

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[1] Rev. Mag. Zool. (2), 9, 1857, p. 101, and Mem. Soc. Geneve, 14, 1858, 457, pl. 3, f. 21.

The words emphasized by me cannot be understood as they stand. But if we conjecture that v. Martens wrote or intended to write, instead of *vorderen* (anterior), *anderen* (other), everything is clear: he meant to say, that the inner plane face of the inner part is adjacent to the identical face of the appendage of the *other* side.

Thus the whole description is intelligible, and indeed, it is a correct characterization of the chief features of this organ. It is very interesting to note, that already v. Martens attributes to the inner part two lobes, and his second one is clearly the accessory spine, which is not horny in the male of the second form; v. Martens, consequently, describes this organ of the male of the second form.

He has also correctly interpreted this organ. There is also in our specimens an outer part, which ends bluntly, and has the anterior margin slightly swollen just below the tip. The inner part is dilated and flattened on the inside, and forms, on the anterior margin, near the tip, a sharp shoulder. Its posterior margin extends considerably beyond the margin of the outer part, which is due to the extreme dilatation of the inner face. Its tip is pointed, and has, in the second form, a rounded, projecting lobe anteriorly.

In the male of the first form, the tip of the inner part is more slender and thin, almost setiform, but soft (not horny). The projecting lobe is replaced by a slightly procurved, horny spine, which is two-pointed, one point being blunt, the other acute and thin.

Faxon's figures (1885, pl. 8, f. 5, $5'$, $5''$, $5'''$) are only partly correct. There is hardly any objection to Fig. $5'''$, which represents the inner view of this organ of the left side of the male of the second form. It shows plainly the pointed tip of the inner part and the lobiform accessory process, as well as the thickened anterior margin of the tip of the outer part. Fig. $5''$ represents the same organ from the outside. The different parts are recognizable, but the outer part is not marked off at the tip, and the accessory lobe of the inner part is rendered incorrectly (as a recurved, blunt hook). Fig. $5'$ is intended to represent the inner view of this organ of the left side in the male of the first form; the inner part is drawn correctly, showing the setiform tip and the horny spine; this spine, however, is drawn triangularly-single-pointed, while it is really slightly procurved and two-pointed. The outer part is represented in this drawing by a blunt, conical process, while actually it resembles the condition seen in the male of the second form, being concealed by the inner part with the exception of the swollen anterior margin, which projects slightly. Fig. 5 (outer view of same organ) is quite unintelligible; the tip of the outer part is not correctly represented, while the horny process is much too thin and is recurved, instead of procurved.

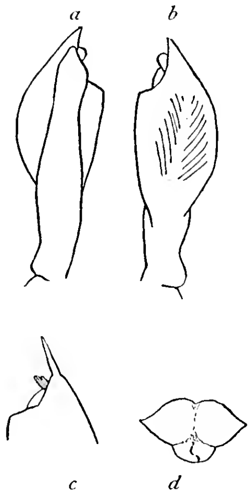

FIG. 3. *Cambarus cubensis* Sauss. *a*, First pleopod (left side) of male (II), outer view; *b*, the same, inner view; *c*, tip of same organ of male (I), inner view; *d*, annulus ventralis of female. All figures enlarged.

That the differences between Faxon's figures and our specimens are due to incorrect rendering of the object by the draughtsman, is evident from the fact that it is impossible to reconcile the different views (inner and outer) of the same object. Correct figures of the organ in question are submitted here.

Thus the copulatory organs of *C. cubensis* clearly belong to the type of the subgenus *Procambarus;* the outer part has no terminal horny teeth, but is soft and blunt; the inner part is flattened and dilated on the inside, with a shoulder on the anterior margin near the tip; the end of the inner part has a soft tip, and, in addition, in the male of the first form, a horny spine, which is replaced, in the second form, by a blunt tubercle.

C. cubensis is closely allied to the species *williamsoni*, *pilosimanus*, and *mexicanus*, but differs in the following characters:

(1) The dilatation of the inner face of the male copulatory organ is much more pronounced; the tip of the inner part is more pointed, almost setiform, in the male of the first form; the horny spine is two-pointed. (2) The rostrum has marginal spines; these are also present in *C. williamsoni* and *pilosimanus*, but are absent in *C. mexicanus*. (3) The carapace has a small lateral spine, which is sometimes absent; this spine is always missing in *C. mexicanus*, while the other two species have two distinct lateral spines on each side.

3. Faxon's description of the *annulus ventralis* of the female (l. c., p. 52) is correct: "composed of a large anterior bilobed tubercle, and a smaller posterior tubercle." I only wish to add that the small posterior tubercle possesses the S-shaped longitudinal fissure commonly seen in *Cambarus*, and it seems to me that only this tubercle ought to be regarded as the annulus. I was able to observe the shape of the annulus only in the largest female of the first set; in all other females, which are small, it is very indistinct, a fact that has also been noticed by Faxon.

For the rest, this species has been well described by Faxon, but in the figure of the anterior part of the animal (*pl. 2, f. 1*), the marginal spines of the rostrum have been omitted. These spines are small, but present in all specimens at hand.

V. CAMBARUS (CAMBARUS) WIEGMANNI Erichson.

Camb. wiegm. Faxon, Mem. Mus. Harvard, X, 1885, 38 (literature). — Hay, Amer. Natural., XXXIII, 1899, 959 and 964.
Camb. (*Cambarus*) *wiegm.* Ortmann, Proc. Amer. Philos. Soc., XLIV, 1905, 102.

Hagen's female type specimen in the Philadelphia Academy agrees rather well with a *male of the first form* present in the same collection. This latter one is from the Cope collections and represents a new locality for the species:

Lake Xochimilco, south of City of Mexico (Federal District). — E. D. Cope coll., 1885.

This male has enabled me to draw up the following *description:*

Rostrum broad, moderately long, plane above; margins elevated, slightly convergent anteriorly, near the tip more strongly convergent, and forming a short, subtriangular acumen; no marginal spines nor marginal angles at base of acumen, and the elevated margins continued to the tip, which is bluntly pointed; postorbital ridges divergent posteriorly, without spines anteriorly; *carapace* ovate, slightly compressed, punctate, slightly granulated on the sides; suborbital angle blunt, branchiostegal spine distinct, but blunt (tuberculiform); cervical groove sinuate; no lateral spine; *areola* longer than half of the anterior section of carapace, rather narrow in the middle, with two to three irregular rows of punctations.

Abdomen as wide as, and slightly longer than, the carapace; anterior segment of telson with three spines on each side; posterior segment semicircular.

Epistoma with anterior part almost semicircular, a little angular on the sides, and bluntly pointed at the middle; *antennal scale* broad, broadest anterior to the middle; *flagellum* shorter than carapace (but damaged at end).

Chelipeds with hand rather wide, not much swollen, compressed, with subparallel margins; surface squamoso-tuberculate, tubercles on inner margin more crowded and stronger, forming an irregular row of serrations; fingers strong, about as long as the palm, with longitudinal ribs and punctations on outer face, and with squamiform tubercles at the bases: cutting edges tuberculated, tubercles irregular, a larger one near the base of each finger, and another large one near the distal end of immovable finger: carpopodite squamoso-tuberculate, inner side with several spiniform tubercles, upper surface with a slight longitudinal sulcus; meropodite smooth, with a few tubercles near distal end of upper margin, and two rows of tubercles on lower margins, the outer ones shorter.

Ischiopodite of third and fourth pereiopods with hooks, those of the third pereiopod are very small, but distinct and tuberculiform. Those of the fourth pereiopod very strongly developed, swollen and inflated, tapering to a blunt point; *coxopodite* of third pereiopod with a semicircular, elevated, compressed tubercle, that of the fourth pereiopod with a strong, triangular spine, directed outward; that of the fifth pereiopod with a small, spiniform tubercle below genital opening, directed downward.

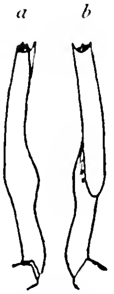

FIG. 4. *Cambarus wiegmanni* Erichson. First pleopod (right side) of male (I). *a*, outer view; *b*, inner view. Enlarged about three times.

First pleopods (Fig. 4) rather long and slender for the subgenus *Cambarus*, reaching to the coxopodites of the second pereiopods, almost straight, very slightly curved; truncated at the tip, with three horny teeth, of which the outer one is compressed and truncated, crescentic in shape; the inner tooth is broadly triangular, and the anterior is short and spiniform,[1] the inner part of this organ terminating in an almost straight spine, which is only slightly directed outward, and is slightly longer than the truncated outer part, and has a distinct horny tip.

Measurements: Total length 60 mm.; carapace 29, anterior part of carapace 18.5, posterior 10.5; width of areola 1.75; abdomen 31; length of hand 25.5, width of palm 9.5 (Erichson gives the following figures: total length 52 mm., length of hand 17 mm., width of hand 6.5 mm. Hagen gives 66 mm. as total length.)

Comparing the present male with the description of the spe-

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[1] This latter one seems to belong to the inner part; but I suspect strongly that such is the case also in other species of the subgenus. The homologies of the sexual organs of *Cambarus* are altogether not well understood, and urgently need a more close study.

cies given by Erichson, and the discription of the female given by Hagen, there is hardly any difference. Hagen describes and figures the epistoma as triangular and rather acute, which is not the case in our individual, and further, Hagen gives only two lateral spines for the anterior section of the telson. These differences are of no consequence, variations in these characters being frequent in other species. I have compared the female in Philadelphia, which served as the base of Hagen's description, and which, since the Berlin types of Erichson have disappeared, must be regarded as the type of the species, and I find it to agree in all essential characters with our male, chiefly so in the shape of body and rostrum. Thus I think, the present male ought to be referred to this species.

As is evident from the characters of the male of the first form described above, *C. wiegmanni* belongs to the subgenus *Cambarus*, to the section of *C. blandingi*, and the group of *C. alleni*,[1] and it has been assigned its correct position already by Hagen and Faxon (allied to *C. barbatus*). The sexual organs are peculiar on account of the crescentic, compressed and truncated outer horny tooth, and do not closely agree with any of the known species of the subgenus; but just this feature agrees with the *alleni*-group in so far as this group is characterized by peculiar and aberrant conformations of the tips of the sexual organs.[2] In shape of carapace, areola and rostrum, this species agrees closely with *C. evermanni*, *barbatus* and *alleni*, and the rostrum represents a rather advanced stage of development, being broadly lanceolate, without any traces of marginal spines or even marginal angles in their place. It resembles to a certain degree, the rostrum of *C. clypeatus* Hay[3] from Bay St. Louis, Hancock Co., Miss., but in the latter form the rostrum is still broader, and almost rounded off at the apex. I should

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[1] See Ortmann, Proc. Amer. Phil. Soc. 1905, 98 and 100; Ann. Car. Mus., 1905, 437 and 438.

[2] The sexual organs agree most nearly with those of *C. hinei* Ortm. from Louisiana, with the exception that in the latter species the crescentic and truncated tooth is absent, and that the distal part of the organ is distinctly curved backward. See Ortmann in The Ohio Naturalist, VI, 1905, p. 402, fig. 1. Also the rostrum of *C. hinei* is transitional toward *C. wiegmanni*.

[3] Proc. U. S. Nat. Mus., XXII, 1899, 122, fig. 2, no. 1.

not be surprised, if this latter species, of which the male is unknown, should finally prove to belong to this group, and not to the second group of Faxon (affinity of *C. cubensis*) as Hay is inclined to believe.

The hooks of the ischiopodites of the pereiopods are very peculiar, and unlike anything else that is known in the genus. And further, the development of the spines and processes of the coxopodites of the three last pairs of pereiopods is very unique; such processes are indeed found in other species in the shape of tubercles or ridges on the fourth or fifth pereiopods, but they never assume such proportions as in this species, and the outwardly directed spine of the coxopodite of the fourth pereiopod in *C. wiegmanni* is without parallel.

Thus it seems that *C. wiegmanni* is to be regarded as a very peculiar, and, in certain features, extremely developed form of the subgenus *Cambarus*, which belongs to a rather advanced and modern group of it (*alleni*-group, see l. c., p. 105) which is characteristic for those parts of the coastal plain of the southern United States, that are most recent geologically. Its presence in Mexico is rather interesting, and the specialized character points to a recent immigration into these parts. But we are to bear in mind that the *alleni*-group in general is comparatively poorly known and needs further study.

VI. Subgenus **CAMBARELLUS.**

For the species of this subgenus I am only able to add a few new locality records:

Cambarus (*Cambarellus*) *montezumæ* Saussure (Faxon, 1885, 121; 1898, 660).

Neighborhood of City of Mexico: Laguna de Santa Isabel. — G. Seurat coll., 1897 (Mus. Paris, 1 ♂ (I), 1 ♀).

Mexico. — Mus. Paris, numerous specimens, collected by various persons, but without more explicit localities.

Lake Xochimilco, south of City of Mexico (Federal District). E. D. Cope coll., 1885 (Philadelphia Academy, 1 ♀).

Most of the specimens seen by the writer belong to the form *tridens* v. Mart. With Faxon, I do not believe that this is worth a varietal name. According to my observations, young examples generally are *tridens*, while the typical form is found only among old individuals, and is comparatively rare.

Cambarus (*Cambarellus*) *montezumæ dugesi* Faxon (1898, 660, *pl. 66, f. 1*).

Guadalajara, State of Jalisco, Mexico. — Diguet coll. (Mus. Paris; many specimens).

Same locality. — Dugès coll. (Mus. Paris, 4 ♂).

State of Guanajuato, Mexico. — Diguet coll. (Mus. Paris, 4 ♂, 4 ♀).

The latter locality is the type-locality recorded by Faxon. The specimens from Guadalajara have been mentioned by Bouvier as *C. montezumæ tridens* (Bull. Mus. Paris, 1897, 224), but they clearly belong to this variety.

Cambarus (*Cambarellus*) *montezumæ occidentalis* Faxon, (1898, 661, *pl. 66, f. 3, 4*).

Hot Springs, Huingo, State of Michoacan, Mexico. — S. N. Rhoades coll., 1899 (Philadelphia Academy; many specimens).[1]

VII. SYNOPSIS OF THE CRAWFISH-FAUNA OF MEXICO, CENTRAL AMERICA AND THE WEST INDIES.

Our knowledge of the chorology of the genus *Cambarus*, south of the United States, is rather poor. Crawfish are now known from Mexico, Guatemala, British Honduras, and Cuba, but not only is the morphology of these forms not well understood, but also we have only a few and often doubtful or unreliable locality-records. In order to call attention to this lack in our knowledge, I want to condense here the known facts, and point out the questionable records.

Four subgenera are represented in this southern section of the range of the genus: *Paracambarus*, *Procambarus*, *Cambarus*, *Cambarellus*. The first two are not found in the United States, while the other two are. *Cambarus* is largely distributed in the United States, and has its main range there, only one species having invaded Mexico. *Cambarellus* has its main abode in Mexico, and only one species is known from a single locality in Louisiana (New Orleans).

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[1] Huingo is near Lake Cuitzeo, and site of large salt works by evaporation from natural springs flowing into the lake. Crawfish were numerous in these springs and streams (communication from Mr. S. N. Rhoades to the writer).

The following is a list of the known species and their distribution:

1. *Cambarus* (*Paracambarus*) *paradoxus* Ortmann.

Tetela, Sierra de Zacapoaxtla, State of Puebla, Mexico.

2. *Cambarus* (*Procambarus*) *digueti* Bouvier.

Tributaries of Rio Santiago, State of Jalisco, Mexico (Bouvier).

Guadalajara, State of Jalisco (Faxon).

Ameca, State of Jalisco (Faxon).

Hacienda de Villachuato, State of Michoacan (Faxon). The location of this hacienda is unknown.

This species consequently belongs to the Pacific drainage in western Mexico.

3. *Cambarus* (*Procambarus*) *williamsoni* Ortmann.

Los Amates, Province of Izabal, Guatemala (Atlantic drainage).

4. *Cambarus* (*Procambarus*) *pilosimanus* Ortmann.

Coche, on river Coban, Guatemala (probably Coban, Province of Alta Vera Paz, see above p. 9, footnote).

Belize, British Honduras. (Both localities in Atlantic drainage.)

5. *Cambarus* (*Procambarus*) *mexicanus* Erichson.

Mexico (Erichson, Ortmann). Probably the City of Mexico is meant, since the presence of this species in its neighborhood is confirmed by other records from the Federal District.

Santa Maria, Mexico (Faxon). There are half a dozen places of this name in various parts of Mexico. One is close to the City of Mexico, and thus we may assume that this is intended.

Tomatlan, Mexico, "terres chaudes" (Saussure). Again there are several places of this name in Mexico: one is south of the City of Mexico, in the Federal District, another in the State of Jalisco, not far from the Pacific Ocean; a third one about 10 miles south of Huatusco, in the State of Vera Cruz. Saussure's specification: "terres chaudes" renders it safe to assume that this latter locality in the State of Vera Cruz was intended.

Puebla, State of Puebla (v. Martens).

Mirador, Mexico (Faxon). This is an observation station in the State of Vera Cruz, 19° 15′ N., 96° 40′ W., alt. 3,600 feet. I was not able to find it on any of the maps at my disposal.

Texolo, State of Vera Cruz (see above p. 11).

Thus this species is known from the states of Mexico (Federal District), Puebla, and Vera Cruz, that is to say, from the central plateau and from the Atlantic slope.

6. *Cambarus* (*Procambarus*) *cubensis* Erichson.

Cuba. Saussure gives the interior of this island, and Faxon creeks in a little town opposite Havana.

7. *Cambarus* (*Cambarus*) *wiegmanni* Erichson.

Mexico (Erichson, Hagen), probably the City of Mexico.

Lake Xochimilco, Federal District (see above, p. 16).

Jalapa, Mexico (Faxon). This is very likely Jalapa in the State of Vera Cruz, although there are other places of this name in Mexico.

These localities are on the central plateau and the Atlantic slope. This species has been recorded with some doubt from the Isthmus of Tehuantepec (Faxon), but we would better drop this for the present.

8. *Cambarus* (*Cambarellus*) *chapalanus* Fax.

Lake Chapala, State of Jalisco, Mexico (Pacific drainage).

9. *Cambarus* (*Cambarellus*) *montezumæ* Sauss.

a. Typical form (including var. *tridens* v Mart.).

Chapultepec, Federal District, Mexico (Saussure). West of City of Mexico.

Lake Texcoco, Federal District (Faxon). East of City of Mexico.

Lake Xochimilco, Federal District (see above, p. 19). South of City of Mexico.

Laguna de Santa Isabel, near City of Mexico (see above, p. 19). I have not been able to locate this, but the statement that it is near the City of Mexico associates this with the first three records given.

Puebla, State of Puebla, Mexico (v. Martens).

Lake San Roque, Trapuato, Mexico (Faxon). I have not been able to find this locality designated on any of the maps, or in any gazetteer consulted by me.

Vera Cruz, Mexico (Ortmann) (Zool. Jahrb. Syst., 6, 1891, p. 12). This locality should be considered as doubtful till confirmed. The specimens upon which this record was founded, were secured from a dealer, and it was not stated whether the city or the state of Vera Cruz was meant. Moreover, it is well known how utterly untrustworthy dealers' localities are.

The presence of this species in its typical form is thus positively known only on the central plateau, near the cities of Mexico and Puebla.

b. Cambarus (*Cambarellus*) *montezumæ dugesi* Faxon.

State Guanajuato, Mexico (Faxon, Mus. Paris).

Guadalajara, State of Jalisco (Bouvier, Mus. Paris, see above, p. 20).

Pacific drainage.

c. Cambarus (*Cambarellus*) *montezumæ areolatus* Faxon.

Parras, State of Coahuila, Mexico (Faxon). Northern part of central plateau.

d. Cambarus (*Cambarellus*) *montezumæ occidentalis* Faxon.

Mazatlan, State of Sinaloa, Mexico (Faxon).

Huingo, State of Michoacan, Mexico (see above, p. 20).

Pacific drainage.

It is hard at present to draw any conclusions from these meagre records. Only a few remarks may be made, but it is very likely that they will be subject to revision when more information comes to hand.

The subgenus *Procambarus* possesses its most primitive form (*C. digueti*) in the western extremity of its range (mountainous region toward the Pacific slope). The most extreme species (*C. cubensis*) is found at the eastern extremity of the range, in Cuba. Intermediate forms are found on the central plateau and the eastern hot country of Mexico (*C. mexicanus*), in Guatemala, and British Honduras (*C. williamsoni* and *pilosimanus*), thus indicating the direction of the dispersal (see Ortmann, Ann. Carn. Mus., 3, 1905, p. 441).

Thus *Procambarus* not only points out the original home of the genus in a general way (Mexico), but indicates especially the western portions of this country. However, further research is very desirable.

Cambarus wiegmanni is the only representative of the subgenus *Cambarus* in Mexico; the bulk of this subgenus being found in the United States, chiefly in the southern parts (see

Ortmann, P. Amer. Philos. Soc., 44, 1905, p. 103 f.). Moreover, it belongs to a rather advanced and modern group of this subgenus (*alleni*-group), which is characteristic for the late Tertiary and Post-tertiary plains of the South Atlantic and Gulf border in the United States. Thus it is very probable, that this species immigrated into Mexico from the United States, representing a direction of dispersal opposite to that generally observed in the genus, for which, however, at least one other instance is known (*C. clarki*, l. c., p. 126). The known habitat of *C. wiegmanni* appears rather isolated, and it is much to be desired that northern Mexico and southern Texas should be investigated with a view to settle this question.

The most primitive species of the subgenus *Cambarellus* (*C shufeldti*) is found in Louisiana. *C. chapalanus* appears slightly more primitive compared with *C. montezumæ* and its varieties, and is found in western Mexico. Of the *montezumæ* forms, *areolatus* is the most primitive and the most northern, nearest to the United States, while *occidentalis* is the most advanced (shape of rostrum), and is western in Mexico. Thus the evidence is partly contradictory. Leaving out *chapalanus*, the general trend of the evidence is to show that the subgenus originated in the southern United States and immigrated into Mexico, first into the central plateau, then into the Pacific slope.

This would, consequently, offer a third case of reversed migration in this region, and my map (1905, pl. 3) should be changed accordingly (the brown color). This would also not conflict with the morphological characters of *Cambarellus*, the shape of the sexual organs inclining more toward the subgenus *Faxonius* of the United States, than toward the Mexican subgenera. But I must confess, that the evidence for this assumption appears at present too scanty, so that we can hardly call it more than a mere theory. It is chiefly with a view to instigate further research on these questions that I have ventured to express at all an opinion on this topic.

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THE GEODETIC EVIDENCE OF ISOSTASY, WITH A CONSIDERATION OF THE DEPTH AND COMPLETENESS OF THE ISOSTATIC COMPENSATION AND OF THE BEARING OF THE EVIDENCE UPON SOME OF THE GREATER PROBLEMS OF GEOLOGY.[1]

INTRODUCTION.

BY O. H. TITTMANN.[2]

IT is my pleasant duty to introduce to you the speaker of the evening, but I shall ask your indulgence for a few moments while I explain to you the reasons which lead up to the investigation of which he will give you an account. You are aware that the governments of the world maintain an international Geodetic Association under the terms of a formal convention for the purpose of furthering the admeasurement of the earth. The countries which are parties to this convention are Great Britain, whose monumental work in India is of the greatest importance and which is also conducting geodetic operations in South Africa; Germany, the originator of the Association; France, the mother of geodesy; Russia, Austria-Hungary, Italy, Spain, The Netherlands, Norway, Sweden and Denmark. The Orient is repre-

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[1] Published with the permission of the Superintendent of the Coast and Geodetic Survey.

[2] At a meeting of the Washington Academy of Sciences on the evening of April 14, 1906, this paper was read by Mr. Hayford. It has been thought desirable to publish in this connection the introductory remarks made by Mr. O. H. Tittmann, Superintendent of the Coast and Geodetic Survey, and the discussion by Major Clarence E. Dutton.

sented by Japan, and this continent by the United States and Mexico. In South America, Brazil, the Argentine Confederation, Chili and Peru, are organizing geodetic surveys and will doubtless become parties to the convention which recognizes the determination of the earth's figure and size as an international function. As the arc of Peru, which was recently remeasured by the French, was measured by a European nation, the United States is the only country among all the American nations, which has contributed to our knowledge of the earth's figure. Leaving out of consideration for the present several minor arcs along the Atlantic seaboard the Coast and Geodetic Survey published in the year 1900 the results of the measurement of the transcontinental arc along the 39th parallel. This was followed in the year 1901 by an account of the oblique arc extending from Eastport, Maine, to New Orleans, La. Since then it has published the results of its trigonometric survey extending from the southern boundary of California to Monterey Bay, California. These great triangulations were begun in many separate localities and when they were connected it became necessary to adopt a uniform system of coördinates for the whole country. The advantage of doing this was recognized by the engineers of the Army, under whom an extended trigonometric survey covering the region of the Great Lakes had been completed, and their triangulation, having been connected with that of the Coast and Geodetic Survey, was, by coöperation between the Departments having charge of these organizations, referred to the same datum adopted by the Coast and Geodetic Survey. The earlier coastwise triangulations of the Coast and Geodetic Survey were projected upon the Bessel spheroid. As the work progressed it became evident that the Clark spheroid of 1866 was in the region of the United States better adapted for the purpose of a reference spheroid than the former, and it was substituted for the Bessel spheroid. It also became clear that for purely geographic purposes the Clark spheroid would suffice, or at any rate that an attempt to substitute, if it were possible, a closer osculating spheroid would involve enormous labor without compensating advantages. This point of view established the policy of referring all the trigonometric work on the United States to a common origin of coördinates on the Clark spheroid of 1866 on which much of it had already been developed.

Side by side with the computations necessary in this great undertaking the investigation of the form of the geoid involving the anomalies which were developed by the trigonometric and astronomical operations was carried on, for the adoption of a reference spheroid for geographical purposes did not relieve us of the duty of trying to explain the discrepancies between it and the existing geoid.

The discussion of the arcs hitherto published proceeded along the conventional lines of treating these anomalies, that is, the deflection of the vertical as though they were accidental errors of observation, though it was well understood that such is not the case. When, however, the arcs were all connected it became possible to treat the triangulations in a much more general way and to have regard to the surface within the area covered by them, which would most nearly represent the geoid. To this very difficult task Mr. Hayford addressed himself. He first devised methods of computation which brought the investigation within reach of the limited force of computers at his disposal. What he will tell you to-night in brief, will be submitted in more detail to the International Geodetic Association as a contribution from this country to a problem which all are trying to solve.

The results will, I believe, make evident to you the great power of geometry, using the word in its etymological sense, to disclose facts which are of the greatest importance to geology and geophysics.

THE PAPER.

BY JOHN F. HAYFORD, C.E.[1]

My intention is to present to you a general view of an investigation which is still in progress, to state some of the principal conclusions reached, and to indicate very briefly some of the relations of these conclusions to conclusions reached by others along very different lines of investigation.

At the outset it is necessary to have a clear conception of the condition called isostasy.

If the earth were composed of homogeneous material, its figure of equilibrium, under the influence of gravity, and of its own rotation, would be an ellipsoid of revolution. The earth is composed of heterogeneous material which varies considerably in density. If this heterogeneous material were so arranged that its density at any point depended simply upon the depth of that point below the surface, that is, if all the material in each horizontal stratum were of one density, the figure of equilibrium would still be an ellipsoid of revolution.

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[1] Chief of Computing Division and Inspector of Geodetic Work, Coast and Geodetic Survey.

If the heterogeneous material composing the earth were not arranged in this manner at the outset the stresses produced by gravity would tend to bring about such an arrangement. But as the material is not a perfect fluid, as it possesses considerable viscosity, at least near the surface, the rearrangement will be imperfect. In the partial rearrangement some stresses will still remain, different portions of the same horizontal stratum may have somewhat different densities, and the actual surface of the earth will be a slight departure from the ellipsoid of revolution in the sense that above each region of deficient density there will be a bulge or bump on the ellipsoid, and above each region of excessive density there will be a hollow, relatively speaking. The bumps on this supposed earth will be the mountains, the plateaus, the continents — and the hollows will be the oceans. The excess of material represented by that portion of the continent which is above sea level will be compensated for by a defect of density in the underlying material. The continents will be floated, so to speak, upon the relatively light material below them and, similarly, the floor of the ocean will, on this supposed earth, be depressed because it is composed of unusually dense material. This particular condition of approximate equilibrium has been given the name, isostasy.

Is the earth to-day in this condition? In connection with a study of this question it is convenient to define two or three phrases which will be found useful and in defining them to add precision to our conception of isostasy.

The adjustment of the material toward this condition, which is produced in nature by the stresses due to gravity, may be called the isostatic adjustment.

The compensation of the excess of matter at the surface (continents) by defect of density below, and of surface defect of matter (oceans) by excess of density below may be called the isostatic compensation.

Let the depth within which the isostatic compensation is complete be called the depth of compensation. At and below this depth the condition as to stress of any element of mass is isostatic, that is, any element of mass is subject to equal pressures from all directions as if it were a portion of a perfect fluid.

Above this depth, on the other hand, each element of mass is subject in general to different pressures in different directions, to stresses which tend to distort it and to move it.

The idea implied in this definition of the phrase "depth of compensation," that the isostatic compensation is complete within some depth much less than the radius of the earth, is not ordinarily expressed in the literature of the subject, but it is an idea which it is difficult to dodge if the subject is studied carefully from any point of view. The data to be discussed to-night indicate that all the isostatic compensation occurs within a thin surface layer of the earth, extending down $\frac{1}{57}$ or possibly $\frac{1}{37}$ of the depth from the surface to the center.

The geodetic evidence which may be used to test whether or not the condition called isostasy exists, consists of determinations of gravity and of determinations of deflections of the vertical.

It is to the evidence furnished by the latter that I wish to call your attention to-night. Within the limits of the United States and connected by continuous triangulation, which has all been reduced to one datum, 507 astronomic determinations have been made; 265 of latitude, 79 of longitude, and 163 of azimuth. These furnish that component of the deflection of the vertical which lies in the meridian at 265 stations, and the prime vertical component at 232 stations. These astronomic stations are scattered from Maine to southern California, in portions of 33 states. This triangulation and the astronomic determinations connected with it are furnished to the world by the Coast and Geodetic Survey and the Lake Survey and constitute a magnificient contribution by the United States toward the determination of the figure and size of the earth.

In deriving the figure and size of the earth from observed deflections of the vertical the usual practice has been to ignore the topography around each station, except that occasionally observed deflections have been rejected because they were in or near a mountainous region. The effect of a possible systematic distribution of density in each horizontal stratum of the earth has also been ignored.

The topographic irregularities are visible and known. The systematic distribution of density below the surface is invisible and unknown. The topographic irregularities and the distribution of density each affect the deflections of the vertical. Therefore, each should be taken into account as far as possible in any attempt to derive the figure and size of the earth from geodetic measurements. They are so taken into account in the investigation now in progress in the Coast and Geodetic Survey.

This investigation seeks to determine not only the figure and size of the earth but also to determine whether the condition called isostasy exists with its peculiar distribution of sub-surface densities, and if so the depth within which the isostatic compensation is complete. Several complete and independent solutions by least squares of the problem of determining the figure and size of the earth have been made in this investigation upon different assumptions as to isostasy and depth of compensation. The residuals of these different solutions, expressing the degree of harmony brought about by the different assumptions, furnish the evidence as to which of the assumptions is nearest the truth.

One solution was made on the assumption that the condition called isostasy does not exist, that no isostatic adjustment occurs when vast masses are eroded from high parts of the earth's surface, and are transported and deposited on the low parts—that the earth is so rigid as to support the continents as local excesses of mass. It is equivalent to the assumption that the depth of isostatic compensation is infinite.

To make this solution it was necessary to compute the effect of all the topography for a considerable distance from each station. The computation was made to cover all topography within 2,564 miles of each of the 304 stations.

The usual solution was also made. This solution is based upon the tacit assumption that no relation exists between deflections of the vertical and the topography. It is equivalent to the assumption that isostatic compensation exists and is complete at depth zero—that there exists immediately below every elevation (either mountain or continent) the full compensating defect of density, and that at the very surface of the ocean floor there lies material of the excessive density necessary to compensate for the depression of that floor. Under no other condition can it be true that the observed deflections of the vertical are independent of the known topography. This assumption, tacitly made in the usual determinations of the figure of the earth, such for example, as the Clark and Bessel determinations, represents an impossible condition. It is a limiting case.

If the depth of compensation is finite, the deflections of the vertical due to topography will be partly counterbalanced by the contrary deflections due to defects and excesses of density below the surface. The counterbalancing will be more complete the greater the distance from the station to the particular topographical features under consideration. Given an assumed depth within which the compensation is complete, and assuming that the compensation is uniformly distributed through that depth, it is a simple matter to compute the corresponding deflections. The computation takes account fully of the amount by which the plumb line is drawn toward a given mountain range by the direct attraction of the mass of the range, and also of the smaller effect of the contrary sign produced upon the plumb line by the relative defect of density below the range.

Three complete solutions were made in turn upon the assumptions that the depth of compensation is 101, 75, and 71 miles. These particular assumed depths were based upon preliminary examinations.

A comparison of the five solutions corresponding to assumed depths of compensation, infinity, 101 miles, 75 miles, 71 miles, and zero, showed that the sum of the squares of residuals was least for the 71-mile solution. Therefore, 71 miles is the most probable of these five assumed values for the depth of compensation.

How strong and clear is the evidence that the actual condition of the earth is that called isostasy, with the isostatic compensation uniformly distributed within the depth of 71 miles, rather than that it is an earth in which there is no isostatic compensation, on which the continents and oceans are maintained by rigidity? Compare the 71-mile solution with that for assumed depth infinity, the last named being the solution corresponding to extreme rigidity.

The sum of the squares of the residuals in the former solution is 8,000 and in the latter is 65,000, more than 8 times as large. In the former solution there are but 19 per cent. of the residuals greater than 5″ and the maximum residual is 16″, whereas in the latter 66 per cent. of the residuals are greater than 5″ and the maximum residual is 44″. In the former solution the average residual is 3″.1 and the latter 8″.8.

The evidence shows clearly and decisively that the assumption of complete isostatic compensation within the depth of 71 miles is a comparatively close approximation to the truth, that the assumption of extreme rigidity is far from the truth—that the United States is not maintained in its position above sea level by the rigidity of the earth, but is, in the main, bouyed up, floated, upon underlying material of deficient density.

The conclusions just stated were based upon the 507 residuals considered as one group. The residuals have been examined in separate groups of 25, each group covering a small region. Not a single group of 25 contradicts the conclusion just stated.

It is certain that for the United States and adjacent regions, including oceans, the isostatic compensation is more than two-thirds complete—perhaps much more.

The departure from perfect compensation may be, in some regions, in the direction of over-compensation rather than under-compensation but in either case the departure from perfect compensation is less than one-third.

In terms of stresses, it is safe to say that these geodetic observations prove that the actual stresses in and about the United States have been so reduced by isostatic adjustment that they are less than one-tenth as great as they would be if the continent were maintained in its elevated position, and the ocean floor maintained in its depressed position, by the rigidity of the earth.

In order to secure the greatest possible accuracy in deriving the figure of the earth it is necessary to determine as accurately as possible the depth at which the isostatic compensation occurs. This is also of great importance on account of its bearing on the greater problems of geology. With what degree of accuracy does this geodetic investigation fix the depth of compensation?

When all the evidence from the solutions for depths infinity, 101 miles, 75 miles, 71 miles, and zero, is also taken into account, it appears that, if the compensation is uniformly distributed with respect to depth, the most probable value of the limiting depth is 71 miles and that it is practically certain that the limiting depth is not less than 50 miles nor more than 100 miles.

No conclusive evidence has yet developed in the investigation that the depth of compensation is different for different parts of the United States.

In all that has been said thus far, and in the corresponding parts of the investigation, it has been assumed that the compensation is uniformly distributed with respect to the depth. This assumption is not necessarily true and it must, therefore, be examined. It was adopted as a working hypothesis because it happened to be the one reasonable assumption which lends itself most readily to computation, and because it also seemed to the speaker to be the most probable simple assumption.

It is probably impossible to determine the distribution of the compensation with respect to depth from investigations based simply upon deflections of the vertical. Possibly pendulum observations combined with deflection observations may detect the manner of distribution.

All that can be done with deflections of the vertical is to determine the depth of compensation on various assumptions in regard to distribution with respect to depth.

Just as the limiting depth of the compensation, if it is uniformly distributed with respect to depth, has been determined by this investigation to be about 71 miles, so it has also been determined by a later portion of the investigation that if the compensation is greatest at the surface and diminishes uniformly with respect to depth until it fades out to zero, the limiting depth is about 109 miles.

Again, it has been determined by the investigation that if the compensation all occurs within a stratum ten miles thick the bottom of the stratum is at a depth of about 37 miles.

My belief is that the depth 71 miles and the corresponding assumed manner of distribution are nearer the truth than either the depth 37 or 109 miles with its corresponding assumption. This belief rests on insecure foundation. If anyone will tell me the manner of distribution of the compensation with respect to depth I believe that from the observed deflections of the vertical now available the limiting depth of compensation can be derived with reasonable certainty, with an error of less than 25 per cent.

Thus far this talk has been confined to the direct deductions from the geodetic observations. In this field the speaker enjoys a peculiar advantage in being in unusually close touch with the subject. He has no such advantage with respect to the suggestions which are about to be made on the bearing of these deductions upon some of the greater problems of geology. Nevertheless, the suggestions seem to be desirable in order to indicate some of the important relations of the geodetic investigation to other investigations.

The direct deductions from the geodetic observations, which have been stated, are a safe and strong foundation which cannot be shaken. The superstructure of suggestions which I am about to build upon it is relatively weak and unsafe. Please remember if you do succeed in knocking down the superstructure, that the foundation is still in place and awaiting an abler architect than I am to put a good superstructure upon it.

The fact is established by this geodetic investigation that the isostatic adjustment brought about by gravity has reduced the stresses to less than one-tenth of those which would exist if the continents and oceans were maintained by rigidity. This gives new and very strong emphasis to the idea that the earth is a failing structure, not a competent structure. The mechanics of the two kinds of structures are very different.

Geologists, and others who deal with the mechanics of the earth, seem to realize only a part of the time that the earth is a failing structure. Even during the periods of realization it is seldom that one acts upon the supposition that the earth is so utterly incompetent to bear the stresses brought upon it as this geodetic investigation indicates. Let me cite two examples taken from speakers before this Academy and in this room within a year.

One speaker, in stating the various methods of estimating the age of the earth, referred to the fact that there is no great excess of land surface about the equator as compared with the remainder of the earth. It has been urged that this indicates that the earth solidified in comparatively recent time. For otherwise, under the influence of a decreasing rate of rotation, the water would draw away from the equator and leave it high and dry. Now if the earth is so weak that it can stand but a small fraction of the weight of a continent before isostatic readjustment begins to take place, of course the equatorial protuberance due to decreasing rotation will be leveled down by failure and isostatic readjustment practically as fast as it develops, even if no other actions tend to level it down. Hence the study of the distribution of land with respect to latitude furnishes a measure of the earth's weakness, not of its age.

Another speaker quoted an article by Mr. G. Johnstone Stoney in which it is suggested that the permanence of the continents is due to elastic expansion of all the underlying material when load is removed by erosion. This idea, viewed in the light of geodetic evidence, seems to be extremely absurd, for it assumes the earth to be perfectly elastic—a competent structure—to great depths, whereas the earth is apparently inelastic to a high degree even near the surface and is apparently failing continuously under the stresses brought to bear upon it.

The expression "failing continuously" has been used purposely. It is possible that the continents and oceans are in their present positions because light material accumulated at the outset in the places now occupied by the continents, and heavier material accumulated where the deep oceans now lie. This would constitute an initial isostatic adjustment. But the geologic evidence is overwhelming that within the interval covered by the geologic record many thousands of feet of thickness have been eroded from some parts of the earth and have been transported to and deposited upon other parts. If isostatic readjustment had not also been in progress during this interval, it would be impossible for the isostatic compensation to be so nearly complete as it is at present.

For example, it is estimated by competent authority that a series of strata from 8 to 10 miles thick have been eroded and carried away from certain areas in the western part of the United States, which are now broad and lofty platforms carrying mountain ridges. The present elevation of these areas is less than three miles—the average elevation, not the elevation of the summits. Yet the present isostatic compensation, as already stated, departs not more than one-third from present perfection. The only reasonable explanation is that the isostatic readjustment keeps pace approximately with erosion and deposition.

Upon the basis that the isostatic compensation is complete and uniformly distributed throughout the first 71 miles of depth, will the computed variations of density be so great as to raise a doubt of the validity of the conclusions which have been drawn?

The highest large area within the region covered by this investigation is the region southwest of Denver, Colorado, with an elevation of about 11,000 feet or 2.1 miles. This is 3 per cent. of 71 miles. Hence, on the basis stated, the average density of the material beneath this region is 3 per cent. less than that beneath the areas along the coast which lie practically at sea level. The deepest ocean area of considerable size within the region of the investigation is in the Atlantic, northeast of the Caribbean Islands, with a depth of 3,000 fathoms or 3.4 miles. On the basis stated the average density of the material underlying this deep spot is only 3 per cent. greater than that of the material under areas which lie at sea level.

This computed variation in density is small, much smaller than the variations in density between different rock samples from different regions. Hence it presents no contradiction to the supposition that the location of continents and oceans may be due to initial differences of density in the materials.

But if there is a continuous isostatic readjustment in progress it is apparently necessary to believe that a given material may change in density as much as 3 per cent., under the varying conditions as to pressure (and possibly temperature) to which it is subjected within the first 71 miles of depth in the earth.

Both laboratory obvervations and geologic observations indicate that this is not only possible but probable.

The elastic effects probably coöperate in producing such changes of density, but probably play a minor part only.

Laboratory experiments have established as a general law of chemistry that increase of pressure favors such chemical changes as are accompanied by decrease of volume, that is, increase of density.

So, too, it is a law well established by laboratory investigations that the mass of a given gas that will remain in solution in a given liquid is proportional to the pressure. According to this law, known as Henry's Law, wherever beneath the surface of the earth gases and liquids are in contact an increase of pressure will drive more gas into solution and so increase the density of the mixture. A decrease of pressure will cause a part of the gas to come out of solution and decrease the density of the mixture.

Considering solution as a chemical process this law is but a specific example of the general law stated a moment ago.

Many other specific examples might be given of changes in pressure producing changes in chemical state and thereby changes in density.

Very important among these, because it is a process apparently in progress very extensively, is the solution of rock constituents in water and redeposition with a net increase of density of the rock so modified.

A quantitative study shows that changes of these kinds in a small part only of the materials in the heterogeneous mixture which makes up each cubic mile are sufficient to account for a change of 3 per cent. in the average density, and that isostatic readjustment brought about in part in this manner is not at all improbable.

The consensus of geologic evidence also indicates the existence of this relation of pressure, chemical state and density. For example, rocks which have been under great pressure because they have been deep within the crust are, in general, more dense than those composed of the same proportions of the elements but which have not been subjected to great pressure. So, too, it is a general law of metamorphism that changes going on in rocks which are now near the surface but which formerly were deep-seated are changes which are accompanied by decrease in density.

The indications are, therefore, that when an elevated area under which there is complete isostatic compensation is unloaded by erosion the underlying material to a depth of 71 miles increases in volume mainly because of chemical changes induced by the decrease in pressure, and partly also because of changes in the gases from solution to the free state. This increase in volume raises the surface. It also increases the pressure at each level above the 71-mile depth, and tends to bring it back toward the value which it had at that level before the unloading.

This expansion process alone is not sufficient, however, to maintain an isostatic adjustment indefinitely.

As the process progresses—a continuous expansion in the underlying material keeping pace approximately with continuous unloading by erosion at the surface—the pressure near the bottom of the expanding column will become considerably less than it is at the same level in other areas at which no unloading by erosion is taking place. So, too, near the top of the expanding column the pressures will tend to be somewhat greater than at the same level in other areas. The result of these differences in pressure at any given horizontal surfaces will be to set up, sooner or later, a great slow undertow from the ocean areas toward the continents, and a tendency to outward creeping at the surface from the continents toward the oceans.

Let me now emphasize the idea that the theory briefly sketched in the last few minutes is one which correlates many groups of observed facts.

It obviously accounts for the marked general tendency for areas unloading by erosion to rise and those loading by deposition to subside.

The theory indicates how the changes in density which accompany matamorphism are a part of the process of continent building.

The theory also accounts for the tangential stresses along the earth's surface of which the crumpled strata, especially of mountainous areas, are the evidence. For the great undertow toward the continents is attached to the surface strata by continuous material and tends to carry them inward. A great contest is waged between the shearing stresses developed between the undertow and the surface strata on the one side, and the compressive stresses exerted in a horizantal direction in surface strata, on the other side. The shortening of the surface strata by bending is a record of the extent to which the surface strata have suffered in the contest.

According to this theory the undertow should be most powerful a short distance inside the continental borders and hence the mountain building should be most active there. Many geologists have stated this to be the fact.

Again, according to this theory, such mountain ranges should be unsymmetrical, thereby indicating that the pressure came from the ocean side. Again, according to the geologists, many mountain systems show this effect as, for example, the Alleghenies.

Many other points might be brought out. But the time is too short.

So, too, the time has been too short to credit ideas to their originators, some of whom are present here to-night. I have tried simply to marshall the ideas and facts in such a way that their relations would become evident.

Discussion.

By Major Clarence E. Dutton.

I have only words of praise for the paper of Mr. Hayford. He seems to have expressed very accurately the conception of isostasy. His definitions of isostatic adjustment and isostatic compensation are very good. The chief point in his paper which makes it a valuable contribution to science is his determination of the depth at which the compensation occurs and is probably limited. That determination proves to be of a greater depth than I had anticipated, but it is none the less satisfactory on that account. Indeed I think it is more satisfactory than I had anticipated. It gives a greater concentration to the isostatic effort and permits us to infer a larger amount of horizontal displacement in the underlying masses than if it were much deeper. Also his determination of the amount of strain to which the rocks are subject is very much less and the amount of outstanding deformation of the earth is correspondingly less than we could have reasonably expected.

I have never supposed that isostasy was a force or condition which produced great elevations and subsidences of the earth. I have always been careful to distinguish sharply between the force which tends to preserve the various elevations and depressions of the earth from the force which tends to raise the lands and depress the sea bottoms. Those two classes of forces are at work independently of each other. The heavy masses of sediment which are formed upon the bottom of the sea can, I conceive, only be elevated by a positive uplifting force. Those portions of the land which are being denuded can only have their profiles depressed by an independent process of subsidence. Isostasy merely tends to keep the levels of the denuded region on the one hand, and the loaded regions of the sea bottom on the other, at constant levels.

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DISTRIBUTION OF THE LYMPHATICS IN THE HEAD, AND IN THE DORSAL, PECTORAL, AND VENTRAL FINS OF SCORPÆNICHTHYS MARMORATUS.

BY WM. F. ALLEN.

CONTENTS.

I. INTRODUCTION.

In some previous work on the Blood-Vascular System of the Loricati (2)[1] the lymphatics were frequently injected to distinguish them from the veins, and, and upon looking over the literature of the lymphatics of fishes, I was impressed with the general incompleteness and obscureness that seemed to characterize it. *Ophiodon* and *Scorpænichthys* differ very materially

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[1] The figures in parentheses refer to a list of the literature at the end of the paper.

in many important details from the forms that have already been studied, namely: *Squalus*, *Raja*, *Torpedo*, *Amia* (= *Amiatus*), *Cyprinus*, *Leuciscus*, *Salmo*, *Lucius* (= *Esox*), *Perca*, *Lophius*, *Pleuronectes* and *Uranoscopus*. The lymphatics of the Loricati therefore appealed to me as a subject worthy of study; hence this paper, which deals with the distribution of the lymphatic vessels in the head, dorsal, and paired fins of *Scorpænichthys*.

Two investigators of this subject in selachians, namely, Robin (23) and Mayer (18) deny the existence of lymphatics in fishes other than the visceral system. They consider the superficial and profundus vessels of the head and trunk as veins, and their sinuses they regard as venous sinuses. If this is true for selachians, it is certainly not true for the teleosts. In *Scorpænichthys* wherever there are blood-vessels and connective tissue there are lymphatics. Strange to say, the lymph and the plasma of the blood of this group has a greenish tinge, so that in an uninjected specimen the lymphatics, although lighter in color, might readily be taken for veins. Lymph usually contains some red corpuscles, often sufficient to give it a red tinge. Whether they have come directly into the lymphatics through the spleen and lymphatic glands, or through venous-lymphatic openings, or have transuded through the walls of the blood-vessels into lymphatic spaces and thence into the lymphatic vessels is still an open question. If, however, some lymph be drawn out with a pipette from the myelonal or superior longitudinal spinal lymphatic trunk, lying in the spinal canal above the cord, or from any of the lymphatic sinuses, and ejected into a bottle, and some blood be placed in a second bottle, the difference can quickly be detected upon the addition of a little alcohol. Most of the corpuscles of the lymph are colorless, while those of the blood have a dark brown color. The entire visceral lymphatic system can often be injected from the myelonal lymphatic trunk, which would hardly be possible were it a vein; and further, the arrangement of what has been designated as the neural lymphatic vessels, goes to prove that they are a part of a distinct profundis system. In front of each neural spine there is a neural lymphatic vessel, which empties into the myelonal lymphatic trunk; also in front of each alternate neural spine there is a neural artery, coming from the dorsal aorta, and in front of the other alternate neural spines, a vein that empties either into the kidney or into the caudal vein. If the neural lymphatic vessels be regarded as veins, there would be one artery and vein in front of one set of alternate neural spines and two veins in front of the other set of alternate neural spines, a very unlikely arrangement. The same correlation can be shown in connection with the hæmal vessels.

Scorpænichthys sometimes reaches a weight of twenty-five pounds and is one of the largest, if not the largest, of the Cottidæ. It is easily obtained close to shore, is little used as food, lives out of water for hours, remains hard some time after death, and taken all in all, furnishes a most excellent fish for anatomical study. These observations were made at the Hopkins Seaside Laboratory, Pacific Grove, California.

The same injecting masses were used that were employed in my studies on the blood vessels (2), and if only the lymphatics were to be injected preference was given to the berlin blue gelatin mass. The fish was severed transversely a little behind the vent and the body was placed head downward in a dish. A glass cannula connected with a piece of rubber tubing was forced forward in the myelonal lymphatic trunk. Usually a little cotton was placed around the cannula and over the cut ends of the dorsal, lateral, and ventral longitudinal lymphatic vessels. The syringe filled with the berlin blue mass was then connected with the rubber tubing, and with slow steady stroke the mass was forced into the lymphatics until they were completely filled, which is usually the case, but should this fail entirely or in part, it can be repeated farther forward, or the lateral and ventral lymphatics can be injected in a similar manner. In other species of fishes having a very small myelonal vessel or none at all, one has to resort mainly to the lateral lymphatic trunks. The tail can be injected caudad in a similar manner from the myelonal lymphatic trunk. It is, however, of primary importance in working with fishes that have been caught with a hook to cut the line if the hook has been swallowed. To attempt pulling it out would, in all probability, rupture the large sinuses surrounding the heart, which would be fatal to a successful injection.

The history of the work done on the lymphatics has been given by Milne-Edwards (16), Robin (23), Trois (28), and Hopkins (8). The general physiology and physiological history is fully set forth in Schäfer (26). A recent paper of unusual interest is that of F. M. Sabin's " On the Origin of the Lymphatic System from the Veins and the Development of the Lymph Hearts and Thoracic Duct in the Pig" (27). Anything further on the history of the lymphatics of Pisces would be simply repetition.

2. GENERAL SURVEY OF THE LYMPHATICS OF SCORPÆNICHTHYS.

As in the higher vertebrates, Milne-Edwards (16; p. 471–2) and subsequent investigators, have separated the lymphatics of fishes into a visceral and a muscular portion, the latter division having been further subdivided into a superficial or subcutaneous and a profundus or submuscular system. These three systems in *Scorpænichthys* are in close connection. Except in the head region the principal superficial and profundus vessels are longitudinal trunks that terminate anteriorly in the cephalic and pericardial sinuses, which empty into the jugular near the proötic process and into one of the branches of the inferior jugular; posteriorly they are collected in the neighborhood of the last vertebra by the right and left forks of the caudal vein.

The superficial or subcutaneous system of the trunk consists of 4 longitudinal canals, respectively — dorsal, ventral, and lateral. Both of the *lateral lymphatic trunks* (Figs. 1, 4, 5 and 6; *L.L. V.*) lie in a median plane, directly beneath the skin in a sheath of connective tissue that separates the dorsal from the ventral myotomes. Posteriorly they unite with the corresponding forks of the myelonal lymphatic trunk in the region of the last vertebra, and the combined trunks empty into the right and left branches of the caudal vein. Anteriorly after passing under the shoulder-girdle each of these trunks bifurcates, the lower fork emptying into the pericardial sinus, and the upper after receiving the corresponding fork of the myelonal lymphatic trunk, finally terminates in the cephalic sinus situated under the hyomandibular bone. Throughout its entire course the lateral lymphatic trunk receives numerous dorsal and ventral intermuscular or transverse vessels, which arise from a network on the surface of the myotomes, and which anastomose with the dorsal and ventral lymphatic trunks. The *dorsal lymphatic trunk* (Figs. 1 and 4; *D.L.V.*) is found under the skin in the dorso-median line, but for the most part it is a paired vessel, running along on each side of the dorsal fin between the superficial and profundus dorsal fin muscles. In the region of the fins both trunks receive numerous cross-branches from the dorsal fin or median dorsal lymphatic vessel, that traverses the basal canal[1] of the rays, and which collects the network from the dorsal fin. Throughout their whole length the dorsal lymphatic trunks are in connection with the intermuscular and the neural or interspinal vessels. Posteriorly this trunk is continued into the basal canal of the caudal fin as the caudal fin sinus, and when the median line is reached, unites with the corresponding ventral trunk in forming the hæmal or inferior spinal lymphatic canal. The *ventral lymphatic trunk* (Figs. 1, 2, 3, 4 and 6; *V.L.V.*) occupies a similar position on the lower side of the body. In the region of the anal fin it is a paired vessel. Between the ventrals it expands into a reservoir, which receives the ventral fin sinuses that collect the lymph from the ventral fins. A few myotomes in advance of the ventrals it pierces the ventral fin musculature and follows along the lower side of the pelvics to empty into the pericardial sinus. Posteriorly it enters the basal canal of the caudal fin as the caudal fin sinus, and as described above anastomoses with the dorsal and hæmal trunks. Throughout its entire course it is in connection with the ventral intermuscular or transverse vessels and the hæmal or interspinal lymphatic vessels. The most cephalic of the ventral intermuscular vessels is much larger than the others and is designated as the *pectoral sinus* (Figs. 1, 2, 3, 4, 5 and 6, *P.S.*). It receives the common trunk formed by the union of the 2 large sinuses situated on either side and at the base of the pec-

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[1] Immediately distad to the basal articulation of each ray there is a sort of foramen, here designated as the basal foramen of the fin or the fin-ray. Trois calls it *cruna* (eye of a needle).

toral fin, and each of these sinuses is in communication with cross-branches from the median pectoral fin sinus, lying within the basal canal and collecting the pectoral fin network.

Two principal trunks constitute the main profundus or submuscular system. The dorsal one, which is undoubtedly the largest and most important vessel in *Scorpænichthys*, is designated as the *myelonal* or *superior longitudinal lymphatic trunk* (Figs. 4 and 5, *My.L.V.*). It runs in the spinal canal directly above the cord from which it is separated by a septum. Between the skull and atlas it divides, and both forks after passing laterad out of this canal unite with the lateral lymphatic trunks in forming two common vesicles that finally terminate in their respective cephalic sinuses. In the region of the last vertebra this trunk again bifurcates to unite with the lateral trunks in forming joint papillæ that undoubtedly empty into the right and left forks of the caudal vein. Along its entire course it receives numerous neural or interspinal vessels that communicate above with the dorsal trunk, and which are often prolonged ventrally to unite with the longitudinal hæmal or inferior spinal lymphatic trunk and the abdominal sinus. Since the *longitudinal hæmal* or *inferior spinal lymphatic trunk* does not come under the head of this paper it has not been figured. It travels in the hæmal canal, is continuous posteriorly with the dorsal and ventral trunks, and anteriorly it appears to empty into the abdominal sinus. Within the hæmal canal it receives the hæmal or interspinal vessels, which are also in communication with the ventral lymphatic trunk. The *abdominal sinus* (Figs. 4, 5 and 6, *Abd.S.*), which lies directly under the kidney and empties anteriorly into the cephalic and pericardial sinuses, receives numerous small lymphatic vessels from the reproductive organs, the great lymphatic trunk from the viscera, and many intercostal vessels that are also connected with the *profundus ventral lymphatic trunk*. The latter vessel (Figs. 4, 6 and 9, $V.L.V._1$) perhaps should have been included as one of the principal profundus longitudinal trunks. It pursues a similar course to the ventral lymphatic trunk along the lower wall of the visceral cavity and terminates anteriorly in the posterior end of the pericardial sinus. Several interlinking vessels were noticed in the region of the ventral fins between this trunk and the main ventral lymphatic trunk.

In the head region there is the same division into superficial and profundus systems. The *superficial facial trunk* (Figs. 4 and 5, *S.Fac.L.V.*) takes its origin in the neighborhood of the snout, and following along the upper inner edge of the suborbital bones, crosses the proötic process to join the jugular papilla of the cephalic sinus. The *profundus facial trunk* (Figs. 4 and 5, *P.Fac.L.V.*) could only be found in the orbit; branches were seen to enter it from the adductor mandibulæ muscles, and it was traced to a point in front of the proötic foramen, where it probably passed under the jugular and entered the abdominal sinus. This point, however, could not be determined. There are 2 hyoidean lymphatic trunks, which run along the upper and lower sides of the arch (Figs. 3 and 4, *A.Hyo.T.* and *P.Hyo.T.*). Of the 2 the lower is the principal stem. It collects the lymph from the branchiostegal region, and after receiving the upper vessel expands into a sinus that empties into the cephalic sinus.

With *Scorpænichthys* nothing has been done in connection with the lymphatics of the viscera. The main trunk, however, was often injected from the myelonal trunk, and was seen to follow the cœliaco-mesenteric artery and empty into the abdominal sinus. The lymph from the reproductive organs was poured into the abdominal sinus through numerous small vessels. In an injected specimen of *Ophiodon* lymphatic vessels were seen to arise from all the organs and empty into trunks that followed the courses of their corresponding blood-vessels, often nearly surrounding them. These canals were collected anteriorly into a main cœliaco-mesenteric trunk that discharged itself in the abdominal sinus, and posteriorly the principal intestinal vessels traveled along with the posterior mesenteric vein between the reproductive organs to culminate in the abdominal sinus.

3. SUPERFICIAL OR SUBCUTANEOUS LYMPHATICS OF THE TRUNK.

Lateral lymphatic trunk (Figs. 1, 4, 5 and 6, *L.L.V.*).—No other of the lymphatic canals of fishes has received the attention that this one has. It is easily located and the one from which this system has usually been injected. According to Milne-Edwards (16, p. 473) and Stannius (24, p. 254) this vessel was briefly described and its connection with the ductus of Cuvier noted by Hewson (5) and Monro (14). Vogt (33) however, was the first to show the connection of this trunk with the caudal vein, but (in 1, p. 134) gives the credit of this discovery to Hyrtl. From the latter (7) one obtains a most excellent account of this vessel. It is represented (p. 233) as arising from numerous dorsal and ventral transverse vessels (Seitenast-Parre) into which empty numerous smaller branches that collect the network coming from the matrix of the scales, and in conversely restating the course of these vessels he says that the longitudinal trunk empties into the blood-vascular system. Further on (p. 234) he adds that in a successful injection the sinuses at the base of the pectoral and ventral fins and their branches were filled, but that no vessels were noted in connection with the dorsal fins. He also states that the lateral trunk terminates in a caudal sinus which empties into the caudal vein, and with *Acipenser*, *Cyprinus*, *Leuciscus*, *Esox* and *Gobio* it ends anteriorly in a thin-walled pear-shaped cephalic sinus situated at the side of the skull directly behind the orbit, which empties into the jugular a little forward of the lower jaw and opercular vein. Shortly before the lateral lymphatic trunk terminates in the cephalic sinus several vessels coming from the jaws, the gills, the tongue and branchiostegal membrane are described as emptying into it. With the salmon and the trout, Hyrtl notes an entirely different anterior mode of communication with the venous system. Here the lateral trunk after curving under the clavicle empties into the sinus of the spermatic vein (Sinus der Holvenen) at its junction with the ductus of Cuvier, and this opening is guarded by a valve opening into the vein. While with *Perca lucioperca*, *Tinca chrysitis*, and *Cottus gobio* both points of union are said to exist. Vogt (1, p. 134–7) also describes this trunk in the salmon with great detail. He noticed the transverse branches emptying into the main trunk, but considered them as extravasations caused by the rupture of the thin-walled lateral canal. Posteriorly this canal is said to end in a sinus that empties into the caudal vein (veine cardinale). Upon reaching the end of the thoracic cavity it expands into a capacious reservoir, lying directly beneath the clavicle. Within the sinus there is a slit covered by a strong valve that leads into a vessel about the diameter of a pin-head, which passes directly into the sinus of Cuvier. Pl. K (Figs. 7 and 8; 64) shows this cephalic sinus papilla entering the sinus of Cuvier from the front. Vogt speaks of this trunk as a mucous canal, and since he could find no lateral mucous canal in the salmon into which the mucous pores emptied, he inferred that they emptied into this trunk. Stannius (24, p. 252–4) states that this trunk takes its source from numerous transverse branches, and following along with the truncus lateralis N. vagi terminates in caudal and cephalic sinuses. In addition the latter receives lymph from the head, gills, and trunk and empties into the precava (truncus transversus). From footnotes Milne-Edwards gives us the following additional information: *Silurus* has three parallel lateral lymphatic vessels. With some fishes, as for example, the pike, roach, grudgeon, barb, and sturgeon, the lateral trunk is prolonged into the head and forms a sinus at the base of the skull, which empties into the jugular through a transverse canal. With the salmon, cod, rays, and sharks, the lateral trunks open into a pair of large cervical sinuses, that descend behind the center of the scapula and reunite in the median line at the point where the abdominal sinus joins them. Each of these scapular reservoirs communicates with the anterior vena cava or ductus Cuvieri through an orifice guarded by valves. Trois (28, 29, 30 and 31) gives a most excellent account of this vessel in *Lophius piscatorius*, *Uranoscopus scaber*, and in several of the Pleuronectidæ. He describes this trunk as ending in cephalic and caudal sinuses, and has satisfied himself that the transverse branches are not superfluous injecting mass as Vogt maintains. These vessels in *Lophius* are portrayed as sending off branches between the myotomes, which anastomose with similarly arranged profundus vessels, forming a sort of ladder network. The transverse rami are represented as also anastomosing with the dorsal and ventral lymphatic trunks. *Uranoscopus* (29, p. 20, and Pl. on p. 37) furnishes a beautiful example of a fish having 3 longitudinal lateral lymphatic trunks, and since the middle one is the largest and is connected with the venous system at either end Trois is right in attributing only secondary importance to the other two. Trois also noted the knotty appearance of the main lateral trunk in *Uranoscopus* (29, p. 21–2) which he thinks is due to rudimentary or imperfect valves that may have been put out of action by death, and the difficulty that he has experienced in injecting this trunk he ascribes to the resistance of these valves. This knotty appearance of the lateral trunk was also noticed in *Scorpænichthys*, but since no trace of valves has been found it seems best to attribute it to the outside resistance of the body musculature, rather than to the existence of hypothetical valves. To a considerable extent this arrangement may check the flow of the lymph and also the injecting mass, but by swelling out in the region of the centers of the myotomes it considerably increases the capacity of the lymphatic system. With the carp and pike Sappey (25, p. 41, and Pl. XII, Fig. 2) describes and figures the lateral trunk as bending ventrad about 15 or 20 mm. in front of the clavicle and emptying directly into the jugular without forming any sinus. Hopkins (8, p. 371–2) in addition to describing the ordinary termination of the lateral trunk in cephalic and caudal sinuses says that in *Amia* this trunk receives a branch from the pectoral sinus before passing under the pectoral arch to open into the cephalic sinus, which is said to extend from the dorsal end of the clavicle to the base of the skull, and which empties into the jugular about 1 cm. cephalad and a little ventrad of the dorsal end of the clavicle.

The *lateral lymphatic trunk* of *Scorpænichthys* (Figs. 1, 4, 5 and 6, *L.L.V.*) in the trunk region corresponds in the main with the descriptions of the previous investigators. As has already been stated in the general survey of the lymphatics this vessel lies beneath the skin in the median lateral line, and except in the cephalic portion of the trunk follows parallel, but mesad of the lateral line canal. It is distinctly a superficial vessel lying in the connective tissue septum that separates the two halves of the great lateral muscle. Throughout its entire course it takes up numerous dorsal and ventral intermuscular or transverse branches, the most cephalic of which is a large ventral sinus to which the name *pectoral sinus* has been given. Passing under the pectoral arch it follows along in front of the first rib across the anterior fork of the kidney. About half way across the kidney it receives a communication from the *pericardial sinus* (Figs. 4, 5 and 6, *Per.S.*), and when the atlas is reached unites with a fork of the myelonal or longitudinal spinal lymphatic trunk, the point of junction being marked by quite a large reservoir, designated as the *occipital sinus* (Figs. 4 and 5, *Oc.S.*). From here on the combined trunk thus formed is a distinct profundus vessel designated as the *cranial lymphatic trunk* (Figs. 4 and 5, *Cr.L.V.*). This vessel finally empties into the cephalic sinus, and is described in detail further on under a separate paragraph.

Had the lateral trunk in *Scorpænichthys*, after having passed under the clavicle, curved downward without expanding into a sinus and emptied into the jugular, we would have the conditions as described for the carp and pike by Sappey (25). Had the lobe of the kidney not extended so far cephalad and the occipital sinus been located in front of the precava a little below its present position in *Scorpænichthys*, and received the branchial, hyoidean, and facial trunks, but not the myelonal, it would have answered to Vogt's description of the anterior termination of the lateral canal in the cephalic sinus with the salmon (1); provided that this sinus emptied into the precava. Finally, had the lateral trunk of *Scorpænichthys* continued to the base of the skull, without receiving the myelonal trunk and the pericardial sinus, but collecting the branchial, facial and hyoidean trunks, and had sinus (*s*) emptied into the jugular we would have had the conditions met with in *Cyprinus*, *Leuciscus*, *Esox*, *Acipenser*, etc. It is of special interest to note in this connection that Hyrtl and Milne-Edwards have vaguely described 2 anterior communications from the lateral lymphatic trunk with the venous system in *Cottus gobio*, a species belonging to the same family as *Scorpænichthys*.

The *intermuscular* or *transverse vessels* (Figs. 1, 2, 4 and 5, *Intm.V.*) described by Hyrtl, Stannius, Milne-Edwards, Trois, Sappey, Hopkins, and which Vogt took to be extravasations of the injecting mass have certainly been found in *Scorpænichthys*, following along superficially in the septa between the myotomes. The ventral vessels anastomose with the ventral lymphatic trunk and the dorsal with the dorsal trunk. These vessels are connected by a lymphatic network, which has its origin from the surface of the muscles and connective tissue, and branches are also received that arise from a very rich network on the subcutaneous layer of the skin. This network is especially conspicuous in fresh-water drum, *Aplodinotus grunniens*, where it can be seen through the transparent scales. The secondary lateral trunks described by Trois in *Uranoscopus* are certainly of only secondary importance in *Scorpænichthys*. For not only is the central vessel much larger and connected at either end with the venous system, but the secondary lateral vessels are only found in the cephalic end of the trunk, and the most dorsal one is not a continuous trunk, but simply a series of regular cross vessels.

Pectoral sinus and lymphatics of the pectoral fin. — This sinus (Figs. 1, 2, 3, 4, 5 and 6, *P.S.*) lies directly below the skin between the base of the pectoral fin and the post-clavicle, or perhaps to more accurately state it, between the superficial pectoral adductor muscle, and the anterior myotomes and the sterno-hyoideus muscle (see fig. 2). In a well-injected specimen it can be traced cephalad between the sterno-hyoideus and superficial abductor muscles to what has been designated as the *ventral pericardial sinus* (Figs. 3, 4 and 6, *V.Per.S.*). Since the ventral pericardial sinus receives the ventral lymphatic trunk, the union of the pectoral sinus with the ventral pericardial sinus is analogous to the union of the ventral intermuscular or transverse vessels with the ventral lymphatic trunk. In addition to its dorsal and ventral connections the pectoral sinus is always in direct communication with the *abdominal sinus* (Figs. 4 and 6, *Abd.S.*) In a very large specimen from which Fig. 6 was drawn an additional connection was also noticed with abdominal sinus, which received a communicating branch from the pericardial sinus. Near the termination of the pectoral sinus in the lateral lymphatic trunk it receives a common trunk formed from the union of the outer and the inner pectoral fin sinuses (see figs. 1, 4 and 6). Of these two sinuses the *inner* is the larger (Figs. 1, 2, 2*a* and 4, *I.P.S.*). It follows along the base of the fin between the superficial and profundus adductor muscles, having blind sacs that pass between the profundus adductor muscles, but which send up short branches between the middle rays that soon fork to anastomose with the corresponding branches of its fellow, thus forming a circle over the bases of the middle rays (Fig. 2). These circular vessels receive short pectoral-ray vessels (Figs. 2 and 2*a*, *P.F.L.V.*$_{(1)}$), which run along the inner surface of the rays. They are much shorter than the main pectoral fin or pectoral fin-ray vessels, but appear in a well-injected specimen to have communicating branches with the main pectoral-ray vessels. The *outer pectoral sinus* (Figs. 1 and 2*a*, *O.P.S.*) occupies a similar position between the superficial and profundus pectoral abductor muscles. It also sends back little pockets between the bundles of the profundus muscle, and receives dorsad a large branch that has its origin from the superficial and profundus abductor muscles (see Fig. 1). The outer pectoral sinus, after curving over the most dorsal ray, joins the inner pectoral sinus in forming a common trunk that empties into the main pectoral sinus. In addition to these 2 pectoral sinuses there is a third or *median pectoral sinus* (Fig. 2*a*, *M.P.S.*), which traverses the basal canal of the pectoral rays.[1] This trunk receives the main *pectoral fin* or the main *pectoral fin-ray* vessels (Figs. 2 and 2*a*, *P.F.L.V.*). Two such vessels accompany each ray and receive the network from the pectoral fin membrane. As is shown in Fig. 2*a* numerous cross-branches pass between the rays from the median pectoral sinus to both the inner and the outer pectoral sinuses.

Very little is to be found in the literature on the lymphatics of the pectoral fin. Hyrtl (7, p. 234) says that a pectoral sinus and its branches are filled in a successful injection of the lateral trunk. Stannius (24, p. 253) briefly describes a sinus at the base of the pectoral which receives numerous branches from the pectoral fin muscles. Hopkins simply states with *Amia* (8, p. 371) that the lateral trunk receives the pectoral sinus. Trois (28, p. 8, and 29, p. 25) says that in *Lophius* and *Uranoscopus*

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[1] See note, page 45.

there are at least 3 pectoral lymphatic trunks emptying into the cephalic sinus. Secondary branches are noted as anastomosing with the intercostals, and a sinus (vaso collettore) is spoken of as lying at the base of the rays and forming a ring about every ray. Lymphatic vessels are described as running along the surface of the rays and collecting the rich network from the skin. It will be seen from Trois' description that the lymphatics of the fin itself correspond somewhat with the arrangement in *Scorpænichthys*, but as regards their mode of termination there is nothing in common.

Dorsal lymphatic trunk (Figs. 1 and 4, *D.L.V.*). — Hyrtl and Vogt seem to have overlooked this canal. Stannius (24, p. 253) says that this trunk can be divided into 2 subordinate stems. First a vessel is described as running along the angle of the intermuscular septa, and a vessel is noted as passing along between the upper border of the great lateral muscle and the longitudinal muscle of the dorsal fin, which would place it at the base of the dorsal fin. Cross-branches are said to exist between the 2 trunks, and the second trunk receives numerous branches that followed along the rays. The first dorsal trunk of Stannius is undoubtedly the same as that described by Trois and myself as the most dorsal of the secondary lateral lymphatic trunks. Trois (28, p. 6) and Sappey (25, p. 47) describe the dorsal trunk in *Lophius* and the pike as a knotty vessel that separates into 3 distinct trunks upon reaching the dorsal fin, two of which run laterad to the base of the rays, while the third, more slender, passes through the holes in the base of the rays. Two vessels for each ray collect the lymph from the fin and empty into the median trunk. With *Uranoscopus* (29, p. 23) the anastomosis with the neural or interspinal vessels was noted. Hopkins (8, p. 373) describes this trunk in *Amia* as anastomosing with the lateral trunk before terminating in the caudal sinus, while anteriorly it bifurcates at the base of the skull, each fork emptying into a cephalic sinus.

The description given of the dorsal longitudinal lymphatic trunk by Trois for *Lophius* and *Uranoscopus* will also answer very well for *Scorpænichthys*. In the region of the dorsal fins this canal separates into three longitudinal trunks, two of which running along at the base of the fins between the great lateral, superficial, and profundus dorsal fin muscles are evidently the main stems, and might be designated as the *lateral dorsal lymphatic trunks* (Figs. 1 and 4, *D.L.V.*); while the third or *median dorsal lymphatic trunk* (Figs. 1 and 4, *D.L.V.*$_{(1)}$) simply passes through the basal canal of the rays and collects the dorsal fin lymphatic vessels. Numerous transverse interlinking vessels were noticed between the median dorsal and the 2 lateral dorsal lymphatic trunks, and the *dorsal fin lymphatic vessels* (Figs. 1 and 4, *D.F.L.V.*) were merely small branches of the median lymphatic trunk, that followed along the cephalic and caudal surfaces of each spine and ray and collected the network from the fin membrane. Some variation, however, is shown in the anterior region of the first dorsal, where there is but one dorsal fin lymphatic vessel between the first and second, and between the second and third spines, both of which empty directly into the lateral dorsal trunks. In addition to receiving the dorsal fin vessels the median dorsal lymphatic trunk collects numerous small branches from the superficial or extrinsic dorsal fin muscles (Fig. 1). Anteriorly these 2 lateral dorsal lymphatic trunks do not terminate directly into cephalic sinus as described by Hopkins for *Amia*, but throughout their entire course communicate with the lateral lymphatic trunk through the intermuscular or transverse vessels, and with the myelonal or longitudinal spinal lymphatic trunk through the *neural* or *interspinal vessels* (Fig. 4, *Neu.L.V.*). The most cephalic neural or interspinal vessel (Figs. 4 and 5, *Neu.L.V.*$_{(1)}$) does not empty into the myelonal trunk, but follows along behind the skull and terminates in the cranial lymphatic trunk.

Ventral lymphatic trunk and lymphatics of the ventral fins (Figs. 1, 2, 3, 4, 6, 9 and 10,[1] *V.L.V.*). — According to Milne-Edwards (16, p. 473) this vessel has been described by Monro (14) and Hewson (5) in *Gadus*, and as was the case with the dorsal trunk this canal seems to have been overlooked by Hyrtl and Vogt, although the former states that a ventral fin sinus is filled from a good injection of the lateral trunk. Stannius (24, p. 253) describes this vessel as unpaired, running

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[1] Figs. 7 to 10 are text-figs. on pp. 73, 74, 76 and 77.

along between the halves of the lateral muscle from the vent to the shoulder-girdle. Caudad the vessel from the anal fin is discharged into it, and in the rump region it receives transverse vessels that follow the intermuscular septa. Trois (28, p. 7) and (29, p. 23) represents the ventral trunk in *Lophius* and *Uranoscopus* as consisting of 2 parallel trunks. With *Uranoscopus* they run close together and are connected by numerous cross-branches. In front of the anal they unite, and the common trunk receives 3 vessels from the region of the anal fin, of which the median is the largest and traverses the basal canal of the rays; the 2 lateral trunks are found at the base of the fin and travel toward the tail, and the 3 vessels are said to be connected by transverse rami. With *Lophius* we are told that the ventral canals bifurcate at a very acute angle in front of the ventral fins, and that these branches collect everything at the base of the ventrals. Sappey (25, p. 47) states with the pike and carp that this trunk is very similar to the dorsal; that it is a single trunk in the region of the anal fin; but in advance of this, between the ventrals and pectorals, it consists of two parallel trunks, which are prolonged to the posterior end of the skull. With the Pleuronectidæ, Sappey (p. 49 and Pl. XII, fig. 4) represents the ventral trunk as consisting of 2 parallel vessels in the region of the anal fin, but uniting in front of it in a common trunk that empties into the sinus of Cuvier. Hopkins (8, p. 372) describes the ventral trunk as beginning at the base of the caudal fin and extending cephalad to the heart, where it divides into two branches that merge into pericardial sinus, which communicates with the cephalic sinus and thence with the veins. On its course it receives the lymph from the anal and pectoral fins, and the sinus at the base of each of these is said to be much smaller than the one at the base of the pectoral.

The *ventral longitudinal lymphatic trunk* of *Scorpænichthys* (Figs. 1, 2, 3, 4, 6, and 9, *V.L.V.*) differs very materially from any of the species described above, although perhaps conforming more closely to Hopkins' account for *Amia* than any of the others. The course of this trunk through the anal fin and its prolongation into the basal canal of the caudal fin is left for another paper. In contrast to Trois' description this is a single trunk in *Scorpænichthys*, extending from the vent to the origin of the pectoral fins. It runs along superficially in the ventro-median line from the vent to the origin of the pectorals, but pierces the body wall some distance behind its cephalic end; the exact position is noted by *V* (Figs. 1 and 4), which is a little cephalad to the point of union with the vessels coming from between the profundus and superficial abductor muscles of the ventral fin. At this point a slight sinus is formed, which might be described as receiving an anterior and a posterior ventral trunk. The combined trunk or main stem thus formed penetrates obliquely between the 2 ventral fin abductor muscles, continues cephalad in a median line along the lower surface of the pelvic bones (Fig. 4), and passing between the clavicles and the pelvics, curves around the anterior end of the pelvics to enter the *ventral pericardial sinus* (Figs. 4, 6, 9 and 10, *V.Per.S.*) directly below the ventricle from the rear. The connection of this sinus with the veins will be described further on under a separate paragraph. Between the ventral fins the ventral trunk expands into a distinct pear-shaped sinus to which the name *ventral sinus* has been given (Figs. 1, 2 and 4, *V.L.S.*). This sinus receives at least one pair of intermuscular vessels and two *ventral fin sinuses* (Figs. 1, 2 and 4, *V.F.L.S.*), which lie on the upper or inner base of the ventral fins. They receive the *ventral fin* or the *ventral fin ray vessels* (Figs. 1, 2 and 4, *V.F.L.V.*) from between each two rays, which soon bifurcate, each fork running along the adjoining rays and receiving the network from the membrane between the two. This is the typical arrangement, but some irregularities are often found as shown by Fig. 2, where some *auxiliary ventral fin vessels* (Fig. 2, $V.F.L.V._{(1)}$) were noticed traversing the innermost rays, which reunited in a common vessel that passed over the lower side of the fin to empty into the ventral fin sinus close to its union with the ventral sinus. The ventral fin sinuses are prolonged cephalad between the external ventral fin abductor muscles and the great lateral muscle as the *ventral fin musculature lymphatic vessels* (Figs. 1 and 2, *V.M.L.V.*), and in route receive at least three intermuscular or transverse lymphatic vessels. Mesad of these ventral fin musculature lymphatic vessels there are still two other *ventral fin musculature vessels* (Fig. 2, *V.M.L.V.*$_{(1)}$), which run between the internal and external ventral fin abductor muscles, and unite with the main ventral trunk immediately before it penetrates the musculature to empty into the pericardial sinus.

From the above description of the termination of the ventral fin vessels into a single sinus outside the fin it will be noticed that this is a very different arrangement from that found in the dorsal and pectoral, where these vessels emptied into a median sinus, which traversed the basal canal of the rays, and having numerous transverse branches, communicating with the two lateral sinuses, lying at the base of the fin.

In the paragraph on the lateral lymphatic trunk it was stated that a typical ventral intermuscular or transverse lymphatic vessel connected the lateral with the ventral lymphatic trunk. The most cephalic of these vessels, however, show some deviation from this general plan. The first one connects the pectoral sinus with the anterior end of the ventral trunk; the second interlinks the pectoral sinus with the ventral fin intermuscular vessel; the third and fourth communicate with the lateral trunk and the ventral fin intermuscular vessel; the fifth unites with the lateral trunk and the ventral fin sinus; while the sixth extends from the lateral trunk to the ventral sinus.

4. PROFUNDUS LYMPHATICS OF THE TRUNK.

The *profundus ventral lymphatic trunk* (Figs. 3 and 4, *V.L.V.*$_{(1)}$), which seems to have escaped the notice of the previous investigators, pursues a parallel and somewhat similar course to the main ventral lymphatic trunk between the great lateral muscles, but follows along the inner or visceral side of them. So far as could be ascertained it arose near the vent and passing cephalad along the median line close to the visceral cavity, terminated in the posterior end of one of the pericardial sinuses (Figs. 4, 6 and 9). Throughout its course it receives or gives off numerous *intercostal lymphatic vessels* (not shown in any of the figures), which follow along the inner side of the intermuscular septa, parallel with the intermuscular or transverse lymphatic vessels and anastomose dorsally with the abdominal sinus. In the region of the ventral fin, and not improbably in other places, interlinking vessels were found between the profundus and superficial ventral trunks.

Myelonal or *superior longitudinal spinal lymphatic trunk* (Figs. 4 and 5, *My.L. V.*).— This trunk with its neural or interspinal branches has been described by Hyrtl (7) and Stannius (24) as ending in the caudal sinus, but nothing whatever is said about its anterior connections. Trois states that this trunk in *Lophius*, *Uranoscopus*, and the Pleuronectidæ (28 to 31) runs along in the spinal canal, receives numerous interspinal branches, and is connected with the hæmal longitudinal trunks by means of transverse vessels. With *Rhombus maximus* and *R. lævis* (30, p. 43) an additional longitudinal trunk was described as traveling along at the level of the bases of the interspinal bones. So far as could be discovered, Sappey (25) is the only one to give a cephalic ending for this canal. He states that it is a very important trunk with the pike and flatfish, and with these 2 fishes it is represented as extending from the coccyx of the last vertebra to the first cervical vertebra — where it turns to empty into the jugular. He further adds that there appears to be no caudal connection with the papilla of the lateral canal. No such trunk was portrayed by Vogt in the salmon or by Hopkins in *Amia*.

In *Scorpænichthys* the *myelonal* or *superior longitudinal spinal lymphatic trunk* (Figs. 4 and 5, *My.L. V.*) agrees very well with the descriptions given it by Trois and Sappey in *Lophius*, *Uranoscopus*, *Esox*, and the Pleuronectidæ, except that its cephalic termination is very different from what Sappey represents it for the pike and the flatfish. This trunk seems to be of different relative importance in different groups. With *Scorpænichthys* it is the longest and undoubtedly the most important of the longitudinal canals. It is located in the spinal canal directly above the myelon or cord, from which it is separated by a rather tough connective tissue septum. The *neural* or *interspinal lymphatic vessels* (Fig. 4, *Neu.L. V.*), which have been described so accurately by Trois and Sappey, are very important branches of the myelonal trunk in *Scorpænichthys*. Their course lies between the neural spines and anastomose dorsad with the dorsal or the 2 lateral dorsal lymphatic trunks. Since there is no special anterior connection of the dorsal lymphatic trunk with cephalic or pericardial sinus in *Scorpænichthys* save through the neural or interspinal and the dorsal intermuscular or transverse vessels into the lateral or myelon trunks, and since the neural or interspinal vessels are much the larger, especially at the junction with the myelonal trunk, it is more than likely that they convey most of the lymph from the anterior portion of the dorsal fin region, while the main supply for the dorsal intermuscular vessels evidently comes from the surface of the myotomes and the surrounding connective tissue. The main myelonal trunk extends from the last caudal vertebra to the skull. Its posterior connection with the caudal vein will be described in a later paper. When the skull is reached it bifurcates, each fork after passing laterad between the skull and the first vertebra or atlas empties into a rather large sinus situated at the side of the atlas, directly in front and a little below the base of the first rib. This sinus is designated as the *occipital sinus* (Figs. 4 and 5, *Oc.S.*) and receives, as has already been stated, the main lateral lymphatic trunk from the side and rear. Very likely this sinus should be considered nothing more than a swelling caused by the union of these 2 important trunks the resultant of which is the *cranial lymphatic trunk.*

The course of this sinus-like vessel (Figs. 4 and 5, *Cr.L. V.*) is along the lateral base of the skull. Following the upper surface of the head kidney for a short distance, it crosses under the first spinal nerve and receives from above the *first neural* or *interspinal lymphatic vessel* (Figs. 4 and 5, *Neu.L. V.*$_{(1)}$); then continuing along the side of the cranial wall between the great abdominal lymphatic sinus and the IX and X cranial nerves expands into a sinus (Figs. 4 and 5, *S.*), which lies directly above the jugular vein, on a level with the optic lobes, immediately behind the proötic process and between the skull and the first internal branchial levator muscle. This sinus has 2 openings; the most cephalic one is simply a tapering down of the sinus into a papilla, which curves outward and downward to communicate with the abdominal sinus; while the other opening leads into a lateral vessel or papilla, which curves around the first internal branchial levator muscle to empty into what has been designated as the *cephalic sinus* (Figs. 4 and 5, *Ceph.S.*). A full description of this sinus and its connection with the jugular behind the proötic process will be given under a separate paragraph.

Longitudinal hæmal or inferior spinal lymphatic trunk and the abdominal sinus. — Hyrtl and Stannius seemed to have overlooked these vessels, but such a canal is represented by Vogt (1, p. 138) as consisting of 2 large lymphatic trunks that follow the aorta, and into which the trunk from the viscera and the vessels from the body wall empty. The posterior connections of these trunks were not given, but anteriorly they are said to empty into a branch of the *third canal*, terminating in the cephalic sinus. Vogt states (p. 138) that this canal (Pl. L, Figs. 1 and 8; 64) comes from a common reservoir which follows the superior plate of the fourth branchial arch, and that it receives 2 important branches, one coming from the fourth branchial arch and the other arising at the middle of the body. The last branch is said to communicate in the median line with the corresponding branch from the opposite side immediately in front of the kidney, and at this point receives the 2 longitudinal trunks which follow the aorta. Two small vessels, which could not be definitely traced, but which appeared to come from the brain, are described as emptying into the cephalic ends of these longitudinal trunks. Milne-Edwards (16, p. 477) says that in general there are 2 lymphatic canals running parallel with the aorta, but expresses some doubt about their emptying into the cervical or cephalic sinuses. He further adds in a footnote that Fohmann (4) found 2 longitudinal lymphatic vessels traveling along with the aorta in the eel, which received branches from the trunk musculature and emptied anteriorly into the cephalic sinus. With the pike Sappey (25, p. 49) represents the trunk *sous-vertébral* as occupying the same canal as the caudal artery and vein, being situated below the vein, and receiving branches which traverse the muscles adjacent to the hæmal spines. With the Pleuronectidæ (p. 50) he states that the inferior spinal trunk empties into the jugular directly below the superior trunk. It is also of interest to note in this connection that he claims to have found the minute lymphatic vessels anastomosing with the blood capillaries in the connective tissue of the muscles and the skin. Trois' description of this canal in *Lophius*, *Uranoscopus*, and in the Pleuronectidæ (28 to 31) is very similar to Sappey's, but so far as could be learned he does not give a cephalic ending for this trunk. With the Pleuronectidæ he finds 2 parallel longitudinal vessels, a superior and an inferior longitudinal trunk, having numerous anastomosing cross branches that form a scale-shaped network on the caudal vein. Hopkins does not mention any longitudinal hæmal trunk, but describes (8, p. 375) a large abdominal sinus running along the right side of the air-bladder. Caudad it is said to anastomose with one of the ducts from the duodenum ; throughout its course it receives branches from the bladder and the stomach and finally empties into the right lymphatic sinus, which terminates in the ductus Cuvieri.

Both the longitudinal hæmal lymphatic trunk and the abdominal sinus were found in *Scorpænichthys*. The hæmal trunk was noticed only in the caudal region, and undoubtedly empties into the abdomidal sinus.

The *abdominal sinus* in *Scorpænichthys* (Figs. 4, 5 and 6, *Abd.S.*) is a very large and important sinus, lying directly below the kidney and extending from the posterior end of the abdominal cavity to the orbit. A little behind the precava it divides, each fork following along under its respective lobe of the kidney continues cephalad along the ventro-lateral surface of the skull, and when the proötic process is reached directly below the jugular, or directly opposite the first internal branchial levator muscle, it turns inward and downward to end blindly opposite the parasphenoid behind the orbit. In some specimens the injecting mass so settled as to give the appearance of 2 abdominal sinuses with numerous cross branches in the visceral cavity. Throughout the abdominal cavity this sinus receives many branches from the reproductive organs, urinary bladder, body wall, and probably from the kidney itself. The body wall vessels are the *intercostals*, which follow along the inner surface of the intermuscular septa and anastomose ventrad with the profundus ventral lymphatic vessel. Numerous interlinking vessels were also found between this sinus and the myelonal trunk. With *Ophiodon* a large posterior mesenteric trunk was seen to pass between the generative organs with the corresponding vein and empty into this sinus; it had its origin from the posterior end of the intestine, being simply a continuation of the main intestinal trunk. As has already been stated the abdominal sinus receives a communication from the pectoral sinus, and a little in advance of this a connection is received from the pericardial sinus (Figs. 4 and 6); while between the two it receives the large *cœliaco-mesenteric lymphatic trunk* (Figs. 4 and 6, *Cœ. Mes. L. V.*), coming from the viscera and following the course of the corresponding artery. In advance of the head kidney each cephalic fork of this sinus swells up considerably upon the receipt of 3 sinuses from the region of the branchial arches. An important communication, which has already been mentioned is the papilla from sinus (*S*) of the cranial lymphatic trunk (Figs. 4 and 5, *S.*). Another possible accession is the profundus facial lymphatic trunk (Figs. 4 and 5, *P.Fac. L. V.*).

Branchial or *dorsal branchial sinuses* (Figs. 4 and 5, *Br.L.S.*). These 3 sinuses appear to arise from the dorsal extremities of the first, second, third and fourth arches respectively, and passing between the obliqui dorsales muscles, unite with each other and the abdominal sinus in such a way as to entirely encircle the 2 internal branchial levator muscles. My injections simply showed these sinuses to be blind pockets off from the abdominal sinus, and no trunks from the branchial arches or even from the dorsal branchial muscles were seen to empty into them.

Vogt in the salmon (1, p. 177–8) describes the *second* canal emptying into the common cephalic sinus as being composed of 3 different branches, each of which is composed of 2 different components. These 3 branches come from the first, second, and third branchial arches, and of their 2 components, one is very small, arising from the superior part of the arch especially from the filaments; while the other is more superficial, continues along the arch and unites with the inferior jugular (Veine de

Duvernoy). Vogt states that he has succeeded in injecting the inferior jugular from the common branchial canal (Fig. L; 63). A somewhat similar arrangement is shown for the fourth arch; the two branchial components unite in a common stem that anastomoses with a large trunk coming from the middle of the body and finally ends in the cephalic sinus as described under the abdominal sinus. Stannius (24, p. 254) says that lymphatic vessels arise from the branchial arches and empty into a trunk running in the canal of the arches. Trois (28 and 29) always found a branchial trunk in the groove of each arch in *Lophius* and *Uranoscopus*, which received branches arising from networks in the arches and in the filaments. The filament networks are represented as being much finer and necklace-shaped, while those of the arch are irregular and much coarser. In connection with *Uranoscopus* (29, p. 26) the author states that Fohman (4) is the only one having described these branchial lymphatic vessels, and attributes the fact that they have not been discovered by other investigators to their faulty method of procedure, namely, of immersing the specimen in alcohol.[1]

Müller (15) and Stannius (24) have shown a somewhat similar arrangementof branchial vessels under the head of *venæ nutritiæ*, and in a previous paper of mine (2) both dorsal and ventral nutrient branchial veins were figured and described; the former emptied into the jugular and the latter into the inferior jugular. These vessels received branches from the arches and the filament nutrient veins, which arose from a capillary network in the filaments. This network could easily be distinguished from the regular gill network on account of its different arrangement and its much coarser meshes.

In not being able to find lymphatic vessels arising from the gills and the branchial arches I am not disposed to contradict their existence, for I can see no reason why the gills should not possess lymphatics.

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[1] In this connection, would state that I see no objection to preserving an injected specimen in alcohol or formalin for future reference. I have kept injected material in formalin for years in as perfect shape as when first injected, and upon writing up a description find them of greater value than reference figures or mere memory.

5. FACIAL LYMPHATICS.

As in the trunk region there is a distinct superficial and profundus system. Strange to say Vogt (1, p. 137) is the only anatomist to have definitely described lymphatics arising from the facial region of Pisces. The *first canal* emptying into the cephalic sinus in the salmon is said to originate on the temporal (pterotic) crest from two trunks coming from the head. The first branch, which is somewhat similar to the vessel described below in *Scorpænichthys* as the profundus facial lymphatic trunk, has its source at the anterior angle of the nasal fossa, and passing through the orbit receives branches from the upper part of the face and head. The second branch, which is evidently analogous to the superficial facial trunk in *Scorpænichthys*, is represented as following along under the suborbital bones and collecting numerous branches from the surface of the cheeks, of which the inferior maxillary vessel is the largest; this is said to run along in front of the preopercle from which it receives several branches. Hyrtl (7, p. 236) describes a swelling of the jugular at the entrance of the optic nerve into the orbit that is in communication with a similar bulb on the opposite side as the *sinus ophthalmicus* (Fig. 8, *d*), and this sinus he thinks receives the lymph from the head. In a previous paper (2) a similar sinus-like vessel was described as crossing the eye muscle canal and connecting the 2 internal jugular veins; but with *Ophiodon* there is no marked swelling of the jugulars at the junction with the connecting vessel, which is evidently nothing more than a venous sinus. Stannius (24, p. 254) claims that the connection of the head and trunk lymphatics has not yet been made clear.

Superficial facial lymphatic trunk (Figs. 4 and 5, *S.Fac.-L. V.*). — With *Scorpænichthys* this trunk has its origin in the region of the first suborbital bone from a dorsal and a ventral fork; the dorsal branch comes from the snout and the space surrounding the nasal sac; while the ventral branch follows along above and behind the maxilla. After uniting the common stem crosses the orbit between the adductor muscle of the palatine arch and the upper and inner edge of the chain of suborbital bones, or suborbital stay as it is in this species. Upon reaching the posterior end of the orbit it crosses over the facialis-mandibularis nerve and vein, and after passing across the lateral surface of the proötic process unites with the jugular papilla of the cephalic sinus (see Figs. 4 and 5) and ultimately reaches the jugular. Numerous branches were received from the surface of the adductor mandibulæ muscles, and soon after crossing the facialis-mandibularis vein, is joined from the rear by a rather large branch, which runs along the dorsal and inner surface of the opercle. No inferior maxillary branch as described by Vogt in the salmon was noticed.

Profundus facial lymphatic trunk (Figs. 4 and 5, *P.Fac.-L. V.*).— In the last specimen dissected the course of this canal could be followed much better than in any of the others. It appears to be entirely confined to the region of the orbit. In this specimen it started from the dorsal side of the orbit, and passing ventrad across the anterior end of the orbit bifurcates at the ventro-cephalic corner of the orbit, but soon reunites. The outer or sinus portion being much the larger, extends some distance ventrad between the adductor muscles of the palatine arch and the mandible; a few branches from the adductor mandibulæ were noticed, and after uniting the common stem passes caudad across the orbit on the surface of the adductor muscle of the palatine arch, a little mesad of the facialis-maxillaris vein, but some little distance inward from the superficial facial lymphatic vessel. This trunk could be traced to a point immediately beneath the junction of the internal and external jugular veins, but no farther. Very likely it continues caudad below the jugular through the proötic process foramen and empties into the abdominal sinus. The final ending of the profundus facial lymphatic trunk could not, however, be determined.

6. LYMPHATICS OF THE HYOID ARCH.

Two distinct lymphatic canals are found running along the dorsal or anterior and the ventral or posterior edges of the arch. Of these the *posterior* or *ventral lymphatic trunk* (Figs. 3 and 4, *P.Hyo. T.*) appears to be the main stem. It traverses the lower and posterior edge of the epi- and cerato-hyals, and from between each 2 branchiostegal rays receives 1 or 2 small branches

(Fig. 3, *Hh.S.L.V.*) arising from the hyo-hyoideus superior muscles and the branchiostegal membrane. Directly behind the inter-hyal the posterior hyoidean trunk expands into a reservoir designated as the *hyoidean sinus* (Figs. 3 and 4, *Hyo.S.*). This sinus also receives the *anterior* or *dorsal hyoidean trunk* (Figs. 3 and 4, *A.Hyo.T.*), which runs along the upper and anterior edge of the epi- and cerato-hyals, and in front of the inter-hyal swells up into a sort of a sinus from which a papilla crosses the outer surface of the inter-hyal and empties into the main hyoidean sinus. At about the center of the arch quite an important branch was seen to join it from the genio-hyoideus muscle. This vessel (Figs. 2 and 3, *Gh.L.V.*) after passing along the inner ventral surface of the muscle, crosses the first and second branchiostegal rays, and at this point makes a sharp curve to cross the outer surface of the cerato-hyal and empty into the anterior hyoidean trunk. The main *hyoidean sinus* (Fig. 4, *Hyo.S.*) gradually tapers down dorsally into a papilla that empties into the cephalic sinus from below and to the rear, and ultimately reaches the jugular through it. This system of lymphatic vessels appears to have been almost entirely overlooked. The only reference found is that of Hyrtl (7, p. 237), where he represents the lymphatics from the tongue and branchiostegal rays as emptying into the lateral trunk near the cephalic sinus.

This concludes the description of the distribution of the lymphatic trunks of the head, dorsal, ventral and pectoral fins of *Scorpænichthys*, but 2 important sinuses into which they empty, and which ultimately terminate in the venous system remain to be described.

7. CEPHALIC SINUS.

With the salmon Vogt (1, p. 136) represents the cephalic sinus as being an expansion of the lateral lymphatic trunk at the cephalic end of the thorax, which lies under the clavicle and has a slit covered by a valve that leads into a vessel about the diameter of a pin head, which terminates in the sinus of Cuvier near the jugular. This sinus is said to have 3 other openings that are also defended by valves. In brief the first comes from the face, the second from the first 3 branchial arches, and the third from the fourth branchial arch, the viscera, and the body wall. Hyrtl (7) states that the lateral trunk in *Acipenser*, *Cyprinus*, *Leuciscus*, *Esox*, etc., ends in a thin-walled pear-shaped sinus situated at the side of the skull, a little behind the orbit, which empties into the jugular a little forward of the lower jaw and opercular vein. This sinus he believes is contractile upon electrical or mechanical stimulation. With the salmon and trout the lateral trunk is said after passing under the clavicle to end in a sinus that discharges itself in the sinus of the spermatic vein (Sinus der Holvenen) at its junction with the ductus of Cuvier. A valve was seen at the point of union, but no vessels were described in advance of the cephalic sinus; doubtless for reasons so fully set forth by Vogt (1), namely, that the vessels emptying into this sinus were all guarded by valves, and the injection mass would naturally find its way into the venous system. With *Perca lucioperca*, *Tinca chrysitis* and *Cottus gobio* both points of union were noticed. Stannius (24, p. 254) speaks of the lymphatics from the head, gills, and trunk as uniting in a sinus that emptied into the truncus transversus (precava) near the jugular, and in a footnote states that this communication was noted by Monro (14) and Hewson (5). Milne-Edwards (16, p. 475) following Hyrtl says that in the pike, roach, grudgeon, barb and sturgeon, the lateral trunk is prolonged into the head and terminates at the base of the cranium into a sinus that empties into the jugular through a transverse canal. While in the salmon, cod, rays and sharks he describes the lateral vessels as opening into a pair of cervical sinuses, which descend behind the center of the scapula to unite in the median line at a point where the abdominal sinus joins them, and each of these scapular reservoirs is said to communicate with the ductus Cuvieri through an orifice protected by valves. Also with *Perca lucioperca* and *Cottus Gobio* 2 modes of communication with the venous system are vaguely mentioned. Trois's description in *Lophius* (28, p. 8) of the termination of the 2 lateral lymphatic vessels in the cervical or cephalic sinuses and their union with the abdominal sinus is almost identical with the descriptions given by Hyrtl and Milne-Edwards, except that no connection is noted with the venous system. According to Sappey (25) there are no cephalic sinuses in the carp or the pike. He states that both the lateral and myelonal or superior longitudinal spinal lymphatic trunks empty directly into the jugular, and with the Pleuronectidæ the inferior spinal or longitudinal hæmal trunk likewise terminates in the jugular, while the ventral trunk empties directly into the ductus Cuvieri. No other vessels were mentioned from the head region, doubtless for the reasons given above. Hopkins represents the lateral lymphatic trunk of *Amia* (8, p. 371) as passing under the clavicle and opening into a cephalic sinus at the base of the cranium. This sinus is described as receiving the pericardial sinus from below; its opening into the jugular is said to be about 1 cm. cephalad and a little ventrad of the dorsal end of the clavicle, and the orifice is guarded by a valve opening into the vein.

Possibly it might simplify matters somewhat to classify the cephalic sinuses and their connections described in the previous paragraph under 5 different heads. *First*, in *Acipenser*, *Cyprinus Leuciscus*, *Esox*, etc., the lateral trunk after passing under the pectoral arch follows the ramus lateralis vagi to the base of the skull, and there expands into a cephalic sinus that empties into the jugular. *Second*, with *Lophius*, the salmon, trout, ray, and shark the lateral trunk immediately after passing under the shoulder-girdle discharges itself in a cervical or cephalic sinus that empties into the precava, and which according to Vogt in the salmon receives other trunks from the face and the branchial arches. *Third*, midway between these two extremes comes *Amia* with a lateral trunk which after passing under the clavicle terminates in a cephalic sinus, that also receives the pericardial sinus, and which ultimately empties into the jugular instead of the precava. *Fourth*, *Perca*, *Tinca*, and *Cottus* are vaguely described as having two communications with the venous system; probably the jugular and precava connections are the ones referred to. *Fifth*, with the carp, pike and flatfish there are said to be no cephalic sinuses, the main lymphatic trunks emptying directly into the jugular and precava.

What is designated as the *cephalic sinus* in *Scorpænichthys* (Figs. 4 and 5, *Ceph.S.*) does not fit very well into any of these classes and seems to constitute one of its own. Here this sinus is a sort of stomach-shaped reservoir situated between the hyomandibular bone and the first internal branchial levator muscle, which would make it nearly opposite and a little below the level of the cerebrum and the optic lobes. Its cephalic dorsal corner gradually tapers down into a papilla, which passes inward and empties into the jugular directly behind the proötic process. At this point the jugular itself expands into a sort of reservoir before greatly diminishing in caliber to pass through the foramen formed by the proötic bone and its process. In a large uninjected specimen of *Ophiodon* from which a portion of the dorsal wall of the jugular had been removed the orifice could be distinctly seen from the inside of the vein. It pierced the ventro-lateral wall a little behind the proötic process, and was guarded by a strong valve that opened into the vein. This valve was attached dorsad, but was free three fourths of the way around. As the cephalic sinus papilla passed behind the proötic process to empty into the jugular it recieves the superficial facial trunk. In the posterior ventral corner of the cephalic sinus there is a second opening into which a prolongation of the hyoidean sinus enters. A third opening remains to be noted in the posterior dorsal corner, which is in connection with a lateral papilla from a sinus at the cephalic end of the cranial lymphatic trunk (Figs. 4 and 5, *S*). As previously stated this sinus corresponds in position to the cephalic sinus described and figured by Hyrtl in *Leuciscus*, however, in *Scorpænichthys* this sinus does not empty directly into the venous system; anteriorly it tapers rapidly down into a papilla that passes ventrad between the cephalic sinus papilla and the first internal branchial levator muscle to communicate with the cephalic end of the abdominal sinus, but in no case was any direct connection noticed between it and the cephalic sinus, the cephalic sinus papilla, or the jugular vein. As stated above the connection of this sinus with the cephalic sinus comes from its lateral wall. Sinus *S* in *Scorpænichthys* (Figs. 4 and 5) is therefore to be regarded as simply an expansion of the cranial lymphatic trunk; a trunk that is formed by the union of the lateral and myelonal canals.

8. PERICARDIAL SINUSES.

Strange to say so far as could be determined Hopkins (8, p. 372–3) is the only one to describe such a sinus; evidently it is absent in the other species studied or else it has been overlooked. The ventral lymphatic trunk in *Amia* is represented as branching at the level of the heart; each fork running between the pericardium and the tough fibrous partition separating the pericardial from the abdominal cavity, is said to merge into large pericardial sinuses that communicate with the sinuses of the lateral trunk (cephalic sinuses). With *Scorpænichthys* this is a very large and extremely important sinus, and appears to be made up of several divisions or sub-reservoirs, which have for convenience been designated as the main pericardial, posterior, and ventral pericardial sinuses.

One of the *main pericardial sinuses* (Figs. 4, 6, 9 and 10, *Per.S.*) is perhaps best shown in Fig. 6, which is drawn from a very large specimen that was well injected and hardened in formalin. It is a retort-shaped reservoir situated directly behind the precava or ductus of Cuvier. Its dorsal stem crosses the corresponding lobe of the kidney to unite with the main lateral trunk. In this specimen a branch was given off caudad at the base of the kidney which anastomosed with a branch of the pectoral sinus that emptied into the abdominal sinus. In no other specimen was this connection noticed, but a little below this level and in front there is always some communication with the abdominal sinus. Here a much larger branch is given off cephalad (Figs. 4 and 6) which soon expands into 3 large divisions (Fig. 6; *a*, *b* and *c*). The most anterior one (*a*) passes cephalad to terminate in the abdominal sinus directly behind the precava. The middle one (*b*), which is the largest of the 3, is a blind sac that extends ventrad directly behind the precava and rests on the dorsal surface of the sinus venosus. Without carefully dissecting out sinus (*b*) it always has the appearance of emptying into the sinus venosus. I have, however, carefully dissected out this sinus in many specimens to make certain that there was no communication with the venous system here, and have satisfied myself in every case that this is simply a blind sac. The third division (*c*) is merely a much smaller blind sac, lying behind (*b*). At about this level the pericardial sinus receives a small lymphatic vessel from the side, which comes from the center of the clavicle (Figs. 4 and 6, *C.L.V.*). In this region it is important to avoid confusing the external subclavian and anterior gastric or œsophagus veins (Fig. 6, *E.Sub.V.* and *A.Gas.V.*) with the lymphatics. The external subclavian vein crosses over the pericardial sinus and its divisions (*a*, *b* and *c*) to discharge itself in the precava; while the anterior gastric veins pass under the pericardial sinus, but over its divisions (*a*, *b* and *c*) and likewise empty into the precava. There is always quite a prominence in the neighborhood of the anterior ventral corner of the pericardial sinus which extends outward and forward some little distance between the external and internal pharyngo-clavicularis muscles.

From a lateral view what appears to be a separate *posterior pericardial sinus* (Figs. 4 and 6, *Per.S.*$_{(1)}$) emptying into the main pericardial sinus is shown in a ventral view (Figs. 9 and 10, *Per.S.*$_{(1)}$) to be nothing more than a posterior continuation of the main pericardial sinus. Each of these so-called posterior pericardial sinuses or posterior continuations of the main pericardial sinuses passes at first ventrad behind the sinus venosus and ventricle, being separated from them only by the pericardium, and when the posterior ventral corner of the ventricle is reached curves backward at nearly right angles. At this point in about half of the specimens a connecting branch (Fig. 6 and 10, *X*) was given off cephalad to anastomose with a papilla of the ventral pericardial sinus (Figs. 6 and 10, *P.V.Per.S.*) that communicates with the main pericardial sinus. In an equal number of specimens connecting vessel (*X*) was absent (see Figs. 4 and 9), and possibly it should be noted that in these specimens the ventral pericardial sinus papilla always followed very close to the posterior portion of the main pericardial sinus. Both of the posterior pericardial sinuses or posterior portions of the main pericardial sinuses continue backward some little distance, gradually increasing in size as they approach one another, until finally they come into contact, but do not anastomose. Both of them end some little distance in advance of the ventral fins, and either may receive the profundus ventral lymphatic trunk.

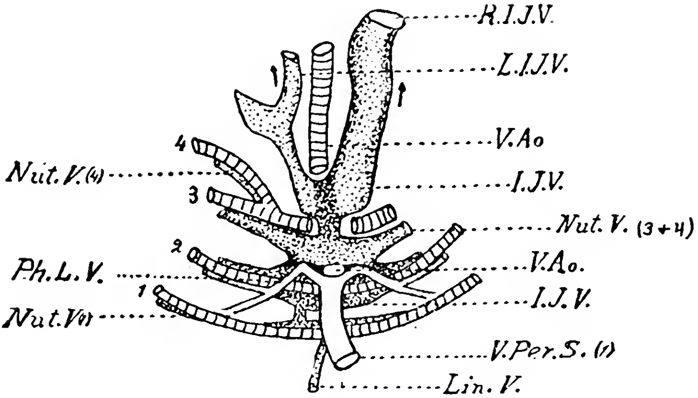

FIG. 7. Shows the branching of the ventral pericardial sinus to the pharynx region, especially to the bases of the first and second branchial arches and the thyroid gland. The anterior ventral pericardial sinus has been cut and turned forward from its natural position. Small *Scorpænichthys*. Natural size.

A list of the abbreviations used in text-figs. 7 to 10 will be found in a general list, p. 87, under 13.

With *Scorpænichthys* there is always a distinct and very important *ventral pericardial sinus* (Figs. 3, 4, 6, 7, 9 and 10, *V.Per.S.*). Since there is always a marked depression in the region of the bulbus arteriosus this sinus might be said to consist of an anterior and a posterior portion. The posterior portion of this sinus (Figs. 3, 4, 6, 9 and 10, *V.Per.S.*) is a somewhat irregularly-shaped reservoir situated below the anterior end of the ventricle and the bulbus arteriosus. Its 2 posterior dorsal corners are prolonged across the posterior half of the ventricle as papillæ (Figs. 4, 6, 9 and 10, *P.V.Per.S.*), which communicate with the anterior ventral corners of the corresponding pericardial sinuses. Between these 2 papillæ the ventral longitudinal lymphatic trunk curves around the cephalic ends of the pelvic bones, and empties in the median line into the posterior end of the ventral sinus. Ventrally this sinus bifurcates and soon forms 2 conspicuous reservoirs situated on the ventral surface of the clavicles (see Fig. 3), and into these sinuses the ventral prolongations of the pectoral sinuses terminate. The anterior dorsal corner of the posterior ventral pericardial sinus is continuous with the anterior portion of the ventral pericardial sinus.

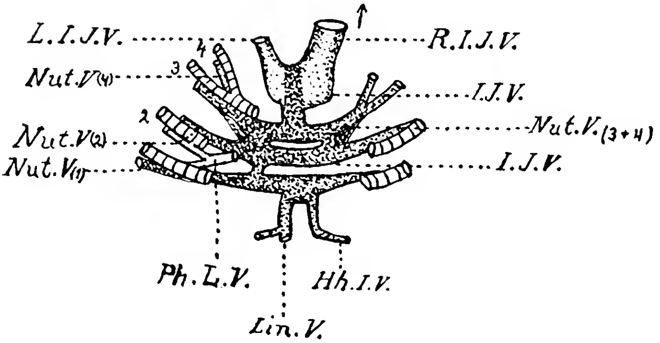

FIG. 8. Deeper dissection of the same specimen as Fig. 7 to show the origin of the inferior jugular from the nutrient branchial veins and its course above the ventral aorta.

This sinus (Figs. 3, 4, 6, 7, 9 and 10, *V.Per.S.*$_{(1)}$) passes cephalad along the lower side of the ventral aorta, and when midway between the combined trunks of the third and fourth afferent branchial vessels and the second pair of afferent branchial vessels, it divides; each fork, designated as the *pharynx lymphatic vessel* (Figs. 3, 6, 7 and 8, *Ph.L. V.*), passes at first obliquely across the thyroid gland and the second afferent branchial trunk. Here it bifurcates, the anterior fork going along the side of the thyroid to the base of the first branchial arch; while the other stem continues along between the afferent and efferent branchial vessels of the second arch and shortly sends off a branch which traverses along behind the afferent branchial trunk. Neither of these branches could be traced farther than to the origin of the first branchial filaments. They evidently only receive lymph from the connective tissue lining the base of the second branchial arch and the thyroid gland. Since no similar branch was found on any of the other branchial arches this fork has been designated as a pharynx rather than a branchial vessel. In well-injected specimens as is shown by (Fig. 6, *Thyr.L. V.*, and Fig. 3) there was found an additional stem emptying into the ventral pericardial sinus between the 2 pharynx vessels. It apparently arises solely from the thyroid gland, and it may have some direct connection with some of the branches of the inferior jugular that run along the dorsal surface of the gland.

During the early stages of this work I had no inference that either the pharynx or the thyroid lymphatic vessels had any communication with the inferior jugular. Later on a specimen was dissected in which the entire venous system, with the single exception of the jugular and its branches, was found to be well filled from an injection of the myelonal lymphatic trunk. This of course led me to believe that there must be another communication with the venous system in the head region other than the cephalic sinus, and most careful search was made of all the lymphatic vessels surrounding the jugular, precava, sinus venosus, and especially lobe (*b*) of the pericardial sinus; still no connection whatever was found. Also every opening into these veins was accounted for. As the work progressed the lymphatics of several heads was injected from the ventral lymphatic trunk, and as a rule in these specimens the pericardial lymphatic sinuses, the thyroid, and pharynx lymphatic vessels were well filled, and the mass entered the nutrient branchial and the inferior jugular veins, but rarely extended in the inferior jugular as far back as the sinus venosus; it would first run out some of the cut lymphatic vessels that were severed in removing the head. In one specimen I first injected the venous system from one of the hepatic veins with a blue mass, and after allowing the mass to partially solidify, injected the lymphatics with a yellow mass from the ventral lymphatic trunk. The lymphatic sinuses, pharynx, and thyroid lymphatic vessels were found to be well filled with the yellow mass, as was also the nutrient branchial veins, and the yellow mass had forced back the blue a short distance in the inferior jugular vein. Upon further dissection the entire venous system, including the jugular and the dorsal nutrient branchial veins, was found to be filled with the blue mass, indicating of course that a connection must exist between either the pharynx or the thyroid lymphatic vessel and one of the branches of the inferior jugular. By dissection I have been unable to find the exact point of union, but am inclined to believe that the thyroid vessel is the one that communicates with the venous system. For a short distance each pharynx lymphatic vessel runs along the ventral surface of the combined trunk of the third and fourth nutrient branchial veins, and at this point several dorsal branches are given off, but they apparently go to the posterior end of the thyroid. The largest of them, however, leads into the sinus situated at the base of the second branchial arch.

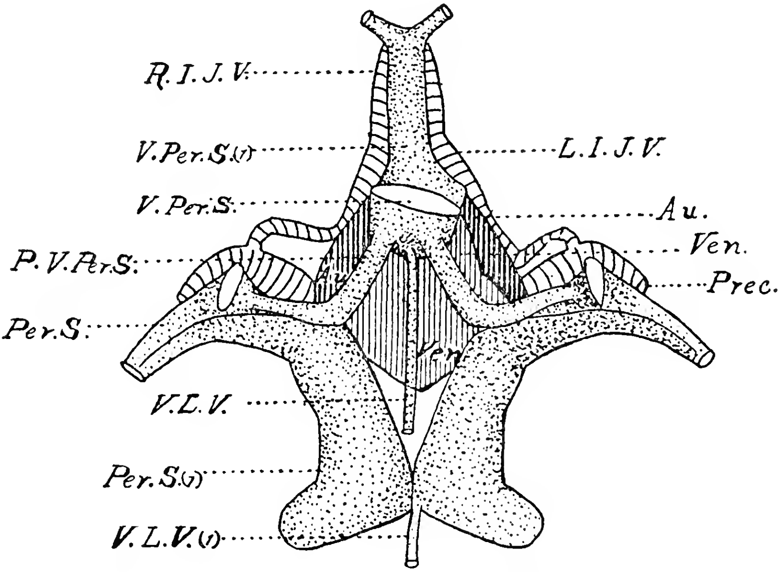

FIG. 9. Ventral view of the large pericardial lymphatic sinuses surrounding the heart. Only a portion of the ventral pericardial sinus is figured. In this specimen the two interlinking arms between the ventral pericardial and the pericardial sinuses had no additional connection with the posterior portion of the pericardial sinus as it has in some specimens, shown in Fig. 10. Medium large *Scorpænichthys*. Natural size.

It is of interest in this connection to again note that Vogt (1, p. 138) in the salmon describes one of the 2 dorsal lymphatic trunks of each branchial arch, which terminates in the cephalic sinus, as being prolonged ventrad and anastomosing with the veine de Duvernoy (inferior jugular), and from Vogt's description it is perfectly clear that he has not confused the nutrient branchial veins for lymphatics, otherwise they would terminate in the jugular and not in the lymphatic trunk that emptied into the cephalic sinus. It will be seen at a glance that this connection of the dorsal lymphatic trunks with the inferior jugular described by Vogt in the salmon is very different from the somewhat hypothetical union described above, notwithstanding that both modes of communication occur in the same vicinity.

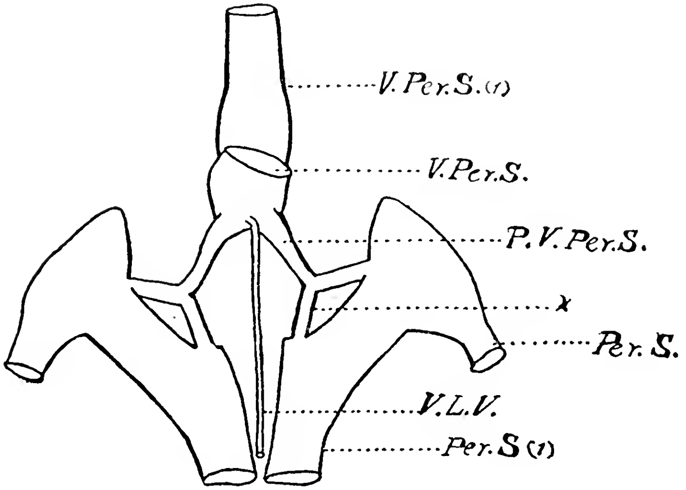

Fig. 10. Same view of another specimen as Fig. 9 in which the interlinking arms of the pericardial and ventral pericardial sinuses had an additional connection (X) with the posterior portion of the pericardial sinus. Medium size *Scorpænichthys*. Natural size.

Possibly at this point a note should be made in connection with the inferior jugular and its branches. In *Scorpænichthys* 2 inferior jugulars empty into the sinus venosus, a large *right* and a much smaller *left inferior jugular* (Figs. 3, 6, 7 and 8, *R.* and *L. I. J. V.*); both of which pass along, above and to the side of the ventral aorta, and unite in a common stem directly behind the common trunks of the third and fourth afferent branchial vessels. Perhaps it would have been more accurate to have conversely stated this arrangement by saying that the common stem of the inferior jugular bifurcated behind the common trunks of the third and fourth afferent branchial vessels, and each fork after passing along the side of the ventral aorta emptied into the sinus venosus. Following the common stem of the inferior jugular cephalad it will be seen from (Figs. 6, 7 and 8) that it may branch and each fork receive first the combined sinus-like trunk of the third and fourth nutrient branchial veins and then in succession the second and first nutrient branchial veins as shown by Fig. 8, *Nut. V.*$_{(3,4)}$, etc.) or as was noticed in other specimens may expand into a broad sinus between the second and third branchial arches, which in like manner collects the nutrient branchial veins. In either case the anterior part of the inferior jugular in spreading out over the thyroid gland took on more the appearance of a lymphatic trunk than it did a vein.

9. GENERAL CONSIDERATIONS AND SUMMARY.

Scorpænichthys has as complete a lymphatic system as is to be found in any vertebrate; in general wherever there is connective tissue there are lymphatics. As in the higher Vertebrata there are distinct superficial and profundus systems. In the trunk region the main lymphatic canals are longitudinal trunks that terminate caudad in the caudal vein, and cephalad empty in one way or another into the cephalic and ventral pericardial sinuses, which ultimately reach the jugular and apparently the inferior jugular veins. These sinuses are simply non-contractile reservoirs in no way comparable to the lymphatic hearts of the Batrachia. In the region covered by this paper no valves were found except at the orifice of the cephalic sinus papilla in the jugular.

1. The lateral lymphatic canal in the trunk region very closely resembles the descriptions already given for other species. Dorsal and ventral intermuscular or transverse branches were regularly received; they arose from a network in the connective tissue of the myotomes and skin, and anastomosed above with the dorsal lymphatic trunk and below with the ventral trunk. In the anterior region of the trunk there are dorsal and ventral lateral lymphatic vessels, which are merely a series of longitudinal cross-branches, lying above and below the main lateral trunk, but which give additional support

to Trois' statement that similar longitudinal trunks in *Uranoscopus* are doubtless of only secondary importance. Before passing under the shoulder-girdle the lateral trunk receives a large pectoral sinus that collects the lymph from the pectoral fin region, and from here on its course and connections are very different from what has been described for any other fish. Following the first rib inward it receives a communication from the pericardial sinus, and opposite the atlas unites with a fork of the myelonal trunk in what is designated as the occipital sinus, from which the cranial trunk has its source.

2. A large and very important myelonal or superior longitudinal spinal lymphatic trunk is found traversing the spinal canal above the cord, from which it is separated by a septum. The neural or interspinal branches noted by previous workers are very conspicuous in *Scorpænichthys;* all of which anastomose above with the dorsal lymphatic trunks, and many of them are prolonged ventrally to connect with the abdominal sinus or the longitudinal hæmal lymphatic trunk. Evidently this trunk is absent in many species or else it has been overlooked. So far as could be ascertained Sappey is the only one to give it a cephalic ending; he represents it with the pike and carp as curving outward at the first cervical vertebra and emptying directly into the jugular. In *Scorpænichthys* the myelonal trunk bifurcates directly behind the skull; each fork passing outward between the skull and atlas unites with the lateral lymphatic trunk in forming the cranial lymphatic trunk, and as stated above the occipital sinus marks the point of union.

3. The cranial lymphatic trunk follows along the ventrolateral wall of the skull above the jugular, and shortly before the proötic process is reached dilates into sinus (*s*), which opens laterally into the cephalic sinus and anteriorly into the abdominal sinus.

4. Trois' description of the dorsal lymphatic trunk in *Lophius* and *Uranoscopus* will answer equally well for *Scorpænichthys.* In the fin region it splits up into 3 parallel vessels, 2 of which run along at the side and base of the rays and the third is a median trunk that traverses the basal canal of the rays; the latter trunk receives branches from the fin membrane, there

being 2 for each spine or ray, and sends outward numerous cross-branches to the lateral trunks; the two lateral dorsal trunks communicate with the lateral lymphatic trunk through the intermuscular or transverse vessels, and with the myelonal trunk through the neural or interspinal vessels. The first neural vessel passes between the skull and the first neural spine and empties into the cranial lymphatic trunk.

5. With *Scorpænichthys* the ventral lymphatic trunk in front of the anal fin is not a paired vessel as described by Trois. Between the ventrals it expands into a large heart-shaped sinus into which the ventral fin sinuses are discharged. They receive the lymph from the ventral fins and are prolonged between the body myotomes and the ventral fin musculature to end in the ventral lymphatic trunk. Two other branches have their origin from between the superficial and profundus abductor muscles of the ventral fin. In the median line the ventral lymphatic trunk penetrates between the superficial and profundus abductor muscles, and following along the lower side of the pelvics terminates in the posterior end of the ventral pericardial sinus. The ventral intermuscular or transverse vessels connect this trunk with the lateral lymphatic trunk.

6. A profundus ventral lymphatic trunk was observed running along the inner surface of the body musculature parallel with the main ventral lymphatic trunk. Connecting branches were noticed between the two in the region of the ventral fins, and it was also in communication with the abdominal sinus through the intercostal vessels; while anteriorly it emptied into one of the pericardial sinuses.

7. A large pectoral sinus is placed at the base of each pectoral; dorsad it unites the lateral trunk and the abdominal sinus, and ventrad it is prolonged to communicate with the ventral pericardial sinus. Into the pectoral sinus is discharged a common trunk formed from the union of the external and internal pectoral sinuses. These sinuses run along at the base of the fin and receive connecting branches from the median pectoral sinus, which traverses the basal canal of the rays and collects the lymph from the fin. Trois is the only one to describe the pectoral lymphatics, and he represents the main trunks in *Lophius*

and *Uranoscopus* as emptying directly into the cephalic sinus.

8. In *Scorpænichthys* there are distinct superficial and profundis facial lymphatic systems. The superficial system arises in the snout region, follows the upper inner surface of the suborbital stay through the orbit, and after receiving a branch from the opercular region joins the jugular papilla of the cephalic sinus directly behind the proötic process; while the profundus system takes its origin from a large orbital sinus, and could be traced to a point directly in front of the foramen formed by the proötic process with the skull, but no further. Very likely it passes through this foramen below the jugular and empties into the abdominal sinus. Vogt describes somewhat similar vessels in the salmon as uniting in a common trunk that emptied into the cephalic sinus, which is located under the clavicle.

9. There are in *Scorpænichthys* 2 lymphatic canals running along either side of the hyoid arch. The ventral or posterior one is evidently the main trunk, since it collects the lymph from the branchiostegal region and expands into a sinus behind the interhyal, which receives the dorsal or anterior trunk. This hyoidean sinus tapers down dorsad into a papilla that empties into the cephalic sinus.

10. Strange to say, my dissections have revealed no lymphatic vessels coming from the cranial cavity; these doubtless exist, but the injection mass has failed to reach them. From the arrangement of the blood vessels one would expect to find one of the trunks passing out of the cranial cavity near the V and VII complex, and joining one of the large lymphatic sinuses attached to the side of the skull. Very likely there is a posterior trunk, which in some way or another unites with the myelonal trunk. In some previous work on the vascular system the myelonal trunk of a large *Ophiodon* was injected, and upon opening up the cranial cavity all of the semi-circular canals of the ear were found to be filled with injecting mass.

11. An extremely important vesicle in *Scorpænichthys* is the abdominal sinus, which is situated directly below the kidney, and forking with it is prolonged cephalad to the orbit. It receives the lymphatics from the reproductive organs, the inter-

costal vessels, the cœliaco-mesenteric trunk from the viscera, the dorsal branchial sinus which could only be traced to the arches, and more than likely the lymphatic vessels from the kidney and the profundus facial trunk; in addition it has interlinking branches with the myelonal trunk, and has communications with the pectoral sinus, the pericardial sinus, and the cranial trunk.

12. What is designated as the cephalic sinus in *Scorpænichthys* may be only analogous to the similar sinus of other fishes that performs the same function, but which has entirely different connections and very different modes of termination. With *Scorpænichthys* this is a non-contractile stomach-shaped reservoir situated beneath or mesad to the upper portion of the hyomandibular. Dorsad it tapers down into a sort of a papilla that empties into the jugular directly behind the proötic process. The orifice of this papilla is guarded by a valve, which opens into the vein. In one way or another the lymph from the entire body can reach this sinus; the superficial facial lymphatic trunk unites with its jugular papilla; the hyoidean sinus empties into it from below; and a connecting branch from sinus (*s*) of the cranial trunk, which is also in direct communication with the abdominal sinus, is received from above and behind.

13. The pericardial sinuses, which surround the heart in *Scorpænichthys* have been subdivided into 3 distinct reservoirs. What has been designated as the main pericardial sinus is situated between the precava and the shoulder-girdle. It is in connection above with the lateral lymphatic trunk, and sends off a vecicle anteriorly that soon divides into 3 lobes, the most anterior being in communication with the abdominal sinus and the other 2 ending blindly. Some little distance below this level the pericardial sinus is continuous posteriorly into what has been described as the posterior pericardial sinus, which either ends blindly or receives the profundus ventral lymphatic trunk. In addition to all these connections it also receives from below and in front a prolongation of the ventral pericardial sinus, a sinus of considerable importance, which can always be separated into a posterior and an anterior portion. The former receives the ventral lymphatic trunk and the ventral prolongations of the

pectoral sinuses; while the latter branches anteriorly into what has been designated as the thyroid and pharynx vessels, one of the other of which, undoubtedly communicate with the inferior jugular. As was noted for the cephalic sinus, the lymph from the entire body can be discharged in one way or another into the ventral pericardial sinus, and doubtless ultimately into the inferior jugular.

10. SYNONYMY.

Abdominal sinus. — Desc. as 2 parallel trunks following the aorta (?), Vogt (1); Vasi longitudinali spinali inferiori (?), Trois (28); Le tronc sous-vertébral (?), Sappey (25); Third abdominal sinus (?), Hopkins (8).

Branchial lymphatic sinuses. — Canaux muciques des branchies and Canaux muciques du 4me. arc branchial, Vogt (1); Linfatici delle branchie, Trois (28).

Cephalic sinus. — Kopf-Sinus, Hyrtl (7); Desc. as spacious reservoir lying under the clavicle, Vogt (1); Desc. Stannius (24) and Milne-Edwards (16); Seni cefalici o cervicali, Trois (28); Cephalic sinus, Hopkins (8).

Dorsal fin lymphatic vessels. — Tronchetti linfatici delle pinne, Trois (31); Réseau cutané de la nageoire dorsale, Sappey (25).

Dorsal lymphatic trunk. — Untergeordnetere oberflächliche Längsstämme, Stannius (24); Desc. Milne-Edwards (16); Tronco linfatico longitudinale dorsale, Trois (28); Les troncs lymphatiques dorsaux, Sappey (25); Dorsal lymphatic trunk, Hopkins (8).

Intermuscular or *transverse lymphatic vessels.* — Seitenast-Paare, Hyrtl (7); Desc. Stannius (24), Milne-Edwards (16), and Hopkins (8); Tronchetti trasversali, Trois (28); Troncules qui s'étendent au tronc abdominal and Troncules qui relient le tronc latéral au tronc abdominal, Sappey (25).

Lateral lymphatic trunk. — Seitengefässe, Hyrtl (7); Grand canal latéral and des canaux muciques, Vogt (1); Seitenlangsstämme, Stannius (24); Les troncs latéraux, Milne-Edwards (16) and Sappey (25); Tronchi linfatici laterali, Trois (28); Lateral lymphatic trunk, Hopkins (8).

Secondary lateral lymphatic trunks. — Probably one of Stannius' dorsal lymphatic trunks; Desc. Milne-Edwards in Silurus; Tronchetti linfatici laterali accessorj (29).

Median pectoral fin sinus. — Vaso collettore profondo (?), Trois (28).

Myelonial or *superior longitudinal spinal lymphatic trunk.* — Wassergefässe im Rückenmarks-Canal, Hyrtl (7); Längsstammes des Canalis spinalis, Stannius (24); Longitudinale spinale superiore (28) and Tronco linfatico sopravertebrale (31), Trois; Tronc lymphatique sus-vertébral ou intrarachidien, Sappey (25).

Neural or *interspinal lymphatic vessels.* — Desc. Hyrtl, Stannius, and Milne-Edwards; Vasi interspinosi, Trois (28); Troncules lymphatiques qui viennent se jeter dans le grand tronc sus-vertébral, Sappey (25).

Pericardial sinus. — Pericardial sinus, Hopkins (8).

Profundus facial lymphatic trunk. — Desc. Vogt (1).

Pectoral sinus. — Desc. Hyrtl and Stannius; Trois (28) desc. three pectoral sinuses emptying into cephalic sinus; Pectoral sinus, Hopkins (8).

Superficial facial lymphatic trunk. — Desc. Vogt (1).

Ventral fin lymphatic sinuses. — Desc. Hyrtl, Trois, and Sappey; Sinus at the base of the ventral fin, Hopkins (8).

Ventral or *abdominal lymphatic trunk.* — Ein unpaarer epigastrischer Längsstamm, Stannius (24); Desc. Milne-Edwards (16); Tronchi linfatici abdominali, Trois (28); Les troncs lymphatiques inférieurs ou abdominaux, Sappey (25); Ventral lymphatic vessel, Hopkins (8).

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12. DESCRIPTION OF THE FIGURES.

Scorpænichthys marmoratus.

All of the figures were drawn to a scale from injected specimens. In the colored figures the lymphatics are indicated by yellow and the veins by blue: while in the other figures the veins are cross-barred and the lymphatics are drawn in outline or stippled.

Fig. 1. Represents a general lateral view of the head region of a small *Scorpænichthys*; the skin being removed to show the superficial vessels of the body, dorsal, ventral, and pectoral fins. × ½.

Fig. 2. Ventral view of the same specimen as above. Shows the superficial vessels of the body, ventral, and pectoral fins. The left pectoral superficial adductor muscle is cut distad and turned toward the body to show the profundus trunks.

Fig. 2*a*. Is from a transverse section through a portion of the pectoral fin near its base to show the termination of the pectoral fin vessels in the pectoral fin sinus.

Fig. 3. Shows a ventral view of a deeper dissection of a small *Scorpænichthys* head. Most of the ventral musculature is removed as is also the left hyoid arch, the left branchial arches, and the left pectoral fin. The right hyoid arch is turned forward and outward and the branchiostegal rays are cut close to their bases. In this figure the ventral aorta and its branches are cross-barred with blue lines. Note especially the anterior branching of the ventral pericardial sinus to the pharynx and the thyroid gland. There is undoubtedly some communication in the region of the thyroid with a branch of the inferior jugular. × $\frac{9}{10}$.

Fig. 4. Deeper dissection of a small *Scorpænichthys* as seen from the left side. The shoulder-girdle and pectoral fin are removed, as is also a portion of the skull, suborbital stay, opercle, and the great lateral muscle. × ¾.

Fig. 5. Dorsal view of the great superficial and profundus trunks and sinuses of the right side of the head. Kidney, brain, and walls of the cranium drawn to show the topography. The entrance of the cephalic sinus into the jugular, lying in front of the VII nerve and directly behind the proötic process, is distinctly shown. Same specimen as Fig. 4. Natural size.

Fig. 6. Lymphatic trunks and sinuses in the region of the heart of a very large *Scorpænichthys* as seen from the left side. × ½.

Figs. 7 to 10 have been changed to text-figures under 8, pp. 73, 74, 76 and 77.

13. ABBREVIATIONS USED IN THE PLATE AND TEXT-FIGURES.

A or *P* prefixed to an abbreviation signifies anterior or posterior; *R* or *L*, right or left. A series is numbered from cephalad to caudad.

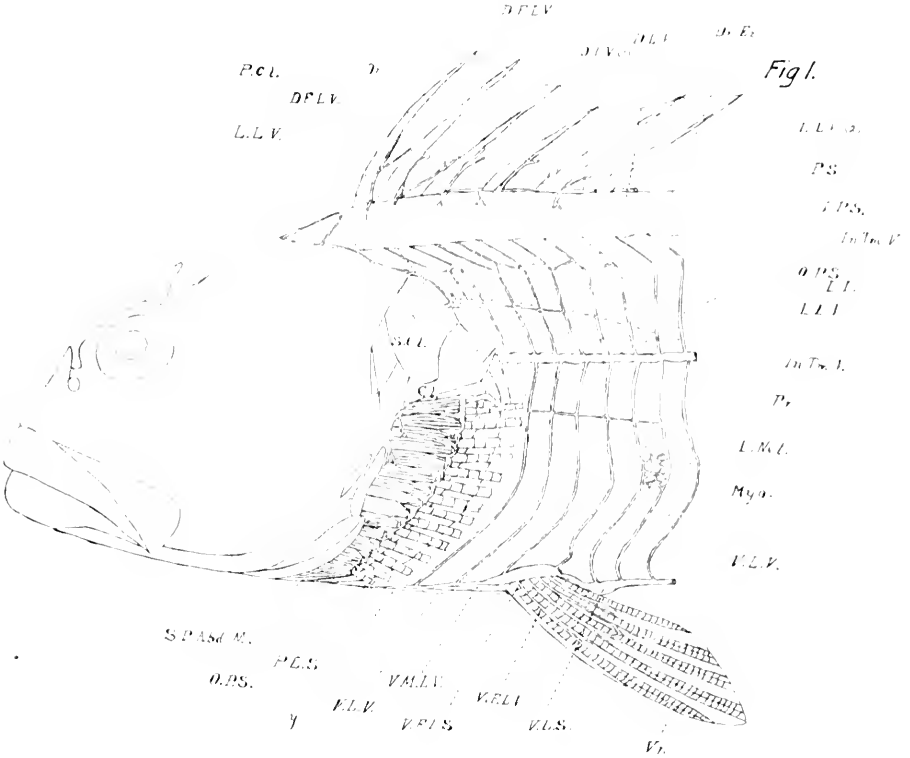
Abd.S.	Abdominal sinus.
A.Br.A.$_{(1-4)}$	Afferent branchial trunks.
Add.M.	Adductor mandibulæ.
Add.P.A.	Adductor arcus palatini.
A.Gas.V.	Anterior gastric or œsophagus veins.

A.Hyo.T.	Anterior hyoidean lymphatic trunk.
Au.	Auricle.
B.Art.	Bulbus arteriosus.
Br.	Branchiostegal rays.
Br.A.$_{(1-4)}$	Branchial arches.
Br.L.S.	Branchial or dorsal branchial lymphatic sinuses.
Car.V.	Cardinal vein.
Ceph.S.	Cephalic sinus.
Cer.	Cerebellum or epencephalon.
Cl.	Clavicle.
Cl.V.	Clavicle lymphatic vessel.
Cœ.Mes.L.V.	Cœliaco-mesenteric lymphatic trunk.
Cr.	Cranial wall.
Crb.	Cerebrum or prosencephalon.
Cr.L.V.	Cranial lymphatic trunk.
D.Dr.M.	Depressor dorsal ray muscles.
D.F.L.V.	Dorsal fin lymphatic vessels.
D.L.V.	Dorsal lymphatic trunk.
D.L.V.$_{(1)}$	Median dorsal lymphatic trunk.
Dr.	Dorsal fin rays or spines.
Dr.Ex.M.	Extrinsic muscles of the dorsal fin.
E.J.V.	External jugular vein.
E.Sub.V.	External subclavian vein.
F.Man.V.	Facialis-mandibularis vein.
F.Max.V.	Facialis-maxillaris vein.
Gh.L.V.	Genio-hyoideus lymphatic vessel.
Gh.M.	Genio-hyoideus muscle.
Gh.V.	Genio-hyoideus vein.
Hh.I.V.	Hyo-hyoideus inferior vein.
Hh.S.L.V.	Hyo-hyoideus superior lymphatic vessel.
Hh.S.M.	Hyo-hyoideus superior muscle.
Hyo.A.	Hyoid arch.
Hyo.S.	Hyoidean lymphatic sinus.
I.J.V.	Inferior jugular vein.
I.L.Br.A.M.	Internal branchial arch levators.
Im.M.	Intermandibularis muscle.
Inh.	Inter-hyal.
Intm.V.	Intermuscular or transverse lymphatic vessels.
I.P.S.	Inner pectoral fin sinus.
J.V.	Jugular vein.
L.Dr.M.	Levator dorsal ray muscles.
Lin.V.	Lingual vein.
L.L.	Lateral line canals.
L.L.V.	Lateral lymphatic trunk.
L.L.V.$_{(2)}$	Secondary lateral lymphatic trunks.
L.Net.	Network of minute lymphatic vessels.
Man.	Mandible or dentary bone.
Max.	Maxilla.
Max.V.	Maxillaris vein.

Max. V.	Truncus maxillaris trigemini or infra-orbitalis.
M.P.S.	Median pectoral fin sinus.
My.	Myelon or spinal cord.
My.L.V.	Myelonial or superior spinal longitudinal lymphatic trunk.
Myo.	Myotomes of the great lateral muscle.
Neu.L.V.	Neural or interspinal lymphatic vessels.
Neu.S.	Neural spines.
No.	Nasal opening.
Nut.V.$_{(1) \text{ to } (4)}$	Nutrient veins (1) to (4).
O.B.	Olfactory bulb or rhinencephalon.
Obl.	Oblongata or metencephalon.
Oc.S.	Occipital sinus.
O.D.M.	Obliqui dorsales muscles.
O.L.	Optic lobes or mesencephalon.
O.N.V.	Orbito-nasal vein.
Op.	Operculum or opercular bone.
O.P.S.	Outer pectoral fin sinus.
P.	Pectoral fin.
P.Cl.	Postclavicle.
P.C.V.	Connecting vessels between the median and the outer and inner pectoral fin sinuses.
Pel.	Pelvic bones.
Per.S.	Pericardial sinus.
Per.S.$_{(1)}$	Posterior pericardial sinus or posterior portion of the pericardial sinus.
P.Fac.L.V.	Profundus facial lymphatic trunk.
P.F.L.V.	Pectoral fin lymphatic vessels.
P.F.L.V.$_{(1)}$	Extra pectoral fin lymphatic vessels.
Ph.L.V.	Pharynx lymphatic vessel.
P.Hyo.T.	Posterior or ventral hyoidean lymphatic trunk.
P.P.Add.M.	Profundus pectoral adductor muscle.
Pr.	Pectoral rays.
Prec.	Precava.
Prem.	Premaxilla.
Pro.P.	Proötic process.
P.S.	Pectoral sinus.
P.V.Abd.M.	Profundus ventral abductor muscle.
P.V.Per.S.	Papilla of the ventral pericardial sinus that joins the main pericardial sinus.
R.Lat.X.	Ramus lateralis vagi.
R.My.L.V.	Right fork of the myelonal lymphatic trunk.
S.	Lymphatic sinus at the cephalic end of the cranial trunk.
S.Cl.	Supraclavicle.
S.Fac.L.V.	Superficial facial lymphatic trunk.
S.Oc.	Supraoccipital.
S.Orb.	Chain of suborbital bones or suborbital stay.
S.P.Abd.M.	Superficial pectoral abductor muscle.
S.P.Add.M.	Superficial pectoral adductor muscle.
Sp.N.	Spinal nerves.

Sub.A.	Subclavian artery.
S.V.Abd.M.	Superficial ventral abductor muscle.
S.Ven.	Sinus venosus.
Thyr.	Thyroid gland.
Thyr.L.V.	Thyroid lymphatic vessel.
V.Ao.	Ventral aorta.
Ven.	Ventricle.
Ver.$_{(1)}$	First vertebra or atlas.
V.F.L.S.	Ventral fin lymphatic sinus.
V.F.L.V.	Ventral fin lymphatic vessels.
V.F.L.V.$_{(1)}$	Auxiliary ventral fin lymphatic vessels.
V.L.S.	Ventral lymphatic sinus.
V.L.V.	Ventral or abdominal lymphatic trunk.
V.L.V.$_{(1)}$	Profundus ventral lymphatic trunk.
V.M.L.V.	Ventral fin musculature lymphatic vessel.
V.M.L.V.$_{(1)}$	Secondary ventral fin musculature lymphatic vessel.
V.Per.S.	Ventral pericardial sinus.
V.Per.S.$_{(1)}$	Anterior portion of the ventral pericardial sinus.
Vr.	Ventral fin rays.
X.	Connection between the ventral sinus papilla and the posterior part of the pericardial sinus.
Y.	Point where the ventral lymphatic trunk pierces the ventral wall to empty into the ventral pericardial sinus.
I to X.	Cranial nerves.
1 to 4.	Afferent branchial trunks 1 to 4.

Fig 1.



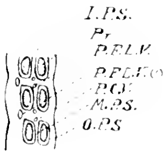


Fig 2a.

Fig. 2.

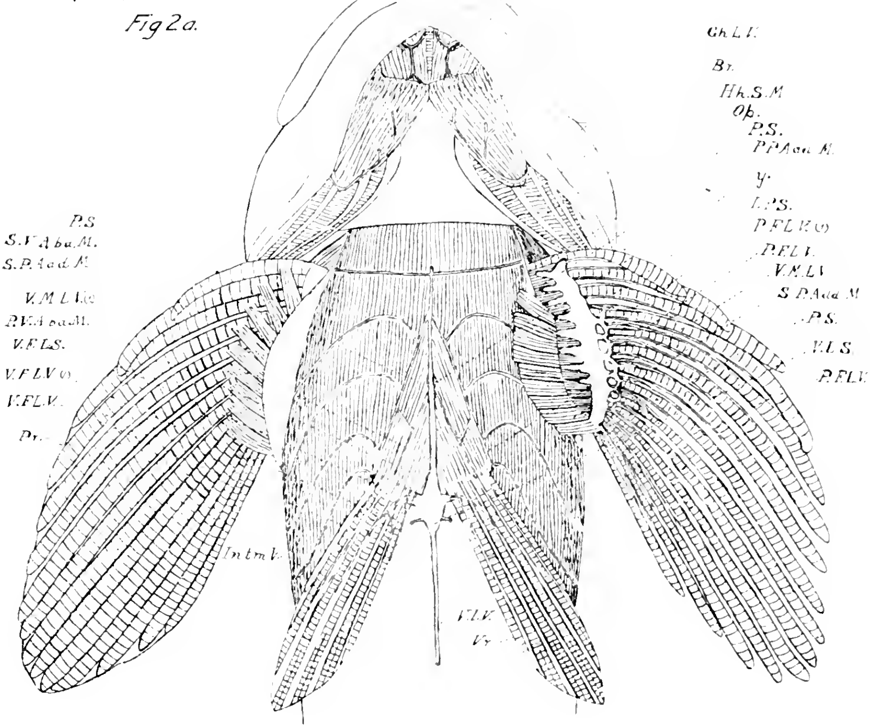


Fig. 3.

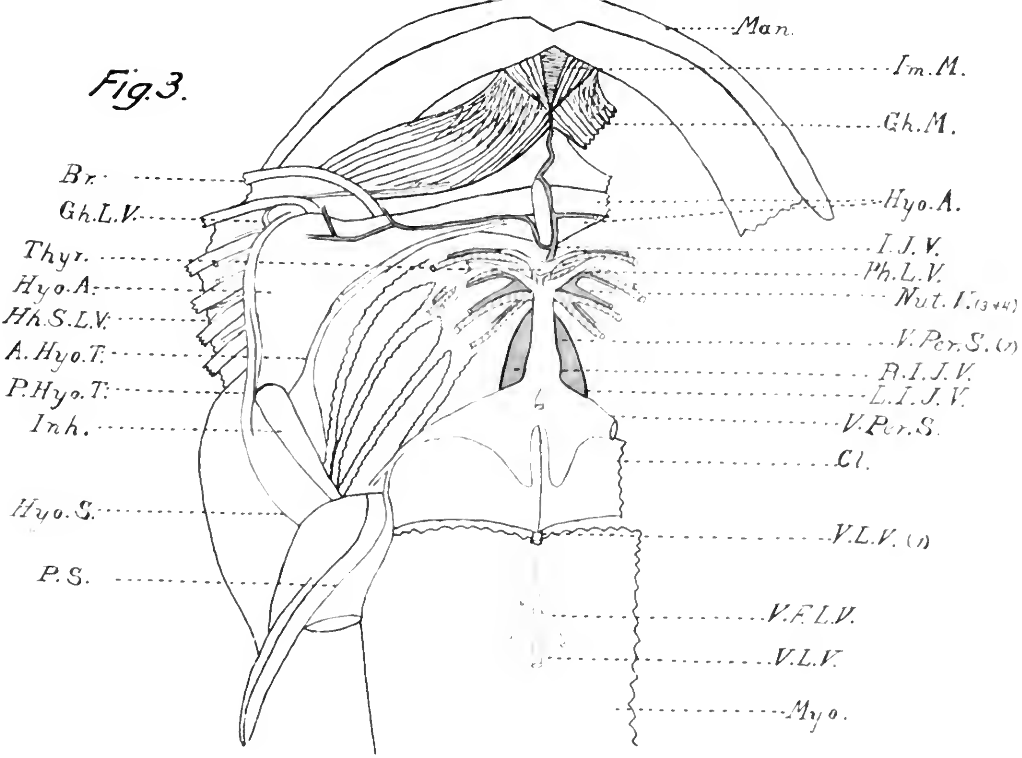
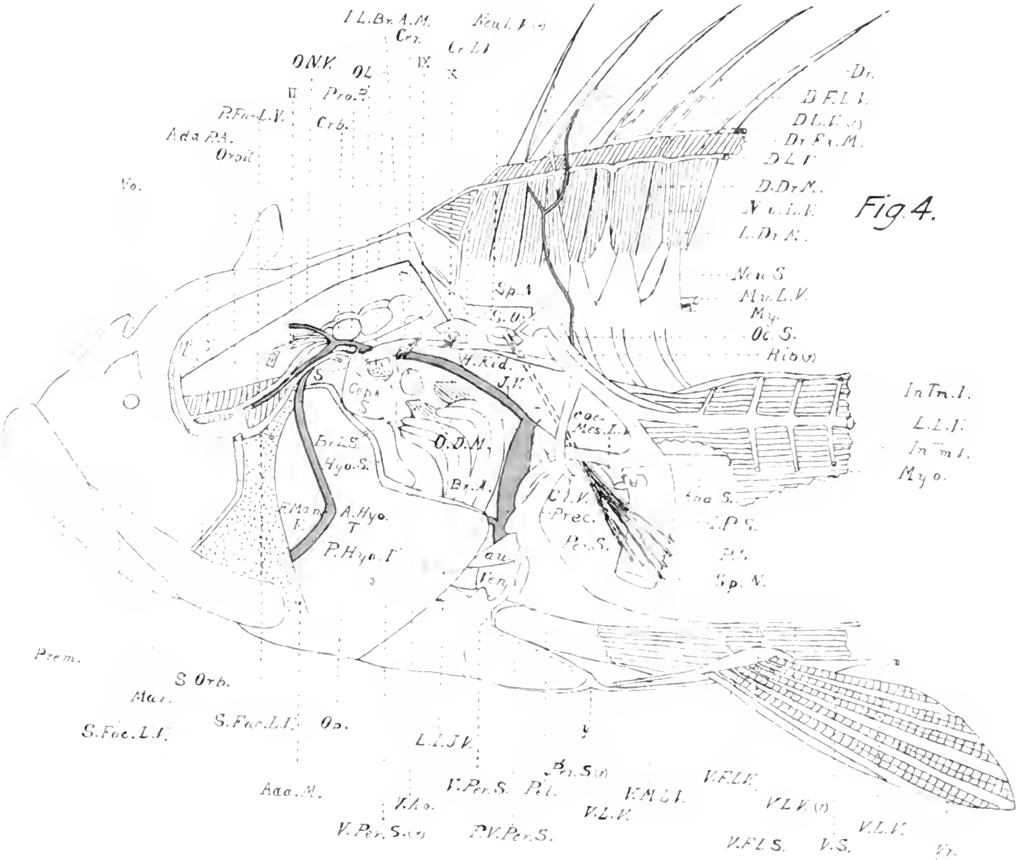

Man.
Im.M.
Gh.M.
Br.
Gh.L.V.
Hyo.A.
Thyr.
I.J.V.
Hyo.A.
Ph.L.V.
Nut.V.(3+4)
Hh.S.L.V.
V.Per.S.(?)
A.Hyo.T.
R.I.J.V.
P.Hyo.T.
L.I.J.V.
Inh.
V.Per.S.
Cl.
Hyo.S.
V.L.V.(?)
P.S.
V.F.L.V.
V.L.V.
Myo.

Fig. 4.


I.L.Br.A.M.
Neu.L.V.(?)
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IX
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Ada.P.A.
Oroil
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Dr.
D.F.L.I.
D.L.V.(?)
Dr.Fx.M.
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D.Dr.M.
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Neu.S.
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Vr.

Fig 5.

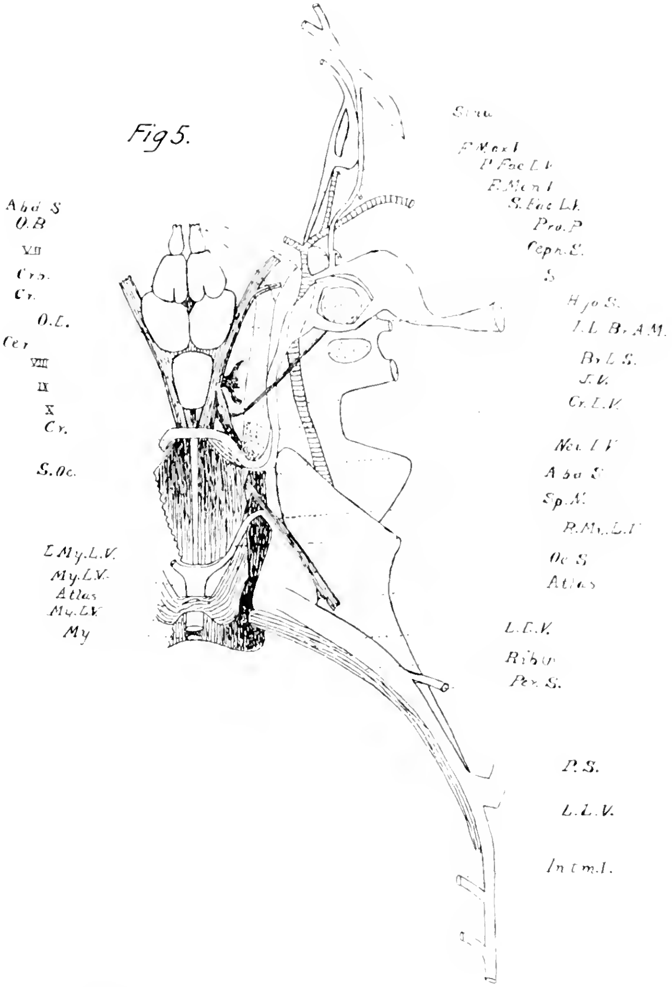
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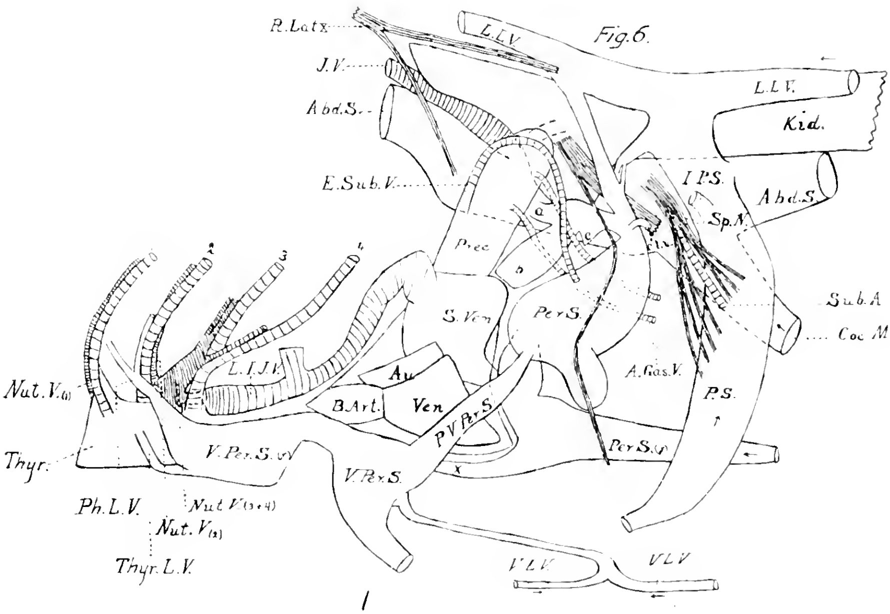
Fig.6.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B.Art.
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P.V.Per.S.
A.Gas.V.
P.S.
Nut.V.(1)
Thyr.
V.Per.S.(v)
Per.S.(v)
x
V.Per.S.
Ph.L.V.
Nut.V.(3+4)
Nut.V.(2)
Thyr.L.V.
V.L.V.
V.L.V.

I,

PROCEEDINGS

OF THE

WASHINGTON ACADEMY OF SCIENCES

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EVIDENCE BEARING ON TOOTH-CUSP DEVELOPMENT.[1]

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IN connection with the work of cataloguing the portion of the Marsh collection of Mesozoic mammals, obtained under the auspices of the U. S. Geological Survey and now deposited in the United States National Museum, I have made some discoveries of seeming importance in the form of evidence bearing on the question of tooth-cusp homologies in the mammalian molars. This evidence I wish briefly to present in the following pages, hoping it may throw some added light on the very important subject of tooth morphology.

Before proceeding, I wish to express my indebtedness to Dr. George P. Merrill for making possible the arrangements for this detailed study of material and for his encouragement in the work; to Prof. Charles Schuchert, of Yale University, for submitting to my hand the type material of the Marsh collection at New Haven; and to Prof. Henry F. Osborn of the American Museum of Natural History, for his courtesy in placing the collection of Mesozoic mammals in that institution at my disposal. My thanks are also due Mr. G. S. Miller, Jr., for his valuable aid in selecting study material from the collection of modern mammals in the National Museum and for a clear translation of Herluf Winge's paper on tooth-cusp development.

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[1] Based on a study of the Mesozoic Mammal Collection in the U. S. National Museum.

Of the several theories thus far advanced for the evolution of the teeth, none has been entirely satisfactory, and there is still a wide disagreement among authorities, especially as regards the position of the primary cone or "protocone" in the upper molars. As proposed by the late Prof. E. D. Cope and supported by Prof. Henry F. Osborn, the primary cone is to be found invariably on the inner or lingual side of the trigonodont upper teeth, and is the homologue of the central cone in *Triconodon*, in which the three main cusps are arranged in an antero-posterior line, the trigonodont molar having been derived from this form through the shifting of the two lateral cones to the outside. The central cone (*protocone*) remaining on the inner side, thus forms a triangle (*trigon*) with the apex pointing inward. In the meantime, according to this theory, the cusps of the lower molars are supposed to have moved in the opposite direction, leaving the central cusps (*protoconid*) on the outside, forming an oppositely directed triangle (*trigonid*). Thus the primary cones of the upper and lower molars in shifting have completely reversed their positions in relation to each other, the primary cone of the upper molars not only moving to the inner side of the crown, but taking a position in the series inside the primary cone of the lower molars as well.

This theory, so skillfully worked out by Osborn, has been widely accepted as satisfactorily explaining the problem of tooth-cusp evolution. But recent paleontological and embryological investigations have thrown a large amount of discredit on the whole theory. As stated by Wortman, Scott has shown most conclusively, from paleontological evidence, that in the upper molariform premolars the primary cone is on the *outer* side and the subsequently added cusps have a very different history from that proposed by the tritubercular theory for the true molars. The embryological researches of Woodward, Tacker, and others have not only confirmed Scott's theory for the premolars, but show also that in all groups of mammals investigated the antero-external cusp or paracone is first to appear in the permanent upper molars and milk molars, as it does in the premolars, and the order of appearance of the other principal cusps is practically the same as proposed by Scott for the premolars.

Woodward[1] found that in *Centetes* and *Ericulus* the main internal cusp, usually termed the protocone, was first to develop, but he believed this cusp to be the paracone, the whole tooth representing only the antero-external triangle of such a form as *Talpa*, the protocone and metacone not having been developed. This, as stated by Woodward, is a modification of Mivart's view published in 1868,[2] in which he states his belief that in *Centetes*, *Chrysocloris*[3] and like forms, the main portion of the crown represents the union of the two external prisms of *Talpa* and like forms. According to Mivart, the main internal cusp of *Centetes*, *Ericulus*, *Chrysocloris*, etc., was derived by the fusion of the paracone and metacone, while the protocone and hypocone are wanting or rapidly diminishing in size and importance. According to both Woodward and Mivart, therefore, in these forms, which have been considered typical trituberculates, the outer cusps are developments of the cingulum, while the main internal cusp has been wrongly termed the protocone and is in reality the paracone, according to Woodward, or combined paracone and metacone, according to Mivart, while the inner cusp (protocone) is greatly diminished in size or has entirely disappeared. These two authorities, therefore, are agreed on the two points of principal importance regarding *Centetes* and *Ericulus*, viz : (1) the location of the paracone in the main internal cusp and (2) the ultimate loss of the protocone. I strongly concur in these views, for in a series of upper molars, including *Potamogale*, *Solenodon*, *Centetes*, *Ericulus*, *Hemicentetes* and *Chrysocloris* (see figs. 1–6, pl. IV), the stages suggesting the gradual diminishing and final disappearance of the protocone are very complete, amounting almost to demonstration, and there can be little doubt that the molars of the *Centetes* and *Chrysocloris* type have been derived from forms similar to that of *Potamogale*, involving the loss of the protocone. In consequence of this the paracone, or combined paracone and metacone, comes to be the principal inner cusp. In *Potamogale* the

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[1] Proc. Zool. Soc. London 1896, 588–589.

[2] Journ. Anatomy and Physiol., Vol. II, 139, 1868.

[3] The form figured by Mivart has since been removed to a distinct genus, *Bematiscus* Cope, Am. Nat., XXVI, 1892, 127. The typical *Chrysocloris* upper molar has no trace of a protocone.

protocone is quite prominent and still typical in form, while in *Solenodon* it is much reduced and is beginning to divide transversely, or more probably is beginning to separate from a likewise reducing hypocone. This is in favor of the view held by Mivart that the simple inner cusp in *Potamogale* and like forms is in reality the fused protocone and hypocone. The reduction is carried still further in *Centetes*, in which two inner cingulum-like cusps appear, one on each side of the enlarged paracone. In *Chrysocloris* and *Hemicentetes* the inner cusp (protocone and hypocone) has entirely disappeared.

Regarding Mivart's " fusion theory," I am inclined to believe that Woodward has not given due weight to the evidence cited by Mivart and that there is considerable support for this theory to be found in the modern bats and insectivores. Mivart considered the *Potamogale* molar as an intermediate form between molars of the *Talpa* type, having two external triangular prisms, and those of *Centetes* and *Ericulus*, having only one such prism. He pointed out that in *Potamogale* there is "a very interesting approximation of the triangular prisms," in which the paracone and metacone, although still remaining distinct, are in very close juxtaposition. This view is strongly supported by a series of bat molars to which Mr. G. S. Miller has kindly called my attention. In this series, which includes *Vespertilio*, *Scotophilus* and *Harpiocephalus*, are suggested the successive steps from *Talpa* to *Potamogale* in the insectivore group. *Vespertilio* represents the normal or more generalized form, in which the protocone is large, the paracone and metacone are widely separated, and the external styles are nearly equal in size. The mesostyle is much reduced in *Scotophilus* and is drawn inward, the paracone and metacone are more closely appressed and the protocone is somewhat shortened. In *Harpiocephalus*[1] the mesostyle has disappeared, the parastyle and

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[1] The skull of *Harpiocephalus* from which this description was taken was obtained by Mr. G. S. Miller through the kindness of Oldfield Thomas, of the British Museum.

Unforunately it came too late to be photographed and figured uniformly with the series. Its place is taken on Plate III, by an outline drawing from a figure for Wilhelm Peters' Fledermäuse des Berlines Museums für Naturkunde (a projected monograph of the bats).

metastyle have drawn closer together and compose the entire outer portion of the crown, while the paracone and metacone are closely approximated, forming the greater part of the inner portion of the crown, the protocone being very much reduced. Thus in *Harpiocephalus* a stage is reached nearly analogous to that of *Potamogale*, the principal difference being that the metacone is the dominant cusp instead of the paracone, as in the latter genus.[1]

From these comparisons it seems reasonably clear that such forms as *Centetes*, *Ericulus* and *Chrysochloris* have attained a secondary or pseudo-tritubercular form by passing through some such stages of evolution as are suggested by the two series here selected. Other examples of a fusing paracone and metacone and reducing protocone may be found in the molars of some of the creodonts and carnivorous marsupials and in the sectorials of many of the carnivores.

From the foregoing it now seems to be demonstrated beyond question that the main inner cone of *Centetes* and *Ericulus* is not the protocone as observed in normal groups, but, if not entirely made up of the primary cusp (paracone), it at least involves that element and Woodward's contention that the evidence of embryology is in entire harmony for the molars and premolars is not controverted by these seeming exceptions as supposed by Osborn.

Wortman of late has strongly opposed what he terms the "cusp migration theory," and has brought considerable evidence to show that, in the creodonts and carnivores, at least, the cusps of the upper molars in general are homologous to those of the molariform premolars and have had substantially the same history in their development.

Against this combined evidence Osborn[2] has recently reaffirmed the tritubercular theory, "as originally proposed," resting the whole question on the point of evidence as to "whether the main reptilian cone, or protocone, of the ances-

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[1] In the Laramie mammals I find that the metacone equals or is larger than the paracone in those forms in which the postero-external heel is well developed in the upper molars.

[2] Amer. Journ. Science (4), Vol. 17, 1904, 321–323.

tors of the mammals was found upon the antero-internal side or on the antero-external side of the upper molars." This evidence, according to Osborn, is in favor of the tritubercular hypothesis, and conclusive evidence of the theory is furnished in the Jurassic mammal molars. However, a study of all the mesozoic mammal material available has led the present writer to exactly opposite conclusions.

Unfortunately, Osborn's observations were confined to a very limited amount of material, and from a careful examination of the teeth of *Triconodon* and *Dryolestes*,[1] two forms especially studied by him, it seems that his conclusions were based on evident, though perfectly excusable, errors of observation, due doubtless to the minuteness of the teeth and their dark color, which make it difficult in many cases to distinguish, between a fracture and the natural surface of the tooth. Thus, according to Osborn,[2] the upper molars of *Dryolestes* are "broadly transverse or triangular and upon the *internal* side of each is a large, conical, pointed cusp, *pr*, supported by a large stout fang, . . . The external portion of the crown is depressed, and bears one large antero-external cusp ? *pa* and one smaller postero-external cusp ? *me* which is either partially worn away or less pronounced in development." But there are two important cusps not noted by Osborn, one an external cusp placed anterior to the main external cusp, the other a small but well-defined intermediate cusp appearing on the posterior transverse ridge. Thus there are five distinct cusps instead of three, as stated by Osborn, and these do not form a trigon in the sense that this term has been used, for the main external cusp is in the middle of the base of the triangle instead of forming one of its angles.

In the upper molars of *Triconodon* the three principal cusps are arranged in a direct line, and are nearly equal in size and form, and the two lateral cones are each supplemented by a small but well-defined internal basal heel-like cusp and an external basal cingulum. The main cusps are flattened externally into a continuous wall in one species (see Pl. V, fig. 1), while they are

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[1] The specimens studied by the present writer and referred to these genera are from the Atlantasaurus beds of Wyoming. These beds are usually referred to the upper Jurassic, although they may be lower Cretaceous.

[2] Amer. Journ. Science (4), Vol. 17, 1904, 322.

much rounded and deeply divided on the inner or lingual side. Thus, there is not the slightest suggestion of a tendency toward an outward movement of the lateral pair of cusps, while it is easily conceivable that the continued development of the two inner heel cusps and outer cingula would early result in a general form of tooth very different in pattern from the tritubercular type which might form the basis for such molars as those of the diprotodont marsupials and many of the rodents or even of the manatee and mastodon. I do not wish to be understood here as implying any relationship between these very diverse forms, but as especially emphasizing the fact that in *Triconodon* is suggested an easy and not improbable way in which some complex molars may have been derived without having passed through the typical tritubercular stage.

Thus, it is shown by this restudy of the two forms, which according to Osborn represent successive stages in the evolution of the mammalian molar, that the gap between them, which was already great, even according to Osborn's interpretation, is very greatly increased especially from the tritubercular theory standpoint. Moreover there is no evidence, in the way of intermediate forms, indicating that *Dryolestes* ever passed through a stage strictly analogous to that of *Triconodon* or that the main internal cusp is in any way homologous to the central cone in the *Triconodon* molars. Furthermore, a critical comparison of these two forms shows that such an hypothesis is beset by many difficulties. The following are the principal ones: (1) The molars of *Triconodon* are larger and fewer in number than in *Dryolestes* indicating a generally higher specialization. (2) The lateral cones in *Triconodon* are already comparatively much specialized, being suplemented by growths of the cingulum externally and heel cusps internally and thus do not especially resemble, either in form or proportions, any two of the external cusps in *Dryolestes*. (3) The external portion of the upper molar in *Dryolestes* (see Pl. V, figs. 2 and 3) is composed of three simple connate cusps supported by two fangs, their general appearance suggesting an arrangement homologous to the three cusps and two fangs of *Triconodon;* while (4) the internal portion of the tooth is a high antero-posteriorly compressed V-shaped cusp supported by a single fang, centrally placed, and exposed on its inner side for the greater part of its length, the maxillary bone apparently not yet having formed a completed socket, or alveolus, for its reception. Thus the whole construction of the inner cusp, which is highly suggestive of a heel development, differs materially from the central cone of *Triconodon*.

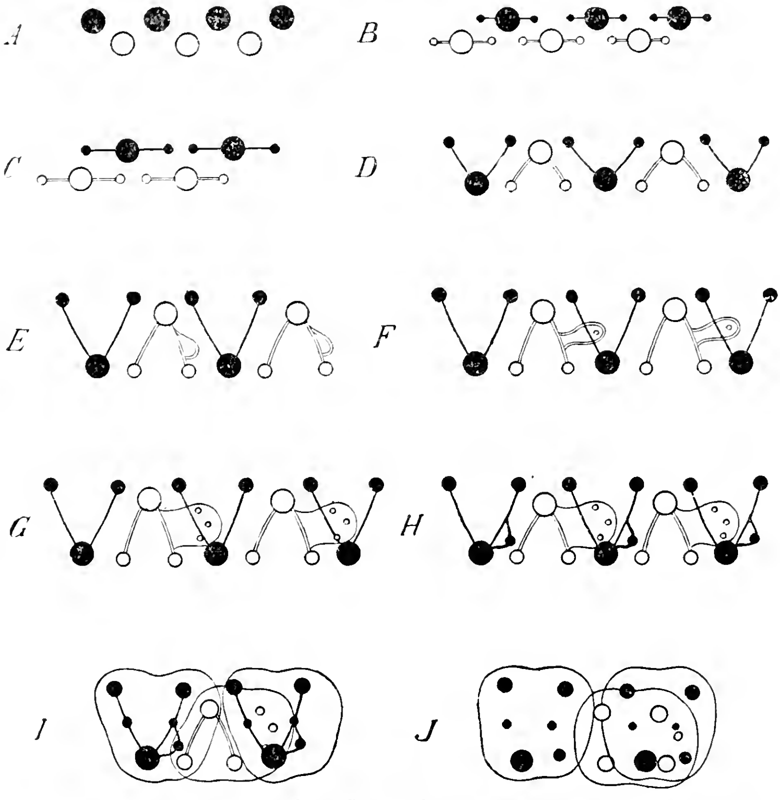

FIG. 11. *Phyletic History of the Cusps of the Ungulate Molars.* *A*, Reptilian Stage, Haplodont, Permian. *B*, Protodont Stage (*Dromotherium*), Triassic. *C*, Triconodont Stage (*Amphilestes*). *D*, Tritubercular Stage (*Spalacotherium*). *E*, Tritubercular-tuberculo Sectorial, Lower Jurassic. *F*, The same, in Upper Jurassic. *G*, The same, in Upper Cretaceous. *H*, The same, Puerco, Lower Eocene. *I*, Sexitubercular-sexitubercular, Puerco. *J*, Sexitubercular-quadritubercular, Wahsatch. (After Osborn.)

Considering the outer portion of the *Dryolestes* molar as homologous to the three cones and two fangs of *Triconodon*,

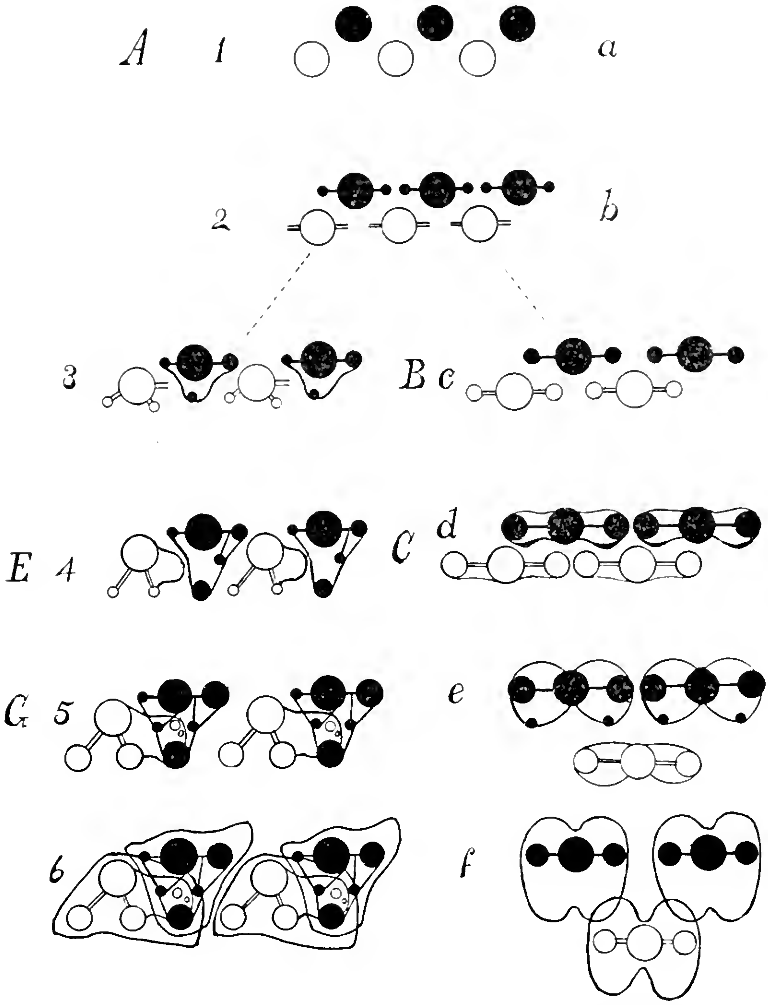

FIG. 12. *Suggested Phyletic History of Two Types of Complex Molars.* [As in Osborn's diagram, the solid black dots represent the cusps of the upper molars, the circles, those of the lower molars.] 1 to 6, Phyletic history of the "Tritubercular" type; *a* to *d*, Phyletic history of the "Triconodont" type; *e*, *f*, From the brachyodont Triconodont stage to the bilobed hypsodont type of molar.

A, *B*, *C*, *E* and *G* compare with *A*, *B*, *C*, *E* and *G* in Osborn's diagram, fig. 11; 4, *Dryolestes* type, Atlantosaurus beds (? Upper Jurassic); 5 and 6, *Protolambda* or *Pediomys* type, Laramie beds (Upper Cretaceous); *d*, *Triconodon* type, Atlantosaurus beds (? Upper Jurassic); *f*, *Palæolagus* type, White River beds (Oligocene).

the derivation of this type of tooth is much simplified, it being not so far removed from the primitive reptilian condition, and though diverging on different lines, is no more specialized, as a whole, than the *Triconodon* type of tooth, the differentiation being carried on more rapidly in the latter in the special development of the anterior and posterior lateral cones and their accessory cusps, while in *Dryolestes* the specialization has apparently been centralized in the development of the high, narrow, heel-like cusp and its supporting fang on the inner side of the molar.

This view is strongly supported by the evidence obtained from still another characteristic Atlantosaurus-beds type of molar represented by *Dicrocynodon*. In this form, Pl. V, fig. 4, the same primitive arrangement of three cusps and two fangs is preserved in the outer portion of the tooth, while on the internal side a large secondary cusp has been developed differing widely in character from that of *Dryolestes*. This cusp is a laterally compressed cone supported by *two* rudimentary fangs and is joined to the outer portion of the tooth by a high, wedge-shaped ridge. The base of the inner cone is greatly expanded antero-posteriorly, curving gently outward toward the external portion of the tooth. Thus the crown, as a whole, is greatly constricted medially with the inner and outer portions superficially resembling each other.

From these observations two important conclusions may be drawn: First, that, leaving out of consideration the multituberculates, there are among the mammals of the Atlantosaurus beds at least three distinct forms of upper molars representing three primitive types of about equal specialization apparently leading off in entirely independent lines. Probably only one of these, *Dryolestes*, represents an ancestral type from which the Upper Cretaceous and later forms possessing trigonodont molars may have been derived. Second, that the evidence derived from the Atlantosaurus beds mammals entirely supports the evidence of embryology and agrees in general with the "premolar analogy" theory. Thus, the evidence from all sources points overwhelmingly to the conclusion that the primary cone is to be found on the *outer* side in the upper molars of primitive trituberculate forms and in all forms derived from a tritubercular type of tooth as well, except where the main inner cone (protocone) has been reduced secondarily. The opposite view held by the tritubercular theory now apparently stands on very insufficient evidence, and the proposition that the protocone, of Osborn, represents the primary cusp is entirely without support.

The lower molars of the Atlantosaurus beds mammals furnish abundant additional evidence along the line of conclusions regarding the shifting of three cusps from a straight line to form the primitive triangle. In such forms as *Dryolestes* and *Paurodon* we have trituberculate molars in the primitive or forming stage, and, what is most significant, the cusps resemble very closely, both in position and relative proportions, those of the premolars of later types in their early stages of transition to the molariform pattern. In the lower molars of *Paurodon* the crown consists of a high, pointed cusp (protoconid), centrally placed, a low posterior heel, a small antero-internal cusp (paraconid), and a very small median internal cusp (metaconid). The last two form the base of the trigonid. In *Dryolestes* both the trigonid and the pimitive heel are somewhat more advanced in development. In still other forms, such as *Manacodon* and *Tinodon*, the two internal cusps are relatively large and the trigonid is fully developed, while the heel, or talonid, is very small or entirely wanting. In all the paraconid and metaconid are entirely on the internal side of the crown, and in these and all the material examined there is not the slightest evidence of any shifting of the cusps, but they seem to have arisen in the positions they now occupy.[1] In *Paurodon* the heel is apparently as much or more developed than either of the internal cusps and seems to have made its appearance even in advance of the metaconid. Also the metaconid is still very rudimentary and is just budding off near the base of the protoconid, but little posterior to its apex and midway of the entire length of the crown, while the place of origin assigned to it by the tritubercular hypothesis is already occupied by the comparatively large heel.

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[1] This is in accord with the general conclusions on tooth cusp development reached by Herluf Winge as early as 1882. Widinsk Meddelelsor fn den naturhist. Florening é Kjobenhavn. 1882. p. 18.

From these observations it seems apparent that the trigonid of the lower molars is not the reverse of the trigon of the upper molars, as held by advocates of the tritubercular theory, and the homologues of the elements of the upper and lower molars, as proposed by this theory, are far from being apparent. (This also accords with the conclusions of Winge.)

The lower molars of *Triconodon* differ from any of the forms just described. They are composed of three nearly equal cone-like cusps arranged like those in the upper molars of this genus in an antero-posterior line. There is no cusp corresponding with the metaconid in *Dryolestes.* There is a continuous basal cingulum on the inner face of the crown, and the posterior cusp is in no way homologous, except in position, to the heel in the lower molars of *Paurodon* and *Dryolestes.*

The mammals from the upper Cretaceous Laramie beds show a great advance in development. The molars of the tritubercular forms of this horizon have passed into a second well-defined stage of specialization which, though varying greatly in detail in the various types, conforms in general to a distinctive pattern which may readily have been derived from some Atlantosaurus-beds form, such as *Dryolestes.* An upper molar of *Pediomys* Marsh, a typical example of the Laramie tritubercular molar, compared with the corresponding tooth of *Dryolestes*, presents the following differences and indicates the principal lines of progression:

(1) The main internal cusp (*protocone*) is much broadened antero-posteriorly; (2) a second small V-shaped intermediate cusp (*protoconule*) has been added; (3) the postero-external cusp (*metacone*) has greatly increased, nearly equaling, both in size and importance, the median external, or primary, cone (*paracone*), while the antero-external cusp (*parastyle*) has remained small and undeveloped. A correspondingly progressive development marks the trigonid and heel of the lower molars.

Thus, the "trigonodont" tooth, or a type of molar with three principal cusps of almost equal importance, arranged in the form of a triangle, makes its first appearance in the Laramie. This pattern of tooth Cope early recognized as a general primitive type, and on its representatives in the lower Eocene he founded the tritubercular theory. That this type is primitive and many, at least, of the later forms have been derived from it, have been too conclusively demonstrated by Cope, Osborn, Scott and others to be seriously questioned; but this early trigonodont form, as is now evident, was derived in a totally different way from that assumed by the tritubercular hypothesis.

An especially interesting feature in these Laramie forms is the oft-repeated appearance in the upper molars of a backwardly extended outer heel-like cusp connected by an elevated ridge with the postero-external cusp. This portion of the tooth is thus converted into a more or less perfect sectorial, or cutting, blade, against which the anterior blade of the trigonid shears, while the greatly broadened heel or talonid of the lower molar, extending backward under the antero-posteriorly expanded protocone of the upper molar, forms a successful crushing apparatus. Thus, so early as the Cretaceous the prevailing molar types were about equally equipped for use as cutting or crushing mechanisms. The creodonts and carnivorous marsupials seem to have early taken advantage of the sectorial blade to the neglect of the crushing heel which gradually diminished in relative size and importance, while in many other forms, using the crushing portion of the tooth most, the sectorial blade was early lost.

Another special character marking the advance of the upper Cretaceous mammal molars is the first indication in a few forms of the postero-internal cusp (*hypocone*), which forms the fourth main cusp in the later quadra-tubercular type of molars. This cusp has apparently been derived, according to the evidence of these Laramie types, from independent sources in different groups of mammals. In a form which Marsh has referred to *Telacodon* a strong cone-shaped cusp has developed on the postero-internal cingulum of the tooth indicating the derivation of the hypocone from that source. Another form, apparently representing an undescribed genus (Pl. V, fig. 7) is evidently developing a hypocone from the primitive posterior intermediate cusp. Still another form, represented by *Proto-*

lambda Osborn, seems to indicate a third source from which the hypocone may have developed. In *Protolambda* the internal heel (protocone) is broadly expanded and flattened posteriorly without a cingulum, yet the peculiar shelf-like form of this portion of the tooth suggests the origin of a hypocone budding off from the protocone independently of either the cingulum or posterior intermediate cusp.

From such a form as that presented in Pl. V, fig. 7, it is but a short step to the typical selenodont artiodactyl type of molar through the progressive development of the V-shaped posterior intermediate cusp. The addition of a second posterior cusp budding off from the enlarged postero-intermediate cusp would readily convert the tooth into a perissodactyl type of molar. Thus is suggested a fourth possible source of origin for the hypocone. This does not necessarily imply an actual relationship of this particular form to the ungulates, but indicates a type closely resembling them which differs widely from the primitive carnivores and insectivores, in which the hypocone, when present, was undoubtedly derived from the cingulum. These observations suggest especially that apparently homologous elements in the teeth of the more highly complex forms may often arise from different sources.

The correlation and homologies of the cusps of the lower molars in comparison with those of the upper series have, for the most part, been left out of this discussion. One observation, in this connection, however, of seeming great importance and significance should be noted here.

In examining a large number of examples of both living and extinct forms, I have found the following associations between the heel of the lower molars and the protocone of the upper teeth to hold constantly true, viz: A functional, broad, crushing protocone is invariably associated with a well-developed crushing heel in the opposing lower molar. A reduced or vestigial protocone is invariably associated with a correspondingly reduced or vestigial heel in the opposing lower molar. Since the heel of the lower molars is admittedly of secondary origin, this feature alone would seem to argue strongly for a like secondary origin for the protocone in the upper molars.

SUMMARY AND CONCLUSIONS.

Summing up the evidence derived from this preliminary study, the following conclusions are suggested:

1. That the evidence obtained from the Mesozoic mammal teeth furnishes no support to the tritubercular theory in so far as it involves the position of the protocone and the derivation of the trigonodont tooth from the triconodont stage through the shifting of the lateral cones outward in the upper molars and inward in the lower molars.

2. That it supports entirely the embryological evidence that the primary cone is the main antero-external cusp, or *paracone*, having retained its position on the *outside* in most upper molars (see exceptions above, p. 95).

3. That it agrees in the main with Huxley's "premolar-analogy" theory, as supported by Scott.

4. That the molars of the Multituberculates, *Triconodon*, *Dryolestes* and *Dicrocynodon*, were apparently derived independently from the simple reptilian cone; hence the supposition follows that the trituberculate type represents but one of several ways in which the complex molars of different groups may have been derived.[1]

5. That in the forms derived from the trituberculate type of molar the order of succession of the cusps is not the same in all groups, and apparently homologous elements are sometimes developed from different sources. Hence it follows that *no theory involving an absolute uniformity of succession in the development of complex molars will hold true for all groups of mammals.*

In the foregoing pages I have restricted the use of Osborn's tooth-cusp nomenclature for the reason that, in this particular discussion, there are some cases in which it is not strictly applicable and might lead to confusion.

On similar grounds Dr. Wortman[2] has expressed the opinion that all attempts to establish a tooth-cusp nomenclature founded on supposed homologies are "foredoomed to failure" and should be entirely abandoned as "useless and confusing." I

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[1] Somewhat similar conclusions have been reached from different reasoning by E. S. Goodrich, M. Tims and others.

[2] Amer. Journ. Science (4), Vol. 16, 1903, 265–368.

agree with the general sentiment expressed (*op. cit.*, p. 366) that, owing to the adoption of different plans in different groups of mammals for increasing the complexity of their molars, no terminology founded on the basis of cusp homologies can be made strictly applicable to all the mammalia. I do not, however, consider this sufficient ground for abandoning absolutely so convenient a system of nomenclature as that proposed by Osborn. Granting that many of the terms proposed are founded on mistaken homologies, it does not necessarily follow that they need be in the least confusing, as suggested by Wortman. For in any system used, in order to make that system of greatest convenience and highest utility, the names once adopted should be permanent and not subject to transfer or substitution on any ground of changed conceptions of homologies or history, for the same reason that generic and specific names are retained regardless of the fact that they may have been given to denote some supposed affinity or characteristic which may later have proved entirely erroneous.

Viewed from the nomenclature standpoint, therefore, the convenient names proposed by Osborn have come to assume an individuality which conveys a far more definite meaning than any purely descriptive terms, be they of relative position or supposed homologies. Moreover, they have the valuable advantages of clearness and brevity in description. On these grounds, in the opinion of the present writer, and for the added reason that great confusion would inevitably result from any change in a terminology that has found its way into so many publications, Osborn's nomenclature should be retained as originally proposed. Thus the term "protocone" always means the main antero-internal cusp of a normal upper molariform tooth, whether that element is regarded as the original primary cusp or otherwise.

The objection that the terms are not universally applicable is scarcely worthy of consideration since they are widely applicable to the great majority of mammalian molar types, without in the least interfering with the use of terms descriptive of "relative position only," which may be used in any cases where Osborn's terms do not apply.

EXPLANATION OF PLATE IV.

(All figures except fig. 9, three times natural size.)

FIG. 1. *Potamogale* — left upper jaw (No. 124327 U. S. N. M.); habitat, Africa.

FIG. 2. *Solenodon* — left upper jaw (No. 2230, U. S. N. M.); habitat, Cuba.

FIG. 3. *Centetes* — left upper jaw (No. 63316 U. S. N. M.); habitat, Madagascar.

FIG. 4. *Ericulus* — left upper jaw (No. 122488 U. S. N. M.); habitat, Madagascar.

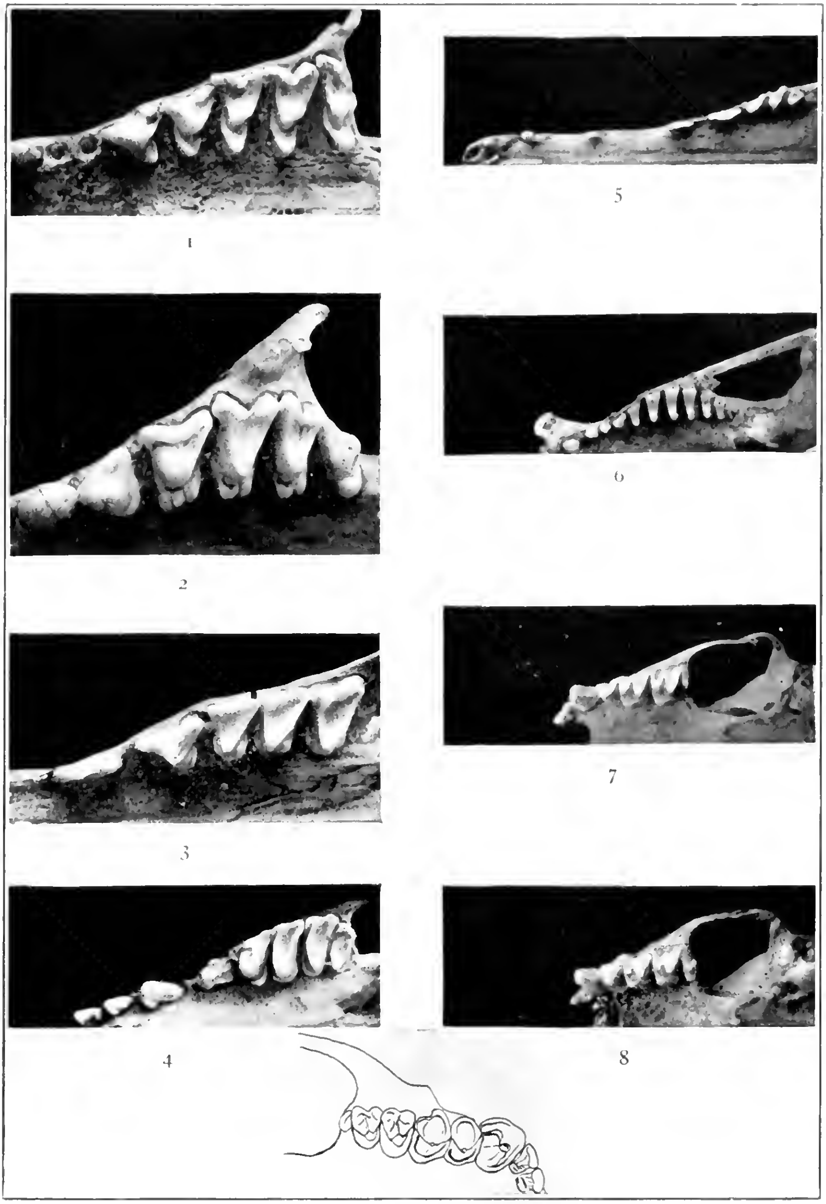
FIG. 5. *Hemicentetes* — left upper jaw (No. 63319 U. S. N. M.); habitat, Africa.

FIG. 6. *Chrysochloris* — left upper jaw (No. 61686 U. S. N. M.); habitat, Africa.

FIG. 7. *Vespertilio fuscus* — left upper jaw (No. 62736 U. S. N. M.); habitat, Washington, D. C.

FIG. 8. *Scotophilus kuhli* — left upper jaw (No. 113463 U. S. N. M.); habitat, Philippines.

FIG. 9. *Harpiocephalus* — right upper jaw. (Outline drawing taken from a plate prepared in 1880 by Wilhelm Peters for a monograph of the bats. This monograph was never published.)



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CHEEK TEETH OF LIVING INSECTIVORES AND BATS

EXPLANATION OF PLATE V.

FIGS. 1 and 1*a*. *Triconodon ? bisulcus* Marsh (Atlantosaurus beds), left upper molars, m^2 and m^3, crown and external views. Six times natural size (No. 2698 U. S. N. M.).

FIGS. 2, 2*a* and 2*b*. *Dryolestes* sp. (Atlantosaurus beds), left upper molars; crown, external, and posterior views. Seven times natural size (No. 2845 U. S. N. M.).

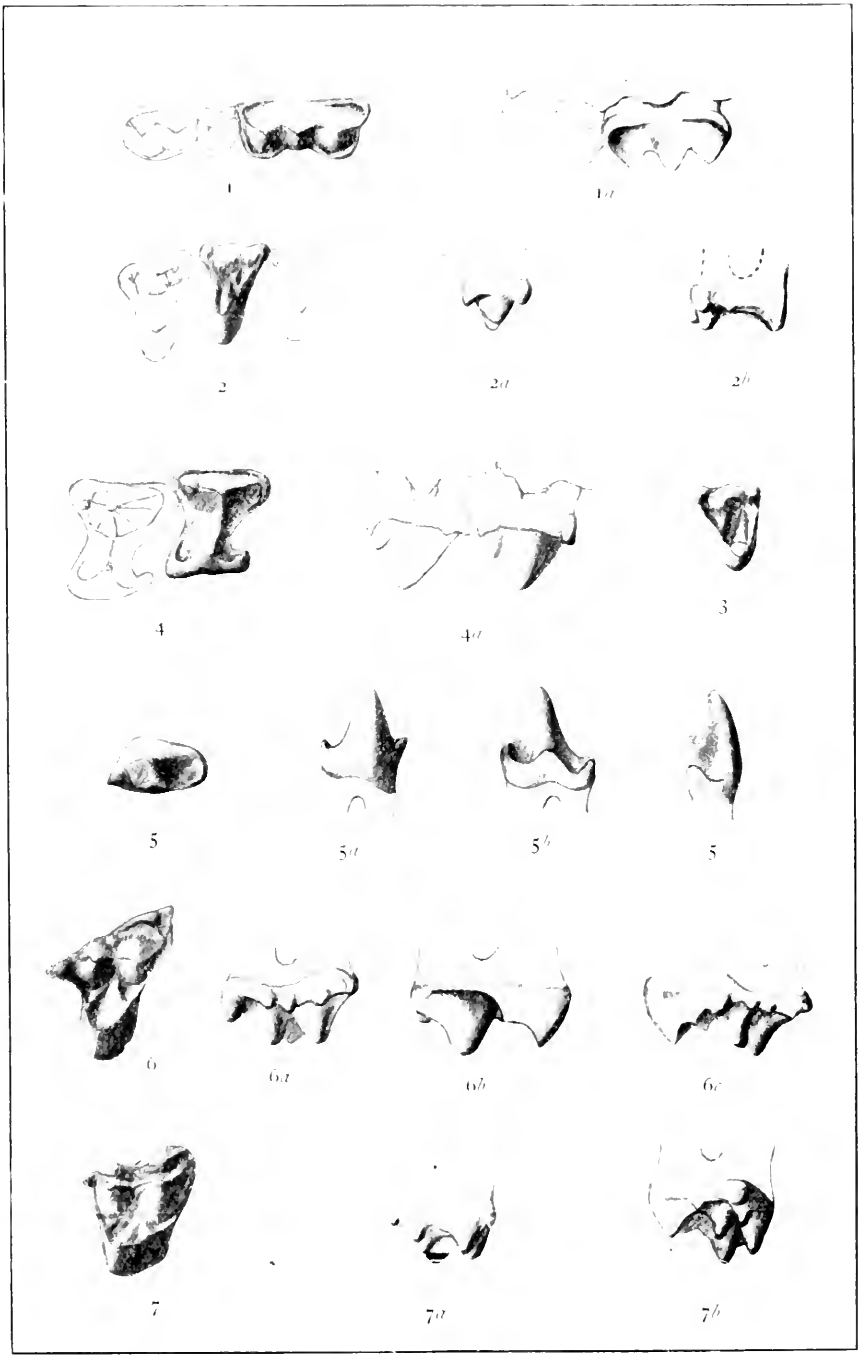
FIG. 3. *Dryolestes*, first right upper molar, m^1; crown view. Eight times natural size (No. 2839 U. S. N. M.).

FIGS. 4 and 4*a*. *Dicrocynodon* sp. (Atlantosaurus beds), left upper molars; crown and external views. Six times natural size (No. 2715 U. S. N. M.).

FIGS. 5, 5*a*, 5*b* and 5*c*. *Paurodon* sp. (Atlantosaurus beds), right lower molar, m_2, crown, external, internal and posterior views. Eight times natural size (No. 2733 U. S. N. M.).

FIGS. 6, 6*a*, 6*b* and 6*c*. ? *Pediomys* sp. (Laramie beds), left upper molar; crown, external, posterior, and anterior views. Eight times natural size (No. 5062 U. S. N. M.).

FIGS. 7, 7*a* and 7*b*. Gen. et sp. indt. (Laramie beds), left upper molar; crown, external and anterior views. Eight times natural size (No. 5076 U. S. N. M.).



TEETH OF MESOZOIC MAMMALS

PROCEEDINGS

OF THE

WASHINGTON ACADEMY OF SCIENCES

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NEW STARFISHES FROM THE PACIFIC COAST OF NORTH AMERICA.

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THE United States National Museum recently sent the writer most of the starfishes in its collections from the west coast of North America. These collections comprise material dredged by the Fisheries Steamer *Albatross*, as well as specimens from other sources. As it will be some time before the final report can be completed and published, the following species are described in advance:

Leptychaster pacificus.
Leptychaster anomalus.
Astropecten ornatissimus.
Luidia ludwigi.
Luidia asthenosoma.
Henricia aspera.
Henricia polyacantha.
Crossaster alternatus.
Crossaster borealis.
Rathbunaster californicus, new genus and species.

In the Bulletin of the Bureau of Fisheries for 1904, Vol. XXIV, June 10, 1905, pp. 291 to 320, the writer published 1 new genus, 2 new subgenera, and 24 new species, based on material collected by the *Albatross* in Alaska in 1903, and off

California in 1904. Most of these forms are found also in the National Museum material, collected at an earlier date.

The new forms described below will be figured in the final report.

Family **ASTROPECTINIDÆ** Gray.

Genus **Leptychaster**[1] Smith.

Leptychaster Smith, Ann. and Mag. Nat. Hist., Ser. 4, XVII, 1876, 110.

Leptoptychaster Smith, Philos. Trans., Zool. Kerguelen Island, CLXVIII, 1879, 278.

LEPTYCHASTER PACIFICUS Fisher, new species.

Rays 5. $R = 43$ mm.; $r = 14$ mm.; $R = 3r$. Breadth of ray at base 16 mm.

General form similar to that of *L. arcticus* (Sars) but disk rather broader. General form flattened; rays evenly tapered, bluntly pointed; interbrachial angle slightly rounded, but abrupt; abactinal surface subplane; margin of rays defined by inferomarginal plates, rounded; superomarginal plates well-developed, relatively larger than in *L. arcticus*, forming a fairly conspicuous margin to abactinal paxillar area; actinal surface slightly convex; actinal interradial areas slightly smaller, and intermediate plates fewer than in *L. arcticus*. Tube-feet pointed, the proximal with a rudimentary subconical disk; superambulacral plates small.

Abactinal paxillar area fairly compact, the paxillæ decreasing in size toward center of disk, midradial line, and end of ray; smallest paxillæ in center of disk, the largest on margin of area at base of ray. Paxillæ similar in character to those of *L. arcticus*, but slightly larger, and spinelets a trifle longer. Base of pedicel flaring into a roundish plate with 4 or 5 short rather irregular lobes by which the plates touch or imbricate slightly, and between which the papulæ emerge. Larger paxillæ with about 25 peripheral and 30 central slender delicate

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[1] This is the original spelling, and, as it is very evident that there is no typographical error, this name should be employed instead of *Leptoptychaster*.

terete blunt spinelets: spinelets occupying center of tabulum form a coördinate flat-topped group, usually stand upright and are crowded; peripheral spinelets usually radiate and are not equal in length.

Marginal plates short, band-like, but both series more conspicuous than in *L. arcticus;* superomarginal plates, 30 in number from interradial line to extremity of ray much wider than long on proximal half of ray, the width rapidly decreasing on outer portion until plates are nearly quadrate. Plates form an arched bevel to margin of abactinal area, are separated by deep fasciolar grooves, and are covered with short delicate terete spinelets which form a close nap all over exposed surface.

Inferomarginals corresponding to superomarginals, beyond which they extend laterally forming margin of ray: separated from superomarginals by rather wide groove; short, band-like, separated by fasciolar furrows, forming well-arched bevel to actinal surface; first plate about twice as wide as corresponding superomarginal; all densely covered with small spinelets similar to those of superomarginals, but a trifle larger, those of transverse median region slightly squamiform and directed outward.

Actinal intermediate areas rather smaller than in *L. arcticus;* one series of intermediate plates extending about three-fourths length of ray or to eighteenth inferomarginal; a second series extending to seventh or eighth plate, and a third series confined to angle bounded by adjacent first 2 plates. Intermediate plates with a low tabulum crowned by a coördinate group of 15 or 20 papilliform spinelets, those in center being slightly thicker and more clavate than the peripheral ones.

Adambulacral plates about as wide as long with a rounded furrow margin, but first 2 or 3 plates wider than long and with more angular margin. Armature consists of (1) a furrow series of 4 (more rarely 5) slender, rather long, blunt cylindrical spinules, the two central being slightly the longest or the 4 subequal; (2) on actinal surface are 2 or 3 longitudinal series of about 4 similar spinules which decrease in size toward outer edge of plate; third series when present more irregular, its spinelets distinctly tapered, slenderer, shorter and sharper. Furrow spinelets usually bent back from furrow, and armature has a decidedly crowded appearance.

Mouth-plates narrow, the free margin of each being longer than that adjacent to first adambulacral, and the combined plates forming a salient angle into actinostome. Margin of plate with a series of about 15 slender tapering spinules, decreasing in length from inner to outer end of plate. About 8 to 10 of these are more regular and occupy the free actinostomial margin, the rest being adjacent to first adambulacral plate, between which and the mouth-plate there is a fairly wide suture. A series of numerous similar spinules stands on edge of suture furrow, and sometimes an incomplete, irregular, intermediate series is present.

Madreporic body situated about its own diameter from inner edge of superomarginal plates, fairly large, surrounded and partially obscured by large paxillæ; striations deep, coarse, irregular, centrifugal.

Type, No. 21925, U. S. Nat. Mus. Type locality, Albatross Station 2862, near north end of Vancouver Island (inside) in 238 fathoms, on gray sand and pebbles.

This well-marked form has larger superomarginals than any previously described species. I have compared the type with a specimen of *L. arcticus* (No. 17992, U. S. Nat. Mus., "Sta. 21, Cashes Ledge") having a major radius of 35 mm. In *L. arcticus* the proximal superomarginal plates are not conspicuously larger than those of outer third of ray. They are roundish and resemble large paxillæ, but in *L. pacificus* the proximal plates are much wider than those of distal half of ray, and the plates decrease regularly in width all along ray. The marginal plates of *L. arcticus* are shorter, hence more band-like, than in *L. pacificus*, there being 36 plates to $R = 35$ mm., while in *L. pacificus*, with R 43 mm., there are but 28 to 30 plates. On account of the difference in size of the superomarginals in the 2 species, the abactinal paxillar area is narrower in *L. pacificus*. The actinal interradial areas of *L. arcticus* are slightly larger than in *L. pacificus* and the paxillæ are more crowded. The present species seems to bring *Leptychaster* nearer to both *Bathybiaster* and *Psilaster*, on account of the larger superomarginal plates. There are, of course, no special spines on the marginal plates of any *Leptychaster*.

LEPTYCHASTER ANOMALUS Fisher, new species.

Rays 5. $R = 27$ mm.; $r = 17$ mm.; $R = 1.6r$. Breadth of ray at base, 19 mm.

In general form and ornamentation greatly resembling *Parastropecten inermis* Ludwig. Disk broad, rays short, broad and blunt; interbrachial arcs shallow and wide; abactinal surface subplane, capable of slight inflation; marginal plates conspicuous, devoid of enlarged spines or spinelets, but covered with granules and granuliform spinelets; actinal intermediate areas broad; adambulacral plates with 3 or 4 furrow spines; small superambulacral plates present; a very tiny anal pore present.

Abactinal paxillar area compact; paxillæ arranged in not very regular oblique transverse rows at sides of ray; without order in median radial area and center of disk. Paxillæ largest at base of ray and in interradial areas decreasing conspicuously in size toward center of disk and tip of ray; larger at sides of paxillar area than in mid-radial region. Paxillæ with subcircular bases having 5 or 6 very short irregular lobes, by which neighboring plates touch, or even imbricate in center of disk and mid-radial area. Papulæ in 5's and 6's (except in center of disk and along mid-radial lines where they are absent). Column of paxilla about as high as breadth of base, flaring at summit, the largest crowned with a coördinate floriform group of about 40 or 45 short, terete, often clavate, round-tipped spinelets; of these about one-half form a peripheral series and are a trifle slenderer and longer. On the smaller paxillæ the spinelets decrease markedly in size, but only slightly in number.

Superomarginal plates, 15 in number from median interradial line to extremity of ray form an arched bevel to border of abactinal surface; plates shorter than wide, but increase in length on outer half of ray. Plates of both series separated by transverse narrow deep fasciolar grooves and a narrow deep groove (not so deep as transverse grooves) separates superomarginal from inferomarginal series. Superomarginal plates covered with short, terete, blunt granuliform spinelets, similar to but larger than paxillar spinelets, becoming well-defined slender spinelets in fasciolar grooves. Superomarginal covering is to be considered as a spinelet rather than granules.

Inferomarginal plates much wider than long, encroaching more onto actinal area than do superomarginals onto abactinal, and corresponding in position to superomarginals. Spinelets, densely covering surface of plates, larger than those of superomarginals, and increasing in size toward outer end of plate which projects slightly beyond adjacent end of superomarginal, thus defining the ambitus. Inferomarginal spinelets granuliform in middle of plate, often attaining a squamiform appearance at outer end; spinelets in fasciolar furrows, slender. No enlarged spines of any sort on either marginal series. Terminal plate small, granulose, deeply notched below.

Actinal interradial areas large; intermediate plates low-paxilliform, arranged in chevrons, the series adjacent to adambulacrals extending about three-fourths length of ray or to eighth inferomarginal. Plates decrease in size toward margin, are strongly imbricated internally, and the paxillar crowns which are composed of about 25 to 30 clavate obtuse, not very crowded, spinelets (slender when dry) surmount a low convex elevation or tabulum. Well-defined fasciolar channels separate these tabula.

Adambulacral plates about as wide as long, with a slightly rounded, angular furrow margin, the angularity being more pronounced in vicinity of mouth plates. Armature consists of (1) a furrow series of 4 (sometimes 3) terete or slightly flattened bluntly pointed tapering spinules about as long as plate and graduated in length orad, the longest spine being on aboral end of plate; or the spinules may be disposed like rays of fan and graduated in length toward either end of series. (2) On actinal surface are about 3 longitudinal series of smaller spinelets, decreasing in length toward outer edge of plate where the spinelets are like those of actinal intermediate plates. Four spinelets commonly occur in the inner actinal series and about 3–5 in each of the outer; or the 2 latter series may be wanting, the spinelets, instead, forming an irregular group, especially on outer part of ray where there are frequently upwards to 16 or 20 actinal spinelets.

Mouth plates narrow, rather prominent actinally, the free margins of the combined plates forming a salient angle into actinostome; free margin of each plate slightly angular near inner end and longer than the margin adjacent to first adambulacral. Armature consists of a furrow series of about 6 or 7 tapering spinules decreasing in length from the inner enlarged tooth, outward, and thence continued along margin adjacent to first adambulacral in about 9 much smaller spinelets similar to those of actinal intermediate plates. A superficial series of similar spinelets follows margin of median suture, increasing in size toward inner angle of plate, and an incomplete more or less irregular series often, but not always, occurs between marginal and superficial series. There is more or less variation in the details of dental armature.

Madreporic body rather large, about midway between center and extreme edge of disk. Striations coarse, centrifugal, very irregular; madreporic body sometimes nearly hidden by 5 or 6 large paxillæ.

Type, No. 21926, U. S. Nat. Mus. Type locality, Albatross Station 3310, Bering Sea, in 58 fathoms, on dark sand and mud.

Remarks.—This species bears a close resemblance to *Parastropecten inermis* Ludwig,[1] and is probably congeneric with that form, although *anomalus* has a minute anal pore. The presence of an anal pore is, I believe, a character of scarcely more than specific importance. For instance one species of *Astropecten* has been shown by Verrill to possess a minute anus. Although I have not yet had an opportunity to make serial sections of the anal region of *anomalus*, I have been able to make out a tiny pore in 2 specimens, and the intestine leading to the pore is well developed. It may perhaps seem heretical to classify the present species with *Leptychaster*, but *anomalus* differs chiefly from *L. pacificus* in having a larger disk, shorter rays, broader actinal interradial areas, and a slightly different ornamentation on paxillæ and marginal plates.

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[1] Mem. Mus. Comp. Zool., XXXII, July, 1905, 76, pl. iv, fig. 21, 22; pl. xxi, fig. 117; pl. xxii, fig. 126. (Gulf of Panama and Cocos Id., 1,271 and 1,408 meters.)

The superomarginals are only a trifle, if any, larger in *anomalus* although the inferomarginals are a little longer and not quite so broad. The chief differences are therefore in proportion. But *pacificus* is an undoubted *Leptychaster*, an evident offshoot of *arcticus*, of the circumpolar fauna. It therefore follows in due course that *anomalus* is a *Leptychaster*, although superficially different enough from *kerguelenensis*, perhaps, to warrant another generic designation if we did not have the intermediate steps.

Without having examined specimens of *Parastropecten inermis* I hesitate to further question the validity of the genus, although frankly I find no generic characters other than the size of the superomarginals that can separate the form from *Leptychaster*. At any rate, *L. anomalus* differs from *P. inermis* in having fewer furrow spines, more paxillæ spinelets, 5 and 6 papulæ about the very short-lobed roundish plates (instead of 4), and finally in possessing a minute anal pore. The general facies of the 2 forms is strikingly alike.

Genus **Astropecten** Schulze.

Astropecten Schulze, Betrachtung der versteinerte Seesterne u. ihre Theile, 1760.

There appear to be 3 species of *Astropecten* off the California coast. One, which I have provisionally identified as *A. erinaceus* Gray, does not range much north of San Diego, and seems to be a shore form. I have been unable to identify the other two species with any previously described form. I have recently described one of these as *Astropecten californicus*[1] and the other is diagnosed below. In order to contrast the principal characters a synopsis of the 3 forms is added.

a. A series of spines along upper edge of superomarginals, and usually, also, a second, parallel longitudinal series, spaced from the above; size large; littoral................................*erinaceus.*

aa. Superomarginals entirely devoid of enlarged tubercles or spines.

  b. Paxillæ larger, about 3 transverse series opposite 2 superomarginals at base of ray; paxillæ not irregular and more crowded along radial lines; the enlarged spine of actinal surface of adambulacral plates, slender, tapering and bluntly pointed. *ornatissimus.*

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[1] Zool. Anzeiger, Bd. XXX, Nr. 10, June 19, 1906, 299.

bb. Paxillæ smaller, about 4 or 5 transverse series opposite 2 superomarginals at base of ray, crowded and more or less irregular along radial lines; enlarged adambulacral spine with rounded or truncate tip, and not conspicuously tapered...*californicus*.

ASTROPECTEN ORNATISSIMUS Fisher, new species.

This species differs from its nearest relative, *A. californicus*, in having shorter rays, larger paxillæ with longer spinelets, longer and slenderer adambulacral spines, and longer marginal spines.

$R = 56$ mm.; $r = 14$ mm.; $R = 4r$. Breadth of ray at base, 16.5 mm.

The paxillæ afford the most evident difference between *ornatissimus* and *californicus*. In *californicus* there is a considerable area around center of disk in which the paxillæ are smaller and more crowded than on remainder of disk and on rays, and paxillæ of midradial regions are more irregular, at least in arrangement, than along margins of ray. In the present form the large paxillæ extend nearly to center of disk, there being only a small area of small paxillæ.

The paxillæ of sides of rays are not in such regular rows and are not easily differentiated from the midradial ones. About 3 or 3½ transverse series of paxillæ correspond to 2 superomarginal plates at base of ray (usually 5 in *californicus*), about 5 at middle of ray, and 6 or 7 near tip. Opposite suture between second and third superomarginal plates about 12 or 13 paxillæ can be counted across ray to same point on opposite side (18 to 20 in *californicus*). Large paxillæ at base of rays with 15 to 18 peripheral and 10 to 15 central spinelets, which are much longer than in *californicus*, terete, with rounded or clavate tips. Tabulum of paxilla fairly broad so that both central and peripheral spinelets appear spaced, giving the whole an open floriform appearance. Farther along ray, 1 to 6 central spinelets to a paxilla, and upwards to 15 or 18 peripheral. At very end of ray the paxillæ are much smaller.

Superomarginal plates 32 to a ray, without enlarged spinelets or tubercles. General surface covered with short spinelets, delicate except along median transverse line where they are clavate to thimble-shaped, increasing in size toward upper end of plate (same spinelets are markedly squamiform in *californicus*).

Armature of inferomarginal plates very similar to that of *californicus*, there being usually 2 or 3 marginal spines obliquely placed, and, in a line, 3 more spaced, smaller, spines along aboral edge of plate. The auxiliary lateral spines situated just adorad to the regular lateral spines on each plate are longer than the same spines of *californicus*.

Adambulacral furrow spines 3 or 4, similar to those of *californicus*. First actinal series with 2 spines, the aboral being much the longer, tapering, slightly flattened, bluntly pointed, longer and slenderer than the corresponding spine of *californicus*. The adoral member is about as long as the furrow spine which stands vis-à-vis. Outer or second actinal series usually consists of 3 slender untapered spines somewhat shorter than furrow spines, and standing in a fairly regular row. Near base of furrow 2 or 3 very small spinelets sometimes stand on outer end of plate.

Mouth spines similar to those of *californicus*, but the marginal series stand slightly spaced from the intermediate spines, so that inner end of combined plates is broader and the 3 series, superficial, intermediate and marginal, are more clearly evident. All spines are slenderer and a trifle longer than in *californicus*. Marginal spines, about 7 between tooth and inner end of first adambulacral plate; and about 6 or 7 more minute spinelets continue the series two-thirds distance to outer end of plate.

Madreporic body concealed by paxillæ, situated as in *californicus* and crossed by sinuous striæ; tiny, spiniform knobs on ridges of *californicus* apparently lacking.

Color in alcohol, bleached yellowish to whitish; color in life unknown.

Type, No. 21927, U. S. Nat. Mus. Type locality, vicinity of Santa Barbara Islands, in 150 fathoms. The vertical range is 67 to 162 fathoms, and the species extends south to Lower California at least, and north to the latitude of Monterey Bay.

Remarks. — This species differs from *A. fragilis* Verrill in having numerous actinal adambulacral spines and shorter rays.

A. regalis Gray, a short-rayed form, also has but one actinal adambulacral spine, scarcely longer than longest furrow spine. *A. verrilli* de Loriol differs from *ornatissimus* in having a different inferomarginal and adambulacral armature. The superomarginal plates of *verrilli* carry small tubercles forming a single longitudinal series. *A. rubidus* de Loriol is allied to *articulatus* (Say), having broad superomarginal plates, a smaller disk than *ornatissimus*, and with rays broader at tip, paxillæ with shorter spinelets, and adambulacral plates with much smaller spinelets — 3 small ones in actinal series.

Family **LUIDIIDÆ** (Sladen) Verrill.

Genus **Luidia** Forbes.

Luidia Forbes, Mem. Wern. Soc., VIII, 1839, 123.

There are three species of *Luidia* occurring off the California coast. In literature two names occur — *Luidia foliolata* Grube[1] and *L. californica* Perrier.[2] According to Ludwig the latter name is a nomen nudum; hence it need not further be considered. Ludwig[3] further states that Grube gives California as the locality of *foliolata*. I have not been able to consult Grube's description, but from the fact that Sladen thinks *foliolata* may not be distinct from *brevispina*, I have considered that the name must apply (if not actually to *brevispina*) to a common, shallow water *Luidia* (Southern Alaska to San Diego, and Mazatlan?) which is closely related to *brevispina*. This form I have compared with specimens of *L. brevispina*, and it is perfectly distinct. If the name *foliolata* does not apply to it, it is a new form.

The other 2 species are evidently new and the more evident characters of the 3 forms are contrasted in the following synopsis.

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[1] Ueber einige neue Seesterne des Breslauer zoologischen Museums < 43 Jahresber. d. Schlesisch. Gesellsch. f. vaterländ. Kultur, Breslau, 1866, 59. (*Fide* Ludwig.)

[2] Étude sur la répartition géographiques des Astérides. < Nouv. Archiv Mus. Hist. Nat. Paris, II ser. I, 1878, 35, 91. (*Fide* Ludwig.)

[3] Mem. Mus. Comp. Zool., XXXII, 1905, 80, footnote.

a. Lateral abactinal paxillæ with a quadrate or subquadrate tabulum.
  b. No pedicellariæ; abactinal surface drab gray or greenish gray in life .... *Luidia foliolata*.
  bb. Pedicellariæ (bivalved) on inferomarginal plates (abactinal end) and on superomarginal paxillæ, and trivalved upright pedicellariæ on actinal intermediate plates; abactinal surface reddish in life, sometimes mottled with lighter ......*Luidia ludwigi*.
aa. Paxillæ with stellate crown; granuliform abactinal 2-jawed pedicellariæ; slender 2-jawed actinal intermediate pedicellariæ; rather prominent lateral spines...........*Luidia asthenosoma*.

LUIDIA LUDWIGI Fisher, new species.

Rays 5. $R = 107$ mm.; $r = 13$ mm. $R = 8.2r$. Breadth of ray at base, 15 mm.

Rays slender, very gradually tapering to a pointed extremity; interbrachial arcs acute; general form depressed as in other species of genus, but abactinal surface well arched; sides of ray rounded; abactinal area with 3 or 4 regular series of quadrate paxillæ on each side, the superomarginal with small 2- and 3-jawed pedicellariæ; inferomarginal plates rather narrow, arched, with 1 to 3, *usually 2*, lateral spines, and 3–6 actinal spinules larger than spinelets of general surface, and on upper end a pedicellaria similar to that of adjacent paxilla; actinal intermediate plates of interradial areas and proximal half of ray each with a rather prominent 3-jawed pedicellaria; adambulacral plates with a curved furrow spine, 3 actinal spines and 1 or 2 smaller spinules.

Abactinal paxillar area rather crowded; paxillæ of 4 or 5 lateral regular series, quadrate; fourth, fifth, or sixth series (according to size of specimen) with many subcircular or not obviously quadrate paxillæ; superomarginal paxillæ slightly smaller than those of adjacent series; paxillæ thence decreasing in size toward mid-radial area where they are arranged without regularity and are roundish or irregular in outline. In some small specimens paxillæ are not so obviously quadrate in lateral series, being subcircular in outline, but nevertheless arranged regularly. Crown of spinelets not so flat as in *foliolata* but rather convex especially in small examples; superomarginal paxillæ with about 35 short clavate spinelets in a radiating coördinate group, and most of them also with a small 2-jawed valvate pedicellaria, slightly longer than spinelets; next series with about 40 spinelets, those in center of tabulum stouter than the peripheral, as in superomarginal paxillæ; small mid-radial paxillæ with about 20 spinelets.

Inferomarginal plates relatively narrower than in *foliolata* (*i. e.*, with reference to transverse axis of plate): fasciolar grooves deep, and wider (with reference to long axis of ray) than same dimension of special raised ridges of inferomarginals. Outer or abactinal end of each plate with a 2-jawed pedicellaria similar to that of adjacent superomarginal paxilla, and with 1 or 2, usually 2, tapering sharp spines, of which sometimes the inner, sometimes the outer, is the longer: the longer (about 4 mm.) equal to about width of its plate; more rarely 3 shorter subequal spines in transverse series on outer end of plate; spines forming a prominent marginal fringe to ray; on actinal surface of plate, 3 to 6 much shorter spinules form a transverse series in line with lateral spines, or a zigzag, or even double series, while margin of plate bears slender terete spinelets, becoming more capillary in fasciolar grooves.

Adambulacral armature consisting of a curved sabre-shaped furrow spine, and on actinal surface 3 tapering bluntly pointed spines, of which 1, the longest, stands behind furrow spine and the other 2 form a slightly oblique longitudinal series just behind first actinal spine; or 2 spines, the adoral the shorter, stand in a longitudinal series just behind furrow spine, and the third just outside of the aboral (longer) spine of the series; 1 to 3 small slender spinelets occur on outer part of plate, frequently 3 at base of ray forming a longitudinal series, or 1 on adoral edge of plate, back of outer adoral spine.

Actinal intermediate plates of interradial region and proximal half of ray paxilliform, surmounted by a prominent 3-jawed pedicellaria which is surrounded at base by numerous slender spinelets in a calyx-like whorl. Each pedicellaria is conical and 1.5 to 2 times as high as its width at base.

Mouth plates narrow, with 6 or 7 marginal spines and 7 or 8 superficial ones, forming together a double series on the raised exposed surface of plate parallel with median suture. Inner spine of superficial series largest, and like the rest, slender, pointed, tapering. All spines decrease in size toward outer end of plate. Innermost marginal spine situated nearer peristome than is the enlarged inner superficial spine.

Madreporic body between second and third lateral rows of paxillæ, and hidden by them.

Type, No. 21928, U. S. Nat. Mus. Type locality, Albatross Station 2970, vicinity of Santa Barbara Islands, in 29 fathoms, on fine gray sand and mud.

Remarks. — This species has the general form of *L. lorioli* Meissner (Mazatlan), but has longer arms, which are more attenuate distally. *L. ludwigi* lacks the conspicuous sharp spinules which are present in many of the lateral abactinal paxillæ of *lorioli*, and the latter has no abactinal pedicellariæ, such as are very characteric of the present species. Another character which separates *ludwigi* from both *lorioli* and *bellonæ* Lütken is the presence of prominent pedicellariæ on the actinal intermediate plates of interradial region and proximal half of ray. Details of adambulacral armature differ in all three forms. *L. ludwigi* differs from *L. quinaria* in having much longer narrower rays, no scattered and abundant abactinal pedicellariæ over the midradial region, and in having 3-jawed, not 2-jawed, actinal pedicellariæ. The abactinal pedicellariæ of *quinaria* are low, and of the bivalved form of some Goniasteridæ. The adambulacral plates also have 2-jawed pedicellariæ in *quinaria*.

Named for Prof. Hubert Ludwig.

LUIDIA ASTHENOSOMA Fisher, new species.

This fragile creature bears a close resemblance to *L. sarsi* Düben and Koren, of northern Europe and the Mediterranean, and may be looked upon as a north Pacific representative of that species. None of the specimens are as large as *L. sarsi* is known to grow. The California species differs from *sarsi* in having very small, abactinal, 2-jawed (rarely 3-jawed), granuliform pedicellariæ scattered along the medioradial area, with larger ones, sometimes, on the regular lateral paxillæ, and on upper end of inferomarginal plates. The inferomarginal spines are longer, the adambulacral armature and minor details of paxillæ are different.

Rays 5. $R = 86$ mm.; $r = 9$ mm.; $R = 9.5r$. Breadth of ray at base, 10 to 11 mm.

Rays long, narrow, pointed, very gently tapering, with a slightly convex abactinal surface usually sunken along midradial line. General form much flattened; sides of rays rounded; inferomarginal plates narrow, not encroaching much upon actinal area, but forming rather the margin of ray; ambulacral furrow wide and shallow; tube feet long, in 2 series; actinal and marginal spines rather long and bristling, the adambulacral armature forming 2 series continuous with that of inferomarginal plates; actinal intermediate plates usually with a rather short, 2-jawed, blunt, papilliform pedicellaria.

Abactinal paxillæ with a stellate crown; those of superomarginal series larger than rest, and each corresponding to an inferomarginal plate, to upper end of which it is closely juxtaposed. Crown of superomarginal paxilla longitudinally oval (as in *sarsi*), the others subcircular. Adjacent to superomarginal paxillæ are about 2 regular series of lateral abactinal paxillæ, about 2 of which correspond to 1 superomarginal paxilla. Paxillæ diminish in size very rapidly toward median line of ray and become less regular in arrangement as they approach it. Superomarginal paxilla has slightly convex tabulum armed with about 30 slender denticulate spinelets, of which about 10 are scattered on surface of tabulum and the remainder about the periphery, the whole forming a diverging group. The superomarginal and other lateral paxillæ sometimes have a blunt 2-jawed pedicellaria similar to but larger than those scattered over the midradial area (see below). The adjacent paxillæ have about 12 peripheral and 3 to 5 central spinelets, while those in midradial region have about 10 peripheral and 3 or 4 central, very much smaller, spinelets, the whole paxilla being notably smaller. Many of small paxillæ of midradial area also bear in center of tabulum, surrounded usually by a few small peripheral spinelets, a small obovoid 2-jawed valvate pedicellaria, resembling a split granule. Viewed from above, the pedicellaria is elliptical in shape when closed. Each jaw is hollowed on inner face and occasionally is larger, springing from a very low paxilla and emerging between the others. Rarely there are 3 jaws. Jaws of pedicellariæ much thicker and more robust than any paxilla spines.

Inferomarginal plates relatively very narrow, transversely arched, encroaching but slightly upon actinal surface, forming rounded margin to ray; chord of width equal to 1.5 times that of adambulacral and actinal intermediate plates combined. Fasciolar grooves deep and wide, slightly wider (*i. e.*, measured on long axis of ray) than corresponding dimension of specialized elevated ridge of plate. Each plate with a transverse series of 3 robust, tapering, sharp spines, of which the outer is often slightly the longest, but frequently the middle one, or the 2 are subequal; inner (actinal) spine of series is sometimes much slenderer than other 2, and only one half or two thirds length of longest spine; latter attains a length of 5.5 mm. or slightly over one half width of abactinal paxillar area, or nearly twice width of plate (*i. e.*, chord of width). General surface of plate covered with slender almost capillary spinelets which become finer in fasciolar grooves; and upper end of plate sometimes bears a pedicellaria similar to those of abactinal surface.

Adambulacral plates with a slender sabre-shaped furrow spine, and forming a linear series with it on actinal surface, 2 slender tapering pointed spines, the inner of which is the stouter and slightly the longer. A couple of very slender spinelets stand on adoral side of outermost spine, which decreases in size toward extremity of ray more rapidly than the inner.

On most of the actinal intermediate plates of proximal two thirds of ray is a small 2-jawed pedicellaria accompanied by 2 or 3 capillary spinelets; when former is absent its place is taken by about 3 to 5 capillary spinelets; jaws of pedicellaria blunt, oblong to obovate, 0.5 mm. high; 3 or 4 pedicellariæ in interradial region, but very few spinelets.

Mouth-plates more like those of *Astropecten* than most species of *Luidia*. Exposed surface of combined plates, ovoid, prominent; suture between plates fairly wide. Armature consisting of a slightly tapering, bluntly pointed tooth and back of that on margin a large 2-jawed pedicellaria nearly as long as tooth. Two shorter spines may take the place of the pedicellaria. In line with the tooth a series of about 10 superficial spinelets follows edge of suture, decreasing in size toward outer end of plate; and along curved margin adjacent to first adambulacral are 4 or 5 slender spinelets, the second from inner end of series often the longest. This series is separated from the superficial by a shallow groove.

Color in life, reddish brown (burnt Sienna) on abactinal surface; marginal spines lighter, often whitish; actinal surface whitish.

Type, No. 21929, U. S. Nat. Mus. Type locality, Albatross Station 3148, off Central California in 47 fathoms, on brown mud.

Family **ECHINASTERIDÆ** Verrill.

Genus **Henricia**[1] Gray.

Henricia Gray, Ann. and Mag. Nat. Hist., Ser. 1, VI, 1840, 184.
Type, *Asterias sanguinolenta* O. F. Müller.
Linckia Forbes, non Nardo, Mem. Wern. Soc. VIII, 1839, 120.
Cribrella Forbes, *non Agassiz*, Brit. Starfishes, 1841, 106.
Cribrella Lütken, Grönl. Echinod., 1857, 30; and most authors since then.
Echinaster M. & T. Syst. Ast., 1842, 22 (pars).
Henricia Bell, Ann. and Mag. Nat. Hist., Ser. 6, VI, 1890, 472.

HENRICIA ASPERA Fisher, new species.

Rays 5. $R = 100$ mm.; $r = 15$ mm; $R = 6.6r$. Breadth of ray at base, 14 mm.

Disk small, rays slender, usually not swollen at base. Abactinal skeleton forming an open meshwork, the individual plates

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[1] *Cribrella* Ag., the name long used for this genus, is a synonym of *Linckia* Nardo. Forbes appropriated Agassiz's name and transferred it to a different group, that is, to the genus which Gray had previously named *Henricia*. *Cribella* Forbes drops out of nomenclature both because it is a synonym of *Henricia* and more especially as it is a homonym of *Cribrella* Agassiz. The *Cribrella* of Agassiz was proposed (Mem. Soc. Sci. Nat. Neuchâtel t. 1, 1835. 191) as a substitute name for *Linckia* Nardo, the latter being now in use. Consequently *Cribrella* Ag. has no status other than as a synonym of *Linckia*.

indistinguishable and spinelets very short granuliform, not arranged in evident pseudopaxillæ as in *leviuscula*. Meshes roundish quadrate, or irregularly polygonal, more open in some examples than in others, containing sometimes 1 or 2 small secondary ossicles with a few granuliform spinelets. Meshes usually considerably wider than enclosing trabeculæ, and with 5 to 12 papulæ on proximal two-thirds of ray, 5 to 7 distally (but fewer in small specimens). Spinelets not crowded, but spaced, short, sharp, much slenderer, and fewer than in *leviuscula*, often reduced to mere granuliform sharp elevations on plate and more or less obscured by a tight thin skin; arranged along ridges irregularly, but in not over three rows, often in only one irregular series. These rows are interrupted, dividing the spinelets and granules into groups probably corresponding to underlying plates, although no divisions are evident. There are commonly 5 to 15 spinelets in one of these groups, but in some specimens they are so obscured by the superficial membranes that only the very tips of the spinelets are visible. They are invisible to the naked eye, and are seen with difficulty under a strong glass. Division into groups more evident on sides of ray.

Marginal plates regularly arranged. Superomarginal series departing from interradial angle about midway between dorsal center of disk and inner angle of jaw-plates; occasionally rather irregular near interbrachial angle; plates sometimes transversely elongated, with 10 to 12 spinelets. Inferomarginals slightly larger or exactly equal to superomarginals; 1 or 2 rows of intermarginal plates on basal fifth of ray; also 1 or 2 rows of actinal intermediate plates, 2 extending about one fifth length of ray, and 1 series for one half length, beyond which point inferomarginals and adambulacrals are in contact. Inter- and inframarginal papulæ; 1 to 6 in an area. Marginal plates also form fairly regular transverse series with adambulacrals, although latter are more numerous than former.

Adambulacral plates with 1 small spine deep in furrow; on some plates, especially in large specimens, a second may be present just above it and in line. On actinal surface 2 larger spines stand in an oblique transverse series on furrow margin (frequently a group of 3); and behind them 3 or 4 much shorter graduated spinelets in a single zig-zag series, all more or less united basally by membrane. Armature varies greatly, sometimes 2 transverse series of spines being present, and the spines themselves vary in shape from slender cylindrical tapering to thick, clavate and blunt. Armature generally has appearance of being in a single series and rather sparse. The outer spinelets of some specimens (those which have very minute spinelets generally) are buried in membrane and all but invisible.

Madreporic body variable — usually subtubercular, roundish, with coarse striations.

Color in life: Abactinal surface deep chrome yellow; papular areas deep saffron yellow; actinal surface pale Indian yellow.

Type, No. 21930, U. S. Nat. Mus. Type locality, Albatross Station 3052, off Oregon in 48 fathoms, on "coral," broken shells and rocky bottom.

HENRICIA POLYACANTHIA Fisher, new species.

Rays 5. $R = 66$ mm.; $r = 11$ mm.; $R = 6r$. Breadth of ray at base, 13 mm.

Rays moderately to decidedly slender, very flexible, tapering gradually to bluntly pointed, upturned tip; abactinal surface usually collapsed more or less; disk rather small; adambulacral plates at base of ray with 30 to 40 actinal spinelets, and in furrow, instead of the usual single spinelet, 2 to 6 such spinelets grouped or in a vertical series; always more than 1 furrow spinelet; at base of ray always more than 3.

Abactinal and lateral surfaces of rays covered with small, evenly-spaced pseudopaxillæ, leaving papular areas considerably larger than the plates; papulæ 1 to an area, large. Without aid of a glass the papular areas appear roundish. Paxillæ more or less elongated in one direction; convex, covered with exceedingly small spinelets, which are numerous, but vary greatly in number, according to the size of pseudopaxilla; 10 to 40 is the usual number. Paxillæ form a more or less evident median radial line along ray.

External to adambulacral plates is a regular series of actinal intermediate plates, and separated from the latter by a regular series of papulæ is a row of smaller inferomarginals. Sometimes a superomarginal series can be distinguished just above the inferomarginals, especially on outer part of ray, where the 2 series are fairly regular. At base of ray the serial arrangement is broken up and 2 or 3 additional series of small intermediate plates are interpolated. The "marginal plates" are larger than dorsolateral pseudopaxillæ.

Adambulacral plates separated by a distinct suture. Armature very dense, consisting of many spinelets, as follows: (1) on furrow face of plates 2 to 6 small sabre-shaped spinelets in a vertical series, or more irregularly in 2 series. The number varies in different individuals. Usually there are 5 or 6 at base of ray and 2 or 3 to each plate beyond middle. Occasionally specimens have more than three on plates of distal portion of arm. (2) On actinal surface of plate are 30 to 40 slender pointed spinelets arranged in 3 or 4 transverse series on inner half of plate, but too crowded on outer half to form rows. Even the inner spinelets are often without regularity. Spinelets decrease rapidly in length and calibre from the furrow outward, the outer spinelets being sharper than the inner and about the same size as those on other actinal plates.

Madreporic body prominent, tubercular, situated midway between center of disk and interbrachial angle, there being small spinelets scattered on the surface. Striations coarse, irregularly radiating.

Type, No. 21931, U. S. Nat. Mus. Type locality, Albatross Station 2936, off Dan Diego, Cal., in 359 fathoms, on mud.

Family **SOLASTERIDÆ** Perrier.

Genus **Crossaster** Müller & Troschel.

Crossaster Müller & Troschel, Monatsber. d. k. preuss. Akad. d. Wiss. Berlin, 1840, 103.

a. Marginal plates of two kinds in a single linear series — conspicuous transversely oriented, prominently spinous, paxilliform plates alternating with 1 or 2 low longitudinally placed plates with short spinelets; proximal marginal plates strictly actinal in position; adambulacral plates with usually four actinal spines. Papulæ very conspicuous; abactinal skeleton more open. *Crossaster alternatus.*

aa. Marginal plates of one kind, viz.: conspicuous transversely oriented paxilliform plates which are strictly marginal in position; adambulacral plates with 2 or 3 actinal spines. Abactinal skeleton less open .... *Crossaster borealis.*

CROSSASTER ALTERNATUS Fisher, new species.

Rays 10. $R = 63$ mm.; $r = 24$; $R = 2.6r$. A larger specimen taken between San Diego and San Clemente (500 fathoms) in 1904 measures as follows: $R = 100$ mm.; $r = 34$ mm.; $R = 2.9r$. Breadth of ray at base, 23 mm.

General form flattened; abactinal surface of disk slightly convex, capable of inflation, but flattened on central part; abactinal surface of rays slightly rounded; margins well rounded; actinal surface nearly flat; interbrachial angles rather acute; abactinal skeleton open reticulate, the ossicles slenderer than in *Crossaster papposus;* papulæ large; paxillæ small, well-spaced; marginal plates characteristic, more prominently spinous transversely placed plates alternating with (usually 2) longitudinally oriented plates with very short spinelets; marginal plates actinal in position on basal half of ray; actinal interradial areas small, with few plates set fairly close together; a single series of very small intermediate plates extending to end of ray; adambulacral plates with 4 to 8 furrow spinules and a transverse series of 4 actinal spinules.

Abactinal integument rather thin but tough and pliable, parchment-like, quite opaque and obscuring the ossicles unless dried. Skeleton open and forming a net-work with fairly wide meshes, which are irregular and largest on disk; connecting ossicles slender, often irregular; enclosed within meshes, small free irregular ossicles; these often absent, but usually present on disk and most numerous near its center. Paxillæ with a 2- to 4-slender-lobed base and a low stout pedicel surmounted by usually 4 or 5 rough, delicate tapering, pointed, spinelets enclosed in a delicate membraneous sac, which fits tightly about each spinule for about half its length, leaving only its basal part obscured. In consequence of the open character of skeleton, paxillæ are well spaced, but are much smaller and more numerous than in *Crossaster papposus.* They are largest and most widely spaced midway between center of disk and margin on radial areas, thence rapidly diminishing in size toward extremity of ray and less toward center of disk. A bare sulcus leads from each interradial angle half way to center of disk. These bare areas are about 1 mm. wide and are paved solidly with ossicles which are the upper edge of the incomplete calcareous interbrachial partition. At the inner end of this bare area, in 1 interradius is the madreporic body surrounded by several paxillæ; in the other radii several slightly larger paxillæ hold a similar position. Papulæ large, partially obscuring the small paxillæ; absent from bare interradial areas; 2 to 7 or 8 to each mesh of skeleton on rays and as many as 15 on disk, or even more where meshes are incomplete. Papulæ commonly 3 mm. long, pointed. In the interradii a number of the abactinal plates are actinal in position because the marginal plates are drawn inward toward the mouth. Thus in the type the distance between marginal plates and interradial angle is 6 to 8 mm., consequently the dorsal integument with plates and papulæ is drawn onto actinal surface.

Marginal plates conspicuous; about 14 or 15 prominent, rather widely spaced, *transversely* oriented, paxilliform plates seem to represent the inferomarginal series, and between each of these, in the same linear series, are 1 to 3, usually 2, *longitudinally* oriented, much lower and slightly smaller plates, which may represent the superomarginal series, although now forming a single series with inferomarginals. Prominent marginals become more conspicuous toward tip of ray, acquiring a heavy, compressed pedicel often higher than its width at top, and very paxilliform in appearance, bearing 2 transverse rows of about 8 to 16 long, tapering needle-like spinules, which increase in length but decrease in number toward extremity of ray. Beyond proximal fourth of ray there are two well-defined series of these spinules, of which the adoral spinules are the shorter, and in the other series about 3 skin-covered spinules become much larger than the rest and have very fine points. Distally the spinules form 2 palmate series, but there is more or less variation in their numbers. The non-prominent longitudinally oriented plates vary considerably in size, and decrease markedly in size distad, whereas the others become more prominent. Except at base of ray, they are not nearly so high as transverse plates and are rounded to elliptical-oblong, bearing upwards to 25 very short spinelets in about 3 or 4 longitudinal series. At tip of ray these plates are very small, bearing a group of 5 or more delicate spinelets.

Actinal interradial areas small, with small, closely-placed, paxilliform plates bearing 4 to 10 spinelets, which are more delicate than those of abactinal paxillæ, although the latter are of about the same size. Interradial paxillæ about 10 to 20 in number. Proceeding along ray almost to its tip is an inconspicuous series of very small actinal intermediate plates, often rather widely separated, a plate usually opposite each adambulacral plate, and distally bearing only a single small spinelet, or none at all, proximally with 2 to 5 spinelets.

Adambulacral plates with a palmate furrow series proximally of 6 to 8, distally of 4 or 5, very delicate, tapering sharp skin-covered spinules united for about a third their length by a web. Mesial spinules longest (about one-third width of plate in length) thence decreasing in length toward either end of series. On actinal surface of plate a transverse comb of 4 or 5 slender, needle-like, sharp spines, the 2 or 3 mesial much the longest, the inner usually slightly longer than furrow spinules, often much longer; outermost spine usually nearly equal to the longest, which exceeds in length width of plate. These spines, like those of furrow series, invested in membrane, which forms vane-like lateral expansions (causing the spinule to appear broad and flat near base) and unites them in a common web by their bases. On distal part of ray the large adambulacral spines are similar in size and appearance to the larger inferomarginal spines, already described.

Mouth-plates of the usual shape, rather prominent actinally. Each plate with 3 long slightly tapering pointed spines at inner end, these decreasing in size outward, so that third spine is about one half length of innermost; thence series is continued to end of plate in 7 or 8 much shorter spines resembling those of first adambulacral plate. All spines skin-covered and united basally by a web. On actinal surface, parallel with median suture and slightly nearer it than free margin, is a comb of 2 to 8 skin-covered sometimes basally webbed spinules similar to but smaller than corresponding series of first inferomarginal.

Madreporic body irregularly circular or oval, situated about midway between center of disk and margin; convex, irregularly and centrifugally striated; about 3 mm. in diameter.

Color in life: " salmon pink."

Young: Young specimens agree very well with the large examples, except that the papulæ are less numerous, and there is a slight reduction in number of spines of interradial, marginal and adambulacral plates, as well as fewer itnerradial and marginal plates. In small specimens there is more often only one superomarginal plate interpolated between the transversely oriented inferomarginals, and the former are slightly more superior in position, at base of ray, than in adults. Adambulacrals commonly with 3 to 5 furrow spinules proximally, and about 5 actinal. Usually only 1 or 2 *large* papulæ to a mesh; abactinal spinelets not fewer in number than in adults.

Type, No. 21932, U. S. Nat. Mus. Type locality, Albatross Station 2839, Santa Barbara Islands, Cal., in 414 fathoms, on gray sand.

CROSSASTER BOREALIS Fisher, new species.

Rays 9 to 12. $R = 140$ mm.; $r = 47$ mm. $R = 3r$. Breadth of ray at base, 23 mm.

Related to *C. australis* Perrier. General form much as in preceding species, but disk usually more arched, and commonly slightly sunken in middle; marginal plates prominent, paxilliform, transversely oriented, spaced; not of two kinds as in the preceding species; situated on margin of ray and disk, not proximally encroaching on actinal surface to any great extent; interradial areas small, paved with small roundish close-set plates bearing very few spinelets; a single series of *small* scattered intermediate plates extending nearly to tip of ray; abactinal skeleton similar to that of preceding species, but slightly less open, *i. e.*, meshes somewhat smaller; paxillæ small, spaced, typically arranged with more or less regularity on disk, in series parallel with median radial; anal aperture prominent.

Abactinal integument entirely obscuring underlying skeleton, unless dried or treated with caustic potash. Paxillæ small, spaced, with a low tabulum surmounted by 1 to 6 slender blunt or pointed, tapering spinelets. In life these spinelets are thick, short and stubby, owing to a membranous investment, and are usually 3 or 4 to each paxilla. In center of disk and along distal half of ray, paxillæ irregularly arranged, but between these two areas an arrangement in longitudinal rows more or less evident. Base of paxillæ with 3 or 4 slender unequal lobes impinging upon those of neighboring paxillæ or connected by short irregular ossicles: latter not numerous: near center of disk there are 1 or 2 isolated ossicles in many of the meshes. Anus surrounded by 4 or 5 large paxillæ. As in preceding species a very narrow bare sulcus extends from interradial angle about half way to center of disk. Papulæ prominent, but usually not quite so large as in preceding species, about 3 to 10 to a mesh on disk, 1 to 3 in distal half of ray where skeleton is closer.

Marginal plates, about 30 to each side of a ray, prominent, confined to side wall of ray, paxilliform with fairly high pedicels (relatively about as in *papposus*), bearing 2 vertical or transverse palmate series of 6 to 9 stout tapering pointed skin-covered spines, the mesial of which are the longest. Sometimes there is 1 main series and 2 or 3 smaller spines stand adorally out of the series, or there may be a second adoral series of less conspicuous spinules, but few in number. Spines of proximal plates shorter than rest, except near tip of ray.

Actinal interradial areas rather small, about 35 to 40 plates to each area. Plates obscured by integument which has fine furrows or wrinkles leading from interadambulacral sulcuses to marginal plates. Plates appear spaced, each bearing 1 to 4 short stubby papilliform spinelets, very delicate when dried. Plates arranged irregularly in rows, between the wrinkles. A series of very small widely spaced actinal intermediate plates extends over three fourth length of ray. They bear usually 1 or 2 stumpy spinelets, or are spineless.

Adambulacral plates with (1) a palmate furrow series of 5 or 6 (distally 3 or 4) slender tapering skin-covered spinelets (united for about half their length by a web) of which the 2 or 3 mesial are subequal, the laterals much shorter. These spinelets are of about same length as in preceding species. (2) On actinal surface a transverse series of 4 (3 on smaller examples, varying to 2 and 5) much longer, slender, terete, blunt, skin-covered spines, the second or third usually longest (exceeding in length the width of plate), the outer about one half length of inner (where there are 3 spines); when 2 spines only are present they are subequal and long.

Mouth plates just a trifle narrower than in preceding species. Free margin with a webbed series of about 11 spinelets increasing in length toward inner end of each plate to 2 or 3 enlarged spines, the innermost stoutest. On actinal surface of plate near inner end of each is a stout, though slender, spine. Sometimes instead of this a small one stands on outer end of plates, or there may be 2 or 3 small spines.

Madreporic body variable in size, similar to that of preceding species, and, like it, situated at inner end of an interradial fasciole. Two or 3 large paxillæ stand near it.

Type, No. 21933, U. S. Nat. Mus. Type locality, Albatross Station 2858, east of Kadiak Island in 230 fathoms, on blue mud and gravel; also found in Bering Sea, in 987 fathoms, on green mud.

Family **PYCNOPODIIDÆ**[1] Stimpson (restr.).

Rathbunaster Fisher, new genus.

Rathbunaster Fisher, new genus of Pycnopodiidæ. (Type, *R. californicus* Fisher, new species.)

Near *Pycnopodia* Stimpson, but differing in having a smaller disk, with the rays constricted at base and easily detachable;

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[1] Used by Stimpson (Proc. Bost. Soc. Nat. Hist., VIII, 1862, 261), as synonymous with Asteriidæ of modern authors. As here employed it includes *Pycnopodia*, *Rathbunaster* and possibly also *Anasterias*, although I have not examined that genus.

in the entire absence of rudimentary annular or calcareous ridges at base of ray, in the abortion of alternate superomarginal plates beyond base of ray, and in the small widely spaced inferomarginals each bearing a slender spine; in the greater prominence of the adambulacral plates which are placed on the same level with the inferomarginals (and each with a single spine as in *Pycnopodia*); in the less crowded condition of the ambulacral ossicles.

The circular isolated plates on abactinal surface of rays are more numerous than in *Pycnopodia* and each bears a wreathed spine, whereas in *Pycnopodia* spines are rare on abactinal plates of arm. There are no large bivalved pedicellariæ as in *Pycnopodia.* Tube-feet quadriserial except at extremity and base of ray where they are biserial. Ambulacral plates being less crowded, the tube feet are really intermediate in arrangement between the biserial and quadriserial type. Mouth plates are more prominent than in *Pycnopodia* and approach in form the type common to Brisingidæ. Actinostome wide, like the Brisingidæ.

Named for Dr. Richard Rathbun.

RATHBUNASTER CALIFORNICUS Fisher, new species.

Rays 17 (varying from 13 to 17). $R = 155$ mm. (variable); $r = 23$ mm. $R = 6.7r$ (variable). Breadth of ray at base, 9 to 11 mm.

Disk nearly flat, circular; rays long, slender, Brisinga-like, deciduous, more or less constricted at base, adjacent to disk. Abactinal integument thin, transluscent on rays, thicker on disk; abactinal skeleton reduced to small circular plates, widely spaced, each bearing a slender needle-like spine heavily wreathed with pedicellariæ; a single superomarginal spine to each plate, widely spaced; a single inferomarginal spine to each plate, twice as numerous as superomarginals; a single long slender adambulacral spine to each plate. Numerous long vermiform papulæ.

Disk resembling that of a Brisinga in general form, only larger, the rays being very insecurely connected and therefore readily broken off. Rays in general form suggesting those of

Freyella. Abactinal surface depressed, collapsed on account of the utter absence of any sort of rigidity. On disk, small roundish plates imbedded in membrane are spaced about 2 to 3 mm. apart, each plate being .5 to 1.25 mm. in diameter, and they are slightly more crowded toward center of disk than near periphery; on ray, plates are rather more widely spaced, and about 4 irregular longitudinal series are sometimes evident, although often no serial arrangement is present. These small plates are a trifle convex in center, and bear a single very delicate needle-like spinule, most of which are encircled about the middle or nearer tip by a very elegant wreath of minute crossed pedicellariæ. This wreath consists of a circular expansion of membrane, the upper surface being thickly beset with pedicellariæ, the lower naked. These wreaths are a little larger, and more crowded near center of disk. Scattered between the primary plates are minute grains. Papular pores pierce abactinal integument, the papulæ being long slender, vermiform, and arranged in groups of 2 or 3 up to 10 or 12. On disk they appear very crowded. Intermarginal papulæ present, more or less grouped.

Marginal spines longer and stouter than abactinal and bearing more prominent wreaths of pedicellariæ. Inferomarginal plates small, spaced (not in contact), closely appressed to adambulacral plates, to every 4 or 5 of which there is 1 inferomarginal. Spine borne on a ventral boss of plate, on about same level with adambulacral spines, not much more ventrally as in *Pycnopodia helianthoides.* Just above each alternate inferomarginal, a somewhat larger superomarginal bears a single subequal wreathed spine. These plates touch the inferomarginals and are elongated transversely. Opposite the remaining inferomarginals they are very small and rudimentary, reduced to a tiny ossicle devoid of a spinelet, and wholly invisible until skin is dried. Near base of ray *each* inferomarginal has a spiniferous superomarginal adjacent to it, but soon the alternate superomarginals, as noted above, lose their spine and atrophy. Comparatively few of the inferomarginal spines have a forficiform pointed pedicellaria at their base .75 mm. in length. This may stand on plate near base of spine.

Adambulacral plates placed obliquely as in *Pycnopodia helianthoides*, but not so crowded. They are not sunken within furrow as in that species, but are on same level with inferomarginal plates and define true margin of furrow. Each plate bears a single spinule, slightly shorter and much slenderer than inferomarginal spine. No pedicellariæ on either spines or plates.

Mouth plates small, each with a marginal spine pointing across mouth of furrow, another over actinostome, and usually 2 upright spines, subequal to furrow spines, on actinal surface near suture — 1 placed behind the other. Furrow spines may bear 1 or 2 small forficiform pedicellariæ but usually they do not; several, instead, being found on inner angle of plate.

Ambulacral furrow wide and shallow; ambulacral plates not so crowded as in *Pycnopodia helianthoides*. Ambulacral pores in 4 rows, except at very base of furrow, and on terminal third or fourth of ray, where there are but 2 rows. Tube-feet large, rather crowded. At base of furrow they are very evidently in only 2 rows and resemble those of Brisinga. Soon the plates become a little more crowded and a not very marked quadriserial arrangement of the feet then becomes evident. Actinostome very wide, 24 mm. on a disk 44 mm. in diameter.

Madreporic body small, situated near interradial angle; distant about its own diameter from edge of disk. Striations radial.

In this species the gonads open to the exterior near base of rays. There is one gonad on either side of ray, much as in *Pycnopodia*.

Type, No. 21934, U. S. Nat. Mus. Type locality, Albatross Station 2925, off San Diego, Cal., in 339 fathoms, on mud.

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NOTES ON JAPANESE HEPATICÆ.

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SCHIFFNER[1] has already emphasized the fact that the Hepaticæ of Japan are of unusual interest. They not only include a very large number of species for the size of the island, over 250 having already been reported, but among these species are both northern and southern types, owing to the many degrees of latitude through which Japan extends and to the varied atmospheric conditions which are to be found there. The flora includes at least 2 endemic genera, *Cavicularia* Steph.[2] and *Makinoa* Miyake,[3] both of which, according to our present knowledge, are monotypic. It also includes a number of species which, although referable to well-known genera, present peculiarities so anomalous that they have necessitated a revision or amplification of the original generic characters. This, for example, is the case with *Ptilidium bisseti* (Mitt.) Evans,[4] which differs from all other known members of the genus in developing a felt of cilia on the outer surface of both leaves and underleaves and which is further remarkable in bearing water-sacs on some of the smaller branch-leaves.

The present paper is a partial report on 2 collections, one made by Mr. T. Yoshinaga (formerly Inouë), of Aki-machi,

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[1] Oesterr. Bot. Zeitschr. **49**: 385. 1899.

[2] Bull. de l'Herb. Boissier **5**: 87. 1897.

[3] Bot. Mag. Tokyo **13**: 21. *pl. 3*. 1899.

[4] Rev. Bryol. **32**: 57. 1905.

and the other by Mr. S. Okamura, of Kōchi. The majority of the specimens in both collections came from the province of Tosa. Most of the species noted are additions to the Japanese flora and include 5 which are here proposed as new. Of these new species 2 have already been named in manuscript by Herr F. Stephani, of Leipzig, but have not yet been described. All of the species noted belong to well-known genera, and more than half are Lejeuneæ. Among the latter is one species which affords an interesting link between the genera *Harpalejeunea* and *Drepanolejeunea*. At least 3 other Lejeuneæ, new to Japan and apparently to science, also occur in these collections. Unfortunately they are represented by sterile specimens only, and it has therefore seemed wise to postpone their description until more complete material can be examined. The types of the new species are deposited in the herbarium of the writer, at New Haven, Connecticut.

1. METZGERIA QUADRISERIATA Evans, new species.

(Pl. VI, figs. 1–5.)

Pale yellowish green, growing in depressed mats; thallus prostrate, repeatedly dichotomous, occasionally giving rise to adventitious branches from the margin or from the postical surface of the midrib, well-developed branches about 0.7 mm. wide and from 1.5 to 3.5 mm. long between the forks, plane or slightly convex; midrib 0.08 mm. wide, bounded both antically and postically by 2 rows of cells, smooth above, bearing a few scattered and simple cilia below; wing mostly from 5 to 8 cells broad, smooth on both surfaces but ciliate on the margin, the cilia scattered and borne singly, usually shorter than the width of the wing, straight or slightly contorted, blunt at the apex or irregularly branched; cells of the wing plane or slightly convex, their walls more or less thickened and sometimes with indistinct trigones, not varying much in size in different parts of the thallus, averaging $42 \times 28 \mu$; inflorescence dioicous; female branch broadly orbicular-obovate, 0.35 mm. long, slightly emarginate at the apex, rather closely ciliate on the margin and usually bearing a few cilia on the postical surface, the cilia similar to those found on the thallus; remaining parts not seen.

Type locality, Ioki-mura, Tosa. Collector, Yoshinaga (no. 11), November, 1903.

In his Hepaticæ Japonicæ Stephani[1] accredits to Japan the 4 following species of *Metzgeria:* — *M. conjugata* Lindb., *M. furcata* (L.) Dumort., *M. hamata* Lindb. and *M. pubescens* (Schrank) Raddi. All of these species have a wide geographical distribution in temperate regions, and *M. hamata* is also common in many tropical countries. Two years later, in his Species Hepaticarum, Stephani[2] throws doubt upon the occurrence of *M. furcata* in Japan but adds a fifth species, *M. consanguinea* Schiffn.,[3] originally described from Java but now known also from the island of Luzon.

Of these 5 species, *M. hamata* and *M. consanguinea* are both closely related to *M. quadriseriata*. They agree with it in their dioicous inflorescence and also in the structure of the costa, which is bounded both above and below by 2 rows of cortical cells. In these 2 species, however, the thallus is more robust than in *M. quadriseriata*, the marginal cilia are borne in pairs, and some of the branches at least are strongly convex. *M. hamata* is further distinguished by its larger cells, and by its longer, more numerous and more contorted cilia, while in *M. consanguinea* many of the ultimate branches are practically wingless and extend outward from the substratum. Whether this last peculiarity is to be considered a specific character or not is somewhat questionable. Stephani implies that it may be due to some unusual condition in the environment and states that he has seen similar branches in other species.

Another close ally of *M. quadriseriata* is *M. lindbergii* Schiffn.,[4] a Javan species, which is now known also from Sumatra, Tahiti and the Marquesan Islands. *M. lindbergii* agrees with the new species in the structure of its costa, and also in the fact that its marginal cilia are borne singly. It is, however, more robust, its wings being often 15 cells broad, and its inflorescence is autoicous. From *M. conjugata* and *M. furcata*

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[1] Bull. de l'Herb. Boissier 5: 81. 1897.

[2] Bull. de l'Herb. Boissier 7: 941, 947. 1899.

[3] Nova Acta Acad. Cæs. Leop.-Carol. 60: 271. 1893.

[4] Denkschr. Mat.-Naturw. Cl. Kais. Acad. Wiss. Wien 67: 30. 1898.

the new species differs in the structure of its midrib. Although in both of these species there are only 2 rows of cortical cells antically, there are normally 4 rows postically.

2. MYLIA VERRUCOSA Lindb.

Mylia verrucosa Lindb. Acta Soc. Sci. Fenn. **10**: 236. 1872.

Locality, Mount Kuishi, Tosa. Collector, Okamura (no. 115), October, 1904. This rare species has already been reported by Yoshinaga[1] under the name *Leioscyphus verrucosus* (Lindb.) Steph. Lindberg first recorded it from Saghalin and Amur, but it was apparently not collected in any other localities until it was found in Japan.

3. RADULA OYAMENSIS Stephani.

(Pl. VI, figs. 6–10.)

Radula oyamensis Stephani, Hedwigia **23**: 149. 1884.

Loosely tufted, dark and dull green; stems 0.15 mm. in diameter, irregularly pinnate, the branches widely spreading, similar to the stem but often with smaller leaves; leaves imbricated, the lobe convex and often reflexed at the apex, widely spreading, broadly falcate-ovate, 1 mm. long, 0.7 mm. wide, attached by an almost longitudinal line of insertion, rounded at the antical base and arching partially or wholly across the axis, antical margin strongly rounded, apex broad and rounded, postical margin also rounded, forming an angle of 90° or more with the keel, margin everywhere entire; lobule subrhombiform in outline, 0.45 mm. long, 0.35 mm. wide, more or less inflated along keel and in basal portion, otherwise appressed to the lobe, inner margin attached by an almost longitudinal line of insertion for half its length or more, not dilated, free margin straight, forming a blunt or rounded angle with the inner margin, extending almost at right angles to the axis and subparallel with the keel, outer margin straight, subparallel with the axis, forming a rounded or very obtuse angle, the apex with the margin free, apex tipped with a hyaline papilla, not borne in a distinct depression, keel more or less arched,

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[1] Bot. Mag. Tokyo **17**: (38). 1903.

scarcely or not at all decurrent; leaf-cells plane or nearly so, averaging 10 μ at the margin of the lobe, 15 μ in the middle and 18 μ at the base, walls thin, trigones small but distinct, cuticle on both surfaces very minutely verruculose; inflorescence dioicous; female inflorescence borne on a leading branch, innovating on both sides, the innovations usually simple; bracts similar to the leaves, but a little smaller, the lobe measuring 0.75 × 0.5 mm. and the lobule 0.45 × 0.25 mm., the latter almost transversely inserted; perianth long-exserted, strongly compressed in the upper part, narrowly obovate in outline, 2.5 mm. long, 0.9 mm. wide, gradually narrowed to a stalk-like base, broad and truncate above; mouth shortly two-lipped, entire; male inflorescence terminating a leading branch, bracts in about three pairs, suberect, strongly inflated, shortly and unequally bifid with rounded divisions; mature sporophyte not seen.

Locality, Hono-Kawa, Tosa; growing mixed with Lejeuneæ. Collector, Okamura (no. 112), July, 1904.

Perhaps the most striking features of *Radula oyamensis* are the strongly convex lobes, the verruculose cuticle and the long and slender perianth. With regard to the peculiarities of the cuticle in this genus, little mention is to be found in the literature, but it is probable that roughened cells occur in other species. In the genus *Scapania*, where the cuticle of late has received a good deal of attention, it has been found that specific characters which are derived from it have to be employed with caution, and it is possible that this same statement will apply to the present genus.

R. oyamensis belongs to group Tumidæ, as defined by Stephani.[1] The original specimens were collected by Dr. C. Gottsche on Mount Oyama, and the species has since been reported by Yoshinaga from the province of Iyo. The plant was first described from male material, and no account of the perianth has subsequently appeared. *R. lindbergii* Gottsche, although placed by Stephani[2] in his group Communes, bears a certain resemblance to *R. oyamensis*, the lobes and lobules

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[1] Hedwigia **23**: 162. 1884.

[2] L. c., 149.

having much the same form in the 2 species. In *R. lindbergii*, however, the lobe spreads more obliquely and is less convex, the lobule is less inflated and is attached by nearly its whole length along the inner margin, the perianth is broader, and the antheridial spike is very long, sometimes bearing 15 or more pairs of bracts. *R. lindbergii* is widely distributed in Europe and has already been reported in Japan from the provinces of Tosa and Iyo.

4. COLOLEJEUNEA FLOCCOSA (Lehm. & Lindenb.) Schiffn.

Cololejeunea floccosa (Lehm. & Lindenb.) Schiffn., Consp. Hepat. Archip. Indici 243. 1898.[1]

Locality, on leaves of *Acrostichum yoshinagai*, Mount Honogawa. Collector, Yoshinaga (no. 1, p. p.), August, 1888. New to Japan. Originally described from Luzon but since reported from Java and Sumatra.

5. COLOLEJEUNEA GŒBELII (Gottsche) Schiffn.

Cololejeunea gœbelii (Gottsche) Schiffn., Consp. Hepat. Archip. Indici 244. 1898.

Locality, on leaf of *Trichomanes japonicum*, Akinokawa, Tosa. Collector, Yoshinaga (no. 25, p. p.), October, 1903. This species was first described from specimens collected in Java. It is also known from the island of Penang and has already been reported from Japan by Yoshinaga.

6. COLOLEJEUNEA VENUSTA (S.-L.) Schiffn.

Cololejeunea venusta (S.-L.) Schiffn. in Engler & Prantl, Nat. Pflanzenfam. **1**: 122. 1893.

Locality, on leaves of *Plagiogyria euphlebia*, Tokimoto, Tosa-gun, Tosa. Collector, Okamura (no. 76), January, 1904. New to Japan. Known also from Java, the type locality, and from Sumatra.

The Japanese specimens do not agree in all respects with the figures of Sande Lacoste.[2] In these the lobules are represented

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[1] Full synonymy of the 3 species of *Cololejeunea* mentioned in the present paper may be found in this volume.

[2] Syn. Hep. Javan. *pl. 12.* 1856.

as being covered over with slender setæ, similar to those found on the lobes, and no trace of a false median nerve is shown, the cells of the lobe being fairly uniform throughout, except that the basal cells are longer and destitute of setæ. In the specimens from Tosa the lobule is perfectly smooth; in the outer portion, close to the end of the keel, the free margin bears a slender tooth, usually composed of 2 superimposed cells, and there is commonly a second blunt tooth somewhat nearer the axis; the margin is otherwise entire. In well-developed leaves there is a fairly distinct false nerve, composed of 1 or 2 rows of elongated cells. Unfortunately the writer has been unable to secure specimens of *C. venusta* for comparison, so that it has been impossible to determine whether these differences are real or simply due to inaccuracies in the figures.

7. LEJEUNEA PLANILOBA Evans, new species.

(Pl. VI, figs. 11–16.)

Pale green, not glossy, scattered or in loose depressed mats; stems prostrate, loosely adherent to the substratum, 0.08 mm. in diameter, sparingly and irregularly branched, the branches widely spreading; leaves loosely imbricated, the lobe obliquely to widely spreading, slightly convex but not reflexed at the apex, scarcely falcate, oblong, 0.7 mm. long, 0.4 mm. wide, antical margin decurrent by a single cell, rounded to subcordate at the base, arching partially or wholly across the axis, outwardly curved to the broad and rounded apex, postical margin more or less outwardly curved, continuous with the keel or forming with it a very obtuse angle, margin entire throughout; lobule ovate-rectangular, 0.25 mm. long, 0.15 mm. wide, inflated in basal half, keel arched near the base, nearly straight in outer portion, smooth, free margin appressed to the lobe except at base, straight or slightly curved, sinus straight or very shallowly lunulate, apical tooth straight and blunt, papilla proximal, usually in a distinct depression, reflexed and more or less concealed behind the margin; leaf-cells plane or nearly so, averaging 12 μ at the margin of lobe, 21 × 15 μ in the middle and 30 × 18 μ at the base, thin-walled but with distinct and rarely confluent trigones and intermediate thickenings, cuticle smooth, ocelli none; underleaves distant to subimbricated, orbicular, 0.2 mm. long. bifid about one half with a narrow and blunt sinus and triangular, erect divisions, rounded to acute at the apex, margin entire or vaguely and irregularly sinuate on the sides; inflorescence autoicous; female inflorescence borne on a leading branch, innovating on one side, the innovation simple or branched, sometimes terminating in a male spike; bracts obliquely spreading, complicate and unequally bifid, keel not winged, lobe oblong, 0.6 mm. long, 0.3 mm. wide, rounded at the apex, entire, lobule oblong to ligulate, 0.4 mm. long, 0.12 mm. wide, rounded at the apex, entire; bracteole connate on both sides at base, ovate to obovate, 0.4 mm. long (to junction with bracts), 0.3 mm. wide, bifid about one half with a narrow sinus and erect, subacute divisions, margin irregularly sinuous; perianth about half exserted, obovoid, 0.65 mm. long, 0.4 mm. wide, narrowed toward the base, rounded at the apex and with a short but distinct beak, inflated and with 5 low keels in the upper part, surface smooth; male inflorescence occupying a short branch or terminal on a longer branch, bracts mostly in from 2 to 4 pairs, closely imbricated, shortly and subequally bifid with rounded divisions, bracteoles present at base of spike, similar to the underleaves, antheridia borne singly; capsule brown, spherical, 0.35 mm. in diameter, spores irregular in form, about 23 μ wide, minutely verruculose.

Type locality, Mount Yokogura, Tosa, on bark. Collector, Okamura (no. 67), March, 1904.

Lejeunea planiloba agrees with other members of the genus in its delicate texture, in the structure of the apical portion of the lobule and in the 5-keeled perianth, as well as in other less important respects. Its subrectangular, relatively large lobule is perhaps somewhat aberrant and will at once serve to distinguish it from *L. cavifolia* (Ehrh.) Lindb. and *L. flava* (Sw.) Nees. Only one other species of the genus has been reported from Japan, namely, *Eulejeunea compacta* Steph. In this species the leaves are described as acuminate, so that it could hardly be confused with *L. planiloba*.

The new species bears a certain superficial resemblance to

Cheilolejeunea intertexta (Lindenb.) Steph., which has also been listed as a Japanese plant. The type specimen of this species was collected by Dr. Mertens in the Caroline Islands, and has been kindly sent to the writer for examination by Dr. von Keisslern, of Vienna. The species has a rather wide distribution in the islands of the Pacific. In well-developed plants the lobule has almost the same form as in *L. planiloba*. The apical region, however, is built up on a different plan and shows the distal hyaline papilla which is characteristic of the genus *Cheilolejeunea*.[1] In some cases the proximal papilla in *L. planiloba* cannot be easily demonstrated, because it bends down behind the apical tooth and is more or less concealed (Pl. VI, fig. 14). From the genus *Rectolejeunea*,[2] which is also characterized by a proximal papilla, the new species must be excluded on account of its 5-keeled perianth. At the same time its close resemblance to certain species of this genus, such as the West Indian *R. phyllobola* (Nees & Mont.) Evans, should not be overlooked.

8. LEPTOLEJEUNEA SUBACUTA Stephani, new species.

(Pl. VII, figs. 1-9.)

Pale yellowish green, often becoming brownish with age or upon drying, growing scattered or in thin depressed mats; stem prostrate, 0.05 mm. in diameter, closely adherent to the substratum, copiously branched, the branches widely spreading, often microphyllous toward the extremities; leaves distant to loosely imbricated, the lobe widely spreading, plane or slightly concave, rhomboid-oblong, the antical and postical margins subparallel, 0.5 mm. long, 0.25 mm. wide, attached by a short and almost longitudinal line of insertion, antical margin rounded near base but scarcely reaching the middle of the axis, slightly curved, or, in the outer part, nearly straight, postical margin straight or nearly so, forming a continuous line with the keel, lobe gradually narrowed to a rounded, obtuse or rarely subacute apex, margin entire throughout; lobule oblong-ovoid, 0.17 mm. long, 0.12 mm. wide, inflated to beyond the middle, keel

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[1] See Evans, Bull. Torrey Club 33: 2. *pl. 1, f. 4.* 1906.

[2] Ibid. 33: 8.

slightly arched, free margin nearly straight, outer portion (including apical tooth) appressed to lobe, inner portion slightly involute, sinus shallow and lunulate, apical tooth short, blunt, slightly curved, papilla in a distinct depression, making the lobule appear bidentate at the apex when flattened; leaf-cells plane, averaging 15 μ at the margin of the lobe, 21 μ in the middle and 30 × 23 μ at the base, thin-walled, trigones and intermediate thickenings minute but distinct, not confluent; basal ocellus measuring 55 × 28 μ, strongly inflated, assisting in the formation of the water-sac, remaining ocelli scarcely larger than the other cells, sometimes indistinct, variable in number but sometimes as many as 8, irregularly scattered through lobe or arranged in from 1 to 3 interrupted and indistinct longitudinal rows; underleaves distant, 0.05 mm. long, 0.085 mm. wide, basal portion rectangular or trapezoidal in outline, abruptly contracted to a narrow line of attachment, consisting of a radicelliferous portion with or without a rudimentary disc and 6 marginal cells, the median marginal cell on each side rounded to obtuse, setæ widely to obliquely spreading, 0.07 mm. long, 0.01 mm. wide, usually composed of 3 cells in a single row, rarely 2 cells wide at the base; inflorescence dioicous; female inflorescence borne on a simple and very short branch (with one leaf and one underleaf besides the involucre), bracts and bracteoles in unfertilized flowers suberect; bracts complicate, unequally to subequally bifid, the lobe oblong, 0.37 mm. long, 0.17 mm. wide (maximum measurements), rounded to obtuse at the apex, margin entire, lobule narrower, ligulate-oblong, 0.34 mm. long, 0.09 mm. wide, apex mostly blunt, margin entire; bracteole somewhat connate on both sides, oblong, 0.37 mm. long, 0.13 mm. wide, bifid one sixth or less with a sharp sinus and erect, triangular divisions, acute to rounded at the apex, margin entire or nearly so, ocelli mostly 2 to 4, scattered; male inflorescence terminating the stem or a branch, bracts in 2 to 4 pairs, imbricated, inflated, very shortly and subequally bifid with rounded divisions, keel strongly arched, minutely crenulate in outer part, bracteole present at base of spike, similar to the normal underleaves but smaller; mature perianth and sporophyte not seen.

Type locality, Akinokawa, Tosa, on leaves of *Gymnogramme* *elliptica* and *Pteris cretica*. Collector, Yoshinaga (no. 25. p. p.), October, 1903.

Leafy propagula are produced by this new species in great abundance and resemble in all essential respects those described by the writer for *L. elliptica*, *L. exocellata* and various species of *Drepanolejeunea*.[1] They occur not only on sterile plants but also on those with sexual organs. In some cases they are borne here and there behind normal leaves, the branch bearing them showing no apparent modifications. It is much more usual, however, to find them on microphyllous branches with closely crowded and aborted leaves (fig. 3). In such a case, each rudimentary leaf gives rise to a propagulum, and the growth of the branch is ultimately limited, although usually not until many propagula have been formed. When the propagula become detached they leave behind them their inflated basal sheaths. It sometimes happens that an entire plant gives itself up more or less completely to the production of propagula, and under these circumstances it becomes difficult to detect upon it normal leaves and underleaves.

The propagula themselves exhibit no new features. The first 1 or 2 underleaves develop radicelliferous discs in the usual way, and the first few leaves are more or less sharp-pointed, the first leaf of all being sometimes but not always reflexed.

L. subacuta is closely related to the widely distributed *L. elliptica* (Lehm. & Lindenb.) Schiffn. and also to *L. exocellata* (Spruce) Evans, of the American tropics. It agrees with these species in its general habit, in its entire leaves, in its cell structure, in its large basal ocelli and in its short and simple female branch. It differs from both in the more numerous ocelli of its leaves and in its broader and blunter perichætial bracts. Its leaves also are a little broader than in *L. elliptica* (being usually from 12 to 14 cells broad, instead of from 8 to 12), and its dioicous inflorescence will further distinguish it from *L. exocellata*.

Another close ally, judging from the description, is *L. foliicola* Steph.,[2] known only from the type locality, the island of

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[1] Bull. Torrey Club **29**: 507–509. *pl. 22, f. 9–13. pl. 24, f. 10.* 1902. **30**: 29, 31, 32, 37, 39. *pl. 5, f. 3.* 1903.

[2] Hedwigia **35**: 106. 1896.

Luzon. In this species the inflorescence is also dioicous and the leaves show 2 or 3 rows of small ocelli in addition to the large basal ocellus. The underleaves are also characterized by spreading divisions, each composed of 3 cells. Unfortunately the female inflorescence of *L. foliicola* is unknown, but its acuminate, acute or apiculate leaves will at once separate it from *L. subacuta*, and its long antheridial spikes, bearing from 10 to 12 pairs of bracts, offer a second distinguishing character.

9. DREPANOLEJEUNEA TENUIS (Reinw. Bl. & Nees) Schiffn.

(Pl. VII, figs. 10–19.)

Drepanolejeunea tenuis (Reinw. Bl. & Nees) Schiffn., Consp. Hepat. Archip. Indici 280. 1898.[1]

Pale yellowish green, not glossy, growing scattered or in thin depressed mats; stems prostrate, 0.035 mm. in diameter, rather loosely adherent to the substratum, sparingly and irregularly branched, the branches widely spreading, usually with smaller leaves than the stem but otherwise similar; leaves distant to subimbricated, the lobe obliquely spreading to suberect, slightly convex but with the apex usually strongly reflexed, more or less falcate especially when flattened, ovate-lanceolate, 0.3 mm. long, 0.14 mm. wide, attached by a short and almost longitudinal line of insertion, antical margin straight or slightly incurved near the base, then strongly outwardly curved to the apex, sometimes arching partially or wholly across the axis, sometimes entirely free from it, postical margin more or less incurved, apex long-acuminate, usually tipped with from 2 to 4 cells in a single row, margin minutely and irregularly crenulate or denticulate from projecting cells, usually but not always bearing from 1 to 5 more distinct teeth between the antical base and the apex; lobule strongly inflated throughout, ovoid, 0.17 mm. long, 0.08 mm. wide, keel strongly arched, forming a continuous line with postical margin of lobe, roughened from projecting cells, free margin involute to or beyond the apex, sinus lunulate, apical tooth strongly curved, hyaline papilla in a distinct depression; leaf-cells plane to strongly convex, aver-

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[1] The synonymy of the species is here given in full.

aging about 16 μ in diameter, a few of the basal cells a little longer and narrower than the others, walls slightly thickened with indistinct and often confluent trigones and intermediate thickenings, ocelli none; underleaves distant, trapezoidal in general outline from a somewhat narrow base, 0.08 mm. long, 0.07 mm. wide, bifid to about the middle, with obliquely spreading divisions and a lunulate sinus, basal region usually with 6 marginal cells around a central radicelliferous region, divisions mostly 3 or 4 cells long and 1 or 2 cells wide at the base; inflorescence dioicous; female inflorescence on a short branch, innovating on one side, the innovation short and simple; bracts obliquely spreading, complicate, unequally bifid, not winged along the keel, lobe ovate, 0.5 mm. long, 0.25 mm. wide, acuminate, margin irregularly dentate or short-ciliate, the teeth from 1 to 3 cells long, lobule more narrowly ovate, 0.4 mm. long, 0.14 mm. wide, apex variable but usually sharp-pointed, margin toothed but less strongly than in the lobe; bracteole connate at the base on both sides, broadly ovate, 0.4 mm. long, 0.25 mm. wide, bifid about one third with erect, acute to acuminate divisions and an obtuse sinus, margin as in the lobule; perianth about half-exserted, oblong-obovoid, 0.6 mm. long, 0.35 mm. wide, gradually narrowed toward the base, rounded to truncate at the apex and abruptly contracted into a short but distinct beak, keels 5, sharp, extending to below the the middle, very indistinctly roughened from projecting cells; remaining parts not seen.

Locality, Takimoto, Tosa, on bark, mixed with *Pycnolejeunea tosana* Steph. Collector, Okamura (no. 103 p. p.), October, 1904. This species has not before been recorded from Japan but has a wide distribution in Java, Sumatra and the Philippine Islands. It has also been reported, probably erroneously, from tropical America.

Since the last published description of this little species appeared over 60 years ago,[1] it has seemed advisable to redescribe it. Unfortunately the male inflorescence seems to be still unknown, and no organs of vegetative reproduction have as yet been detected.

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[1] G. L. & N. Syn. Hep. 390. 1845.

D. tenuis is a somewhat aberrant member of the genus. In the majority of the species which have been described the keels of the perianth are spinose, ciliate or distinctly toothed, sometimes being prolonged as horns. In *D. tenuis* the keels are rounded in the upper part and are practically smooth (Pl. VII, fig. 10). It is not, however, unique in this respect, but agrees with 2 American species, *D. subulata* Steph. and *Lejeunea* (*Drepanolejeunea*) *anoplantha* Spruce. This peculiarity, although important, is hardly sufficient to exclude these species from *Drepanolejeunea*, as it is unsupported by differences in vegetative structure.

The differential characters which separate *D. tenuis* from the 2 American allies just mentioned have already been noted by the writer in another connection.[1] The marginal teeth which are there alluded to are exceedingly variable and on many leaves are absent altogether (Pl. VII, fig. 12). On other leaves they are very pronounced (Pl. VII, fig. 11), and there are all gradations between these 2 extreme conditions. There is apparently no definite correlation between the size of the leaves and the length of these marginal teeth. Another variable character is found in the leaf-cells. These are sometimes plane and sometimes markedly convex or even papillate.

10. HARPALEJEUNEA INTERMEDIA Evans, new species.

(Pl. VIII, figs. 1–11.)

Pale green, more or less tinged with yellow or brown, growing in depressed mats; stems prostrate, 0.045 mm. in diameter, loosely adherent to the substratum, sparingly and irregularly branched, the branches widely spreading, similar to the stem; leaves contiguous to imbricated, the lobe obliquely spreading to suberect (widely spreading when flattened out), convex and reflexed at the apex, falcate-ovate, 0.28 mm. long, 0.17 mm. wide, abruptly dilated from a narrow basal region and attached by a short and almost longitudinal line, antical margin slightly incurved near base, then strongly outwardly curved to the apex,

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[1] Bull. Torrey Club 30: 25. 1903.

postical margin somewhat incurved, forming an almost continuous line with keel, apex usually acute, tipped with 1 or 2 cells, whole margin (except close to the antical base) irregularly denticulate from projecting cells; lobule inflated throughout, ovoid, 0.17 mm. long, 0.1 mm. wide, keel strongly arched, free margin involute to the apex, curved, sinus (in flattened leaves) deeply lunulate, apical tooth abruptly curved, papilla in a slight depression; leaf-cells plane to somewhat convex, averaging 14 μ at the margin of the lobe, 18 μ in the middle and 28 × 18 μ at the base, walls with large, irregular and often confluent trigones and intermediate thickenings, ocelli mostly 1 to 3 at base of lobe, 35 μ long, 23 μ wide, often indistinct or wanting: underleaves distant, broadly obcuneate, 0.05 mm. long, 0.05 mm. wide, narrowed toward the base, bifid about one-half with spreading obtuse divisions, separated by a rounded to obtuse sinus; divisions mostly 3 cells long (beyond the basal region) and 2 cells wide, usually tipped by a single blunt cell, sometimes by 2 cells side by side, more rarely by 2 superimposed cells, basal region commonly with 6 marginal cells surrounding a central radicelliferous portion; inflorescence dioicous: female inflorescence usually borne on a leading branch, sometimes on a short branch, innovating on one side, the innovation long and often again floriferous; bracts obliquely spreading, unequally bifid, complicate, lobe ovate, sometimes falcate and reflexed at the apex, 0.6 mm. long, 0.3 mm. wide, acute to acuminate, margin irregularly dentate or denticulate, keel sharp, occasionally with a narrow, interrupted and entire wing in the upper part, lobule ovate, 0.5 mm. long, 0.2 mm. wide, apex usually acute, margin as in the lobe: bracteole somewhat connate on one side, ovate from a narrow base, 0.45 mm. long, 0.35 mm. wide, bifid about one-third with acute divisions and a sharp sinus, margin crenulate or denticulate, often unidentate on the sides; remaining parts not seen.

Type locality, Mount Myoken, Tosa, on bark. Collector, Yoshinaga (no. 7 and no. 6 p. p.), October, 1903. In no. 6 the new species grows mixed with *Odontoschisma denudatum* (Mart.) Dumort. No. 7 may be designated the type.

As a general rule the species of the Lejeuneæ in which innovations are developed show but a single pair of perichætial bracts. In other words there is an abrupt transition between the bracts with their explanate lobules and the normal leaves just below them with their well-developed water-sacs. *H. intermedia* offers a certain exception to this rule, the leaf below the innovation being distinctly intermediate between a normal leaf and a bract (Pl. VIII, figs. 1, 2). In this leaf the lobe is larger than on ordinary leaves and also less convex, while the lobule is acutely pointed and almost plane. The underleaves also show a gradual transition toward the bracteole, but this is a much more usual condition.

The new species is also of interest because in some respects it is intermediate between the genus to which it has been referred and *Drepanolejeunea*. The most important differences between these 2 genera are found in the underleaves. In typical species of *Harpalejeunea* these are divided by a shallow sinus into 2 broad and divergent divisions, rounded at the apex and usually 3 or 4 cells wide. The radicelliferous region is commonly indistinct. In *Drepanolejeunea* the divisions of the underleaves are setaceous and usually widely spreading; in most cases they consist of from 2 to 5 elongated cells in a single row, but they may be 2 cells wide at the base. These divisions arise from a basal portion in which the radicelliferous region is bounded by a distinct margin of larger cells. In *H. intermedia* the underleaves show a basal portion with a fairly distinct border (Pl. VIII, fig. 7), and the divisions vary at the apex from rounded and 2 cells wide, to pointed and tipped with 2 superimposed cells (Pl. VIII, figs. 8, 9). They therefore combine the underleaf-characters of the 2 genera. In some respects these underleaves bear a resemblance to those of *H. pseudoneura* Evans,[1] of the Hawaiian Islands, which is also a somewhat aberrant member of the genus.

H. intermedia is apparently the first species of *Harpalejeunea* which has been recorded from Asia, and it has no very close allies among species known from other parts of the earth. *H. pseudoneura*, with which its underleaves have just been compared, is at once distinguished by the continuous row of ocelli

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[1] Trans. Conn. Acad. 10: 427. *pl. 50, f. 1–9.* 1900.

running through the lobes of the leaves. More typical members of the genus, such as *H. ovata* (Hook.) Schiffn., show a group of basal ocelli in the same position as in *H. intermedia*, but of course their underleaves conform to the normal type. In the form of its leaves the new *Harpalejeunea* agrees with certain species of *Drepanolejeunea*, such as the recently described *D. setistipa* Steph.,[1] of Java and Celebes. In this species, however, the lobes of the leaves are strongly dentate and show scattered ocelli.

11. BRACHIOLEJEUNEA SANDVICENSIS
(Gottsche) Evans.

Brachiolejeunea sandvicensis (Gottsche) Evans, Trans. Conn. Acad. **10**: 419. 1900.

Locality, on bark, Utsutsumai, Tosa. Collector, Okamura (no. 105, p. p.), September, 1904.

The writer has already pointed out the fact, in the place above quoted, that *B. gottschei* Schiffn. is a synonym of the older *Phragmicoma sandvicensis* Gottsche. When *B. gottschei* was first published it was somewhat doubtful whether Wichura's type specimens came from Japan or Java. Since this time, however, it has been twice recorded as a Japanese plant, once by Schiffner,[3] whose specimens were collected at Tokyo by Miyake, and once by Yoshinaga. Its occurrence in both Japan and the Hawaiian Islands would seem to indicate that it has a wide geographical distribution, but it does not seem to have been reported from any intermediate localities.

12. FRULLANIA DENSILOBA Stephani, new species.[2]

(Pl. VIII, figs. 12–22.)

Brownish red, dull or faintly glossy, growing in depressed mats; stems prostrate, rather loosely adherent to the substratum, 0.12 mm. in diameter, at first regularly pinnate with short, obliquely to widely spreading branches, some of the branches

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[1] Hedwigia **35**: 83. 1896.

[2] Oesterr. Bot. Zeitschr. **49**: 390. 1899.

[3] Published as a *nomen nudum* by Yoshinaga in Bot. Mag. Tokyo **15**: (92). 1901.

remaining short and simple, others becoming themselves pinnate in the same way as the stem: stem-leaves contiguous to loosely imbricated, the lobe widely spreading, somewhat falcate, oblong-obovate, 0.4 mm. long, 0.3 mm. wide, slightly convex, rounded at the antical base and arching partially across the stem, rounded at the apex, margin entire: lobule clavate, 0.17 mm. long, 0.08 mm. wide, inflated throughout, subparallel with the stem and separated from it by about half its own width, mouth obliquely rounded, stylus minute, filiform or subulate, tipped with a hyaline papilla, mostly 4 or 5 cells long and 1 or 2 cells wide at the base; branch-leaves smaller than the stem-leaves, relatively narrower and more closely imbricated, 0.35 mm. long, 0.25 mm. wide, lobules similar to those of the stem but close together and oblique, lying with their rounded ends upon the axis and forming with it an angle of about 45°; leaf-cells plane or nearly so, averaging about 8 μ at the margin of the lobe, 9 μ in the middle and 18 × 12 μ at the base, walls more or less thickened and with indistinct trigones, the portion lining the cavity being usually pigmented, ocelli mostly in a single row of from 3 to 6 cells, running obliquely from the stem between the axis of the lobe and the postical margin, averaging 28 × 23 μ in size, contents dark red, ocelli of leaves subtending branches often in 2 rows; underleaves of stem distant, oblong with subparallel sides, 0.22 mm. long, 0.17 mm. wide, neither cordate nor rounded at the base, bifid one-half or less with a narrow, acute sinus and broad, erect, rounded divisions, margin entire; underleaves of the branches contiguous to subimbricated, often partially covered over by the lobules, narrowly ovate or ligulate, 0.14 mm. long, 0.05 mm. wide, with narrow and often acute divisions; inflorescence dioicous; female inflorescence borne on a leading branch; bracts in 2 or 3 pairs, passing by insensible gradations into the leaves, complicate and unequally bifid, lobes of innermost bracts ovate to oblong, 0.75 mm. long, 0.35 mm. wide, narrowed toward the apex but usually obtusely pointed, margin irregularly sinuate, ocelli usually in 2 rows in lower third of lobe, lobule ovate-lanceolate, 0.6 mm. long, 0.25 mm. wide, subacute at the apex, bearing a cluster of short and irregular cilia at the base, the uppermost one or stylus a little longer than the others, margin otherwise entire; innermost bracteole free, ovate, 0.7 mm. long, 0.4 mm. wide, bifid to about the middle with a narrow sinus and acute divisions, margin indistinctly short-ciliate at the base, otherwise entire; perianth about half-exserted, obovate in outline, 1.1 mm. long, 0.7 mm. wide, gradually narrowed toward the base, rounded to truncate at the apex, beak short, cylindrical, entire or nearly so at the mouth, perianth compressed, but with a distinct, rounded postical keel, narrowing toward the apex, surface smooth; spores brownish, 35 μ in diameter; male plant not seen.

Type locality, Mount Konomine, Tosa. Collector, Yoshinaga (no. 32), November, 1903. Another specimen (cotype) from Mount Ishidachi, Iyo. Collector, Okamura (no. 119), August, 1904. Determination made by Stephani.

The specific name of the present species probably refers to the crowding of the lobules. This peculiarity is not always apparent on the main stem or on leading branches but is especially well seen on short branches with limited growth (Pl. VIII, fig. 15). The crowding of the lobules is accompanied by a change in their position with respect to the axis. Instead of being erect, they tend to become oblique, the inflated ends being more or less appressed to the axis. The underleaves on these branches are sometimes almost hidden by the lobules and are much smaller and narrower than when normally developed.

F. densiloba belongs to the subgenus *Thyopsiella* of Spruce, which includes a large proportion of the tropical Frullaniæ. The row of ocelli in the lobes of its leaves and bracts is a character which it shares with many other species of the genus. Of those which occur in Japan, *F. appendiculata* Steph., *F. moniliata* Nees and *F. makinoana* Steph. may be especially mentioned. The first 2 of these are more robust than *F. densiloba* and are further characterized by their obtusely pointed to acuminate leaves. The third species is somewhat more closely allied but differs in the large and semicircular stylus, which it develops between the lobule and the stem, and also in the broader underleaves, lunately excised at the apex with broad and obtuse lobes.

The publication of new specific names without descriptions is a practice which is unfortunately becoming more and more prevalent in the literature of hepaticology. In certain cases the authors of the names are not directly responsible. Collections, for example, are sent to them for determination and, if they include new species, these are often named in manuscript, the authors intending to publish them with descriptions later on. When a list of the determinations is sent back to the collector he is very likely to have it printed and to include in it the manuscript species, as well as those which are already known to science. In other cases manuscript names without descriptions are published by the authors themselves, apparently in the vain hope of securing priority for their species.

Of course such names have no claims whatever to recognition; they are *nomina nuda*, and the species to which they are assigned cannot be considered published in any sense. At the same time, without adding to our knowledge, these names increase the difficulties of the student, who cannot help feeling that they ought to be investigated. A case in point is with reference to *Scapania brevis* Steph. and *S. japonica* Steph. Both of these species were published as *nomina nuda* by Yoshinaga[1] but no direct reference is made to either of them by Müller in his monograph of the genus *Scapania*.[2] Under *S. stephanii*, however, he notes the fact that this species, proposed as new, is based on 2 of Stephani's manuscript species, and there is reason to believe that these 2 species are the *S. brevis* and *S. japonica* referred to above. If the publication of these 2 names had been deferred until the plants could have been properly described, no such confusion would have arisen.

SHEFFIELD SCIENTIFIC SCHOOL,
YALE UNIVERSITY.

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[1] Bot. Mag. Tokyo 15: (92). 1901. 17: (38). 1903.

[2] Nova Acta Acad. Cæs. Leop.-Carol. 83. 1905.

EXPLANATION OF PLATE VI.

Metzgeria quadriseriata Evans.

FIG. 1. Part of thallus, just beyond a fork, postical view, × 40.
2. Midrib with adjoining cells, antical view, × 50.
3. Marginal cilia, × 225.
4. Cross section of midrib with adjoining cells, postical edge below, × 225.
5. Female branch, × 40.

The figures were all drawn from the type specimen.

Radula oyamensis Stephani.

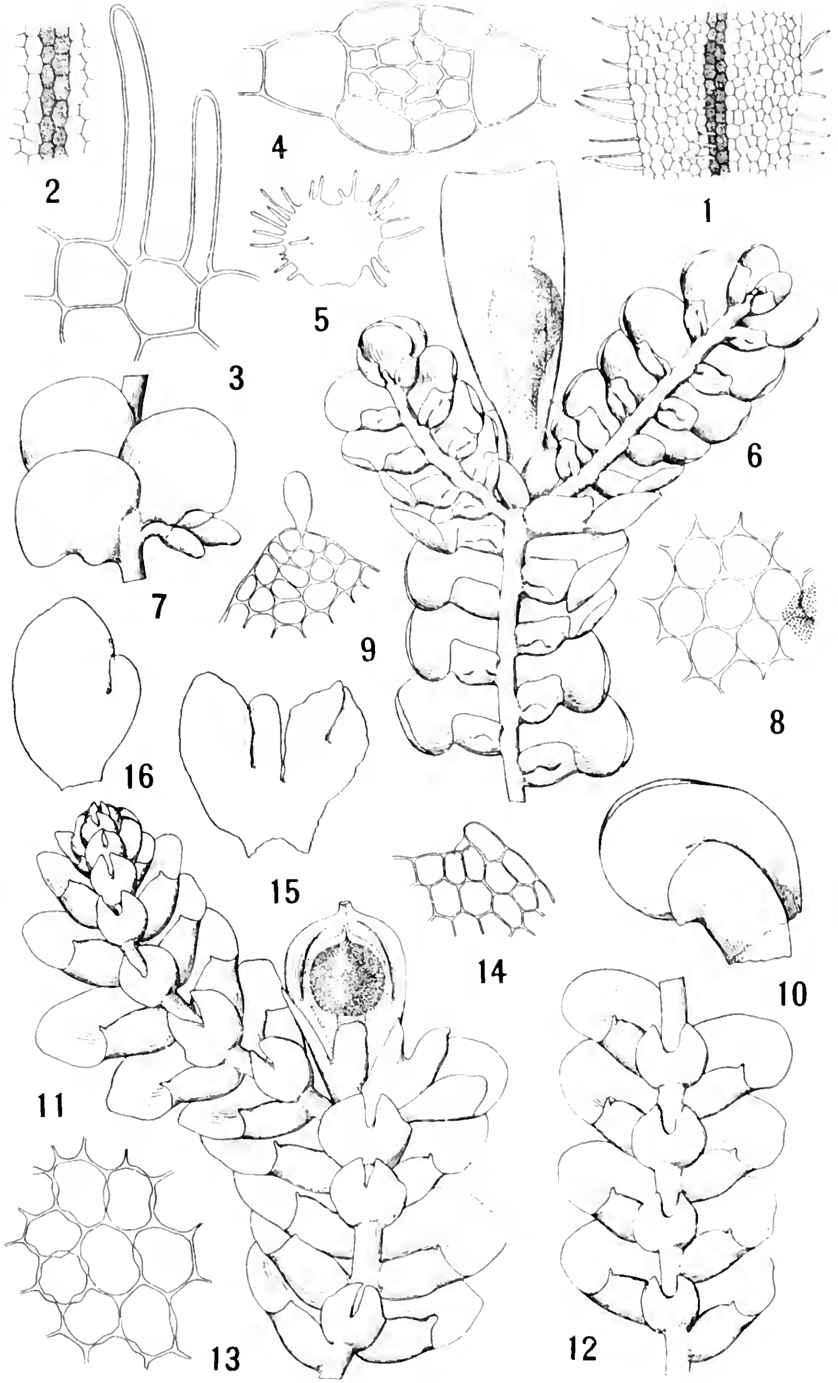
FIG. 6. Part of female plant with perianth and subfloral innovations, postical view, × 17.
7. Part of stem, antical view, × 17.
8. Cells from middle of lobe, some of the verruculæ showing at right, × 300.
9. Apex of lobule, × 225.
10. Perichætial bract, × 40.

The figures were all drawn from Okamura's specimens.

Lejeunea planiloba Evans.

FIG. 11. Part of female plant with perianth, postical view, the lobule of a bract lying over the stalk of the capsule, × 40.
12. Part of stem, postical view, × 40.
13. Cells from middle of lobe, × 300.
14. Apex of lobule, × 225.
15. Bract with connate bracteole, × 40.
16. Other bract from same involucre, × 40.

The figures were all drawn from the type specimen.



FIGS 1-5. METZGERIA QUADRISERIATA EVANS.

FIGS 6-10. RADULA OYAMENSIS STEPHANI.

FIGS 11-16. LEJEUNEA PLANILOBA EVANS

EXPLANATION OF PLATE VII.

Leptolejeunea subacuta Stephani.

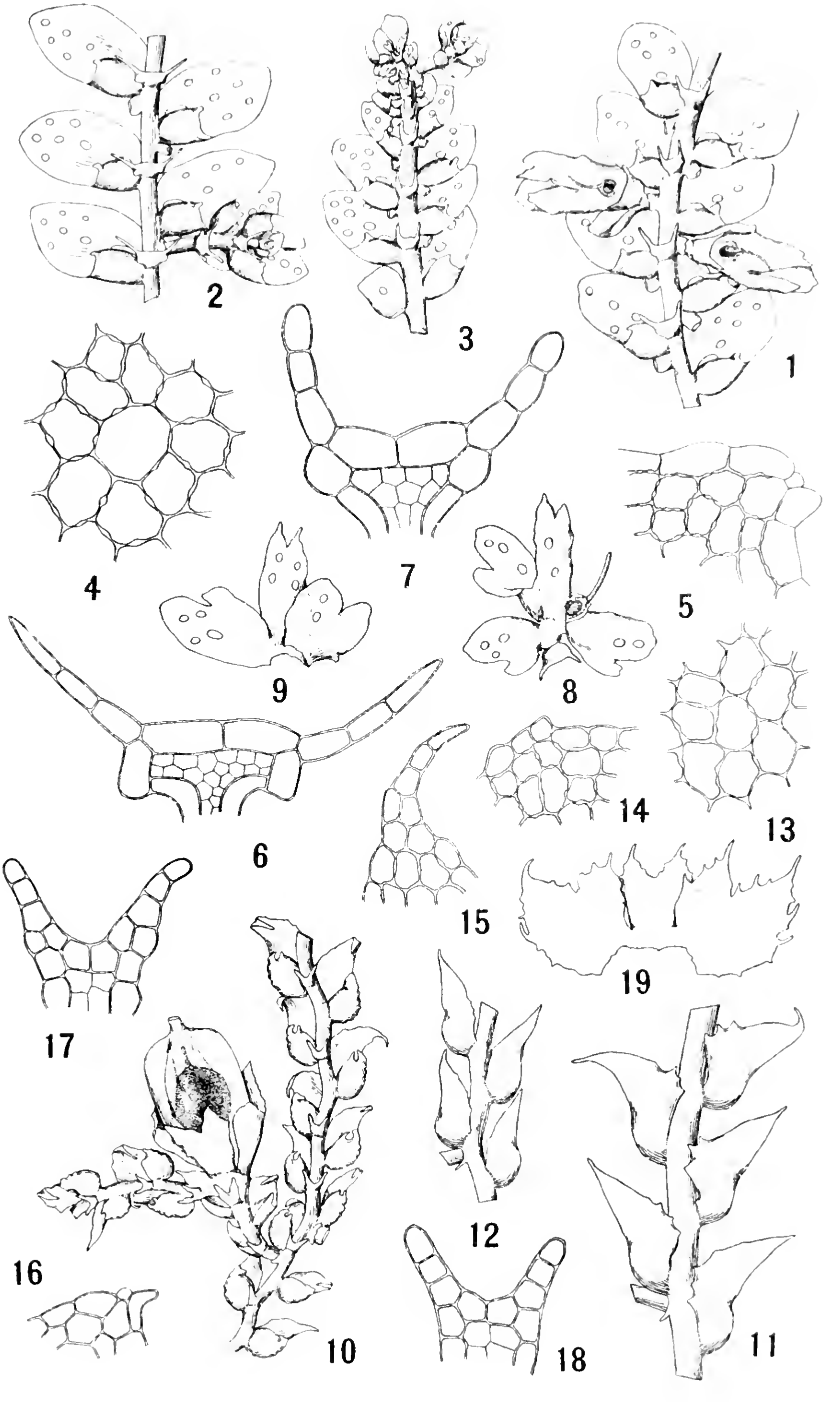
FIG. 1. Part of female stem with two inflorescences, postical view, × 40.
2. Part of stem with branch, postical view, × 40.
3. Propaguliferous branch with one propagulum about to be separated postical view, × 40.
4. Cells from middle of lobe, the middle cell an ocellus, × 300.
5. Apex of lobule, × 225.
6, 7. Underleaves, × 225.
8. Bracts and bracteole with subfloral leaf and underleaf, × 40.
9. Bracts and bracteole from another involucre, × 40.

The figures were all drawn from the type specimen.

Drepanolejeunea tenuis (Reinw. Bl. & Nees) Schiffn.

FIG. 10. Part of female plant with perianth, postical view, × 40.
11, 12. Parts of stems, antical view, × 40.
13. Cells from middle of lobe, × 300.
14. Cells from antical margin of lobe, × 225.
15. Apex of lobe, × 225.
16. Apex of lobule, × 225.
17, 18. Underleaves, × 225.
19. Bracts with connate bracteole, × 40.

Figs. 11 and 12 were drawn from specimens collected by Teysmann in Java and determined by Gottsche; the others from Okamura's Japanese specimens.



FIGS. 1-9. LEPTOLEJEUNEA SUBACUTA STEPHANI.

FIGS. 10-19. DREPANOLEJEUNEA TENUIS (REINW. BL. & NEES) SCHIFFN.

EXPLANATION OF PLATE VIII.

Harpalejeunea intermedia Evans.

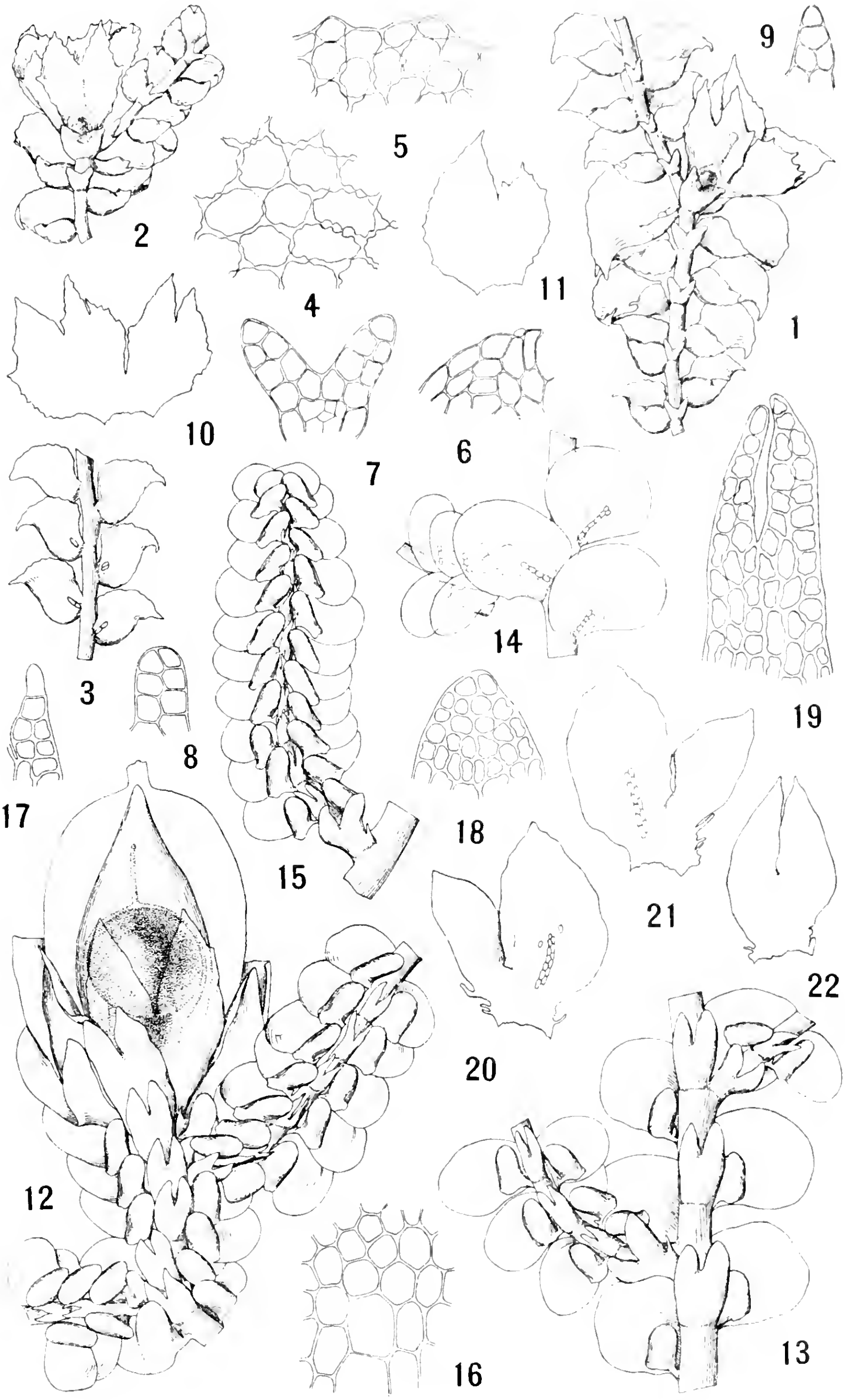
FIGS. 1, 2. Parts of female plants, each with an inflorescence, postical view × 40.
3. Part of stem, antical view, × 40.
4. Cells from middle of lobe, × 300.
5. Cells from antical margin of lobe, × 225.
6. Apex of lobule, × 225.
7. Underleaf, × 225.
8, 9. Apices of underleaf-divisions, × 225.
10. Bract with connate bracteole, × 40.
11. Other bract from same involucre, × 40.

The figures were all drawn from the type specimen.

Frullania densiloba Stephani.

FIG. 12. Part of female plant with perianth, postical view, × 40.
13. Part of stem with bases of 2 branches, postical view, × 40.
14. Part of stem with base of branch, antical view, × 40.
15. Branch with limited growth and crowded lobules, postical view, × 40.
16. Cells from middle of lobe, including one ocellus and part of another, × 300.
17. Stylus of stem-leaf, × 225.
18. Apex of one division from a stem-underleaf, × 225.
19. Branch-underleaf, × 225.
20–22. Innermost bracts and bracteole from a single involucre, × 40.

Figs. 12, 20, 21 and 22 were drawn from the type specimen; the others from Okamura's specimens.



FIGS 1-11. HARPALEJEUNEA INTERMEDIA EVANS.

FIGS. 12-22. FRULLANIA DENSILOBA STEPHANI.

PROCEEDINGS

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A STUDY OF RHUS GLABRA.

BY EDWARD L. GREENE.

INTRODUCTION.

THE genus *Rhus* as Tournefort restricted it two centuries ago, and as many another systematist since his day has held it, is clearly marked and easily defined. As to habit — that foremost indication of a good plant genus — this generic type stands well aloof from all its allies; even distinctly apart from each and every one of those kindred generic groups which, like *Cotinus*, *Toxicodendron*, *Metopium*, *Lobadium*, *Rhoeidium*, and *Styphonia*, in another than the Tournefortian school of taxonomy, have been thought of as preferably constituting mere subgenera of *Rhus*. But not a species in any of those other genera named makes the least approach to typical *Rhus* in habit. Every species and variety of this appears as a shrub or tree with few stout staghorn-like branches, each clothed heavily near its summit with odd-pinnate leaves, these usually large and of many leaflets. In our silva the only tree which in aspect recalls the sumachs is that naturalized alien, the *Ailanthus*, a genus of no near affinity to *Rhus*. But between the last and its near relative *Schmaltzia* there is no habital resemblance. In this regard they are quite as unlike as are currant bushes and elder trees; and, as for *Toxicodendron*, its habit is as remote from that of *Rhus* as the habit of a grape vine or English ivy is remote from that of walnut trees.

Over and above its marked habit, the characters by which this *Rhus* of Tournefort establishes itself as a model genus are, the terminal origin of its inflorescence, the firmness and compactness of that inflorescence, concurring with small red velvety or plushy drupelets for fruits.

Of the genus, in this which seems to me the most reasonable and natural acceptation of it, there exist in North America, according to classic standards, four species, — *Rhus glabra*, *typhina*, *pumila* and *copallina*.[1]

To the last of these there is attributed a geographic range somewhat incredible for that of any one species of shrub of whatever genus; almost incredible, I say, to any experienced student of climatology as affecting plant life and the distribution of species. But according to the books *Rhus copallina* occurs as one and specifically the same in several widely sundered and very different floral regions. It is said to be common in the hard soil and severe climate of New England, and as much at home in the subtropic lowlands of Florida, twelve hundred miles southwestward; even running away to the arid cactiferous hills of further Texas that lie westward from Florida another thousand miles; and yet again, in a region so extremely different from either of these as that of the Great Lakes in Minnesota and Wisconsin, the same *Rhus copallina*, it is said, recurs.

An European celebrity more than twenty years ago, without field knowledge of the shrubs, and with no experience in problems of North American phytogeography, but using the imperfect light of European herbarium material only, made out and named a half dozen varieties and subvarieties of our *Rhus copallina*;[2] all which work is ignored or suppressed by later American compilers of books; to whom the following out of the vivid suggestions of Engler would entail the expenditure of much time and energy, whereas suppression is of all things the most easily done.

Rhus copallina is one of many hundreds of North American phytologic problems awaiting investigation and solution.

Another of our four species, namely *Rhus pumila*, stands in most marked contrast to the preceding in point of geographic

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[1] Torrey & Gray, Flora of North America 1: 217. Gray, Synoptical Flora 1: 384.

[2] Engler, in DC. Monographiæ Phanerogamarum, 4: 383.

distribution. It is almost local, occurring nowhere but in lower and middle districts of the Carolinas and Georgia.

Rhus typhina, the largest and most tree-like of our species, ranges widely, at least when compared with *R. pumila*. It is catalogued for all the states from Maine to Georgia and Mississippi, thence northward to Minnesota and the Dakotas, but is everywhere less common than *R. glabra*, and more particular than either that or *R. copallina* as to its environment. Everywhere southward it is of the mountains or the hill country only, never coming down to the lowlands or to the seaboard. Neither at the northwest does it come out from its woodland habitat to adorn the copses bordering the prairies where a subspecific ally of *R. glabra* is so much in evidence. It seems to have little adaptability to varying conditions other than those of heat and cold; though in this regard its adaptability is very marked. The climate of Minnesota and the Dakotas, and that of Georgia and Mississippi are extremely unlike as to temperature. Yet between the *Rhus typhina* of the most northerly locality and that of the stations farthest southward, one does not discover notable differences other than those of the size of the shrub and the number of the leaflets. In other respects they seem to be much the same; so that the type is apparently one of a singular degree of stability under somewhat varying conditions.

Concerning *Rhus glabra*, the type species of the genus as to North America, one may note first of all its nearly universal distribution. In this regard it is most unlike any of its congeners here. From beyond the river St. Lawrence northward, down to the very shores of the Gulf of Mexico, its range is across the continent. Within these parallels, into every floral region between the oceans, however different — excepting only that of California — there enters that which, according to the books and lists of plants, is *Rhus glabra*.

There is no one species of tree or shrub of any continent that really holds the geographic range which the books and lists ascribe to *Rhus glabra*. By all the analogies of things there ought to be several marked species or subspecies of this type in the southern Appalachian region between Maryland and Tennessee and Georgia; another and an equally distinguishable set between northern New England and the headwaters of the Mississippi beyond Lake Superior; another species or two peculiar to that vast empire of the Middle West, the prairie country; as many more in that different and equally extensive stretch of country lying between southern Missouri and the shores of the Gulf of Mexico. Then, since there is a *Rhus glabra* all up and down the two thousand miles' length of the Rocky Mountain region, this ought to be thoroughly distinct by plenty of characteristics, and to resolve itself naturally into a number of varieties or subspecies. Just the same should be looked for in the shrub accredited to another empire, that of the Pacific slope northward lying between the sources of the Columbia and Puget Sound; while the scores of isolated mountain ranges rising up out of the deserts of Nevada, Utah, Arizona and New Mexico — for the type in question is there also — should furnish another and presumably the most marked group of *Rhus glabra* segregates.

Our herbaria cannot to-day be supposed to be well supplied with specimens representing this type. No author has investigated it, and no special call has been made for the collecting of these shrubs from different regions. Nevertheless, the mass of material that has been before me during some months past is amply sufficient to enable the investigator to point out characters by which a number of species may be, and reasonably must be, given recognition; characters of foliage in abundance, and characters of the fruiting panicle and the fruit itself.

Perhaps more trying than the task of examining and comparing specimens to find out specific characters, is the great amount of bibliographic work that is necessary in order to determine which one of the several eastern species ought to bear the name *Rhus glabra;* for even this, as indicated — though never described — by Linnæus was an aggregate. In the botanic gardens of Europe several species had been long in cultivation, had been recognized as species and even described as such, when Linnæus in the middle of the eighteenth century came along, and, bundling all the glabrous kinds together, named not any one of them, but the whole bundle of species, *Rhus glabra*.

If Linnæus is to be credited with some one particular *Rhus* *glabra* that we must if possible segregate from the bundle of species which bundle he so named, our task is one demanding the very best skill of both the taxonomist and the historian.

EARLY HISTORY.

Prior to the discovery of America the *Rhus* of all botany was a monotypic genus. It began and ended with *Rhus coriaria*, also by some authors called *Rhus obsoniorum*, a shrub of the Mediterranean region, well known in the useful arts from immemorial ages.

No second species of *Rhus* was known until as late as the year 1620, when Caspar Bauhin, publishing an illustrated quarto containing names and descriptions of more than 600 new plants from various parts of the world, brought to the notice of botanists what he chose to name *Sumach angustifolium*.[1] This was known to have come from the New World, though in an herbarium specimen only. Historically this is the earliest and oldest element entering to the confused *R. glabra* Linn. Bauhin himself in the year 1620 showed a preference for the Arabic name *Sumach*, the exact equivalent of the Greek and Latin *Rhus*; but in his more comprehensive work of three years later, the Pinax, as if having decided to use the Greek and Latin rather than the Arabic name of the genus, he adopts *Rhus*, renaming his new American species, *Rhus angustifolia*.[2]

At the time of its publication in 1620, and long afterwards, the material on which it was founded was believed to have been derived from some island off the coast of Brazil; but a century later, no further specimens of it having been received from any part of South America, and because of its now having come to be known as certainly North American, the idea of its being indigenous to Brazil was abandoned.

In so far as I have been able to examine early records, the next mention of any American *Rhus* is in Banister's Catalogue of Virginian Plants, published in the year 1688. That this was some member of the group of *R. glabra* we are assured by his note that the branches are glabrous. The one with soft hairy

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[1] Prodromus Theatri Botanici, p. 158.

[2] Pinax Theatri Botanici, p. 414.

branches, *R. typhina*, was by this time well known by Bauhin's description of it, and had perhaps already appeared in some gardens in Europe. In 1726 both the hairy and the smooth sumachs were to be found in some London gardens and parks, and in 1732 Dillenius published a folio plate and a full description of what must apparently stand for the *R. glabra* Linn. of 1753.

CHARACTERS FOR SEGREGATE SPECIES.

Linnæus' statement of the characters of *Rhus glabra* reads thus: "Leaflets pinnately arranged, lanceolate, serrate, glabrous on both faces." This is the same as no description at all. If one assume said compound leaf to be odd-pinnate rather than equally pinnate, one does so without any warrant in any word that author said about either the species or the genus. Equally without warrant will be any assumption that the leaf is of 7 leaflets, or that it is of 17, or of 27. Linnæus gives no hint of its character in these most significant particulars. One will also reasonably infer that the leaflets are not notably pointed at the upper end; and whether at base they be stalked or sessile you have no means of judging. It must also be assumed that there is no distinction of coloring noticeable respecting the two faces of the leaf; also whether of a dark-green, or of a bright-green, or of a glaucous or blue-green, one is not informed. Such a description as Linnæus gives of *Rhus glabra* might easily apply to each one of five species, or of fifty, or of five hundred species in a genus. It is therefore worthless for diagnostic purposes.

Coming down from the middle of the eighteenth century to near the close of the nineteenth, we shall find that in American books of American botany the Linnæan diagnosis of *R. glabra* has met with a little amendment. That in Gray's Manual in 1890 reads thus: "Smooth, somewhat glaucous; leaflets 11–31, whitened beneath, lanceolate-oblong, pointed, serrate." The expression, "whitened beneath," is one that helps us to fix on certain shrubs, mostly southern, as representing this author's *R. glabra*; but in New England there are at least two different sumacs which this phrase completely excludes; one of them, inhabiting Massachusetts, shows not even a trace of bloom on the lower face. Both of these, and with them several more species of the east and south, are excluded as having hardly half of the "11–31" leaflets.

In Britton's Manual of 1901 is that of Gray somewhat amplified and therefore less safe. Here Gray's evasive term, "pointed," gives place to the more definitive word "acuminate," but this excludes yet another set of forms in which no leaves are acuminate. Moreover, leaves and leaflets have different ways of being acuminate, in so much that, in order to be able to really describe the apex of the leaflet in each segregate of *R. glabra*, I find it necessary to use such truly definitive terms as subulate-acuminate, cuspidate-acuminate, and such phrases as slenderly acuminate and caudately acuminate. But more unfortunate still is the Britton's Manual description of the leaves as being dark-green above. That indeed applies to what I take for real *R. glabra*, and to several of its Atlantic slope allies: but it holds good in not one of those far-southwestern species of New Mexico, Arizona and Utah, which said Manual goes far out of its way to speak of as forming a part of *R. glabra*. Even in the middle west and far-northwestern districts not a tithe of the definable species can be said to have leaves of other than a dull lightish green.

Finally, the authors of none of the books knew anything of the differences of fertile inflorescences in this aggregate. That these in the fruiting and mature state are narrowly oblong in a few, oblong-fusiform in many, and almost or quite exactly pyramidal in many more, a discovery the importance of which will not be disputed, is a fact which is herein first brought to notice.

It is my belief that even the flowers in some species will be found to present characters available for the further establishment of species here. Both calyx and corolla are far from being the same in all; but I have declined to make any use of these for the reason that in the herbaria exist such multitudes of specimens that are in flower only, and of which the fruiting panicles are yet unknown.

In true *Rhus glabra*, and also in by far the greater proportion of the segregates herein proposed, both branches and foliage are wholly glabrous. In the diagnoses I permit this to be taken for granted, never mentioning such a matter except in the cases of those two or three of the new species in which there occurs a trace of pubescence.

KEY TO THE SPECIES.

* Leaves deep or dark green above (except in No. 9), usually white with bloom beneath.

† Panicles of fruit oblong, or oblong-fusiform.

Leaflets very many, 17–21 or more, and large.
  Leaflets oblong-lanceolate, obtuse at base and subsessile, at apex abruptly pointed............ .... 1. *R. glabra.*
  Leaflets oblong-lanceolate, sessile, slenderly long-pointed. 2. *R. oreophila.*
  Leaflets linear-lanceolate, sessile and auricled at base, at apex caudate-acuminate. ....3. *R. auriculata.*
Leaflets less numerous, commonly 13–17.
  Leaflets lance-oblong, tapering abruptly at base and less abruptly at apex...4. *R. ithacensis.*
  Leaflets oval to oblong-lanceolate, merely acute at apex. 5. *R. ashei.*

†† Fruiting panicles broadest near the base and pyramidal.

Leaflets rather few (except in Nos. 6 and 8).
  Leaflets 17–21, sessile, oblong-lanceolate, acuminate. 6. *R. pyramidata.*
  Leaflets very large, but only 13–17, subsessile, acute rather than acuminate.. ....7. *R. caroliniana.*
  Leaflets 19–23, narrowly oblong-lanceolate, obtuse at base, the apex subulate-linear..8. *R. atrovirens.*
  Leaflets 13–17 and small, oblong-lanceolate, coarsely serrate, slenderly acuminate. ....9. *R. pulchella.*
  Leaflets only 11–15, notably thin, attenuate-acute. 10. *R. ludoviciana.*
  Leaflets 11–13, small but firm, subpetiolulate, abruptly but sharply acuminate.. ....11. *R. arbuscula.*
  Leaflets 13–15, large, petiolulate, subfalcate, sharply acuminate. 12. *R. petiolata.*
  Leaflets 13–17, oblong-lanceolate, subpetiolulate, triangular-subulate at apex...13. *R. valida.*
  Leaflets 13–15, sessile by a rounded base, the apex short, slenderly attenuate....................................... ....14. *R. longula.*
  Leaflets only 11–13 and small, sessile, subulate-acuminate, their rachis pubescent....................................15. *R. sandbergii.*

* * Leaves ample (except in No. 25), of a lighter green above, less glaucous beneath. Panicles in almost all pyramidal. All the species far western and northwestern.

Leaflets 13–17, subsessile, sparsely pilose, subulate-acuminate. 16. *R. borealis.*

Leaflets 11–13.
Large, sessile, subfalcate-oblong, abruptly broad-pointed. 17. *R. media.*
Oblong, subsessile, abruptly acuminate ....18. *R. cismontana.*
Large, acutish at base and subpetiolulate, abruptly short-pointed. 19. *R. sambucina.*

Leaflets 13–17.
Shining above, sessile by an obtuse base, cuspidately acute. 20. *R. nitens.*
Checkered light and dark green above, subsessile, cuspidately acuminate ....21. *R. tessellata.*

Leaflets 9–15, oblong-lanceolate, sessile, acuminate. 22. *R. macrothyrsa.*

Leaflets 17–19, oblong-linear, sessile, acutish at base, long-acuminate. 23. *R. arguta.*

Leaflets 13–17, oblong, sessile, obtuse at base, the apex merely acute. 24. *R. aprica.*

Leaflets 11–13, narrowly lanceolate, sessile, acuminate. 25. *R. occidentalis.*

* * * Leaves smaller, of fewer leaflets, altogether pale, very glaucous beneath. Panicles small, less definitely pyramidal. All of arid southwestern regions (But No. 9. *R. pulchella*, of the southern Appalachian mountains is naturally of this group).

Leaflets 11–15.
Sessile, oblong-lanceolate, short-acuminate...........26. *R. albida.*
Petiolulate, subfalcate-lanceolate, slenderly acuminate. 27. *R. elegantula.*

Leaflets 9–11, sessile, oval to oblong-lanceolate......28. *R. sorbifolia.*

Leaflets 7–9, subsessile, lanceolate, slenderly acuminate deeply incise-serrate ....29. *R. asplenifolia.*

1. RHUS GLABRA Linnæus.

Rhus ramis ex stipite pullulantibus glabris, Banist. Catal. in Ray, Hist. 2: p. 1928. 1688.

Rhus Virginicum panicula sparsa, ramis patulis glabris, Dillen., Hort. Elth. p. 323, t. 314. 1732.

Rhus glabra Linn. Sp. Pl., p. 265. 1753, in part, excluding both the shrub of C. Bauhin and that of Catesby.

Rhus glabrum, Mill. Dict. 1768?

Shrub commonly 2–3 m. high, with very few and stout divergent branches: leaves mostly 5–7 dm. long, the rachis and petiole very stout, the latter 1–1.5 dm. long; leaflets about 17–21, not crowded, very large, 8–13 cm. long, 3–3.5 cm. wide, oblong-lanceolate, subsessile, abruptly and not slenderly acuminate, evenly serrate, the serratures 12 or 13 on a side, texture in maturity rather firm but not subcoriaceous, upper face deep green and smooth, lower face glaucous but not excessively so: staminate panicle very large, often 3 dm. high, pyramidal, almost 2 dm. wide at base in the largest, the pistillate, when in flower nearly as long but fusiform, less than 1 dm. wide up and down the middle part, in fruit oblong-fusiform, 6–10 cm. wide below the middle; drupelets very many, round-ovate.

This is the common and apparently the only glabrous *Rhus* of the Potomac Valley in southern Maryland and eastern Virginia, ranging eastward and northward through southern Pennsylvania, to Delaware, New Jersey, and to Connecticut, if I refer here a flowering specimen in the National Herbarium from Green's Farms, 1894, by C. L. Pollard. The type from which the above description is drawn is the shrub as it grows in the District of Columbia, and up and down the Potomac above Georgetown.

The choice between this and the next for something to bear the name *R. glabra* Linn. is made rather arbitrarily, perhaps; for either one may have been that grown in the Eltham garden and figured by Dillenius. The two are distinct by their fruiting panicles, and the fruit of the Dillenian type was unknown, because only the staminate shrub was raised from the seed by which it was introduced into Europe. As to the size of the leaves and leaflets, however, the present species alone answers to the account given by Dillenius; hence the probability in favor of this as identical with his.

Since Linnæus himself did not describe the species; and since the one only synonym, quoted by him which carries with it a description is that of Dillenius, the name *R. glabra* must be applied here unless it be left to fall into synonymy altogether.

Philip Miller, as a contemporary of Dillenius and Linnæus, and as a cultivator of these shrubs, might have been expected to identify correctly the *R. glabra* of Linnæus when he adopted the name; yet to what he so named in his Dictionary, the name *glabra* does not really apply, for he describes its branches as downy, thus awakening a doubt as to whether his *R. glabra* was not some possible segregate of *Rhus typhina*.

2. RHUS OREOPHILA, sp. nov.

Shrub 2–3 m. high: leaves 3–4 dm. long, the petiole 6–8 cm. long: leaflets 19–27, closely approximate, not of the largest, 7–9 cm. long, 2.5 cm. wide, narrowly oblong-lanceolate, sessile, rather slenderly acuminate, lightly and almost obsoletely serrate, the serratures 10–12 on each side, texture firm, almost subcoriaceous, lower face whitish with a dense bloom, upper face by no means deep or dark green, of a rugulose-roughened rather than smooth surface: fruiting panicle large and much elongated, oblong-fusiform, 18–28 cm. long, only about 5 cm. wide, very compact, the drupelets subglobose, nearly 5 mm. in diameter.

Mountain districts of Maryland, Virginia, the Carolinas and eastern Tennessee; not in the lower hill country of the Potomac Valley outside the mountains, nor at all northward. The type specimen in the National Herbarium is on sheet No. 327800, from Chapel Hill, North Carolina, by W. W. Ashe, no date of collecting given, nor any specific locality. Two sheets from the Biltmore Herbarium, the material gathered at different dates in 1896 and 1897, without indication of either the collector or special station, except the name Biltmore, represent the species beautifully. So does another, from the mountains of Cocke County, Tenn., by Mr. Thos. H. Kearney, September 14, 1897. Yet another U. S. Herbarium specimen, in good foliage but young fruit, is from near Luray, Va., by Mr. and Mrs. Steele, August 30, 1901.

The species is in contrast with *R. glabra* by smaller leaflets, with denser bloom beneath, and a longer, narrower thyrsus of larger and more closely compacted drupelets.

It may not perhaps be determinable to a certainty that the preceding rather than this, was grown in London, and formed the type of Dillenius' figure of leaves and staminate panicle. But Banister's field, and probably that of Catesby also, by both of whom seeds were sent to England, was the lower country, where only what I have here called *Rhus glabra* is found.

3. RHUS AURICULATA, sp. nov.

More slender than *R. glabra*, all the parts somewhat smaller, the fruiting panicles especially only about one-third as large: leaves 2.5–3.5 dm. long; leaflets about 19, approximate, often alternate, 7–10 cm. long, never more than 2 cm. in width, often less, of linear-lanceolate outline, the apex caudately long-attenuate, the sessile base showing definite though small auricles, the serratures light but rather close, 14–18 on a side, texture subcoriaceous, the upper face light green, transversely rugose, the somewhat sunken veins correspondingly prominent on the very glaucous lower face; fruiting panicles oblong or slightly verging toward the pyramidal, 10–13 cm. high; drupelets comparatively few, large.

A remote southwestern ally of *R. glabra*, with very definite specific marks. It is known to me only as collected by Mr. C. L. Pollard, August 11 to 12, 1896, the special locality, Agricultural College, Oktibbeha County, Mississippi. The type specimen occupies sheet 271931 of the National Herbarium. There is a duplicate in Herbarium Field Museum which I have seen. Mr. Pollard's distribution number 1261 is on these two of his labels that I have seen.

The species must quite surpass *R. glabra* in beauty. Its narrow slender-pointed leaflets seem to droop from the rachis rather than to spread away from it horizontally. This, however, is characteristic of several other allies of *R. glabra* belonging to regions lying westward.

4. RHUS ITHACENSIS, sp. nov.

All the parts smaller and more slender than in *R. glabra*, the branches not glaucous, seldom glaucescent: leaflets 13–17, sessile by an abruptly acutish base, 6–7 cm. long, saliently serrate, the serratures 13–15 on a side, upper face dull deep green, lower glaucous but less so than in *R. glabra*, the texture thinner: fruiting panicle small comparatively, long-peduncled, 12–18 cm. long, oblong fusiform, not very compact, its branches thinly tomentellous: drupelets below medium size, notably smaller than in *R. glabra*.

Seems to take the place of *R. glabra* everywhere to the westward of the Alleghenies in western Pennsylvania and New York, and in northern Ohio. The station for the type is near Ithaca, New York, as the name might indicate; the type specimen is on sheet No. 225037 U. S. National Herbarium; was collected at Fall Creek, September, 1893, by K. M. Wiegand. Sheet 292227 is the same from Westmoreland County, Pennsylvania, 1878, by P. E. Pierron, consisting of uppermost leaves and a panicle each of staminate and pistillate flowers. It is also in U. S. Herbarium in flower only, from Elyria, Lorain County, northern Ohio, as collected in flower only by A. E. Ricksecker, August 1, 1894.

Excellent specimens, true to the type, are in the Herbarium of the Geological Survey of Canada as follows: sheet 34165 from Sandwich, Ontario, by John Macoun, July, 1901; also another from Bellville, Ontario, by the same as early as 1867, this in male flower only.

All the so-called *Rhus glabra* from the geographic region so indicated, differs from the southern *R. glabra* and the New England *R. pyramidata* in points quite sufficient to establish it in the rank of at least a strong subspecies.

5. RHUS ASHEI (Small).

Rhus Caroliniana Ashe, Bot. Gaz. **20**: 548, 1895, not of Miller, Dict. 1768.

Schmaltzia Ashei Small, Fl. 729.

Shrub erect but low, only 3–5 dm. high; leaflets 13–17, oval to oblong lanceolate, 5–7 cm. long, acute, not acuminate, sessile, rather coarsely subserrate-dentate, the teeth about 10 on each side, pale beneath but not glaucous: panicle of ovoid outline, large for the plant, 10–15 cm. long.

In old fields and low woods of middle North Carolina, collected by Ashe, who correctly indicated it as a good new species but under a name long preoccupied.

6. RHUS PYRAMIDATA, sp. nov.

Both the shrub and its foliage smaller than in *R. glabra*, the mature leaves firmer, almost subcoriaceous, equally white with bloom beneath, the whole leaf 3 dm. long or less; leaflets 17–21, sessile, oblong-lanceolate, acuminate, lightly serrate, the serratures 12–16 on each side: fruiting panicle large, notably compound, the primary branches being again widely branched, the whole subpyramidal, 8–12 cm. wide toward the base and only 12–18 cm. high; drupelets very numerous, smaller than in southern allies, 3 mm. wide, suborbicular inclining to ovate.

This definition I trust may prove to include a large part of what has been called *Rhus glabra* in northern New York, New England and adjacent Canada. That which I wish to cite as the type specimen is on sheet 312308 of the National Herbarium, and was collected near Lake Waccabuc, Westchester County, New York, by Mr. C. L. Pollard, August 12, 1894. The locality lies easily within the range of Colden's field studies made in the middle of the eighteenth century or earlier. It might therefore be guessed that *R. pyramidata* also entered into, and formed a part, bibliographically speaking, of Linnæus' aggregate *R. glabra*. But this cannot be established as a fact; nor would it alter the situation in the least if it could be; for Colden did not describe the shrub, and his work is of later date than that of Dillenius, to which we are obliged to resort for any described and definable thing that may bear the appellation *Rhus glabra* Linn.

The *Rhus glabrum* of Philip Miller, which he said was from New England, and which he reported as cultivated in his time under the name of New England Sumach, cannot have been the present species; for he attributes to that "downy" branches, as I have already remarked under *R. glabra*.

There is presumptive evidence in the herbaria of the existence in southern New England of at least two more species, the diagnoses of which cannot be safely made for want of fruiting panicles. One of these I have seen only in the herbarium of the Field Museum, sheets 13682 and 18510. Both specimens were collected and distributed by the late D. C. Eaton, somewhere near New Haven; no date. Another is from South Hadley, Mass., 1887; the collector's name illegible. This is on sheet 275445 of U. S. National Herbarium. By evident marks of foliage and detached flowering panicle this is certainly distinct from all others known, and nearest *R. ithacensis*, unless the panicle be pyramidal.

7. RHUS CAROLINIANA Miller.

Rhus glabra, panicula sparsa coccinea, Catesby, Carol. App. 4, t. 4.
Rhus glabra Linn. Sp. Pl. 2 ed. 380 (1762) in part only, and as to the shrub of Catesby.
Rhus Caroliniana Mill. Dict. ed. 1768.
Rhus elegans Ait. Hort. Kew. **1**: 365. 1789.

Shrub 2–3 m. high: leaves large, but of only 13–17 leaflets, these not closely approximate but large, commonly 8–11 cm. long, 2–3 cm. wide, subsessile, acute rather than acuminate, strongly serrate, the serratures about 9 on a side, upper face deep green, lower glaucous: fruiting panicle large and not compact, exactly pyramidal, 2 dm. long or more, 1.5 dm. wide at base; drupelets uncommonly small, bright scarlet rather than dark-red in maturity.

A South Carolinian species, collected, described and illustrated by a large folio plate, in the middle of the eighteenth century, by Catesby, who also was the medium of its introduction into English parks and gardens at the same time; from which, also, it is probably long since lost. That it is thoroughly distinct from *R. glabra* Catesby's description and figure demonstrate, to all who know *Rhus glabra*. Philip Miller also knew it to be distinct, and in the year 1768 gave it the trivial name of *R. caroliniana*. Again, as still grown in Kew Gardens twenty years later than the date of Miller's work, Aiton, as if ignorant of Miller's name *R. caroliniana*, published it again as distinct from *R. glabra* under a new name, *R. elegans*.

From a highly instructive paper on some small trees observed in Georgia, published by Mr. Roland M. Harper last year,[1] it appears to me probable that this zealous explorer of southern fields and woods has, without knowing it, rediscovered this large scarlet-fruited *Rhus* of Catesby. Mr. Harper says that he found what he took for *Rhus glabra* "in a cane-brake on the bank of the Coosa River, in Floyd County, about twelve miles below Rome, Georgia, a veritable little grove of this species, in which many of the specimens were as much as seven inches in diameter and thirty feet tall, with the lowest branches higher up than I could reach." Mr. Harper describes the drupelets of this tree as "bright scarlet," just the color mentioned by Catesby more than a century ago, as being one among several marks by which *R. caroliniana* was to be distinguished readily from the then well known *R. glabra*, the fruits of which are unvaryingly of a dark crimson when mature.

8. RHUS ATROVIRENS, sp. nov.

Stout upright shrub, the young branches and lower face of foliage not very glaucous: leaves about 3 dm. long, with unusually stout petiole and rachis, the whole more firm and ascending than in allied species: leaflets about 23 and closely approximate, subcoriaceous, of a dark green above, pale but not white beneath, of only middle size, 5–7.5 cm. long, narrowly oblong-lanceolate, subsessile by an obtuse base, the apex subulate-linear, entire, the serratures of the margin, though obscure very numerous, 16–22 on each side: panicle of fruit narrowly pyramidal, 1.5 dm. long, compact; drupelets larger, than in the last, quite rotund, 4 mm. wide, deep crimson as in most species.

Mountain region of northern Alabama; type in the National Museum No. 19814, from near Gadsden, 1888, by Gerald McCarthy. Distinguished from one and all the foregoing by its narrow and crowded dark green and rather rigid leaflets.

9. RHUS PULCHELLA, sp. nov.

Branches not stout, angular, glaucous, minutely lenticellate: leaves not large, about 2 dm. long, rather long-petioled, of a

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[1] Torreya, 5: 163.

somewhat glaucescent green above, very glaucous beneath; leaflets 13–17, small, sessile, drooping on the rachis rather than spreading away from it on the same plane, oblong-lanceolate, 5–6 cm. long, slenderly acuminate and somewhat irregularly and coarsely serrate-toothed below the acumination, as well as more lightly and evenly serrate in the middle: panicle pyramidal, small, about 8 cm. long, slender-peduncled, somewhat recurved or drooping.

Known only from Yellow River, near McGuire's Mill, Guinnett County, Georgia, July 11, 1893, John K. Small; type in National Museum, sheet No. 19816. A small and very graceful species, recalling some of the far-southwestern forms found in Arizona.

10. RHUS LUDOVICIANA, sp. nov.

Shrub with quite slender branches, the foliage not large ascending, glabrous except as to the hairy line of the rachis, about 2.5 dm. long; leaflets 11–15, opposite, of thin texture even in full maturity, dull green above, moderately glaucous beneath, 5–8 cm. long, attenuate, acute rather than acuminate, evenly serrate, the serratures 12–16 on each margin: panicle small, pyramidal, 8 cm. long, 4 cm. broad toward the base; drupelets obliquely orbicular, of a dark red-purple and not strongly pubescent.

The type specimen is in my own herbarium, from along the seaboard in southwestern Louisiana, at Cotes Blanches, October 10, 1884, by A. B. Langlois. A strongly-marked, probably small species, said to form low thickets in a peculiar maritime region that is still almost unknown botanically.

If the *Rhus angustifolia* Bauhin, believed to have come from the coast of Brazil, was derived from some North American coast by that voyager of nearly or quite three centuries ago, it would be easy to fancy that the specimen in Burser's herbarium, which became Bauhin's type, was from some shore of the Gulf of Mexico, and even may have been identical with what is here described as *R. ludoviciana*, and which is the only known maritime ally of *R. glabra*. And that which may elevate this fancy almost or quite to the rank of a probability is the at least highly interesting coincidence that my type specimens of *R. ludoviciana* bear the only leaves and leaflets known to me that answer to Bauhin's description of those of Burser's specimen. He gave the number of the leaflets, their form and dimensions, the serrated character of their margin, and the narrowly attenuate apex, not omitting mention of the darker green upper and paler lower faces of the leaflets.

This, as I have said before under *R. glabra*, is the earliest element, historically speaking, that enters into Linnæus' aggregate; and had the latter described his *Rhus* species as carefully as Bauhin had described his a hundred and thirty years before him, the task of the twentieth century botanist at this juncture would have been much less difficult.

11. RHUS ARBUSCULA, sp. nov.

Shrub low, tree-like in form though commonly less than 1 m. high: branches of the season glabrous, glaucous, obscurely angled, not very stout, but foliage large and ample; largest leaves 3 dm. long, of 11 to 13 rather remote leaflets, these lance-oblong, 7 to 9 cm. long, often subfalcate, notably inequilateral at base, never quite sessile, the petiolule definite though very short, upper face of leaflets light or deep-green, the lower very glaucous; serratures moderately salient, 10 to 15 on each margin, the apex abruptly and sharply acuminate: panicle pyramidal, very small for the foliage, usually but 7 to 9 cm. long; drupelets of the smallest.

Near Culver, Marshall County, Indiana; collected August 18, 1906, by Mr. H. Walton Clark, of the United States Bureau of Fisheries.

The type locality, and thus far the only known station, is a barren hill above the eastern shore of Lost Lake, near Culver, Indiana. The specimens at hand are two, both of them excellent, but evidently not from the same bush, and, as I suspect, from somewhat different exposures. One of them has a maturer foliage beginning to redden for the autumn; and the branch, as well as the rachis of the leaves in this all show much bloom.

This I designate as the type specimen. The other differs only in having foliage of a clear and vivid green, and the stem shows but little bloom. Both specimens have been presented to, and will be preserved in, the U. S. National Herbarium.

12. RHUS PETIOLATA, sp. nov.

Branches not stout, glabrous, glaucous, striate, roughened also by small and very protuberant lenticels: leaves ample, not long, though long-petioled: leaflets about 13, large, 8–10 cm. long, oblong-lanceolate and often subfalcate, distinctly petiolulate, the base obviously inequilateral, apex sharply acuminate, the sides sharply but unevenly serrate, the serratures 13 to 15, upper face of leaflets of a rich deep green, the lower very glaucous: panicle small for the foliage, pyramidal, 10 cm. high, compact, the branches thinly and rather stiffly hirtellous; drupelets rather large.

Prairie region of the interior of Minnesota, the type from near Spicer, Minn., August, 1892, W. D. Frost, Herb. Field Mus. sheet No. 140259. Well marked by the large definitely petiolulate leaflets.

13. RHUS VALIDA, sp. nov.

Branches very stout and robust, upright, at the end of the first season no longer glaucous but light brown, between cinnamon and chestnut-color, striate, copiously lenticellate: leaves not large in proportion, less than 3 dm. long; leaflets about 15, approximate, short-petiolulate, oblong-lanceolate, 6–10 cm. long, with about 11 serratures on each margin and a short triangular-subulate point, texture subcoriaceous, upper face dull deep green and transverse-rugose, lower fairly glaucous but not white: panicle rather oblong-pyramidal, large, 12–14 cm. high, its branches thinly tomentulose-pubescent: drupelets many, large, little compressed, rather thinly plushy.

Even in the herbarium specimens this impresses one as something wholly apart from any and all eastern and southern shrubs that have been called *R. glabra.* The very stout striated, lenticellate and upright branches, with smallish foliage evidently more ascending than is usual in the genus, and the large rather narrow panicle — all these marks indicate a species, and one possibly somewhat local about Lake Michigan. The type specimens, all in Herbarium Field Museum, are from Hinsdale, a suburb of Chicago, and were collected October 12, 1902, by Ernest C. Smith, his distribution No. 577. I also refer here without hesitation Mr. O. E. Lansing's No. 1111, as in Herbarium Field Museum, from West Pullman, Ill., September 8, 1900.

Later than all these are specimens sent me late in August, 1906, from near Nashotah, Wisconsin, by Dr. H. V. Ogden of Milwaukee. These came to hand after the above diagnosis of *R. valida* had been finished, and the type specimens returned to the Field Museum. But they answer perfectly to my description of the species in every particular, and therefore only further confirm it while extending its range.

14. RHUS LONGULA, sp. nov.

Stem and branches not known: leaves about 3 dm. long, with long stout ascending petiole, and 13 or 15 approximate leaflets, these 7–9 cm. long, sessile by a rounded base, the apical acumination short though slenderly attenuate, the margins lightly and almost subcrenately serrate with about 11 or 12 serratures, texture firm, hardly subcoriaceous, color dark dull-green above, whitish-glaucous beneath: fruiting panicle narrowly oblong and greatly elongated, 18 cm. long, hardly 5 cm. wide at the widest part, the short branches hirtellous-tomentulose; drupelets of middle size and numerous.

Bluffs of the Mississippi River far northward; the special station for the type somewhere near Stockton, Minnesota; the type specimen in U. S. Herbarium, No. 19813, collected by Mr. John M. Holzinger, August 23, 1888. Also on sheet 19811 is a flowering specimen by the same collector, of "May, 1889," which appears to be the same specifically. The station for this is not named.

That *R. longula*, away at the western North should flower in May is noteworthy; for its ally, *R. glabra*, so far southward as the valley of the Potomac does not begin to flower until July.

The eastern analogue, *R. ithacensis*, in Pennsylvania, does not come into flower before the end of July or early August. These segregates of *R. glabra* from the northwest, by their almost vernal flowering, reassert for themselves a more distant relationship to the eastern types than that which we should infer from their visible characters alone.

15. RHUS SANDBERGII, sp. nov.

Rhus glabra var. *sandbergii*, Vasey & Holzinger in Herbarium Field Museum.

Very dwarf, flowering and fruiting freely at 1.5–2 dm. high; branches of the season 4–5 cm. long, angular, rusty-tomentulose and with also a few hirsute hairs, older branches glabrate: leaves small, barely 1.5 dm. long, the slender rachis pubescent on all sides; leaflets 11–13, sessile, oblong-lanceolate, 4–6 cm. long, appressed-serrate, the serratures 15–17 on each margin, apex subulate-acuminate, both faces nearly or quite glabrous, the upper deep green, the lower glaucous: panicle very small, seldom exceeding 5 cm. long, subpyramidal, its branches densely and subtomentosely hirsute: drupelets of the ordinary size and color.

Said to grow in crevices of rocks, near the head of Lake Superior at Thompson, Minnesota, where it was collected in flower in July, and in fruit in August, 1891, by J. H. Sandberg, who afterwards distributed it under numbers 401 and 921. His locality for it is the only one known. I would indicate as the type specimen the fruiting one on sheet 19898 of the National Herbarium. Happily Mr. Sandberg, unlike most collectors of *Rhus* specimens, gathered this in both flower and fruit.

Prof. John M. Holzinger of the Normal School at Winona, Minnesota, would have proposed this species as new, in his paper published in the Minnesota Botanical Studies, part 8, in 1896, but was deterred by the opinion of some authority who would have reduced *R. typhina* and *R. glabra* to one species, with this as a connecting link between them.

16. RHUS BOREALIS, sp. nov.

Shrub evidently large but not stout, at least as to the branches, these smooth, glabrous, glaucous: leaves ample as to breadth, but not greatly elongated, 3 dm. long, the usual hairy line of the rachis quite hirsute, but other parts of the rachis, and also the midvein of the leaflets on both faces showing a few pilose hairs; leaflets 13–17, subsessile, broad and approximate, oblong-lanceolate, 8–11 cm. long, subulate-acuminate, coarsely and closely subcrenate-serrate, the serratures about 14 on a side, texture of leaflet uncommonly thin, upper face of a light but rather lurid green, the lower glaucous almost to whiteness: panicle not large, 11 cm. long in fruit, narrow-pyramidal, distinctly pedunculate, the peduncle and branches of panicle hirsute, the hairiness more or less distinctly retrorse: drupelets larger than the average and of a lighter color, being bright crimson.

Central Michigan near Alma, on dry ridges, collected August 12, 1895, by Charles A. Davis, the type specimen in the Herbarium of the Field Museum, Chicago. A fine species, perhaps common enough in central Michigan, and probably beyond the boundaries of the State southward, a region in which little or no effective collecting has been done in late years. But there is a poor flowering specimen, or fragment, in the National Herbarium which, by the one leaf it bears, I can refer here. This appears to have been sent by Mr. Beale, in 1899; but there is nothing to indicate who collectêd it, or where. Although pubescent, this bears no relation to *R. hirta*.

17. RHUS MEDIA, sp. nov.

Branches rather sharply angular in maturity and sparsely dotted with small lenticels: leaves large but not elongated, only 2 dm. long, rachis not stout, whitish with bloom, glabrous except as to a tomentulose line; leaflets about 13, large, sessile, oblong or subfalcate-oblong, broadly and abruptly pointed rather than acuminate, appressed-serrate, the serratures 13–15 on a side, the whole leaflet of firm texture and about 8 cm. long, 2–2.5 cm. wide, of a dull lightish green above, quite glaucous beneath:

fruiting panicle rather lax, slender-peduncled and as if somewhat drooping but of pyramidal outline, its branches rather finely pubescent; drupelets of middle size, notably oblique, acutish.

Inhabits the region of scattered woodlands and small prairies in southern Michigan and northern Indiana and Illinois, if I rightly refer to it rather numerous specimens, collected in various places, all in young leaf and flower only. Such are in the herbaria from Warrenville, Ill., by L. M. Umbach, July 2, 1895, and by Charles C. Deam at Bluffton, Indiana, 1897; but the type sheet, No. 124146 of the Field Museum, a perfect fruiting specimen, is from Jackson County, Michigan, by S. H. and D. R. Camp, September 19, 1898. Sheet 6072 of the same herbarium, from Stark County, Illinois, may or may not be the same. Its detached fruiting panicle may well belong here, but the one leaf shown is attached to a flowering branch, and therefore immature.

18. RHUS CISMONTANA, sp. nov.

Shrub doubtless low, all its parts reduced in size and rather slender as to branches and leaf-rachis, all these pale and glaucous: leaves 1.5–2 dm. long, ascending; leaflets 11–13, not crowded, of a pallid green above but only glaucescent beneath, mostly oblong and abruptly acuminate, 4–6 cm. long, only subsessile, or some of the more basal leaflets definitely petiolulate, sharply and rather closely serrate, the serratures 10–12 on each side, even the most mature state of foliage not subcoriaceous, though firm: fruiting panicle about 9 cm. high, pyramidal but narrowly so and compact; outline of drupelets slightly inclining to ovate, being a trifle longer than broad, not depressed but rather acutish at summit.

Open hills of the more westerly parts of Nebraska and Kansas, as well as probably in adjacent Colorado, if not Wyoming. The type specimens are in U. S. Herbarium No. 210241, collected by Mr. Rydberg in Thomas County, Nebraska, 1883; and Mr. J. B. Norton's so-called *R. glabra* from Riley County, Kansas, collected in 1895, appears to be quite the same; probably even Mr. Clements' specimens from northeastern Nebraska, 1893, belong here, for, while in these the foliage is larger, the leaflets seem to have all the marks of *R. cismontana*, even to the petiolules, these being very evident.

19. RHUS SAMBUCINA, sp. nov.

Stem and branches unknown: leaves of few leaflets, the whole leaf, including the rather long petiole, little more than 2 dm. long, the leaflets 11 or 13, approximate, large, 7–10 cm. long, oblong-lanceolate, acutish at base and subpetiolulate, the apical acumination rather abrupt and short, the sides with 11 or 12 quite large and sharp serratures, the texture of mature foliage not known, color of upper face a pale glaucescent green, of the lower only paler, with nothing of the white bloom of real *R. glabra:* panicle not pyramidal even in flower, but rather oval, or at most oval-subpyramidal, in fruit oval, decidedly lax, the branches villous-pubescent; drupelets of middle size.

Singular species, with broad short leaves made up of few and much serrated leaflets, all pale green on both faces. The locality of this is remote and but little known. The type specimens are in Herbarium Field Museum, sheet 140404, and are from near Piedmont, South Dakota, by Alice Pratt, June and August, 1895. Unfortunately only the young foliage is present; the one fruiting panicle was preserved only as detached from the branch; yet this matches perfectly, in its peculiar branching and laxity, the flowering panicles.

In the same herbarium, sheet 123606, are flowering specimens of what seems to be the same, from southern Iowa, Decatur County, T. J. Fitzpatrick, June 13, 1896.

20. RHUS NITENS, sp. nov.

Shrub stoutish, perhaps low, young branches and also petioles and lower face of foliage merely glaucescent: leaves short and short-petioled, the whole leaf barely 2 dm. long, the petiole and rachis stout, ascending; leaflets 13–17, closely approximate, seldom opposite, lance-oblong, 4.5–6.5 cm. long, subcoriaceous, sessile by an obtuse base, the apex cuspidately acute rather than acuminate, evenly but not deeply serrate, the serratures 10–12 on a side, upper face of a lightish green but somewhat polished, the lower only pale, not whitened: fruiting panicle small, only about 8 cm. high, definitely pyramidal, its branches short, sparsely hirtellous: drupelets immature but perhaps full grown, orbicular, or a little broader than high.

At 6000 feet in the mountains near Provo, Utah, July 10, 1894, as collected by Mr. Marcus E. Jones, his No. 5612 as in the National Herbarium. This differs from all other far-western species in that its foliage is almost as highly polished as that of *R. copallina*.

21. RHUS TESSELLATA, sp. nov.

Shrub low, copiously and densely leafy, the leaves rigidly ascending, about 2.5 dm. long, the pinnæ approximate; leaflets about 15, lance-oblong, 5–7 cm. long, not quite sessile, cuspidately acuminate, evenly and quite sharply serrate, the serratures 13–17 on a side, the texture subcoriaceous even at flowering time, upper face very smooth and somewhat shining, in general dark green, showing very prominently the fine whitish midvein and veinlets, but some intervals between veinlets wholly of a light green, exhibiting the whole surface as notably checkered, lower face merely pale and glaucescent, not glaucous: panicle small for the foliage; fruit not seen.

Foothills of the Rocky Mountains in northern Colorado, at altitudes of 6000 to 7000 feet; type specimen in U. S. Herbarium No. 257466, collected by J. H. Cowen, July 20, 1895; no special locality mentioned. The species by leaf characters alone is a very good one, even if the checkering of dark and light green be but accidental or occasional. The species here defined may or may not include all the so-called *R. glabra* of eastern Colorado mountains.

22. RHUS MACROTHYRSA Goodding.

Rhus macrothyrsa Good. Bot. Gaz. 37: 56. 1904.

Shrub 1.5–2.5 m. high, glabrous except as to vigorous young growing shoots, these at base ferruginous-tomentose: leaves 2–2.5 dm. long; leaflets 9–15, green above, not glaucous beneath, oblong-lanceolate, sessile, acuminate, sharply serrate:

fruiting panicle open, large, oblong-fusiform, 15–25 cm. long, recurved, its branches coarsely pubescent: drupelets little compressed, 3 mm. wide.

Calientes, Nevada, 1902, L. N. Goodding. No specimens seen by the writer, but by the description the species must be distinct enough, and probably local in southern Nevada.

23. RHUS ARGUTA, sp. nov.

Shrub said to be 1–3 m. high, the branches stoutish, smooth, glabrous, glaucous even in full maturity; leaves notably ascending rather than spreading, 3 dm. long, the petiole uncommonly elongated and, like the rachis, very glaucous; leaflets 17 or 19, narrowly oblong-linear or subfalcate, 6–8 cm. long, sessile by an acutish base, closely, sharply and saliently serrate, the serratures 15 or 16 on a side, the acumination long and narrow, upper face deep green but dull, the transverse veins conspicuously paler, lower face very glaucous: panicle not large, 10–12 cm. high, pyramidal, its branches hirsutulous; drupelets of the largest.

Species of the Pacific slope, apparently common in the Columbia River region, at least eastward; very possibly an aggregate, resolvable into several; but the type of the above diagnosis is from Rhea Creek, Morrow County, Oregon, and was collected by J. B. Leiberg, September 11, 1894, his No. 893 as in U. S. Herbarium. The following, all from western Washington, are more or less true to this type: sheet 93075 in Herbarium Field Museum, from near Spokane, in flower only; sheet 93076 of the same, from the same region with lax pyramidal panicle very much larger, leaflets larger, greener on both faces and by no means sharply serrate; A. D. E. Elmer, Wawawai, 1897; Frank Kreager, Spokane County, 1902; Sandberg & Leiberg, Rock Island, 1893, and Robert Horner, Waitsburg, 1897, these last all as in U. S. Herbarium, likewise from Idaho, A. A. Heller, Nez Perces County, 1896, his No. 3421. This is quite true to the type as to foliage, but in flower only; a fruiting specimen, from Salmon River, Vernon Bailey, 1895, with leaflets not so typical.

Among all these there is nothing of Torrey's *Rhus glabra*, var. *occidentalis*. Nearly all that I have seen of Pacific coast material which matches that of the Wilkes Expedition, comes not from Oregon or Washington, but from British Columbia.

24. RHUS APRICA, sp. nov.

Dimensions of shrub, and characters of branches unknown: leaves as a whole remarkably broad and short, the leaflets being few and approximate but large, subcoriaceous, deep green above, light green beneath, but without bloom; leaflets about 15, oblong, 6–8 cm. long, obtuse at base and sessile, at apex only cuspidately acute, not acuminate, very evenly and quite distinctly though not sharply serrate, the serratures 10 or 11 on each margin: panicle pyramidal, small, about 8 cm. high, its branches only sparingly and obscurely villous-pubescent; drupelets rather large.

Very well marked by its few and large leaflets green on both faces; but known only as collected by M. W. Gorman, on Camas Creek in the Washington State Forest Reserve, August 20, 1897. It is said to occupy dry open grassy slopes. The type specimen is in U. S. Herbarium. Its label bears Mr. Gorman's collection number 632.

25. RHUS OCCIDENTALIS (Torrey).

Rhus glabra occidentalis Torr. in Bot. Wilkes' Exp. 257. 1874.

Only flowers and young foliage known: leaflets (in what should be the type specimen, U. S. Herbarium sheet No. 19819) 11–13, oblong-lanceolate, sessile, notably acuminate, beneath only glaucescent; the panicle small and very slender peduncled; even the branch slender, but quite glaucous.

The label bears, in the handwriting of Asa Gray, the legend, "Okanogan, Wash. Territory."

The Okanogan region lies partly in Washington and partly in British Columbia, and all the more recent specimens seen by the writer which match the type are from the Canadian part of the region. Sheet 4471 of the Canadian Survey Herbarium, Arrow

Head Lake, near Lake Okanogan, is every way true to the type, except that the leaflets are less numerous; nine in most of the leaves and none with a greater number, a few having seven only. In the same herbarium 4473, from Spence's Bridge, in the same general region, has mostly 13 leaflets. The like is true in the case of number 63749, collected at Cascade, B. C., by Mr. J. M. Macoun in 1902. But all these specimens are in one and the same unsatisfactory condition of early flowering, with foliage, of course, not fully grown. They indicate, however, a northerly species, from which the two Washington species herein characterized are sufficiently distinct. Not, however, until mature foliage and fruiting panicles of it shall be brought to light can *R. occidentalis* be properly described.

26. RHUS ALBIDA, sp. nov.

Probably low, the branches not robust, very light-colored and, with the rachis and lower face of leaves, much whitened with bloom, even the upper face of foliage of a pale color and glaucescent: leaves 1.5–2.5 dm. long; leaflets about 13, not crowded, not deflected but spreading, subsessile, 4–6 cm. long, oval to oblong-lanceolate, abruptly acute or short-acuminate, saliently serrate, the serratures 10–14 on each side: fruiting panicle about 1 dm. high and quite broadly pyramidal, its branches only very delicately but rather densely velvety: drupelets much compressed and acutish.

As far as known this very beautiful *Rhus* is local on the San Francisco Mountain not far from Flagstaff in northern Arizona. The type specimen, sheet No. 410696 of the National Herbarium, was collected there, at an altitude of between 6000 and 7000 feet, August 18, 1901, by J. B. Leiberg, his distribution No. 5871. A perfect male flowering specimen is in my own herbarium, as collected by myself at the same station, July 13, 1889. Again, National Herbarium sheet 334404 holds a flowering branch from the same locality by D. T. MacDougal, his distribution No. 309, July 18, 1898. This, too, from an altitude of about 7000 feet. The late date of its flowering, as an ally of *Rhus glabra* in the generally torrid climate of Arizona, indicates the subalpine character of its habitat.

27. RHUS ELEGANTULA, sp. nov.

Branches slender, glabrous, of a distinctly pinkish brown underneath a coat of bloom: leaves small, 1.2 – 1.8 dm. long, the slender rachis quite white with bloom, its villous line very marked; leaflets 11–15, loosely arranged, spreading or slightly deflected, distinctly petiolulate, 4–6 cm. long, narrowly subfalcate-lanceolate, at least the long and slender acumination falcate, sometimes the whole leaflet, the serratures, about 8 on a side, more or less sharply prominent, the texture rather firm, color of upper face pale bluish-green, the lower whitish with bloom: fruiting panicle large in proportion to the foliage, commonly more than 1 dm. high, pyramidal but narrowly so, its branches thinly villous with ascending or spreading hairs: drupelets small, arranged upon simple racemose branches of the panicle, compressed, acutish.

Mountains of extreme southern Arizona along the Mexican boundary, the typical specimens from about Fort Apache, by Edward Palmer, June, 1890; these on sheet 19808 of the National Herbarium; others distributed by Dr. Palmer under his No. 585. Probably the same as a specimen from the Santa Catalina Mountains, September, 1896 by J. W. Toumey, U. S. Herbarium sheet 441724. Lastly rather larger specimens, but otherwise true to the character, have come in this season from the Huachuca Mountains, sent by Mr. J. C. Blumer, who collected them late in August, 1906.

28. RHUS SORBIFOLIA, sp nov.

Shrub apparently low and not stout, the young branches and lower face of foliage not whitened, hardly paler than glaucescent: leaves small, only 1–2 dm. long, spreading away from the stem divaricately, or even a trifle deflected, the petiole and rachis rather slender; leaflets few, only 9 or 11 and loosely arranged, dull deep green above, glaucescent beneath, of small size, 2.5–6 cm. long, oval to oblong-lanceolate, sessile by an abruptly acutish base, at apex subulate pointed rather than acuminate, rather remotely and sharply serrate, the serratures only 7–9 on each margin: panicle of staminate flowers pyramidal, 12 cm. long: sepals triangular, acute; petals twice as long, oblong, obtuse, the anthers equaling them.

Type from mountains west of Las Vegas, New Mexico, G. R. Vasey, 1881; U. S. Herbarium No. 19510. Species with most characteristic habit and foliage.

29. RHUS ASPLENIFOLIA, sp. nov.

Shrub evidently dwarf or at least low, the leafy branches short, slender, tortuous, glabrous, glaucous: leaves small, about 1.5 dm. long, the rachis slender, deeply and narrowly furrowed and the hairy line obvious; leaflets only 7–9, pale green above, moderately glaucous beneath, oblong-lanceolate to lanceolate, 3.5–5.5 cm. long; subsessile, acuminate, very irregularly and somewhat incisely serrate, even coarsely so, the serratures now and then so deep and large as to amount to lobes rather than serratures: only a staminate panicle seen, this narrowly pyramidal, 5 cm. long.

Type from Wolf Creek, Wyoming, July 12, 1896, A. Nelson, distributed to U. S. Herbarium, under No. 2303, mounted on U. S. Herbarium sheet 285144. Manifestly intermediate between the Nebraskan *R. cismontana* and the characteristic species of Arizona; the foliage peculiar.

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ASPECTS OF KINETIC EVOLUTION.

BY O. F. COOK.

THE kinetic theory of evolution finds in the facts of organic development indications that the characters of species change spontaneously, or without environmental causation. Evolutionary progress is further conceived as accomplished through the union of the normally diverse individual members of species into a coherent network of interbreeding lines of descent, rather than by the isolation of variant individuals or by the selective restriction of descent to individuals possessing particular characters.

Former theories have undertaken to explain the method of evolution by reference to the dendritic figure of descent as shown in the ever-branching relationships of species, genera and families. The kinetic interpretation of the evolutionary process is based on what may be called the intraspecific figure of descent, the relationship of organisms inside the species, which is reticular or net-like, and not tree-like.

Theories based on the dendritic conception of descent may also be described as differential; that is, they have given attention chiefly to the problems of distinction and separation of organic groups. The kinetic theory is integral or synthetic, and conceives the evolutionary process as conducted by the accumulation and combination of the variations which appear among the members of the species.

These simple distinctions are fundamental, and will necessitate an extensive readjustment of methods of thought and investigation in the field of evolution.

Various aspects of the kinetic theory have been presented in earlier essays, of which the present chapters are a continuation. Indeed, it is likely to become apparent to the reader that they have been written at different times and that they often lack unity and consistency. The same ground has in some cases been traversed repeatedly and in different directions, but the frequent restatement of the same distinctions appears to be necessary in the development of so large and complicated a subject. My thanks are due Mr. Walter T. Swingle for much helpful interest and criticism.

1. KINETIC EVOLUTION AND THE FITNESS PROBLEM.

The theory that evolution is caused by natural selection and the survival of the fittest is now commonly admitted to be inadequate, but our studies tend, as usual, to follow the beaten paths of thought, and adjust themselves only with reluctance to new interpretations. The point at which the selection theory becomes obviously deficient is that it does not account for the fitness to which the evolutionary progress is ascribed. This has given rise to the attempt in recent years to penetrate farther into what has been called "the problem of fitness," on the natural assumption that more light could certainly be reached in the quarter whence came the first suggestions of evolutionary illumination. Nevertheless, those who have followed closely on the route of natural selection have not yet come through into regions of clear vision.

Fitness is the primary idea of the doctrine of evolution by selection. Fitness affords the cogs, as it were, by which evolution is supposed to be worked by the environment. Even if we were to admit, for the argument, that evolutionary motion could be caused by selection towards greater fitness, the evolutionary factory would still lack the very important facility for providing these cogs of fitness by which the environment could gain a hold upon the species and roll them along. Some selective evolutionists have assumed that environment could form the cogs by impressing itself upon the species, and others that the species could, as it were, wrinkle itself in response to external stimuli, and thus give the environment a selective impingement.

These suggestions have not been able to retain the full confidence of biologists for the selective theory, as witness the recent remarkable diversions towards Mendelism and mutationism. The prompt acceptance of these doctrines by so many students of evolution is not justified by any indication of general pertinence for the facts on which they are based. They met with immediate welcome because they afforded a suggestion, at least, of methods by which new characters or character-combinations could be produced. They promised, in other words, the long-needed supplement of the selective theory, the cogs which selection might turn.

The kinetic theory recognizes that evolution does not depend upon selection nor upon the environment, and still less upon mutation and Mendelism. The evolutionary causes are in the species, not in the environments. They are resident, moreover, in species as constituted in nature, and are exemplified only abnormally in the phenomena which become prominent in the close-bred domesticated plants to which the studies of Mendel and De Vries were mostly directed.

TWO TYPES OF ORGANIC FITNESS.

The current belief in the environmental causation of evolution is largely due to the confusion of two different kinds of organic fitness. (1) The general fitness of the species for the environments in which they exist; and (2) the special fitness or power of adjustment of the individual organisms to particular conditions which they may encounter. An interesting example of the extent to which these two distinct phenomena have been confused may be found in so well known a work of reference as the Standard Dictionary. Adaptation is defined as "an advantageous conformation of an organism to changes in its environments," but the quotation given to illustrate the use of the word in this sense alludes to the "special adaptations" of deep-sea organisms. The definition applies to the second type, fitness by individual adjustment, while the example refers only to the first type, the general fitness of the species, genus or family as a whole.

No method has been suggested whereby either type of fitness can be caused by the environment, but the fact that individual adjustments do have definite relations to the environment, has served to sustain a belief in the environmental causation of evolution. All species have, of course, fitness for their environments; otherwise they would not continue to exist. They must be more fit than other species which have had access to the same environments, or they would be driven out. Nevertheless, inside of the general environment, or place of the species in the economy of nature, there is still a very great diversity of individual experience to which each organism must adjust itself. The environment at all times determines the relation of fitness, but the characters which afford the fitness are as truly results of evolution as any other characters. It has not been shown that they are caused by the environment or that they can be inherited from it.

The doctrine of environmental causation of evolution supports one assumption by another equally baseless. It takes for granted that adjustment differences between individuals of the same species are caused by the environmental differences which are met by these same adjustments. It also takes for granted that the general fitness or adaptation of the species is merely a product of the fitness of individual adjustment, whereas there are two phenomena of fitness which are quite distinct in their relations to the problem of evolutionary causes, though neither of them affords any special indication regarding the nature of such causes. The adjustment of individuals to differences of environment is a form of organic elasticity which permits lateral vibrations or displacements of characters, while the fitness of a species or genus as a whole is, obviously, an accomplished result of evolution instead of being a formative principle or cause.

ADAPTIVE VERSATILITY OF ORGANISMS.

To say, as has been the custom of writers on evolution, that organisms are plastic or susceptible of environmental influences, is only half of the truth. *Organisms are not merely plastic, but versatile.* Under different conditions they are able to grow in different ways, and often in ways which qualify them better for existence in these particular conditions, though not necessarily so. A Guatemalan variety of the cotton plant takes on in Texas a robust, upright habit of growth very distinct from that of its Central American ancestor. It might be held that this deviation from the previous type serves a purpose in the internal economy of the plants, in enabling them to carry on more efficiently the process of vegetative development. Nevertheless, it cannot be reckoned as a truly adaptive change, since it does not improve the chances of the survival of the variety in the new environment. These very large and vigorous plants are relatively infertile, and ripen their fruits much later than those which retain the normal low-growing parental form. This behavior of the cotton plant is not the exception, but accords with a general tendency of tropical plants toward excessive vegetative development when first planted in northern latitudes. The longer days and higher temperatures of our summer seasons are not utilized for earlier and larger production of fruit, but are wasted in riotous vegetative expansion often cut short by frost before a single seed has been formed.

New environments may also throw plants into a condition of morphological instability which can scarcely have any relation to adaptation, since the result is an endless diversity of abrupt variations or mutations along many different lines, including the most opposite. The hereditary coherence of the species or variety is lost, and the individuals scatter, as it were, in all directions. This explosive type of variation is occasioned, obviously, by changes of environment, but it is equally obvious that one and the same change of environment cannot be directly described as having caused many diverse variations; it need only be thought of as having occasioned an abnormal intensification of normal individual diversity.

In some manner, quite unknown as yet, changes of conditions do *induce* changes of methods of development, but to infer that these changes are always advantageous, or that the external causes *actuate* the modified development of the organisms, is bad logic and worse biology.

Curiously enough, it is only at one particular point that such reckless conclusions are indulged. When we find a dozen different species of plants growing on the same square yard of soil, it does not occur to us to suppose that their diversities are due to the different conditions under which they have grown, for the conditions are the same. We accept without debate the fact that the plants are developing each according to the methods of its own species. It is only when we find plants of the same species following different methods of growth when under different conditions that we can be betrayed into supposing that the conditions are producing the characters of the organisms. In reality this reasoning has no more propriety when we compare a plant or an animal with another member of its own species than when we compare it with a member of a different species.

As long as the adjustments are physiological only, we do not find it necessary to marvel, but when they become appreciable from the morphological standpoint our interest is aroused. And when accommodations cause taxonomic difficulties by affecting the characters by which we have described species, some are ready to believe that environment must be responsible for evolution because it can be alleged to change the characters of species. To reach this conclusion the amassing of detailed knowledge of plants and animals was superfluous. It could have been based quite as logically on the fact that rain "causes" us to carry umbrellas, and to wear waterproof coats. The African variety of mankind adopts the reverse policy, but no less appropriate to the occasion. He discards all of his scanty wardrobe and gives his naked skin a coat of palm oil. The birds can not change or take off their feathers, but their own organization provides a convenient supply of oil, and an instinct to use it when needed. Plants can neither go in when it rains nor oil themselves, but many plants grow a water-shedding coat of wax or of fine hairs on the upper surfaces of their leaves.

All species of plants and animals have, as already remarked, not only their general specific methods of development, but they have in addition certain ranges of adjustment to the different conditions under which they are able to exist. The environmental qualifications of a species are not to be represented by a single point, but by maximal and minimal boundaries, like the geographical latitudes and longitudes which may be used to indicate its position on the earth's surface.

It is usually possible to discover somewhere between the prohibitive extremes an optimum condition, or a locality where the fullest development of the species takes place. Unfavorable conditions multiply as the boundaries are approached, and development is variously impeded and restricted, but surely the ability of the organisms to accept or to avoid a measure of such restrictions and to achieve an existence in spite of them, is small warrant for concluding that the conditions afford an adequate biological explanation of the characters. Still less are we justified in supposing that the unfavorable peripheral conditions are any more truly causative than the central optima. Adverse circumstances, by restricting development, would seem rather to require the organism to put forth more active energies, not of development merely, but of accommodation as well. And yet it is in abnormal features arising under abnormal conditions that the evidences of environmental causation have been chiefly found.

If each species were restricted to an absolute uniformity of conditions and materials, the doctrine of environmental causation would have had at least a partial justification, whereas the versatility of organisms, instead of demonstrating environmental causation, renders it highly improbable. The individual members of species in nature are different, even under the same conditions; why should we expect them to be alike under different conditions?

For some species the range of environmental conditions is very broad, in others very narrow. The fitness of the latter type of species may appear to be greater than the former, in the sense of being more highly specialized. It is not, however, the extent of narrowly specialized fitness, but the extent of widely varied adjustment which generally determines the range of distribution and the numerical prosperity of the species.

In a general way the power of a species to accommodate itself to different environments might be held to favor evolution, because it would improve the chances of sustained numerical prosperity, which is an evolutionary advantage. It does not appear, however, that "plasticity" would be especially helpful in the evolution of the particular characters which might be modified in adjustments to the different conditions. The "plasticity" might hinder, even, as Professor Metcalf has recently pointed out, for the ability of the species to accommodate itself promptly would render unnecessary any permanent progress in the direction of these particular changes.[1]

Of permanent effects arising from the influence of environment upon adjustment changes, there would remain only the possibility that a species which had once possessed a wide range of accommodation, might lose this by long disuse, and might thus become more narrowly specialized as a result of environmental influence. Thus an amphibious species, if confined long enough to a strictly terrestrial habitat, might forget, as it were, how to grow in water.

That experiments have not yet demonstrated such an effect does not justify a general denial of the possibility. The phenomenon would be no less real if it took a hundred or a thousand years to produce it than if it required only five or ten.[2] But in any case the result would be negative rather than positive, involving a diminution of the powers of the species rather than an enlargement of them. There would be a loss of characters instead of an addition, and no occasion to infer that environment had aided evolution. The case would be quite analogous with the influence of environment through natural selection, which is likewise not constructive, but wholly restrictive.

Much of the existing terminology of evolutionary discussion is calculated to commit us in advance to the doctrine that the adjustment is caused by the environment, whereas the fact is that the organisms are active instead of passive, and are able to put forth their own efforts toward adjustment to the varied external circumstances. It is only in a loose and figurative sense that the environment can be said to cause the adaptive adjustments. The arctic climate "causes" the Esquimaux to clothe themselves in furs, but it does not skin the fur-bearing

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[1] Metcalf, M. M., 1906. The Influence of Plasticity of Organisms upon Evolution, *Science*, N. S. 23: 789.

[2] An additional reason for caution in denying the possibility of a loss of the power of accommodation from disuse is found in the phenomenon of "fixing the type" of a variety by selection. The normal diversity tends to disappear when only one carefully selected type of the variety is bred for several generations.

animals and sew their pelts together. We say, similarly, that a desert climate "causes" a plant to become more hairy, but this is as yet a mere figment of speech. We have no notion of the chain of biological events coming between the dryness and the hairs. We can appreciate the advantage of the reduced transpiration, but we do not know how the plant puts on the additional protection against the dry atmosphere.

ALTERNATIVE ADJUSTMENT CHARACTERS.

We shall hardly come to understand aright the relation of fitness to evolution until we accustom ourselves to thinking of these variations of accommodation or so-called "environmental reactions" as expressions of the power of the plant or animal to choose, as it were, between alternative methods of growing and of conducting the functions of existence.

Organic versatility, plasticity, or whatever it may be called, does not conduce to the rapid development of specialized characters (adaptation), or to the multiplication of new groups (speciation), but it is undoubtedly of vast practical importance in the economy of species. Some species have little of this readiness of adjustment, while others are able to adopt a great variety of forms and can thus take advantage of opportunities of existence under a great diversity of natural conditions. By keeping open a larger number of alternative lines of progress, the power of accommodation very greatly increases the ability of species to solve their environmental problems. The environment is unable to prevent such groups from accumulating many kinds of variations or from making trial of them, as it were, in a great variety of combinations. This affords the best of opportunities for the construction of new types with enlarged environmental resources, instead of providing merely for the differentiation of narrowly localized and specialized species.

The different characters assumed by a species in accommodating itself to different environments are not less characters of the species because they are shown simultaneously than if they were developed in successive epochs of evolution. The only sense in which they are not characters of the species is the narrowly taxonomic one in which species are treated as having "identity of form and structure." Characters changed when conditions change are to be reckoned as alternative characters, no less than sexual differences. Indeed, the sex determination itself sometimes appears as an incident of environmental adjustment.[1]

Alternation of generations and dimorphism afford further analogies. There is no warrant for the supposition that the evolutionary status of any of these kinds of characters is different from that of characters which appear in all individuals of the species. Professor Metcalf says:

"A high degree of plasticity hinders evolution by selection, of characters similar to those acquired by plastic response to the environmental influences."

This seems to imply that alternative characters which appear responsively have to be acquired over again by selection in order to become genuine results of evolution. If this were true selection might indeed be impeded. Such a distinction is not illogical, but it applies only in the metaphysical systems of evolution which assume that selection causes evolution and that environment causes characters.

A character which can be varied readily and which thus increases the power of the species to accommodate itself to varied environments is much more valuable than one which is not capable of such adjustment, and there is no reason to suppose that selection would favor the development of a non-adjustable form of the same character. Moreover, both the character itself and its adjustability or "plasticity" are already genuine evolutionary results reached by the same processes as any other characters.

It is only when we have allowed our meanings to slip from harmless abstractions to fictitious concretions that we explain evolution by selection and characters by plastic response to environmental influences. However unobjectionable such expressions may be if used in sufficiently general, literary senses, they are dangerously misleading as the basis of physiological inferences, because they take for granted unproved and improbable assumptions, such as the causing of characters by environ-

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[1] See Fink, B., 1906. Plant World, 9: 183.

ment and the causing of evolution by selection, assumptions which rest in turn on the still more general and obviously erroneous assumption that species are normally uniform and stationary, whereas they are neither. It will some day be reckoned as one of the paradoxical incidents of biological history that this static theory, which is simply a relic of pre-Darwinian doctrine of special creation, should have been cherished most jealously by the ultra-materialistic school of biology.

ENVIRONMENTAL ADJUSTMENT ANALOGOUS TO LOCOMOTION.

The power of locomotion is a very important adaptive character of organisms because it gives great freedom of choice of environment. The hippopotamus, for example, is an aquatic animal, but the brief nocturnal excursions to the grassy river-bank or to the neighboring rice farm keep the huge bulk alive. Being animals ourselves and accustomed to use our powers of locomotion to change our environments, we fail to appreciate this form of adaptation and view with much wonder the fact that organic types have other means of dealing with environmental problems.

Unable to change their environments, they have the alternative power of changing their characters and of behaving in different ways in different environments. Some of the most striking instances of this kind are afforded by a series of plants (belonging to diverse and unrelated natural families) which can live either in water or on land, and which have two sets of characters appropriate to the alternative habitats. On land they have the characters of other land plants, in water the characters of other aquatics. The mystery is that they can change from the one to the other. Some have imagined that if we could find out how this change is accomplished we would have penetrated to the causes of evolutionary changes in general. The analogy between locomotion and environmental adjustment has been overlooked, along with the probability that both these methods of adjustment have been attained by the same evolutionary processes. They are finished products and not merely characters in the making.

The elasticity of muscular tissues is only one of the many methods by which organisms are able to place themselves in more advantageous relations to their environment, and to manifest a power of choice with reference to external circumstances. Even among the simplest types of organic structure this faculty is definitely in evidence. The slime-moulds (myxomycetes) pass the vegetative period of their existence in rotten wood or other decaying vegetable matter. By simple amœboid movements the naked, softly slimy protoplasm, of which these primitive organisms consist, is able to creep out at maturity to an exposed surface before giving up its water and separating itself into dry, wind-blown spores.

To better accomplish the work of dissemination many of the myxomycetes have the hereditary talent or instinct to subdivide their colony into small masses, each of which builds itself a stalk to climb upon. There is then built out from this stalk a network of threads to hold the spores so that they can be sifted out and scattered gradually by the wind, instead of falling at once to the ground. The stalk-building myxomycetes do not work, however, by any arbitrary or merely mechanical standards. When the surface of the decaying log over which they have spread themselves at maturity is uneven, so that a part of them must stand in wet depressions or chinks of the bark, these have longer stems than the others. In some species only those in the wet situations will have stems, while those in exposed places will remain seated directly on the substratum.

The building of the stem and the climbing up are not two different adaptations, but are merely the two aspects of the same act of adjustment to environmental conditions. In some connections it may do no harm to say that the wet situation causes the long stem and causes the slime mould to climb up, but for biological purposes all such statements must mean very little until we know something of the chain of events between the wetness and the building and climbing. Still less defensible is the policy of saying that the stem is "caused" by the environment while the motion is "spontaneous" in the organism. Mechanical biologists would be consistent, at least, in ascribing both acts to "stimuli."

The myxomycetes have long been objects of special interest in the scientific world because they have been thought to combine the characters of animals and of plants and thus to afford a connecting link between the two organic kingdoms. Beginning with such a primitive and undifferentiated form of life, it is easy to think of the animals as gradually specializing the power of locomotion, the plants the alternative powers of morphological and physiological adjustment. The animals excel in seeking their own environments, the plants in the ability to take what comes.

The purpose of this rehearsal of elementary facts is merely to convey, if possible, the suggestion of an idea of organic elasticity, so to speak, of which muscular contractility and locomotion are the extreme specializations, but which extends into all departments of organic activity, morphological as well as physiological. Some may still prefer to say that the environment "causes" the adjustments to be made, but it will remain none the less true that the organisms themselves make the adjustments.

Zoölogists speculate on such questions as whether the eggs of Vancouver wood-peckers, if transferred to Arizona, would hatch Arizona wood-peckers, or whether the transferred individuals would gain Arizona characters in a few generations. What the wood-peckers might or might not do depends on the amount of organic elasticity which they may happen to possess, but the experiment is unnecessary for answering the general question, since plants show a high development of these powers of prompt adjustment to diverse conditions. It is not even necessary that the eggs be hatched in Arizona. Many plants, as already noted, can adjust themselves to such changes at any stage of their existence, and are regularly accustomed to do so. They are both fish and flesh. In water they have the form, structure and functions of other strictly aquatic species; on land they are equally ready to behave as terrestrial species.

Needless to say, hundreds of plants have been described as new species which proved afterward to be only land, water, shade, sun, or other environmental forms of previously known species, and such unnecessary "species" continue to be described. There is no way to ascertain from a few herbarium specimens whether their differences represent the results of evolution as isolated groups or are merely adjustments to different conditions, any more than it could be ascertained without local study whether an individual bird-skin represented a regular resident, a migrant, or a still more accidental visitor.

In this merely taxonomic or nomenclatorial sense the environment can be said to cause species, but such a statement has no warrant in the field of evolution. If we have undertaken to diagnose species by characters which represent merely environmental adjustments our only course for the future is to recognize and rectify our mistakes, and not attempt to utilize them as the basis of doctrines of environmental causes of evolution.

For physiological and evolutionary purposes the species is not to be thought of in the mere systematic sense, as represented by the original specimen or even by the form in which the plant appears in what are supposed to be its normal conditions. *The physiological and evolutionary species covers all the forms under which the organism can maintain itself and complete its life-history*, to say nothing of the definitely abnormal results shown when conditions are too adverse.

Adjustment characters, as such, are not inherited, according to the usual definition of inheritance, that is, they are not necessarily repeated in each generation, but are readily recoverable when needed, even after long periods of time. The plant or animal if kept for many generations under the same environment may continue to show the same adjustment, but this may be completely changed by transfer to other conditions of growth. Thus at 4000 feet coffee has a more strict and upright habit of growth, darker, firmer foliage and larger seeds than at 2000 feet, but if seedlings from the two altitudes be exchanged they always grow into trees showing the characters appropriate to their new situations.

It appears, therefore, that both kinds of fitness, the general features which adapt the species as a whole to its place in nature, and the special powers of adjustment which assure to the individual a certain latitude of environmental opportunities, are normal characters of species, quite as much as those which have no such acute relations to the environment. Unless we can resume and carry to completion the Darwinian task of proving that all characters have arisen as useful adaptations, other methods and causes of evolution must be sought. To question the adequacy of selective and environmental causes is to admit at least the possibility that such theories are completely erroneous, for any causes which are adequate to produce and develop useless characters can produce, *a fortiori*, useful ones.

There are enough adaptations to occupy many naturalists for many life-times. They can, if they prefer, live and die without hesitating to entertain doubts of the efficiency of enviromental causation. And yet the fact will remain that the great majority of the differences between related species and between the individuals of the same species have no environmental utility at all, and are quite unlikely to have had any. This is not to be ascertained by denying or affirming the theoretical utility or uselessness of a few selected characters, but by observing whole orders and classes of organisms to learn the general proportions between differences of characters and differences of environmental relations, and by perceiving that the former vastly outnumber the latter.

The fitness which the individuals of a species of plants can attain by adjusting themselves to the special conditions is, as we have seen, a kind of stepping aside, a morphological motion, put forth by the organism itself as truly as are the coördinated muscular acts which enable the higher animals to move from place to place and thus to choose their own environments. A perennial plant must arrange to tolerate whatever extremes of temperature, moisture, and exposure to sunlight its habitat may provide. Its powers of making such adjustments may be reckoned as functions of its tissues and organs in quite the same sense as locomotion and sustained high temperature are functions of the animal organism. The plant withstands a temperature range of a hundred degrees and more, but mammals and birds establish their own temperatures and keep them adjusted to tenths of degrees. It is a regular custom for many of them to travel annually for thousands of miles to find congenial conditions. The arctic plover is said to fly every year the whole length of the continent from Greenland to Patagonia and back again.[1]

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[1] Knowlton, F. H. 1902. The Journeyings of Birds, Pop. Sci. Mon. 60: 323.

The power to make or maintain such adjustments, whether by changes of muscular or other tissues, may well be reckoned as a character of a species, but there is nothing to show that morphological powers of adjustment are different in any evolutionary respect from the others, or that they afford any warrant for the inference that evolutionary changes are due to environmental differences, or that they arise first as adjustments to external conditions. Any change which increases fitness has the advantage of selective encouragement, and is thus able to exert a larger influence in determining the evolutionary course of the species, so that evolution tends ever toward greater fitness, though other lines of progress are not excluded. If changes could take place only in adaptive characters, the difficulty of maintaining fitness would be greatly increased, because characters would need to be useful from their very inception, whereas they have now the possibility of becoming useful at any stage of their expression. Selection begins to discriminate against a character only when it has become harmful.

SELECTIVE PERFECTION OF ADAPTATIONS.

It is not intended to imply that there are never any direct reactions to environmental influences or that such reactions are never of advantage to the organism. The Washingtonia palm of the deserts of Southern California has a complete covering of dead leaves over the whole length of its trunk, and secures, no doubt, a very desirable protection against the extreme heat and dryness. The retention of the leaves is made possible because the climate is dry. Palms native in humid regions usually drop their dead leaves promptly, but if not they are soon weakened by decay and fall away. Such coincidences could scarcely be avoided in any relations so complex as those of biology, but it does not appear that they are of a nature or frequency to give them more than a very subsidiary importance in evolution.

A plant or animal that encounters adverse conditions and is not able to obtain sufficient food will remain stunted. This small size is an advantage, however, in a region where food is scarce or uncertain. Nevertheless it is those individuals of the species which are naturally small, that is smaller than most of their kind, even under favorable conditions, which would be able to make this reaction most successful, since they would be less stunted, or less abnormal, than the others. Thus even the simplest cases of environmental reaction are not to be separated, for evolutionary purposes, from the phenomena of normal diversity among the members of the species. Selection, as far as it influences the movement of the species toward adaptation, works through this intraspecific diversity rather than through the environmental reactions. The reactions are not selected, but the individuals which happen to excel in making the reactions.

Another case illustrating the same principles is that of the inconspicuous colors of the desert animals. Selection is supposed to have produced these inconspicuous colors because they conceal the animals, and thus give them protection against the enemies to which they would otherwise be very much exposed. The insecurity of this assumption becomes apparent as soon as we consider the equally striking fact of nature that desert plants also have the same series of dull shades of pale grayish and brownish colors. It would seem, therefore, that evolutionary inferences regarding the colors of the desert organisms will have to provide for the plants as well as for the animals, and that they must not depend wholly upon the idea of protection against predaceous foes.

From the plants it is very easy to gain another clue to causes of the obscure coloration. The vegetative tissues of desert plants are usually as green as those of species native in humid regions, but in arid climates the soft, thin-walled, green cells have to be covered by thick integuments to protect them from the dry air, and from too great intensity of light and heat. The modified colors seem to be purely incidental to the modified integuments which mask the green tissues within. The thickened, specialized outer skins simply protect the plants against the too rapid loss of water, and enable them to withstand more severe conditions of drouth. Many other species living under exactly the same conditions of exposure are nevertheless able to retain the fresh green colors of plants of humid regions, because they have solved their transpiration problems in other ways, just as there are a few bright colored desert animals. The pigments which determine the color lie in the deeper layers of the skin, and are readily concealed by a thickening of the superficial layers, or by the development of darker pigments above to protect the lower cells from sunlight, as in the human species. When the color is resident in an outer covering of hairs, feathers, or scales, a very direct environmental reaction takes place, for these are no longer actively living, and the strong sunlight can bleach out the colors as well while the animals are alive as after they are dead. This is true of many insects and also of the horned toad, young or recently moulted individuals showing a bright yellow which is lacking in the old.

Finally, the protective coloration doctrine loses another instalment in the fact that in the brilliant lights of deserts no colors are very conspicuous. There is no occasion, so to speak, for the development in desert animals of the brilliant tints which may enable the members of the same species to more quickly recognize each other in the sombre depths of tropical forests.

There have been, no doubt, many cases where the protective colors have been of immense advantage in the severe struggle for existence to which animals are often exposed. Selection must have had an immense influence in perfecting the marvellous adjustments which many species have with their environmental conditions. The nicety of some of these adjustments cannot be exaggerated — it is already past credence. A little fish, common in Liberia, is so exactly the color of the water-covered sandy stream-beds over which it swims that its presence is often betrayed only by the darting shadows. A little frog living in the sandy pools of the California desert canyons has the same elaborately speckled browns and grays, and likewise becomes invisible, except for the shadows. A slender pale gray lizard of the Colorado desert of southern California even excels the fish and the frog, for it seems to have the instinct of always facing the sun when it stands upon a stone to gain a lookout. In this position both its color and its shadow coincide with those of the stone, and the concealment is perfect.

The subject is one of tempting interest of detail, but enough has been said, perhaps, to make it evident that the dull coloration of desert animals is a very complex phenomenon, not to be explained merely by coincidence, nor by environmental reaction, nor even by the selection of reactions.

The possibility of developing such elaborate contrivances is not adequately conceived until we are able to think of the species as having an active instead of a merely passive evolution, until we recognize that species have internal as well as external reasons for continuing to put forth variations of all the characters they possess, as long as the environment does not forbid. The endless possibilities of adjustment can then be realized, for the narrower the environmental road the more definitely adaptive must be the evolutionary motion of the species.

ORGANIC UTILITY AND ENVIRONMENTAL FORTUITY.

The utility of new characters is not to be narrowly restricted to the environmental sense. New characters can be thought of as having what may well be termed an organic utility, quite apart from their effects upon environmental relations. They may afford a desirable stimulation like that commonly shown in the greater vigor of crosses between organisms not too unlike, and they may also contribute to the structural perfection and general efficiency of the organism. Both these effects of new characters would give the new type environmental and selectional advantages, but indirectly, and not to the exclusion of other more definitely adaptive contributions to constructive evolution.

In the recognition of physiological values for new characters the kinetic theory of evolution diverges widely from the older doctrine that species are normally constant and stationary until changes are brought about by environmental influences. Although often misnamed dynamic, this conception was in reality static, for the organisms were supposed to have no power of change except as worked upon by the external causes. Nevertheless, variations, even when ascribed to the environment, were often held to be merely fortuitous in their relations to evolution, for it was not believed that they would be preserved and accentuated except by natural selection. The development of useless characters could not be admitted under this theory, although it has become increasingly obvious that many of the characters which differentiate related species and genera are quite lacking in environmental utility, and probably always have been. Many characters which are now useful could have had little or no utility at the time of their inception unless they appeared suddenly in a highly developed state, as suggested by the now popular doctrine of mutation.

The kinetic theory enables us to understand that during the earlier period, while a character has only an organic utility, it nevertheless tends to be preserved and to become more and more accentuated, in accordance with the principle of kinesis or prepotency of new variations and recently acquired characters, just as though the species were actively concerned to test the environmental possibilities of each of the new characters it may be able to develop. In this view there is no period in which the new character is entirely useless. Its continued development is normal and advantageous on the ground of organic utility, unless it happens to encounter some environmental obstacle which forbids further advance, or unless an excessive development is attained which weakens or unbalances the organism.

In comparatively rare cases an acute natural selection may intervene and establish a standard for the species by eliminating all individuals which do not have a certain character developed to a required degree. If only one course of evolution remains open, progress in this direction may be greatly accelerated, for as the normal diversity of descent is eliminated the prepotency of the remaining variations appears to increase. This is not because the environment is hastening the perfection of a new form of fitness, but because it is of the nature of species to change, and to continue in the direction of further development of the characters already possessed.

As far as environmental causes are concerned, there appears to be complete fortuity in the appearance and development of characters, except as selective specialization intervenes. This may occur, of course, at any time in the development of the character, and may lend it an environmental significance not possessed before, and perhaps not continued except for a limited period or stage of development. Thus the monkeys and anthropoid apes seem to have secured from their larger brains no special advantage over other animals. No species of anthropoids seems to have become very abundant or widely distributed. Only one member of the group continued brain-development to the point of utility in the struggle for existence, and gradually gained supremacy over the mundane creation. But mental development has by no means remained restricted to simple environmental requirements. Cerebral convolutions have continued to multiply among the more specialized or highly civilized varieties of mankind until they have become, if recent statistics are to be trusted, a positive hindrance to the well-being of the species, like the overgrown plumage of the pheasants and birds-of-paradise, or the burdensome antlers of the extinct Irish elk. Civilized man is now facing a crisis in his own evolution. He must soon decide whether he will make use of his over-developed intellect for solving the problems which now beset his existence, or allow it to carry him entirely out of contact with his environment and compass his destruction. As the supply of barbarous peoples of high mentality has almost run out, the present experiment of our race with civilization presents an element of historical finality which adds, if possible, to the natural interest of such phenomena. All former civilizations of the European or Mediterranean peoples have proved suicidal. It remains to be seen whether the modern faith in science will be justified by the finding of means to avoid another repetition of history.

Capable individuals tend always to assume parasitic habits and to become infertile, until the race is represented only by the relatively incapable immunes, upon whom civilization gets no hold. Science must make plain to capable people the folly of becoming parasites, or of permitting parasitism. Scientific discoveries have placed civilized man in many new relations with his environment, but these relations must have complete biological adjustment if they are to contribute to the evolutionary progress of the race. Scientific discoveries have transformed the arts of production and transportation, but they have had no corresponding influences upon social organization. Luxury, idleness and over-education are dangers to society, not merely nor principally because they are connected with an unjust division of material wealth, but also because they rob the race of its most capable elements. However cruel and pitiful the fate of the incapable who are being eliminated in slums and factories, deterioration is no less real at the other end of the social series, and the loss to the race is far greater.

Instead of dwelling, as has been customary, upon the fortuity of variations and of evolution, we might often gain a clearer insight by reversing the points of view and appreciating the fact that it is the environment which is fortuitous rather than the development of species. Whether a character be useful or useless depends entirely upon the circumstances in which the organism is obliged to exist. Nowhere is this better shown than in man himself. The qualities necessary to a safe and prosperous existence in barbarism may be thoroughly disadvantageous in a member of a civilized community. The only way in which the development of desirable qualities may be substantially encouraged is by furnishing conditions in which they are advantageous, not, perhaps, in the way in which advantage is commonly reckoned, but in ways which shall conduce to the biological end of increasing, relatively at least, the better elements of the race, instead of tending to eliminate them.

The causes and remedies of these conditions are not to be considered here, the object being merely to illustrate from the history of man what is no doubt a general experience of species in nature, the change of the status of a character from useless to useful and then to harmful, depending upon this fortuitous relation between the character and the conditions. That only one species out of the millions which share with us the surface of our Earth should have developed intelligence, reason, consciousness, and personality, has appeared very strange, but it seems still more remarkable, when the vicissitudes of the journey are considered, that even this one should have reached so unique a distinction, and more mysterious yet that it should continue to climb the same summit far beyond any environmental or selective requirements, and even in despite of such requirements. Nevertheless, we are but doing what other species of organisms and other races of men have done before, with the single exception, perhaps, of a better appreciation of the fate that is already befalling us.

Another highly specialized animal, the fig insect, affords an equally instructive illustration of the possibility that a character may develop past the point of fitness, and become dangerous to the species. The fig insects are much too highly specialized to be able to lead a free existence. They live only in the fruits of fig trees, which may very properly be said to have domesticated them as their only means of securing cross-fertilization. The two species, the insect and its fig tree, have thus a mutual interdependence of a very complete kind. In addition to their physical peculiarities, the female insects have the highly specialized instinct to find the young fig fruits and to force their way into them, often with much difficulty and the loss of their wings, so that further flight is impossible. The utility of the insect depends finally upon the fact that it is stupid enough not to distinguish between the male and female fig trees. The difference is a fatal one for the individual insect, for those which enter the female figs are lost. Their eggs never develop, and they leave no progeny, the perpetuation of the species devolving upon the relatively few insects which happen to reach male instead of female trees. Young male flowers are extremely scarce at the time when the principal generation of insects emerges, as though to definitely force them to carry pollen to the female trees.

It is evident that the continued success of this method of pollination depends upon a very acute adjustment of the intelligence of the insects. They must know enough to seek, enter and fertilize the fig flowers, but not enough to distinguish between those of the male and of the female trees. All of the insects which are really useful to the fig species in enabling it to ripen its seed are lost to the insect species, for their eggs have no chance of development. From the standpoint of the insect species there is an acute natural selection in favor of those which go to the flowers of male trees, but if there should anywhere be developed an instinctive preference for the male trees so that the fruits of the female trees remained unvisited, the fig would cease, in that region, to produce seed, and would become extinct, along with its insect tenant.

The selection which would eliminate the over-wise insects would not be applied to them directly, but to the trees which have become completely dependent upon their insect servants. Their highly specialized flower-receptacles are so tightly closed that no other insects will enter.[1] When once such a delicate adjustment of structures and instincts breaks down, the parts are as useless as a watch that will not keep time. The utility depends only on the adjustment, and when the adjustment has become highly complex changes are far more likely to disturb than to improve it. Highly specialized types, those upon which selection has exerted the most successful influence, are ever the most liable to sudden and complete extinction, as geological history has already shown.

Close adjustments induced by selective influence are not, in the long run, truly advantageous. The chances of survival are not increased by close adjustment, but by the continuation of development of characters which allow a wide range of possibilities of existence under different environmental conditions. From the standpoint of the species, changes of the environment are fortuitous, and the utility of adjustments is also fortuitous and temporary. Indeed, the study of adaptations alone might have suggested caution in the acceptance of the doctrine of environmental causation, for a vast number of adaptations, and perhaps the majority of them, do not have reference to the environment, but are devices for keeping the species together, that is, for facilitating symbasic interbreeding. To this class of symbasic adaptations belong the whole series of specializations of flowers to secure the visits of insects, the group of phenomena which has probably figured more largely than any other as an evidence that adaptation is a genuine phenomenon of nature and not merely an elaborate collection of coincidences. These cross-fertilizing adaptations are real and wonderful, but the plants instead of having been acted upon by external influences have taken advantage of the environment to enable them to

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[1] A wild species of fig native in the Comitan district of the Mexican state of Chiapas has its fruits so completely closed that even the fig insects can no longer emerge by the natural aperture, but are obliged to bore through the wall of the fruit to let themselves out. Mr. W. T. Swingle informs me that this is true also of the sycamore-figs of the Old World.

maintain and extend the normal organization of the species. The individual plant gains no advantage from cross-fertilization; the advantage appears only when the results are viewed from the standpoint of the species.

FITNESS BY CORRELATION OF VARIATIONS.

No one has appreciated more keenly than Darwin himself the limitation of his doctrine of selection in the way of providing new characters of fitness on which selection could work. He continued with persistence the search for adaptive significances of characters, and supplemented his discoveries in that direction by the hypothesis of the correlation of variations. This assumes that the characters which are being developed by selection carry with them the development of other characters, some of which may remain useless while others attain utility and thus become in turn the objects of selective education. It is as though characters were fastened together in groups like chairs and tables so that they could be hitched along first by one leg and then by another.

Instances of correlation between characters have been found, and the suggestion gains somewhat from the fact that mutations of independent origin often show close similarity although differing from the parent type in numerous characters instead of in one only. Such a mutation might receive a selective advantage for one character, though the others would be preserved at the same time. Nevertheless, this suggestion would be subject to the same objection as the mutation theory as a whole, that the phenomena are abnormal and do not afford a true indication of the method of evolution in nature, for there the diversity appears not to be of the mutation type, but shows unlimited intergradations of all the characters, as though to give absolute freedom in the making of truly constructive combinations.

Correlations between different parts and tissues undoubtedly exist, but we may believe that they are brought about by normal evolutionary processes instead of supposing that characters have been tied up in arbitrary groups or bundles, which only explains one difficulty by imagining others still more mysterious. Such a character-complex would be, in effect, a suborganic organization, if such an expression may be permitted. The hereditary instinct or spirit of the species would be subdivided, like the spirits of the gods of the Japanese mythology. We would then need to speculate on the nature and relations of these subordinate entities whose only purpose, after all, was to stop a gap in a theory. While selection appeared as the only method of actuating evolutionary motion it was justifiable, perhaps, to use a charitable imagination on this suggestion of fitness by correlation, but in the kinetic interpretation, where it is perceived that selection is not the cause of evolution, the correlation assumption does not need to be invoked. It is excluded, as the logicians would say, by the law of paucity, a beneficent selection which eliminates unnecessarily complicated hypotheses.

KINETIC ORIGIN OF ADAPTIVE FITNESS.

Weismann's recognition of the noninheritance of "acquired characters" or "direct adaptations" destroyed the foundation of the older selective doctrine of evolution by environmental causation, and left the means by which adaptation had been attained a complete mystery, especially for those who continued to hold the other half of the doctrine of selection, that species are normally stationary. To logical minds it has appeared obvious that a new foundation must be found or that the whole doctrine of evolution must be given up, whence the special attention given in later years to the "Origin of Fitness," in the hope of finding some way in which the external conditions can produce heritable internal changes in organisms. If the present interpretation of the facts be correct, this is a completely insoluble problem, or rather it is a gratuitous and artificial one, for there is no such relation as that which the selective school of "Genuine Darwinians" has hoped to ascertain.

The non-inheritance of "acquired characters" proves that the changes which the environment "causes" are not those on which evolution proceeds, and forbids us to assert any directly causal connection between evolution and environment. Progress toward greater fitness arises and goes forward in quite the same manner as other forms of evolutionary change. The environment establishes, however, requirements of fitness, at times very rigorous with regard to some particular faculty or feature, but generally allowing wide liberty of chance and choice in other respects. The adaptations are seldom so close that no further beneficial or indifferent changes can be made. If we attempt, by artificial selection, to enforce too narrow restrictions and maintain a closely uniform type, the effort always fails through the deterioration of the organism. The total fitness of species to their environments is simply the summary of their past histories. It has nothing in particular to do with evolutionary causes.[1] The problem of fitness appears to be truly insoluble under the idea of normally stationary species. The postulates of the older selective doctrine are in direct logical agreement with each other, but one without the other is completely inoperative as a working hypothesis. Some have even denied adaptation because they despaired of explaining it, but all these difficulties disappear when the point of view is changed. Kinetic evolution supplies more abundant materials on which selection can act, and explains how fitness can come about without environmental causation. We are not obliged to discredit the evidence of our senses that adaptations exist, nor to reject the obvious probability that they are induced, though not caused, by the environment itself. All the difficulties are surmounted when we appreciate the fact that the environment works by the restriction and deflection of a normal evolutionary motion, and not as a direct or actuating cause. The environment furnishes certain specifications regarding what may be built, but builds nothing itself. Changes of the environments imply changes of the vital specifications; they enable new evolutionary steps to be taken, but the species itself must originate and develop the appropriate variations before selection can favor them with its discriminating encouragement.

The strength of the theory called Darwinism, that evolution is caused by natural selection, lay largely in the fact that it presented a solution of the problem of fitness, and could then explain evolution through adaptation. Darwinism was rational

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[1] The word environment is itself the occasion of great ambiguity in evolutionary literature, some writers using it with reference to its supposed power to cause favorable variations, and others merely as a summary of selective influences. Between these two extremes there are many gradations of emphasis, so that two writers may use the same words in expressing contradictory opinions.

as a theory, but the facts have refused to sustain it. Subsequent efforts by Naegeli, Weismann, De Vries, and others to supplement or supplant selection as an evolutionary cause have failed to command general confidence, largely because they provided no logical or adequate solution of the fitness problem, and undertook to deny adaptation or to explain it away as a mere coincidence. The best that could be done under the static hypothesis was to suppose that if the new types happened to differ from the old in characters of greater adaptive utility they could survive, and, it might be, exterminate their parents. No means not wholly hypothetical were suggested whereby the environment could exert a definite influence upon the course of evolution.

The kinetic theory more than makes good these deficiencies. It removes all need or temptation to minimize the extent of adaptation or the obviously very important role of selection in evolution. Though providing more generously than Darwinism itself the materials for selection to work upon, it does not carry us upon the dangerous ground of supposing that selection itself is an evolutionary cause, or that evolution is limited to adaptive characters. Darwinism assumed too much and explained too little. It predicated an important causal relation where none existed, and could still explain the evolution of adaptive characters only. Kinetic evolution assumes less and explains more. In recognizing the fact that the species are normally in motion it allows for the development of useless as well as of useful characters, and explains also how selection can contribute to adaptive specialization.

SUMMARY OF INFERENCES REGARDING FITNESS.

The problem of fitness is a crucial defect in the doctrine of evolution by selection, because in this theory selection does not become effective until enough fitness has been obtained to give a character selective value. The fact that organisms are often able to adjust themselves to different environments has been taken to prove that the environment causes variations of selective value. Environmental selection of these adjustment characters yielded the logically complete idea of an evolution initiated and actuated by environment.

The kinetic theory rejects the hypothesis of environmental causation of evolution as fatally discordant with the facts of organic nature. The individual members of species are normally diverse, even under the same conditions; the fact that they may differ under different conditions is not to be accepted as a proof of environmental causation of evolution.

There are two phenomena of organic fitness: first the adaptation to environment afforded by the general characters of the species; and second, the power often shown by individual plants and animals to adjust themselves to varied environmental conditions. The latter is a form of organic elasticity comparable, in a general evolutionary sense, to muscular contraction and locomotion, and with no special significance as a factor of evolution, nor any special pertinence as an example of the method of evolution.

Both kinds of fitness are results of evolution, instead of being causes. They are fruits of the tree, not the roots. Fitness is maintained because evolution continues, not because the environment works changes in organisms. For the static evolutionist, fitness becomes an abstract and insoluble problem. Viewed from the kinetic standpoint, it appears as a natural and necessary consequence of a spontaneous evolutionary motion controlled or deflected by selective influence.

Environments continually change, and with them the relative utility of characters. A feature useless in one environment may be of value in another, or a useful character may become useless or even detrimental, depending on external circumstances.

There is thus a real and intimate relation between fitness and environment, but not a relation which can justify recourse either to natural selection or to direct adaptation, as causes of evolution. It is not to be taken for granted that all the differences shown by plants or animals when environments are changed are in the direction of fitness. With different conditions and materials, organisms build differently, or they may wander from the pathway of normal development in unwonted surroundings. Natural selection encourages fitness by preserving the fittest, but there are also environmental differences with no adaptive relation, and upon which selection exerts no influence.

To find that organisms differ in different environments is, after all, only to find that they exist, for where the conditions of existence differ the organisms must differ. The power of organisms to form adjustments is a measure of their ability to exist, for no environments are absolutely constant. Species strive, as it were, by every artifice at their command to enlarge their environments, to conquer more opportunities of existence. Now and then a successful combination is attained.

Causes which can bring characters of selective value into existence can bring other characters as well, and can carry forward their development. It is no longer necessary to suppose that natural selection is an evolutionary cause at all, in the strict sense of the word. Selection may still be recognized as a condition or an influence in evolution, but there is nothing to show that evolutionary progress is actuated by selection. Fitness, in last analysis, comes by evolution, not evolution by fitness. Selection helps to explain adaptation, but it does not explain evolution; it enables us to understand why evolution follows some courses and not others, but it does not show how the evolutionary advance is accomplished, nor how a new character can develop to the point of utility or harmfulness, so that selection can encourage or restrict it.

The Lamarckian and the Darwinian theories ascribed evolution to causes resident in the environment. The kinetic theory ascribes it to causes resident in the species. The causes of evolution are not to be ascertained by the solution of the problem of fitness, but lie rather in the constitution of species and in the methods of organic descent.

2. INTRASPECIFIC DIFFERENCES AS MATERIALS OF EVOLUTION.

The time has gone by when it was supposed that new knowledge could be gained by the analysis and rearrangement of old data and deductions. Nevertheless, it remains true that every advance in science requires, sooner or later, a new and consistent arrangement of the materials of investigation, and of the language to be used in describing them. Words are not things, but they often control the predisposition of the mind and thus obscure or illuminate the field of mental vision.

Science deals primarily with facts, and only incidentally with inferences or theories, though the latter are of immense use in helping to ascertain facts and test their causal relations. Useful theories arrange facts in what appear to be connected sequences, and enable us to project ourselves into the realm of the unknown without hopelessly losing our way in the maze of unrelated data which we are otherwise likely to encounter. We follow the theory until we encounter facts which prove or disprove it, or until a more direct or more coherent theory has been suggested.

Theories are like legislative enactments; the surest way to be rid of a bad one is to enforce it. A false theory, if studied with sufficient care will correct itself, because the places will be found where it is inapplicable. Moreover, the theories and laws which are the most difficult to repeal are those which contain a large measure of truth and justice, and which have been long in force, so that many vested interests have grown up around them. They take possession, as it were, of the field of investigation, divide it up and place on guard a multitude of technical terms and distinctions which defend the approaches of the citadel of error by a battery of words, which go far to keep a new idea unintelligible.

The prevalent doctrine that evolution is caused or actuated by natural selection is such a theory, containing a large and important truth, and at first immensely fertile in scientific results and practical applications, but essentially erroneous, and in some fundamental respects dangerous to agriculture and to man himself.

The basal axioms, the things taken for granted in the selection theory are (1) that species are normally stationary and constant in their characters and (2) that their evolutionary progress is caused by the environment, but neither of these assumptions proves to accord with the facts. It has not been shown that either environment itself or the selection which it exerts are true, efficient causes of evolution. Neither has evidence been found to prove that a species has ever remained stationary in all its characters, or that the component individuals tend to become "exactly alike," even under the most uniform conditions.

Nature abounds in striking evidence of the alternative kinetic view that species are normally in motion, and that the individual organisms of which they are composed have a normal and necessary intraspecific diversity, quite independent of environmental influences. Moreover, there is reason to believe, from the prevalence of sexual and other diversities inside the specific lines, and from the degeneration which follows attempts at maintaining a stable and uniform type, that diversity among individuals of a species is not only universal and normal, but necessary and advantageous. The prevalent doctrine that evolution is caused or actuated by natural selection has been characterized as a static theory because species are thought of as normally at rest, that is, as stationary or constant in characters and tending to be uniform as far as external conditions will permit. The causes of variation and of evolution were sought in the environment and not in the species itself. The problem was to show how the external causes produce the internal effects, but the task was hopeless from the beginning, for the variations which the environment causes are not those through which evolution goes forward.

It is apparent, therefore, that the abandonment of the static point of view, and the placing of a new interpretation upon a large class of familiar facts calls for a new plan for the study and discussion of the phenomena familiarly called variations, in the older and looser sense of the term, meaning all the differences to be found among the individuals of a species. Differences not caused by environmental influences were, of course, quite unconsidered in static theories and classifications. There was not even a scientific term for this universal phenomenon of intraspecific diversity.

A complete treatment of the subject would involve the rearrangement of a large part of the data which have figured in the evolutionary literature of the last half-century. The scope of the present statement permits only a brief and imperfect outline. It is not possible even to adequately describe and illustrate the details of the facts of original observation to which reference is made. Particular instances are not given, therefore, with any idea that they are adequate to demonstrate the truth of the interpretation which has been put upon them. They serve only as samples of groups of facts to which the interpretation is applicable, the primary object being, not to demonstrate conclusions by formal arguments, but to indicate a standpoint, the correctness of which may be judged by other observers from the facts encountered in their own fields of investigation.

To learn the nature and causes of evolution it has not been sufficient to explore and explain the barriers between the species. It is necessary to go inside the species and to ascertain, if possible, which of the many differences between the component individuals represent forward steps in organic development, and which mere lateral diversions or displacements.

DARWIN'S DISCOVERY OF VARIATION.

Much has been written to show that Darwin did not discover evolution, as popularly supposed, since the idea may be traced back to the Greek philosophers or to the Hindus, and had been entertained in modern times by Lamarck and several others of Darwin's predecessors. And yet, the popular impression, though perhaps inexact as to technical terms, is more just than that of many scientific critics. Darwin was able to secure general interest and confidence in an idea previously indefinite, intangible and practically useless. If Darwin did not discover evolution or even invent entirely new arguments in its favor, he performed a more valuable and unique service in establishing the fundamental fact of variation, without which all evolutionary ideas would have remained empty and sterile speculations, as they had remained during the two thousand years preceding.

Darwin discovered what is still more important to the scientific world than the abstract idea or theory of evolution, namely the means of evolution, which is variation. Darwin was the first to adequately appreciate the fact that species do not consist of individuals identical in form or structure, but of those which are diverse, each different from the others in a greater or lesser degree. Upon the fact of variation Darwin also based his theory of evolution by natural selection and other environmental causes, a theory which has had great popularity in the general scientific world, because it afforded the most concrete suggestion regarding the nature of the causes of evolution. It is desired therefore, to distinguish clearly at this point between the facts of variation first adequately recognized by Darwin and the theory of environmental causes of evolution often called Darwinism. Naturalists do not all believe in environmentally caused evolution, but nearly all are now agreed in thinking of species, not as single morphological points, but as large groups of similar individuals.

Since the time of Darwin it has been believed that evolution has been accomplished by means of variations, but there is still the widest divergence of scientific opinion regarding the kinds of variations which cause or contribute to developmental changes. Some theories depend upon one or another of the different kinds of variations and ignore the others, and some hold that all variations are caused by the environment and that evolution itself is merely a summary of environmental influences.

Many writers have approached the subject from the standpoint of formal definitions and narrowly technical distinctions, but the practical divergences between the different views become most apparent from the types of variation — the kinds of intraspecific differences — upon which they depend as showing the nature of evolutionary motion. To correctly fix upon the kind or kinds of variations which contribute to evolution, is the first step of progress toward knowledge of the true evolutionary factors, and brings us by the most direct route to the determination of the primary question, whether the true, efficient causes of evolution lie in the environment or in the organisms themselves. Are the variations which are induced by the environment those by which evolutionary progress is accomplished?

In Darwin's original suggestion environment was held to bring about evolution, first by inducing variations and then by selecting those which proved to be advantageous. The environment was considered as at once the cause of variations and of evolution. This view is still generally accepted as the teaching of science regarding organic evolution, although many modifications and collateral suggestions have appeared necessary to Darwin himself and to many of his successors. Some have approached the Lamarckian idea of direct adaptation, in ascribing much to the moulding influence of the environment, and in requiring correspondingly little of selection. Other writers have gone to the opposite extreme, making little of environmental factors and much of natural selection of fortuitous individual variations. The latter tendency has been dominant since Weismann showed that "acquired characters," the results of direct environmental influences, are seldom or never inherited.

In the original Darwinism and its various amended forms there seems usually to have been included the tacit assumption of a constant of variability. It is taken for granted that a certain amount of variation shall be manifested by each species, so that selection by paring off the species on one side can cause it to grow out on the other, and thus compel a gradual change of characters. Without selection the average is thought to remain stationary, and if selection be withdrawn the progress already made may be lost by retrogression. Selection, in this view, is the true actuating cause or principle of evolution.

Mivart, and recently many others, have considered that both the environmental variations and the minute and fluctuating individual differences were alike in adequate to accomplish evolution through selection, and have advocated a return toward the older doctrine of special creation. They hold still to the evolutionary idea that species arise one from another, but suppose that the new types originate suddenly by "extraordinary births," or by abrupt mutative variations, that is, by individuals which depart widely from the type of the older species. The occurrence of many such abrupt variations is a definitely established fact. Among plants they often come true to seed, and among animals they are often prepotent when bred with other members of their own variety or local species. Nevertheless, it does not appear that this is the method by which species originate in nature. The prepotency of new variations indicates the probability that old species are tranformed by this means rather than that new species are abruptly originated.

Darwin appreciated better than many of his successors in the field of evolutionary literature the fact that variations are of many kinds, of very different evolutionary significance, and due to many different causes. As an evolutionary pioneer it was a sufficient service to have shown that enough variation exists to make evolution feasible or even plausible. The scholastically educated public, which often appreciates arguments much better than facts, was obliged to approach evolution through Darwin's deductions rather than through his perceptions. Evolution was accepted or rejected on the merits of natural selection, though the two ideas have no necessary connection. Natural selection and evolution are both facts, but in proving that the one is the adequate practical cause of the other it would be necessary to show that the variations through which evolution goes forward are caused by natural selection. No such causation has been demonstrated. Natural selection does not furnish the variations nor explain why variations are accumulated and carried forward into evolution. It only explains why some variations are preserved instead of others. It does not explain evolution, but shows how the direction of evolution may be influenced by the environment. The causes of evolution, or, to be more explicit, the causes of evolutionary variations, are as mysterious to us as they were to Darwin, and indeed, more so, since the greatest step in evolutionary investigation since the time of Darwin has been a negative one, the destruction of the theory of the inheritance of characters acquired from the environment. Darwin sometimes placed much importance on variations induced by environment, and invented the theory of pangenesis to explain the inheritance of such, and bring them within the field of natural selection. Without pangenesis and direct inheritance, natural selection loses its place as a positive factor in evolution and becomes purely negative; it *neither causes variations nor causes them to accumulate.* The most that can be claimed is that it hastens the development of some characters by retarding others, or by forbidding them entirely. It is apparent in some groups of organisms that the influence of natural selection has been very great, in others that it has been very small,[1] but its effects are in all cases dependent upon the underlying facts, that variations do appear and are accumulated. Natural selection does not explain evolution, except in a very loose and super-

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[1] Cook, O. F., 1902. Evolutionary Inferences from the Diplopoda. Proc. Entomological Society of Washington, 5: 14.

ficial sense; the first step toward a better solution of the riddle is to reorganize the vocabulary of variations so that it can be used to express something more than erroneous deductions from natural selection. Many words and distinctions of use in presenting the idea that natural selection is a true, actuating cause of evolution, may be spared, but there are others whose utility is not destroyed by this change of view.

VARIATIONS AND INTRASPECIFIC DIFFERENCES.

Before entering upon a discussion of a general scheme of variations it is necessary to notice a fundamental error commonly attached to the word variation itself. Most of the exponents of selective theories of evolution have made, either tacitly or avowedly, the assumption that all the individuals of a species are normally alike and tend to remain uniform, and that the differences found among them are of external origin and of the same nature as the differences between species, and hence of evolutionary significance. It has been assumed, in other words, that all the *differences* to be found among the members of a species are *variations* in the evolutionary sense, and hence that a cause of difference among the members of a species is necessarily a cause of the evolution of species. It is not too much to say that this assumption of normal specific stability and uniformity, either absolute or within constant limits, begs in advance the whole question of the nature and causes of evolutionary change. Notwithstanding the popularity it has enjoyed, this static idea of species is worthy of no more respect than any other unsupported hypothesis.

For the former purposes it appeared desirable to divide the variations, that is, the differences to be found among the individuals of a species, into two classes — (1) those with which they are endowed at birth, and (2) those which they acquired later from the external conditions of their existence. Variations were classified, in other words, as either congenital or acquired. The distinction is not illogical, but it has proved worse than useless for evolutionary purposes, because the static theory by which it was suggested was an erroneous assumption.

Many objections to natural selection, or to evolution as based upon it, have been raised from the time of Darwin to the present day, but a doctrine with so many merits was not to be displaced until another could be found. Furthermore, the alternative views hitherto presented have shared either one or both of the false premises of natural selection, or they are built, like that theory, on some one group of biological phenomena, and leave out of account other data equally pertinent to the general conclusion, and equally in need of evolutionary explanation.

One of the ways in which the search for evolutionary causes went far afield was in assuming a close and essential relation between evolution and the origin of species. It was thought that if it could be known how new species came into existence the secret of the diversity of nature would be revealed. As a matter of fact evolution has very little to do with originating or multiplying species. The evolutionary process continues, we may believe, whether the group becomes divided or not. The two parts become different because evolution continues in both, but it would also have continued if the separation had not taken place. Isolation, of one kind or another, is the cause of the multiplication of species, but not of evolution. We would gain no special advantage for evolutionary observation by stationing ourselves at the point of bifurcation of one group into two; the only lesson would be that isolation isolates, that segregation segregates. Evolution, it cannot be repeated too often, does not take place in the gaps which are left between the species, but inside of the species, among the interbreeding organisms; it is an *intra*spective phenomenon, not *inter*specific.

To learn how species differ is only to ascertain what roads they have traveled over, it is only by canvasing the differences between the individuals of a species that we can hope to ascertain how the evolutionary progress is accomplished. It will not suffice, when when we find that the individuals of a species differ in a certain respect, to assume that this is the line of evolutionary advancement. We must be content first to recognize and describe the several kinds of intraspecific differences before we can hope to estimate with confidence the contribution of each form of change to the general and permanent progress of the species.

CLASSIFICATION OF INTRASPECIFIC DIFFERENCES.

Intraspecific differences may be classified by reference to three considerations; the nature of the diversity, its origin or occurrence, and its relation to environmental fitness. Such a classification is open to the objection that it requires an advance decision upon the evolutionary bearings of the facts which are being classified for evolutionary purposes. This objection also applies, however, to all preceding efforts at classifying variations. Such classifications have no value, of course, as the basis of arguments. Their use is purely that of permitting an orderly arrangement of materials and of illustrating distinctions. They aid in discrimination, not in demonstration.

The utility of the proposed arrangement may be best appreciated by thinking of it, not as a classification, but as affording points of view or avenues of approach to the study of the intricate complexities of evolutionary problems. The purpose of physiological study is not classification, but the comprehension of causal relations.

Differences of Growth Stages. — Changes of size, form, structure, and function shown in the life-history of normal members of the species, including metamorphosis and alternation of generations and structural phases. The forms of diversity grouped under this head would not be called variations except in the most general sense of the term, but they must be taken into account in making a complete outline of intraspecific differences.

Differences of Normal Descent (*Heterism*). — Individual and other differences, including those of sex and polymorphism, which appear among the members of the species under normal conditions of interbreeding in the same environment, and even among the simultaneous offspring of the same parents.

Differences of heterism have no relation to accommodational fitness, though they may assist in the evolution of adaptive characters. They have sometimes been called fortuitous or fluctuating variations because they had no apparent utility, the organic advantage of diversity of descent not having been recognized.

Differences of Accommodation to Environment (*Artism*). —

Differences resulting from the ability of individual organisms to adjust or accommodate themselves to different environments. These are the variations which have the most intimate connection with the environment, though they have no special significance as causes of evolution.

Differences of Deficient Accommodation (*Topism*). — Differences resulting from the inability of organisms to fully adjust themselves to special conditions. The result is a non-hereditary divergence from the normal characters of the species.

Differences under New Conditions (*Neotopism*). — Variations induced by the transfer of organism to new and unwonted conditions. Three stages of new place effects may be distinguished, (1) those in which there is merely a stimulation of growth, (2) those in which there is also a definite mutative change of the hereditary characteristics of the variety, (3) those in which the new conditions call forth a promiscuous mutative diversity.

Differences of Partial or Recent Interruption of Interbreeding (*Porrism*). — Differences arising from the unequal distribution of variations, that is, from a recent or partial interruption of interbreeding. Such are the differences that exist between individuals from the remote parts of the range of a species (geographical differences) and the differences of segregated local varieties of domesticated species. The nature of these differences is the same as that of the differences between species. They are the result of divergent tendencies of evolution.

Differences of New Genetic Variations (*Neism*). — Prepotent variations which arise under normal conditions of free interbreeding, without having existed previously among the ancestors of the variant individuals. They can be preserved without isolation, and are the characters which probably contribute most to heterism, and to the normal evolutionary progress of species in nature. There is no evidence that the appearance of such variations has any connection with adjustment or environmental fitness. Their preservation depends, of course, upon their being useful, or at least not positively detrimental.

Differences of Aberrant Heredity (*Teratism*). — Failure of the organism to attain the normal form, structure or size of the species. Teratism occurs whenever there is any accidental deviation from normal developmental processes, whenever conditions change beyond the practicable limits of normal adjustment, and whenever the specific network of descent is abnormally narrowed. Thus there are many kinds of teratisms, and many gradations between them and the other more normal kinds of variations.

Mutations are abnormal or teratic neisms which appear abruptly in inbred or narrowly segregated groups, and which require isolation in order to be preserved. Even when induced by changes of environment, mutations are to be reckoned as aberrations rather than as accommodations.

This classification makes no claim to final completeness, since still other kinds of intraspecific differences may be discovered. No doubt the schedule will appear to some as already too extensive and complex, but it will be evident that none of the alleged kinds of differences can be left out of account without misinterpreting one or more of the other groups of phenomena. To overlook the facts of heterism would make hopeless confusion under artism, topism and neotopism. To fail to distinguish between neism and teratism is to mistake degenerative mutations for examples of progressive evolution.

Characters, in the morphological sense, cannot be classified and catalogued as heterisms, artisms, or teratisms. There is an intimate and even interchangeable relation between these different kinds of differences. An individual may be larger than others of its species, either as an inheritance or as a new variation, or because the conditions are favorable, or even because they are new. Finally its greater size may be abnormal, or of the nature of a monstrosity. The same character may thus have great diversity of evolutionary significance.

DIFFERENCES OF GROWTH-STAGES.

Under this class of intraspecific differences it is proposed to include all the general forms and growth-stages in which the members of a species normally appear in any part of their life history. Only in the lowest and most primitive groups do all the separate, individual organisms belonging to the same species have even a general similarity of structure and external appearance.

There have been extensive and not altogether profitable discussions of the relation of growth-characters to those of the adult and to the evolutionary history of the species. The older embryologists worked out a doctrine of recapitulation to explain larval and juvenile characters, but it is evident in some groups, such as the insects, that preliminary stages may be quite as adaptive as the adult form of the species, and sometimes distinctly more so. The differences of growth-stages are themselves of very different types in the various natural groups, as a result of the great diversity of methods by which evolution has been accomplished.

THREE TYPES OF CELLULAR STRUCTURES.

The most fundamental diversity of form and structure which exists among the members of the same species is that which arises from the existence of different types of cell-organization. In many of the lower groups of plants the vegetative organism, like a filamentous alga or a moss-plant, is composed of simple cells which have not conjugated and which have in many cases no power of conjugation. In the higher types of plants and animals the body of the organism, in its highest and most complete form, is built up of cells in a double or conjugating condition. The higher fungi differ from the ferns, flowering plants, and higher animals in that the cells associate themselves while in the first stage of conjugation, before the nuclei have fused, while the cells of the other groups represent the second stage of conjugation. The nuclei have fused, but the chromatin granules still remain distinct.[1]

The great diversity of the cells which compose the bodies of the higher plants and animals may be viewed as a phenomenon of social organization. The lower the organism the more alike are the cells until in the lowest all cells are similar and equal. Where socialization, the habit of joining together or living in groups, has not progressed too far, the cells of compound indi-

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[1] Cook, O. F., and Swingle, W. T., 1905. Evolution of Cellular Structures. Bulletin 81, Bureau of Plant Industry, U. S. Department of Agriculture.

viduals may still be alike; the organization is still a mere gregarious association. Later, there may come about a division of labor among the cells, and a corresponding diversification of structure and form. The common pond-scum (*Spirogyra*) consists of threads formed of cylindrical cells, joined end to end, and all alike in their vegetative and reproductive powers. Another similar organism (*Œdogonium*) consists, for the most part, of similar chains of equal cells, but these have only vegetative functions. The power of reproduction has been restricted to two kinds of special sexual cells different from the vegetative cells.

Advance in the scale of organization not only maintained this distinction between the reproductive and vegetative cells, but continued to increase the numbers and differentiate the structures and functions of the latter, until the immensely complex bodies of the higher plants and animals had been built up.

The primitive type of cell organization, that which built up the filaments of the lower algæ and the vegetative tissues of the liverworts and the mosses was not able, however, to reach the higher possibilities of cellular structure. The cells which compose the bodies of the higher fungi have two nuclei, and those of the flowering plants and higher animals have two sets of chromosomes. These double-celled conditions have arisen through a lengthening out of the process of cell-conjugation as it occurred in primitive types like *Œdogonium*. Instead of conjugating at brief and distant intervals, the cells which compose the bodies of the higher plants and animals are in a condition of prolonged conjugation, the cell fusion which begins when the egg-cell is fertilized by the sperm not being completed until after the whole compound cellular structure has been built.

Several groups of plants have two structural phases, one built of the primitive simple type of cells, the other of the double or sexual type. The moss-spore, when it germinates, first produces a delicate tube like a pond-scum, and the fern-spore a small plate of simple cells, much like a liverwort. These diverse stages or phases of structure of the same organism have usually been described as alternation of generations, but the case is in reality entirely different from the phenomenon of alternation found among animals.

ALTERNATION OF GENERATIONS (METAGENESIS).

In many animals and plants the usual method of propagating new individuals by new sexual conjugations gives place to a more or less regular alternation with generations which are propagated vegetatively, or without a new conjugation. Among the animals, such as the tunicates and plant-lice, the generations which propagated vegetatively have a form different from those which propagate by renewed conjugation.

Alternation of generations, in the proper sense of the words, occurs when the same species exists in two alternative forms, and especially where the two forms have different methods of propagation. The plant-lice furnish the most familiar example of alternation of generations. We may suppose that, like other insects, they were confined originally to normal sexual reproduction, but their evolution has been in the direction of smaller size and simpler structure, and they have also developed the power of multiplying for several generations by parthenogenesis, the parthenogenetic generations being further distinguished by the absence of wings, and by being very short-lived. At the end of the season winged insects of both sexes are produced, and normal fertilization and egg-laying ensues.

No such alternation of sexual and parthenogenetic generations is known to have arisen among plants, though a similar interpretation might be placed upon the bamboos, for example, which propagate vegetatively by the branching of their root-stocks for a long series of years. Then all the plants of the species blossom, bear fruit and die, at the same time. Each sterile shoot of the bamboo might be interpreted as parthenogenetic generation if compared with the sexually propagated generations of a plant like Indian corn.

METAMORPHOSIS.

Among the insects in particular, and to a somewhat less degree in many other animals (mollusca, crustacea, batrachia, fishes, etc.). pronounced changes of form and structure, sometimes very abrupt, take place during the life-history of each individual. Thus caterpillars change by metamorphosis into butterflies, grubs into beetles, maggots into flies, tadpoles into frogs, etc.

Metamorphic differences are largely adaptive, but it is none the less probable that the alternation of bodily forms and the change of food and environment may contribute something to the same physiological results as diversity of descent. In the more specialized insects metamorphosis is accompanied by a complete disorganization of the larval tissues, the pupæ representing, as it were, a return to the egg stage, the change of external form affording an opportunity for a complete rebuilding of the cellular structure of the body. It may be that this fact, viewed in connection with the extremely complex nuclear organs of the cells of insects, will assist in explaining the unique efficiency of the insect organism.

Metamorphosis is not restricted, however, to animals. In plants like *Eucalyptus* and *Juniperus* there are sudden changes of form and structure from the juvenile to the adult phase of the species.

HETERŒCISM.

Many plant and animal parasites infest two or more hosts in different stages of their life-history. Changes of hosts are then usually coincident with metamorphoses, or with change of generation or of structural phases. It has been inferred by some that the abrupt change in the organism is due to the change of food and other conditions of existence, but this does not find confirmation in the studies of the life-histories of the parasites. The indications are more favorable to the opposite suggestion that the great diversity of conditions has enabled the parasites to proceed on two or more independent courses of evolution.

The parasites have developed the power of living in two or three distinct environments at different periods of their life-history, and the characters which adapt them to this variety of conditions have been attained, apparently, in quite the same manner as the characters of other less specialized plants and animals.

The more primitive simple-celled stage, or haplogamic phase, of many species of rust-fungi is confined to pines or to others of the more primitive families of plants, while the more advanced and efficient double-celled phase of the parasite has been able to attack plants of more highly developed families, such as the Leguminosæ or Compositæ. There can be little doubt in such cases that the evolution of the later phases of the parasites have taken place in coincidence with the advancing development of their host-plants to which they are so strictly confined.

GROWTH SPECIALIZATIONS ARISING FROM SOCIAL ORGANIZATION (POLITISM).

Just as cells have become diverse by specialization in the building up of compound cellular structures, so individual organisms of the same species may become diverse under conditions of social organization, that is, when the individual organisms do not live singly and independently, but in groups, colonies or compound individuals. The bionomic unit of such species is no longer the individual but the colony, since it is only in the colony form that it meets its environmental problems or enters into relations with other species. A good illustration of politism is to be found among the compound types of higher plants, those which take the form of shrubs or trees and consist of aggregates of large numbers of the individual twigs or branches which correspond to whole individuals of simpler types.

The primitive herbaceous types of flowering plants have a root and a stem, the latter with a series of leaves and a flower at the top. If this be considered an individual, larger plants with many stems or branches and many flowers are compound individuals. Each branch or flowering twig of a tree may be thought of as corresponding to the small individual herb. Usually the branch-individuals are all of one kind, or at least equivalent and able to replace each other, but in some species such as cacoa, coffee, cotton and the Central American rubber tree (*Castilla*) the branches are strictly dimorphic, that is, of two or more distinct kinds with different forms, structures and functions, and also taking definite positional relations in the building up of the compound individual plant or tree.

It is among the animals, however, that specializations of politism exist in vast variety, and the diversity becomes obvious and familiar. In many different groups there have grown up social organizations, so that all stages may be found between the merely gregarious condition in which the individuals are still equal and alike, to those in which the diversity inside the same species may be greater than that of genera and families in other groups. In man himself social organization has scarcely gone farther than the gregarious state, though some races of mankind have more pronounced social instincts than others, and such instincts have undoubtedly been important factors in their progress or backwardness in civilization. In some countries distinct castes exist, but these are racial or historical in origin and scarcely amount to the attainment of intraspecific diversification.

By far the most compact and highly specialized forms of social organization are to be found among the insects. Remarkably similar conditions have been attained independently in several different families belonging to two very different orders, the termites and the hymenoptera. In these highly specialized insects the individuals of a species are no longer capable of independent existence, but, like the cells of the higher plants and animals, have no meaning except as parts of a collective, super-individual organism. The nest or colony has become the true unit of the species, and its members are differentiated into numerous castes adapted to particular functions by pronounced differences of size and structure. Among the hymenoptera only the females have social instincts and take part in the labors of the nest or the hive, but among the termite both sexes are equally involved. Reproduction is restricted to a single royal pair, who do no work beyond burrowing in the ground after their first and only flight. The king and queen and their numerous progeny are fed and cared for, and the architectural and agricultural labors of the state are performed by hosts of sterile dwarfs, of which in some species there are as many as four different castes — soldiers, foremen, workers and nurses, each distinct in form and highly specialized in instincts for its particular part in the labors of the city.

The body of the termite queen may be hundreds of times the size of that of a worker, and the head and mandibles of a soldier twenty times as large as those of a nurse. Termite communities often contain millions of inhabitants. They build structures far exceeding, proportionally, anything attempted by man, and maintain underneath them immense systems of subterranean fungus gardens and chambers for storing and curing the comminuted wood of which the gardens are built. This material is brought in from long distances by means of tunnels bored through the earth or covered passages built over rocks and tree trunks.

Politism is to be classed as a specialization of growth-stages, because among the bees, at least, it has been found that the differentiation of the sterile worker from the fertile queen is determined by the amount and quantity of food given to the growing larva. It is difficult to believe, however, that this is true of the termites, for the young are not stationary grubs as among the bees, but active creatures which circulate to all parts of the nest, so that a consistent policy of feeding seems quite impracticable. Moreover, the workers and other sterile castes of the termites are not undeveloped females alone, as among the bees, but consist of stunted forms of both sexes.

DIVERSITY OF NORMAL DESCENT (HETERISM).

The individuals of a specific group may appear closely alike when compared with those of other species, but when compared with each other their diversity becomes obvious. Many evolutionary writers have believed in a principle of heredity which would make all the members of a species "exactly alike," and have then assumed that intraspecific diversity is due to variation of environmental experiences in one stage or another of the life-history of the differing individuals. The kinetic theory depends upon neither of these hypotheses, but recognizes the diversity of individuals inside the species as a normal and highly significant evolutionary phenomenon, for which the term heterism has been proposed. Plants and animals propagated under the same conditions may appear more similar than others of the same stock grown under diverse conditions, but they do not tend to any complete uniformity except as this is brought about by the abnormal inbreeding to which domesticated varieties are usually subjected.

Heterism might be defined further as the morphological aspect of symbasis. To support and hold together the organic structure there must be an interweaving of lines of descent among *diverse* individuals. This requirement is most conspicuously met by the familiar phenomena of sex-differentiation, but can be traced upward through all the intermediate stages from simple heterism, or mere individual diversity.

As manifestations of heterism are to be included all stages of intraspecific diversity, from individual differences to the extreme specializations of the sexes and polymorphic forms of the higher plants and animals. The function of heterism is to afford diversity of descent, under conditions of symbasic interbreeding. Narrow segregation or selective inbreeding tends to eliminate heterism, but with the inevitable result of degeneration. Heteric characters are highly heritable and though sometimes affected by environmental conditions are in no way dependent upon them or caused by them.

Purity of stock and *uniformity* of characters are not synonymous terms, as commonly supposed. A very "pure" inbred strain may degenerate and become inconstant through mutation, or there may be the diversity of dimorphism or polymorphism in a species or variety which has not been crossed with any alien blood.

Heterism, in its most general and unspecialized sense, is what has been called by some authors individual variation or fluctuating variation. It includes the regular and normal individual diversity of the memhers of a species which is not induced by differences of external conditions. Some writers do not admit that there is any such diversity, not caused by external conditions.

It is very difficult, of course, to say that any given character or difference may not be connected with an environmental change, but it is very easy to ascertain with reference to most of the so-called individual differences, that the environmental relation, if any, is not at all constant, and not to be established on the basis of any form of scientific observation yet suggested. We are perfectly aware that the children of the same parents, born and raised under the same roof are often very unlike, while on the other hand, close family likeness may persist between children born and bred in remote parts of the earth involving the completest possible change of climate, food, and other conditions of existence.

Intraspecific differences, or variations, as they have been called, have been interpreted hitherto either as results of environmental influences or as steps toward evolutionary change. The recognition of heterism, or the diversity of normal symbasic descent, is incidental to a third explanation of the value of variations, that they help to maintain the vital strength or organic efficiency of the species.

Indeed, the frequency and extent of the differences of sexes, castes, races and alternating generations show not only that organisms may change without being divided into separate species, but also that diversity inside the species has an evolutionary as well as an environmental significance.

Heterism has, if this suggestion be well founded, a concrete physiological value in the economy of the species, quite as real as food and water, though of a different kind. The fuel and water are necessary to keep the engine going, but it is also necessary that the machine be kept in repair and from time to time replaced by another built on the same plan.

Environmental variability or power of accommodation, enables the species to operate under a variety of external conditions, but heteric variability provides diversity of descent, even under uniform and favorable conditions, and thus makes it possible for the species to continue to produce new individual organisms as good or better than the old.

Theories of evolution by environmental causation have overlooked heterism and have assumed that the individual members of species would be alike if there were no environmental inequalities to make them different. This assumption is contrary, however, to all the pertinent facts observable in nature. Acquaintance with the members of any wild species of plants or animals soon shows that individual differences exist, as great, and often greater, than those recognized everywhere among men and women, or among horses, dogs, tulips, roses, grapevines or apple trees. Definite individual diversity, as of stature, features, and thumb marks is not confined to the European races, nor to the human species. Travellers newly arrived in Africa or China often have the impression that the natives are all closely alike, but with longer residence they appear as different as Europeans.

Likewise with plants and animals; it is necessary only to become personally acquainted with them to appreciate their individual differences. The shepherd knows all his sheep as individuals, also the poultry-raiser knows the eggs of the individual hens, and the farm boy knows the kind of nuts which each hickory tree produces.

An instructive instance of natural heterism was observed in a species of agave which is extremely abundant on the mountains to the north of Chiantla, in the department of Huehuetenango, Guatemala. The size, shape, color and spine-development of plants growing by the hundreds along the roadside varied endlessly. Some were pale-green and heavily pruinose, some slightly pruinose and much darker green. Some tapered rather gradually to the point, some carried their width to near the end. On some the spines were very numerous and prominent, on others scattering and small, and with all grades and combinations of these and other varying characters. It is not claimed that these agaves have essentially greater individual differences than other plants. The phenomenon of heterism is rendered unusually striking because their large leaves have a very definite form and are closely alike on the same plant, and thus give unusually favorable opportunities for observing and comparing the differences which exist.

SPECIALIZATIONS OF HETERISM.

The recognition of the facts of heterism, the existence of intraspecific diversity for its own sake, and of its own physiological value to the species might appear to rest on merely theoretical ground were it not for the many specializations of heterism for which no use or meaning has even been imagined, other than that of maintaining a desirable diversity of descent.

In some species heterism has remained unspecialized. The individuals are different, but still all equivalent and alike, possessing all the essential vegetative and reproductive parts. Such species secure the benefits of heterism only by the introduction of new characters, for each character can be shared ultimately by all the members of the species and thus ceases to be of value as a means of maintaining diversity of descent.

Heterism becomes specialized when there are permanently established differences among the members of the species, as in the familiar phenomenon of sex. There is also a series of many gradations between unspecialized heterism of merely individual differences, and the fully established sex-differentiation. The separate sexes of the higher animals are so familiar a phenomenon that we have been satisfied to consider them merely as incidental to the process of reproduction, and have thus overlooked the additional physiological value of sexual differences as specializations of heterism, to insure diversity of descent.

In man himself and the higher mammals and birds the principle of sexual selection enunciated by Darwin may have had an influence in the further accentuation of sexual differences such as beards, wattles, combs, tail-feathers and other means of rendering one sex or the other conspicuous and thus attracting their mates, but secondary sexual differences are not confined to the higher groups or even to animals. Many plants are unisexual and the two sexes often have differences other than those of the essential organs. As the two sexes of plants neither see nor come near each other, the pollen being carried by the wind or by insects, there can be no question of sexual selection here. Even types as lowly as the mosses and liverworts often have the sexes separate and very unlike. Nature furnishes, indeed, hundreds and thousands of instances of independently acquired sexual diversity without use either in environmental relations or in reproductive processes.

The use lies, we may believe, not in the particular differences but in the diversity of descent which the species is enabled to maintain. Diversity is of value to a species not only to enable it to exist under a variety of conditions, but also because diversity in descent is an important factor in maintaining the organic strength or vital efficiency of the individual organisms. We may still believe that all character differences have their uses, but the use is not confined to environmental or selective considerations. More fundamental than these is the use of the diversity to the organisms themselves.

Sexual differences contribute, in other words, to the increased effectiveness of sexual reproduction, that is, they intensify the effects of fertilization or cell-conjugation in endowing the new organism with the power of vigorous growth. With this interpretation of sexual differences in mind we are the more ready to entertain the idea that specializations of heterism would be beneficial, even apart from the sexual diversification of the species, and are thus able to recognize and appreciate a group of phenomena which has hitherto remained meaningless and neglected.

Since the time of Sprengel and especially since Darwin, it has been known that many plants, even those which are bisexual, or provided with both pollen and egg-cells, have many specialized habits and devices which serve to secure cross-fertilization. Although possessed of pollen of their own the flowers are often so formed that the pistils receive pollen only from abroad, and in many species foreign pollen is a necessity, pollen from the same plant being entirely ineffective. The advantage of cross-fertilization being admitted, the value of these adaptations for securing it becomes obvious, but the benefits lie, as Darwin discovered, not in the "crossing by itself" which "does no good," but in the diversity of parentage which may in this way be brought about. These specializations have, in other words, a double function; they assist in the crossing and also minister to the diversity of descent which is the object of the crossing. They have, in other words, the same function as sexuality, and have been interpreted by naturalists as a simple or incipient form of sexuality.

Still simpler specializations of heterism have only one of these two functions, that of maintaining the diversity, but without assisting in the bringing of the diverse parents together. The crossing is left, apparently, to chance, but when it takes place the diversity renders it the more effective. As instances of this simple type of specialized heterism may be cited such species as *Verbascum blattaria*, the flowers of which are pink on some plants and yellow on others. The two types grow freely intermingled over wide ranges of country but no intermediates are found.

DIFFERENCES OF ADJUSTMENT TO ENVIRONMENT (ARTISM).

The notion that all of the differences to be found among the individual members of species are caused by inequalities of environmental experience finds no warrant in the vast mass of experimental facts accumulated by agricultural experience with domesticated plants and animals, nor in observations of species in undisturbed natural conditions. The differences which can be ascribed directly to environmental influences are relatively few and of little importance for evolutionary purposes. Of indirect effects of environment there are two principal classes, those which arise from the ability of organisms to adjust or accommodate themselves to different environments, and those which result from a disturbance of heredity by new and unaccustomed conditions.

The individual members of species often differ among themselves as a result of the possession of a certain range of organic elasticity or power of adjustment to different environmental conditions. Such differences are commonly greater among plants than among animals, for the latter are often able, through the power of locomotion, to choose or to control the conditions under which they shall exist, while stationary plants are subject to much wider ranges of environmental vicissitudes. It has often been taken for granted that these differences of accommodation are direct results of environmental influences, the organism being thought of as having a merely passive plasticity. The fact is, however, that this power of accommodation is as positive a phenomenon, as truly a form of organic activity, as growth, locomotion or reproduction, and as worthy of a definite and appropriate designation in evolutionary literature.

Indeed it is no mere figure of speech to term these differences accommodations. The word can be used of plants and animals in their environmental relations in quite the same sense as for the change of convexity executed by the human eye to enable objects to be clearly seen at shorter or longer distances.

This group of intraspecific differences has received a large amount of study from evolutionary specialists, and especially from ecologists and others who hoped to find the causes of evolutionary progress in mechanical effects of environmental influences. A large number of special phenomena of artism have been named, such as heliotropism, or the power of plants to grow toward the light or to turn themselves to face the sun. Geotopism is the opposite tendency of the roots to bury themselves in the soil.

Some writers on "evolutionary mechanics" have gone so far as to name the tendency of birds to stand or fly facing the wind as pneumotropism, and of fish to head up stream as rheotropism. Consistent prosecution of this tendency to ascribe special "forces," and to give technical names to each habit or instinctive act could result only in confusion, worse, indeed, than the older practice of ascribing all unexplained organic phenomena to a general "vital force." Even the operations of agriculture are conducted by many primitive peoples on an instinctive rather than a rational basis. In spite of permanent employment and a fully assured supply of food, the Indians of Central America obey an internal compulsion to scatter upon the land, when the proper season comes, to clear and plant their corn fields. Owners of mines and plantations have reconciled themselves to a complete suspension of work during the corn-planting weeks, having learned by experience that it is useless to oppose or to reason with this irresistible agricultural impulse.

It would be possible, of course, to describe this agricultural instinct as a form of geotropism, a turning to the land for food as the root turns to the soil. The practical point is not, however, the choice or application of terms, but to note the probability that the instinctive actions by which man and the higher animals adapt themselves to environmental needs belong to the same general class of phenomena as the accommodative changes of plants. We know why we clear the land and plant our crops, and if the need or the advantage be not present we have no difficulty in discontinuing our agricultural labors, but it is not likely that agriculture arose, in the first place, as a conscious and deliberate art. Its beginnings are probably to be traced back by imperceptible stages to the primitive root crops of tropical America which grow readily from cuttings of the stems and rootstocks, so that the digging and harvesting of one crop plants and cultivates the next.

We permit ourselves to say that agriculture was learned in some such accidental way, but we forbear to say that plants also learn to adapt themselves to take better and better advantage of environmental requirements. We base the distinction on the fact that we have reasons for our actions, but in the great majority of comparable cases the reasons have been discovered long after the arts had been perfected. We have theories of swimming, but young children often swim quite as instinctively as animals.

This may appear an entirely irrelevant digression, but a useful purpose may have been served if we are ready to recognize the essential unity of the phenomena of accommodation or direct adaptation and cease to demand special explanatory terms and hypothetical forces for each of the multifarious forms of adaptive change. The explanation will come when our knowledge of protoplasmic organization has sufficiently increased, but in the meantime we gain nothing by multiplying the mystery or by giving it a multitude of names.

Under the theory that environment causes evolution a very real and important relation was supposed to exist between artisms, or adaptive alternative characters inside species, and ecology, or the study of the adaptive characters of species.

Artisms or environmental adjustment variations have received much consideration from those who have held that evolution is caused by the environment, and who have believed, in accordance with this view, that the environmental variations were true examples of progressive evolutionary change, carried forward by external influences.

This doctrine became untenable when Weismann showed that characters directly "acquired" from the environment are not inherited, that is, they do not show any tendency to repeat themselves unless the inducing conditions are present. Weismann proposed to explain the possession by the same species of alternative characters by his theory of determinants, or internal "mechanisms of heredity." These determinants were thought to control in advance the characters of the organism, and alternative characters were explained as the work of two or more sets of determinants which could be brought into action by particular conditions. Where the alternatives are sharply defined as in the two sexes of man and the higher animals this theory might appear to be applicable, but where, as in many plants, there are, even in the same species, all stages of sexual differentiation, or many distinct castes or forms, with or without reference to the sexes, the theory of determinants becomes impracticably complex.

In the experiments of Standfuss with butterflies it has been found possible, by changes in the temperatures in which the pupæ are kept, to influence the colors of the adults so as to approximate those of a different geographical variety or seasonal form. It has been inferred as a consequence that temperature is a direct evolutionary factor in causing one species to change into another. In reality, however, this is but one of the many instances in which failure to distinguish between the taxonomic and the evolutionary standpoints has permitted confusion to enter. Some of these seasonal and geographical forms of butterflies have been named as distinct species, but if it be found that the supposedly distinctive characters are merely artisms or accommodations to temperature, the proper step is to revise our classification before attempting to use it as a basis of evolutionary inferences. The largest possibility suggested in the present instance is that abnormal temperatures may induce in one part of a species a character which another part has reached by normal evolutionary process. The fact that the different geographical color races may have been described and named as species and varieties cannot be made to prove that temperature is a cause of species-formation.

This power of accommodation to the environment, specific elasticity or artism, may be thought of for evolutionary purposes as a general character of the species, but like other characters it is possessed in different degrees by different individuals, and this difference of degree is as heritable as any other feature. Some individuals and strains of a species may have greater range of elasticity on both ends of the series, while others have greater freedom of change in one direction than in the other, for example, they can become very hairy, but not very smooth. Still again, we find mutative variations toward a restriction of the normal range of development. Some of the coffee mutants have extremely short internodes. None of these complications need obscure the fact that the phenomena of artism can be viewed as entirely distinct from those of heterism, though neither phenomenon excludes the other.

DIFFERENCES OF USE AND DISUSE.

One of the reasons for the persistence of the belief that adjustments to external conditions represent direct effects of environment, lies in the fact that several other kinds of intra-specific differences have been confused with environmental adjustments. Most of these additional types of diversity are rather uncommon, but they are well calculated to confuse thought and even to vitiate experiments, especially when these are undertaken without fully considering all the sources of possible error.

If an animal or a plant be kept in captivity or placed otherwise under conditions where its normal activities are not called into use, muscles or other organs may fail to reach their normal development, or they may actually decline in size and deteriorate in structure under continued disuse. There are certain senses, of course, in which it may be said that the environment, by determining the use of parts, causes them to prosper or decline, but closer attention will show that these are phenomena of growth and nutrition rather than of environmental adjustment. The use of a muscle is as truly a condition of its development as the food from which the tissue is nourished, and the decline of such a part may be reckoned as a starvation phenomenon, or interference with the normal processes of growth.

The fact that so much has to be learned through precept and practice by the young of the human species has led some to overlook the existence of definite instincts and muscles which develop without use, just as the internal organs and functions develop in the embryo before birth.

The idea that there is a natural and general tendency to evolutionary motion, to change of organic form and structure, need not be confused with the predication of a principle of evolutionary perfection by which some writers have thought that organisms might be carried along in an ever-upward direction. Some species have gone forward or upward, but for each of the groups which has been able to perpetuate itself by continuing upward there have been hundreds and thousands which have not continued in lines of effective progress, but have turned aside and have been extinguished. This is as true of man and of human societies as of species. They do not *tend to go upward* but they do *tend to change* and these changes have carried a few upward to higher levels, where new planes of development and expansion were possible, but where the probabilities of still further steps were as doubtful as before, and as truly dependent upon correct, if unconscious choice. One view is teleological, the other purely causational.

The phenomenon of degeneration, the reduction or elimination of unused parts or organs, has led to the placing of undue emphasis upon the utilitarian aspect of evolution. Darwin attempted to connect the deficient size and strength of the unused organs of the individual with their reduction in the species by means of his theory of pangenesis which assumed that all parts of the body contribute to the reproductive cells. Degeneration was made a converse of natural selection; the reduction was believed to appear first in the adult, and then the negative acquired character was transmitted to the next generation. Many characters of adult organisms consist in part of a genetic or hereditary contribution, which might be called a qualitative element, to which is added during growth a quantitative reaction to more or less favorable conditions, depending not only upon external circumstances but also upon the perfection and efficiency of the remainder of the organism. Disuse undoubtedly affects the quantitative side of the development of voluntary muscles and other analogous organs, but it is not easy to understand how a progressive reduction could be brought about on Darwin's hypothesis.

After the elimination of the quantitative element due to use, a state of stability might be expected to ensue, unless there be predicated in addition a principle of organic economy tending to the gradual and continued elimination of useless characters and organs. In other words, the effect of pangenesis acting alone would be limited to comparatively few generations, and would dispose of superficial and recently acquired characters only, an inference apparently supported by the persistence of many rudimentary organs.

The extreme constancy of vestigial characters confirms the *a priori* expectation that selection would have little to do with them except to eliminate; but differences, nevertheless, occur, of which progressive modification without selective influence must necessarily be predicated.

Weismann's panmixia was intended to represent a view diametrically opposite to that of Darwin, approaching the question of reduction from the side of heredity only, and laid emphasis on the opinion that, selection being discontinued, indiscriminate crossing without reference to the character previously at a premium would result ultimately in the reduction of the selectively developed parts. But even if it be admitted that a reduced average would be attained within specific limits or where intercrossing is possible, panmixia remains entirely inadequate to explain the progressive elimination of wings, legs, eyes or other important parts of the body, unless it be extended, as in the previous case, to an organic law of economy, a proposition logically quite distinct from panmixia. It is of incidental interest to note that both Darwin and Weismann have thus tacitly admitted a law of organic motion in the direction of the simplification of organisms, and that this proposition is again the exact opposite of that of Nägeli whose "*Vervollkommungsprincip*" works from the simple to the complex.

The phenomena of degeneration may appear to militate against the idea of a spontaneous organic motion. The belief has been that though organisms are in a sense elastic, in that one or more characters can be far drawn out by selection, they tend more or less promptly to return to what might be viewed as the previous condition of rest or equilibrium. Especially would this be the case where selection has been very acute and has accentuated one character at the expense of the total efficiency of the organism with reference to conditions other than that which has determined the special selection. The removal of the latter would then involve the loss of the advantage gained by selective response to the special demands. In groups subjected to an active struggle for existence this would mean a change of direction rather than a cessation of selection. In many other instances, notably among parasitic forms, the loss of normal organs ascribed to disuse is better explainable by selection, since the apparent degeneration is of decided advantage from the standpoint of the actual life-history of the animals.

The principle of panmixia seems, indeed, to involve an unwarrantable extension of the idea of organic elasticity, since it implies that organic structure is maintained by selection alone, without which everything would drop back to simple protoplasm. Of such a general tendency to degeneration there is, however, no indication. As explained elsewhere, the reversion of inbred highly selected types to the wild form of the species is not degeneration, but a recovery of normal structure after restoration to normal conditions of interbreeding.

DIFFERENCES OF DEFICIENT ACCOMMODATION (TOPISM).

Environmental differences are not all of one kind. Some of them are the results of the power of accommodation or adjustment (artism), while others represent rather a deficiency in ability of this kind, so that the organism, though perhaps able to maintain an existence, fails to attain one or another of the normal characters of the species. Thus there is a variety of canary bird which if fed on cayenne pepper during its period of moulting produces red feathers instead of yellow.

The South American Indians are said to be able to alter the color of the feathers of their domesticated parrots by inoculating them with the blood of toads. The colors of certain flowers can be modified by special conditions or by treatment with chemicals. The injury of the white pigs from paint-root, while black pigs escaped, as related by Darwin, would be another example of the same group of phenomena.

The relations of topism to artism and to teratism are sometimes very intimate. A character assumed by one plant as a means of accommodation may appear in another as a limitation of the power of accommodation or as a complete abnormality. The need of discrimination and the difficulty of exercising it are frequently apparent in the literature of the subject. Thus it has been inferred from experiments on a spiny New Zealand plant that the spines, instead of being a means of protection against grazing animals, of which there were none in New Zealand, are in reality an adaptation against transpiration, because they do not appear when the plants are cultivated in a humid atmosphere.

"After being placed in the moist chamber, the plants developed no more spines and are now seedling plants in all respects except for the few spines, which were developed prior to the culture in moist air. Moreover, it seems evident that such plants would remain in the seedling form so long as they were kept in an atmosphere constantly moist and exposed to a feeble light.

"Even an adult shoot on a full grown plant in the open and freely producing spines, may have any further production of such suppressed at once, if the shoot should continue its growth under slightly more hygrophytic conditions. Thus quite recently, I observed on the clay hills near Wellington, a shoot creeping near the ground whose apical portion was covered by grass. This shoot where fully exposed to the light was spinous as usual, but where shaded and in a slightly moister atmosphere was quite without spines.

"From the above it follows that the production of spines in *Discaria Toumatou* can be controlled at will by specifically changing its environment — a plant exposed to a dry atmosphere and normal light producing spines, whilst one exposed to a moist atmosphere and a feeble light produces no spines, but in their place leafy shoots of unlimited growth.

"That spines on xerophytic plants are an adaptation against the attacks of grazing animals is a matter of such general belief as to be admitted into certain botanical text-books as a proved fact.

"It seems, however, to me that my experiment, detailed above, is a fairly crucial case, and that in *Discaria Toumatou*, at any rate, the spines are a direct response to conditions of dryness, and function as a special contrivance for checking transpiration. If so, then they have nothing to do primarily with attacks of grazing animals, especially when it is borne in mind that New Zealand never contained such, excepting the various species of *Moa*."[1]

That the spines did not develop under conditions of moisture and feeble light can scarcely be accepted, however, as proving that they are a special contrivance for checking transpiration, for many analogous adaptations do not fail to appear in advance of the conditions which require them. Cacti, and other spiny plants often make most of their growth in periods of humid weather, but they do not on that account fail to put on spines.

The possibility that the spines may be a useful form of tissue for the plant when living in the normal desert habitat is not a sufficient explanation of the failure to produce the spines under conditions of humidity and deficient sunlight. The spines might be an adaptive character and still appear under all conditions of growth. They might represent an adjustment character or artism and still be only reduced instead of being eliminated in the shade form. That the spines disappear entirely indicates that another factor may need to be recognized, that certain conditions are necessary for their development, and that without these conditions the plant is unable to make spines, just as the pepper-fed canary birds may be thought of as no longer able to produce yellow feathers.

The interest of the *Discaria* experiment would have been increased if it had included a test of the behavior of the plants in shade conditions without excessive atmospheric moisture, to determine whether deficiency of light might not of itself inhibit the formation of the spines, simply by restricting the activity of the cells. The formation of the spines is a specialization which the seedling plants do not attain until they have grown to considerable size, perhaps not until they have encountered conditions of drought and exposure to strong sunlight. It is, therefore, not unreasonable to suppose that these conditions are a necessity to enable the plant to produce the spines, and hence that its failure to produce them represents not so much an accommodation as a lack of accommodation, that is, topism, instead of artism.

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[1] Cockayne, L., 1905. Significance of Spines in *Discaria Toumatou* Raoul (Rhamnaceæ), New Phytologist, 4: 79.

The prompt loss of wool by sheep brought to tropical countries is one of the most striking instances of response to environmental conditions, but there are several elements which need to be taken into account in attempting to arrive at a clear understanding of the nature of the process. The continuous heat and excessive humidity may induce an abnormal condition of the skin and cause the hair to fall out, as often happens in human fever-patients. On the other hand, the failure of the sheep raised in the tropics to produce wool may be due to a lack of sufficiently normal conditions of existence which disturbs the normal heredity and affects first the most highly specialized character of the animal. The loss of wool could be explained in this way as a deterioration or reversion rather than as a new or adaptive character. The domestic sheep is now supposed by Lydekker to be descended from wild types which had a hairy summer coat and produced wool only as cold weather approached.[1]

Many animals and plants require the seasonal vicissitudes of heat and cold as a normal part of the conditions of existence, and refuse to behave normally in tropical regions where wide ranges of temperature do not occur.[2] Indeed, the changes of temperature appear to supply to some of them the same kind of bodily vigor to which diversity of descent contributes. The plants and animals of. tropical regions appear to have relatively great rapidity of evolutionary progress, as pointed out by President Jordan, who finds that the tropical fishes are much more highly specialized than those of extratropical waters.

"The processes of specific change, through natural selection or other causes, if other causes exist, take place most rapidly there and produce most far-reaching modifications."[3]

It has not been shown, however, that natural selection is less acute in the colder regions of the globe; in fact, the general impression has been that the requirements are the more stringent and exacting.

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[1] Lydekker, R., 1904. The Field, 104: 654.

[2] Apples, cherries and many other temperate trees and cultivated plants fail to reach productive maturity under consistently tropical conditions, just as the seeds of lettuce may refuse to sprout without alternations of temperature, and the eggs of some mosquitoes refuse to hatch unless they have been frozen.

[3] Jordan, D. S., 1901. Science, N. S., 14: 566.

TEMPORARY EFFECTS OF NEW CONDITIONS (NEOTOPISM).

Experiments to test the effects of different environments upon plants are often interfered with by a temporary stimulation of growth, due, apparently, to the fact that the conditions are new, rather than to any essential superiority of the new place.

Like travelers in foreign countries they may often behave in a manner very different from their habits at home. Organisms, as well as men, though not built by their environments, are often built into them to such a degree that where the accustomed supports and restrictions are taken away the usual courses of action are no longer followed. New and unexpected characteristics assert themselves, not only or chiefly because the new conditions cause the organism to vary, but because they give it an opportunity to do so, or strengthen and bring to expression some tendency or instability of equilibrium. The new characteristics which have a definite connection with the new environment and are in the nature of adjustments to it may be expected to continue, but there is, in addition, a temporary effect, a temporary lack of adjustment, or a stimulation or aberration which sooner or later disappears.

This phenomenon may be called neotopism, or the new place effect. It is often strikingly shown in plants, and is not lacking in animals. The most familiar example of it is, perhaps, that of the tonic medicines. A vast number of substances, utterly unlike among themselves and having utterly diverse specific actions upon the human system when taken in large quantity, may nevertheless produce the same beneficial effect of temporarily increasing the efficiency of the organism, when taken in extremely small doses.

Neotopism is also to be reckoned as one of the factors contributing to the great vigor and rapid distribution of plants and animals immediately following their introduction into a new region. It is true that they may also have the advantage of immunity from diseases or natural enemies to which they were subject at home, but this is by no means a sufficient explanation of the unusual vigor and fecundity which they manifest for a time and which disappears after a series of years. Many plants, like the Russian thistle, which terrified the agricultural regions of the Middle West a decade ago, after threatening for a time to become permanently injurious pests, have taken their places as comparatively peaceful settlers among the older plant inhabitants.

Neotopism is a phenomenon long known in practical agriculture, but hitherto not explained and generally not accepted in the scientific world, because the requisite evolutionary viewpoint was lacking. Having come to appreciate the physiological functions of heterism in maintaining the vital efficiency of organisms, we are in position to understand that a transfer to new conditions may also act as a direct stimulant of organic vigor, an artificial symbasis, as it were, which has probably contributed much to the sustained vitality of our inbred cultivated plants.

Likewise the heterism of the species might be thought of as increased by the extension to the new locality, and the added neotopic diversity might serve the same purpose as normal heterism in helping to maintain the organic vigor of the species as a whole, under conditions of free interbreeding. Thus devices for securing wide distribution serve the interests of the species in a variety of ways. They not only tend to increase the numerical prosperity of the group, but increase the facilities for interbreeding among the members of the species and also give it the benefit of as widely different conditions as possible. The diversity of conditions accentuates diversity of descent and thus contributes to the vigor of the species. With sedentary plants in particular we should be prepared to learn that changes of conditions of growth are as beneficial as changes of diet for man and the higher animals.

In many crops it has become a regular agricultural practice to exchange seed between more or less distant localities. Seed planted in a new locality often produces better and more fertile plants than in the place where it was grown, and better than the same stock after it has been planted in the same place for a series of years. The new conditions afford, for a time, the same physiological benefits as diversity of descent and new variations, and constitute, indeed, a striking confirmation of the physiological relations of these groups of phenomena.

In many other cases neotopism may only bring to the surface and accentuate conditions of degeneration. Many varieties of domesticated plants and animals have been bred so long and so narrowly in one particular locality that any change is accompanied by notable deterioration. Thus it comes to be believed that seeds of one particular plant, such as the radish or the cauliflower, can be grown to perfection only at Erfurt. Transferred to any other point, neotopic mutation at once appears and brings diversity and commercial inferiority. In a similar way many high-bred animals like the Jersey cattle also deteriorate or show special susceptibility to disease when subjected to new conditions, even to those in which other less closely adjusted breeds are able to thrive.

BEARING OF NEOTOPISM UPON ACCLIMATIZATION.

Neotopism must also be taken into account in another department of agricultural investigation. The phenomenon is often very marked in plants introduced from tropical countries into temperate regions, and has had the opposite effect of deceiving us regarding the possibility of acclimatizing species or varieties of tropical origin. The popular impression is that the colder climate of our more northern latitudes will restrict the growth of plants from the tropics, but this is the reverse of what usually happens, as a matter of fact. It seems to be a general law that annual-crop plants, whether of temperate or of tropical origin, are most vigorous and productive near their northern limit of growth. The reason for this is that the longer days supply a greater amount of heat and sunlight than in the tropics themselves.

Plants newly introduced from the tropics commonly misuse these exceptionally favorable conditions to put forth an abnormal amount of vegetative growth and are often killed by frost before they commence fruiting. It has been usual to explain the failure of such experiments on the simple ground that our northern season has proved too short for these tropical varieties, but as a matter of fact the time may have been equal to that required by these same varieties for normal growth and maturity at home in the tropics. Thus the Kekchi variety of Upland cotton, which matures seeds in Eastern Guatemala in five months from planting, required in Texas over six months to produce a much smaller crop the first year after its introduction, and might have produced no seed at all if the tendency to abnormal luxuriance of growth had not been checked by a long period of dry weather. Other tropical varieties of cotton have consistently refused to produce seed when introduced into Texas, even though the same length of season would have been sufficient in their home localities.

With the superior conditions of growth supplied by our northern summers most of the tropical varieties would be able, if they utilized their opportunities properly, to develop even more rapidly than they do in the tropics, and this result has been reached with some of the Mexican varieties of corn. During their first seasons in the United States they became greatly overgrown and ripened scarcely any seed, but after a few years they recovered their short-season qualities and became especially useful as extra-early varieties, like the "Mexican June" corn.

The conditions under which such experiments are usually made are well calculated to intensify neotopism instead of holding it in check. It has been reasoned after the analogy of our domestic varieties that fertile soil and thorough cultivation will conduce to the early maturity so much desired. Moreover, it is the regular practice to keep testing gardens and experimental plots in the best of condition. The result is that the newly introduced tropical variety is surfeited with the unwonted supply of readily available food and moisture, which still further increases the tendency to abnormal vegetative growth.

Many such varieties have entirely failed of acclimatization because they ripened no seed at all in the localities in which the first experiment happened to have been made. Nevertheless, the inference is not warranted that such varieties cannot be acclimatized in temperate regions. Experiments in the introduction of new types of Upland cotton from Guatemala have shown that the tendency to rank and sterile vegetative development can be controlled by carrying the new stock far enough to the north and placing it in comparatively sterile soil. In the latitude of Washington the Guatemalan varieties of cotton showed much more normal habits of growth, and made more progress toward fertility and seed-production than in the much longer growing season of Texas. These experiments afford a definite intimation, to say the least, that by the proper choice of conditions for the first planting the neotopic stimulation of tropical varieties can be held sufficiently in check to permit the maturing of at least small amounts of seed. This opens the way to the practical acclimatization in the United States of useful varieties of cotton, corn and other important food-plants of tropical origin.

Further experiments have shown that the second generation of cotton in the United States is notably earlier and more productive than the first generation, when grown from seed of the same origin and planted in adjacent rows. It has also become evident that there are at least three stages or kinds of new place effects to be considered in the acclimatization of different varieties and types of cotton. The changes of hereditary behavior which can be induced by the transfer to new conditions are not limited merely to increased size or vigor, but have obvious bearing upon the phenomena of mutation, since the plants may change in a very definite manner in characters which would usually be considered of varietal or even of specific importance. The lack of fertility which accompanies the aberration from normal characters affords a further analogy with mutations. Nor does the interest of the experiment end here, for it has been proved that this neotopic form of mutation may supervene in a perfectly definite manner even after the plants have grown for a time according to the specifications of normal form and habits of the variety.

When the change takes place early the whole plant may show the abnormal characters and may be more or less completely sterile. In another locality plants of the same origin may grow for a time in a normal manner and remain normally productive, but may then change suddenly and completely to the abnormal, infertile, neotopic condition. In this form of neotopism the behavior of the individual plants grown from the same lot of imported seed is often remarkably uniform and the result is closely parallel to that described a few years ago by Dr. C. A. White in tomatoes. Two lots of seed produced, with much uniformity, progeny so unlike their parents that Dr. White described and named them as a new species.[1]

A third result sometimes reached by transferring plants to new conditions is to induce a more or less general outbreak of miscellaneous variations of an abruptly mutative character. In such instances the stimulation effect may be lacking or very inconstant. Some individuals may be several times as large as their parents, while others are as much smaller.

Although the new conditions evidently *induce* the mutative variations, they can not be said to *cause* them, in any definite evolutionary sense, as proved by the great diversity of the mutations which the same change of conditions may call forth. The unfavorable conditions unbalance the organisms, but the individual lapses from normal heredity take many different directions, without reference to particular requirements of the environment.

The practical significance of the new-place-effects is, therefore, entirely different in different instances. As long as the result is an increase of vigor and fertility, the phenomenon is a useful one; but if the stimulation be so great as to change the characters of the plants and render them infertile the crop may be ruined, and this misfortune may also be reached when many miscellaneous variations and degenerations appear.

DIFFERENCES ARISING FROM PARTIAL ISOLATION (PORRISM).

Members of the same species are often more or less unlike in the different parts of their geographical range of distribution. Some of these differences will be found to have relations to differences of environment, but others will persist even when brought into tne same conditions. These geographical diversities represent, no doubt, the results of partial isolation, and are of the same nature as the differences between species. If interbreeding were adequate, evolutionary progress would be kept uniform over the whole species, but if the organism is sedentary or lacking in facilities of dispersion local diversities may accumulate.

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[1] White, C. A., 1905. The Mutations of Lycopersicum, Popular Science Monthly, 47: 151.

Individuals from neighboring localities may maintain the usual amount of similarity, but if specimens from remote parts of the geographic range of the species be compared they may prove notably different. If the climatic or other conditions of the two localities are unlike it is very natural to infer that this is the cause of the differences between their organic inhabitants.[1]

That this explanation may prove, in some cases, to be correct, does not justify us, however, in neglecting to perceive that the remote members of a species may have opportunities to accumulate diverse characteristics, much as though they belonged to two distinct species. The extent to which they can do this will depend upon the habits of the particular plant or animal. Sedentary species of animals or plants which have no means of securing wide dissemination of seeds or pollen, tend to manifest local divergencies. The cause of this is, apparently, that new characteristics appear in different parts of the range of the species more rapidly than they can be distributed through the whole interbreeding group. Thus the quail, or Virginia partridge, a nonmigratory bird extending from New England to Central America, shows a large number of appreciably different local varieties or subspecies, which might not exist if the bird were migatory and there were a more general intermingling of the members of the species. The differences which characterize such local subspecies may be quite the same, both in character and amount, as those which distinguish completely segregated species, but they are treated as subspecies because the distribution of the whole group still remains continuous, and provides a complete series of connecting links between the local forms which happen to be described as subspecies.

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[1] Engler, A., 1904. Plants of the Northern Temperate Zone in their Transition to the High Mountains of Tropical Africa. Annals of Botany, 18: 539.

"I am convinced that in such cases the somewhat different climate is the cause of all or at least of a part of the modifications. Sometimes in connection with these new variations are also to be observed (cf. *Cerastium cæspitosum*), which may become the beginning of other new forms. The constancy of such climatical adaptations may be a different one and often become fixed through a geological period. I may add that systematic studies have also convinced me that many of the xerophytes, and that a good deal (I do not say all) of the qualities of xerophytes, which are usually called adaptations for protection against a dry climate, are caused by the climate itself."

The essential difference between a species and a subspecies does not lie, as commonly supposed, in the nature or amount of the differences as such. The practical question is whether two groups are actually separate in nature or are still connected. Subspecies may be more different than other completely segregated species. On the other hand, groups which are really segregated in nature and thus unable to interbreed, are by that fact on the road to the acquisition of specific differences. That they may not have become *very* different from each other does not prove that they are not good species or that it is undesirable to accord them recognition as such.

It does not follow, as some have supposed, that subspecies are always incipient species, or that there is any inherent force or tendency which will insure a subsequent separation into distinct species. The existence of these diverse local forms has not been shown to be any disadvantage to a species, and may, indeed, conduce to its greater vigor, since it tends, like heterism, to insure a certain amount of desirable diversity of descent.

If the habits of a species were to change in the direction of an increase of its power of dissemination and wide interbreeding, the local differences would tend to disappear, since new variations could then spread more rapidly throughout the whole group and render its evolutionary progress more uniform.

Porrism corresponds, inside the species, to many of the differences between species. It is true that when species of the same genus live in different environments and have different habits they usually have structural difference corresponding to their respective needs. Examples of such adaptations are frequent among the higher plants and animals, and their superficial similarity to artism inside the species has been the basis of the doctrine that evolution has been effected by environmental causes. The best corrective of this misapprehension is a study of one of the lower groups of plants and animals in which the same family, order or class has the same habits and the same place in the economy of nature. Many excellent examples will be found among the mosses, liverworts and algæ among plants, and among the myriapoda and lower insects where the number and character of the diversity of the species is out of all imaginable proportion with differences of conditions, habits or selective requirements. Hundreds of species, genera, families, and even orders, have been differentiated notwithstanding complete and long-standing adjustment to the same kind of existence.

The multiplication of species under such circumstances has little reference to environment or to natural selection, and the characters by which the groups differ are not explainable on the basis of utility. The diplopod fauna of tropical Africa changes almost completely every thousand miles, but the tropical forest conditions under which a large proportion of the species live are, for their purposes, practically identical the world over. But with these wingless, slow-moving creatures unable to bear exposure to daylight and dry atmosphere, the opportunities for segregation are greater than those for dissemination. The environment allows a wide freedom of choice, and evolution by means of useless changes has far outrun the natural selection of advantageous differences. As far as their external characters are concerned, these animals appear to have been quite as well adapted to their environment in the carboniferous age as they are to-day, but they have not ceased to differentiate species, although preserving much more than in some groups the same general form. Indeed, the wealth of definite structural differences is, if anything, greater than among the higher insects, where the progress in adaptive structural changes would seem to have removed the necessity of accentuating the inconsequential differences which the diplopoda have utilized as means of evolutionary motion.

DIFFERENCES OF NEW VARIATIONS (NEISM).

Much of the heterism or normal individual diversity of the members of a species can be described as resulting from different combinations and proportions of what have been called the unit characters of the species. The interweaving of the lines of individual descent brings, as we know, an infinite diversity of form and features, and with these differences accentuated by environmental influences there is almost an infinity of possibilities of diversified characters in the same species. Nevertheless, the making of all possible permutations of the characters which may exist in a species at any particular period would lead, after all, to no truly progressive change. Nothing is gained for evolutionary purposes by attempting to explain new characters merely as reversions or as new combinations.

Nor can such assumptions fully account for the facts, since it is often obvious that absolutely new and unprecedented evolutionary departures sometimes appear, which could not be accounted for by any combination of characters existing in the remaining members of the group. Such are the remarkable crests developed on a few of the anterior segments of East African millipedes of the family Oxydesmidæ, specialized structures which are entirely without analogy in the remainder of the order Merocheta or, for that matter, of the entire class Diplopoda.

It would be altogether presumptuous, of course, to insist that any particular variation or mutation represented the very first appearance of its type in the history of the species. It is usual to ascribe variations to possible admixtures of blood at some point in the genealogy of the individual, near or remote. But these suggestions, even if justified for particular cases, should not be allowed to obscure the more fundamental consideration that the very idea of a progressive evolution implies the origination and development of new characters, both of form and of structure, and the opening of new environmental relations for the species.

Of the causes of new characters we are, as yet, in ignorance, but of their uses we need be in no doubt. New characters not only make evolution possible, but by true symbasic interbreeding they help to maintain the vitality or organic efficiency of the species. Neism reinforces heterism and contributes to evolutionary progress. New characters are not averaged away and obliterated by interbreeding, but are prepotent. They tend to spread throughout the species and to become more and more accentuated.

That variation may bring an increase of the vegetative vigor or vital efficiency of the organism could not be more clearly shown than in the numerous instances where unusual bodily strength and hardiness accompany reproductive debility or even complete sterility, as in the familiar instance of the mule.[1] Many similar instances were observed in Guatemala. Coffee plantations which, owing to unfavorable conditions, were dead or dying, often showed occasional mutations which remained healthy and luxuriant. Through some strange internal difference they were able to carry on their vital functions with conspicuous success while all their normal neighbors had completely failed. If coffee were grown for the leaves like tea or for other vegetative parts, these mutations would furnish new types of great economic value, but of thousands of such variants which have come under the observation of planters not one has proved to be equal in fertility or normal seed production to the parent type, under favorable conditions.

PREPOTENCY OF NEW VARIATIONS.

If only a small proportion of the progeny showed the new character it might still gain a footing in the species, especially if favored by selection. Those who have relied on the mathematical doctrine of chance have felt it necessary to claim generous assistance from the principle of selection. Experiments with new variations seem all to agree, however, that among their own relatives, or under equal conditions of symbasis, they have not merely an equal chance of reproducing themselves, but that probabilities are distinctly in their favor. The variation is not resisted but welcomed. The majority does not set the fashion; it is the few who are able to make pleasing modifications of style. The new pattern may not be better or more beautiful than the old, but change is pleasing in itself and may secure a wide vogue for an ugly or uncomfortable garment. With organisms as with clothes the essence of beauty is fitness, as Socrates long ago pointed out. The changes which make a permanent contribution to evolutionary progress are those which fit best into the existing structure and increase its fitness to its surroundings. Our admiration for changes and likewise for fitness in nature and in art, may be an intellectual reflection of the evolutionary properties of organisms.

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[1] Cook, O. F., 1904. The Vegetative Vigor of Hybrids and Mutations. Proc. of Biological Society of Washington, 17: 83.

DIFFERENCES OF ABERRANT HEREDITY (TERATISM).

There are many biological accidents, so to speak, as when in the laboratory, or perhaps in the surf of the sea beach, an egg of one of the simpler animals is shaken apart and develops into two organisms instead of one. In a similar manner, through some mistake of division, two-headed monsters and other malformations occur. No less abnormal are many of the freaks which can be produced by unfavorable conditions of growth. Another series of abnormalities is caused by violations of the law of symbasis, that is, through inbreeding which eliminates heterism and normal diversity of descent.

Teratic characters which are the result of accidents of growth or environment are not inherited, except as they may give rise to a general weakness or debility of the organism. Teratic neisms, on the other hand, are readily heritable.

Teratisms, like accommodational variations, have received much study, especially from those who hoped to gain from organic derangements an insight into the nature of the agencies by which organic structures are built. The field of teratology affords many interesting and significant data, but the correct interpretation of them has been hindered, as in other departments of evolution, by the confusion of issues which are essentially distinct. There are at least as many kinds of teratisms as there are of normal differences, and probably more, and endless gradations of each kind. This is well illustrated by the phenomena of mutation which have received so large an amount of study in recent years. Mutations show all degrees of abnormality, and they grade imperceptibly into the differences of normal individual diversity (heterism) as well as into those of normal and prepotent new characters (neism).

ABNORMAL MUTATIVE DIVERSITY.

That species are not normally constant and stationary in their characters could not be better proved experimentally than by the many attempts of breeders of plants and animals to maintain constancy of characters in domesticated varieties. Selection conduces at first to such a constancy or uniformity among all the members of the breed, those not conforming to the approved standard being ruthlessly weeded out. The type having been once established by this means, the variety remains for a period of years more or less uniform, generally very much more so than the members of wild species in nature. It is the experience of all history, however, that varieties decline after a time from their original excellence and have to be replaced by other, newer sorts, which by reason of their more recent origin have been subjected to shorter periods of inbreeding. The degeneration of the older variety may be indicated in a number of ways, such as a decline in fertility or weaker vegetative growth, or susceptibility to fungous and insect parasites, so that it usually disappears from cultivation or husbandry before the final stage of sterility and extinction is reached, though the tendency in this direction often becomes very obvious.

One of the symptoms of degeneration is the appearance of numbers of freaks, sports or mutations, as they are variously called. These variations of domesticated plants and animals are often interesting, and sometimes valuable on account of some special peculiarity, such as long hair, double flowers, albino color, etc. This is especially true among the plants cultivated for their flowers, where the never-ending diversity of garden varieties is obtained by the preservation of the numerous mutations into which wild species commonly "break" after a period of domestication and inbreeding.

A general tendency among all such sorts is towards lessening of seed production, and finally complete sterility may ensue. The last is not a calamity in species which can be propagated by cuttings, and many of our cultivated species have reached this condition. With others, as for example, the "seedless" green-house or forcing cucumbers, the extreme scarcity of seeds which renders the variety desirable is at the same time a serious obstacle to its cultivation.

On the strength of the older static, uniformitarian theory of life, some writers have insisted that mutations must be caused by environment, there being, in their opinion, nothing else to cause them. The diversity of the mutations could be explained, under this doctrine, only by environmental differences, such as the variety of chemical compounds which might be found in the soil of the same seed-bed. But no evidence of any constant relation between any particular chemical and any particular mutative character has been adduced. That any will be forthcoming may well be doubted, in view of the fact that the same or closely similar mutative characters often appear under very different conditions of soil and climate, and very diverse mutations under the same conditions.

The diversity of the mutations among themselves shows that it is not safe as yet to assert more than this general organic instability; detailed causes are not yet revealed. The necessity of this caution is rendered still more obvious by the behavior of neotopic mutations, those induced by changes of environmental conditions. If in a given environment a plant mutated only in one direction, we would still be far from knowing adequately that the environment *caused* the mutation, but even when we have reason to believe that a change of environment has *induced* mutation we are forbidden to go farther, because of the very great diversity of the mutations which the same change of environment or the same history of selective inbreeding can induce.

It has been shown in the discussion of neotopism that new conditions may conduce to the appearance of abruptly discontinuous mutative variations. The percentage of mutants is notably larger in some regions than in others, but even this does not compel us to believe that the conditions are the true cause of the mutations, in any detailed sense. They are rather to be thought of as merely the occasion of the change, by having brought the coffee, the cotton or the Capsicum the sooner to the point when it can no longer follow the hereditary road over which the individuals must travel to attain the ancestral type of adult form.

The mutative individuals are not to be thought of as the evolutionary pioneers of the species; they represent rather those who are falling out by the wayside. They may be classed together with normal new variations in the sense that they are outside of the specific norm or average, but they have a different position with reference to the evolutionary route of the species. They represent the criminals and cranks, but not the leaders and reformers of the specific organization. For special agricultural purposes mutations are often extremely valuable, but when the desire is for the general improvement of the species or the race, the essentially degenerate nature of mutations cannot be left out of account.

The kinetic theory, if correct, shows that variations, to be of evolutionary value, must take place in the species, or in full contact with society, as it were, and not alone, or in disregard of the condition, interests, and evolutionary direction of the species at large.

Mutations are physiological phenomena, just as evolution itself is a physiological process; they will undoubtedly be found to have causes when we are able to appreciate them. They may be thought of as functional reactions from the restriction of normal heterism and diversity of descent. This abnormal condition of inadequate symbasis renders the organism unstable and it falls down, degenerates or mutates.

Inbreeding is to be studied as a condition of existence, and the manner in which the species reacts may be observed with the same propriety as any more purely environmental problem. Mutations may be abnormalities induced by abnormal conditions of descent, but the reaction which produces them need not be considered abnormal, since it is evidently the same tendency which contributes to the maintenance of the normal heterism.

Indeed, the mutations might restore the normal intraspecific diversity if interbreeding were permitted, as in nature. The very fact that mutations of plants so frequently tend toward diœcism might be accepted as another evidence of their value as a corrective of inbreeding and deficient heterism.

Coffee mutations are often largely or completely unisexual, or have greatly accentuated proterogyny or proterandry. A condition entirely analogous to a diœcious species could be obtained by the crossing of such staminate and pistillate trees. Nevertheless, Professor De Vries has described and named such a unisexual mutation as a new species, without regard to the taxonomic consequences of the application of this policy to sexually differentiated higher animals.

If similar results justify the predication of similar causes the appearance of similar mutations under diverse conditions may be accepted as proof that they were induced by the common condition of inbreeding. Otherwise it would be necessary to suppose that different topic factors have produced like results, all of which shows the hopelessness of connecting mutations with environment. Mutations represent abnormally accentuated individual differences, and it seems not unlikely that most of them follow lines of variation already established within the species.[1] It has been found in all the species thus far canvassed that a few mutative tendencies are much more frequently shown than the others.

Nevertheless, it is not safe to assume that the same mutation reappears even twice in identical forms. Whenever two similar mutations of coffee, cotton, or Capsicum have been brought together and compared they have always been found to be very distinctly different, even more so than the unmutated individuals of the uniform type from which they have arisen.

3. EVOLUTION, SPECIATION AND ADAPTATION.

One of the most frequent causes of confusion and error in evolutionary thought is the failure to distinguish clearly between evolution, speciation and adaptation; to distinguish, in other words, between the process of evolution itself and two of the relatively incidental results of environmental interference.

As long as a group of organisms remains united so that all its members interbreed freely with each other, evolution remains a unit in the sense that the whole group, though it may be changing any or all of its characters, still keeps together and retains its specific coherence. But if such a group be split into two or more parts which do not interbreed, evolution has as many separate courses, and the isolated parts attain differential characters, or, to use the words of former days, new species originate. It is obvious, however, that the differentiation of the new groups, while accomplished by evolution, is occasioned by isolation.[2] The multiplication of groups, which as a process may be

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[1] The oranges, lemons and pomelos afford, according to Mr. W. T. Swingle, many excellent examples of this parallelism of mutative variation.

[2] Confusion often creeps in at this point from the field of geology, for the paleontological species is usually a random sample or section of the network of

called speciation, is brought about by isolation, and is not a necessary cause nor a necessary result of evolution.

In a similar way another group of evolutionary writers have confused evolution with adaptation. Evolution results, not uncommonly, in the production of characters which give a species a specialized fitness for some particular environment. From such facts it was argued that the increase of fitness or "survival of the fittest" represented the method of evolution, or in other words, that evolution is merely a process of adaptation actuated by the selective power of the environment. The facts of nature show, however, that evolutionary motion is not at all restricted to directions of fitness, and it is also obvious that an evolution so restricted could not produce even the characters of fitness upon which it would depend for its supposed power to transform species. Fitness must be attained by evolution before the environment can give the character selective specialization by limiting the evolutionary motion and deflecting it into more definitely adaptive directions.

Evolution is the process of change by which the members of an organic group become different from their predecessors, or from other groups of common origin.

Symbasis is the normal evolutionary condition of free and extended interbreeding among the individual members of natural species.

Symbasis implies adequate diversity of descent; it is to be distinguished on the one side from the narrow inbreeding which induces abnormal mutations, and on the other from the wide cross-breeding which produces abnormal hybrids.

The continual interweaving of the lines of descent from diverse and unrelated ancestors appears to be necessary to sustain the vitality and evolutionary progress of the higher plants and animals. The constructive evolution of new organic types does not take place on simple or narrow lines of descent, but requires

descent. When considered with reference to each other, the contemporaneous species of a horizon have the same significance as species of the present day, but species of different horizons may have a relation which two simultaneous species would never have, that is, one may be the true ancestor of the other. The same word species is used for several categories of organic groups. See, Four Categories of Species, American Naturalist, April, 1899.

that large numbers of organisms advance in company, as in specific groups A species is an organization of diverse, interbreeding individuals, dependent for its continued existence upon its ability to maintain a broad and intricately interwoven network of descent.

Speciation is the attainment of differential characters by segregated groups of organisms, that is, by subdivisions of older species.

Isolation of an organic group implies such a separation that interbreeding with members of other groups is excluded.

Isolation is of primary importance in speciation, since isolated groups of organisms always become different, but there is no indication that isolation is an evolutionary factor in the sense of causing or contributing to organic development. Its influence is negative rather then positive, for small groups of individuals advance less rapidly then large, and often deteriorate through inbreeding and inadequate diversity of descent.

The multiplying of species is a process distinct from developmental progress, and constitutes a distinct scientific problem.

Evolution might be explained without explaining speciation, and speciation without explaining evolution. Recognition of the diversity of the problems enables the factors to be separated; evolution depends upon symbasis, speciation upon isolation.

The segregation of a new group, whether by geographic barriers or by selective discrimination, merely affords opportunity for a new evolution to go forward. The means by which the progress is accomplished are to be sought inside the group, and not in the mere fact of isolation or selection. The multiplication of the number of evolving groups is a phenomenon distinct from that of the evolution itself. The evolutionary question is not how the species become isolated, but how they become different after they have been isolated.

Adaptation is the attainment of characters which place the species in a more advantageous relation with its environment.

Selection is a form of isolation which eliminates from the species individuals lacking in the expression of certain characters.

Under unconscious or natural selection only the most deficient in these characters are rejected; under conscious or artificial selection by man only the most proficient are saved. Selection, by deflecting and confining the evolutionary motion of the species to particular channels, conduces to the adaptive specialization of characters, but it is not an actuating cause of their development.

Symbasis is a primary factor in evolution, an obstacle or negative factor in speciation. Selection often accounts for the accentuation of differences between related species, but is not on this account to be reckoned as an actuating cause or principle of evolution. It may explain the direction which evolution has taken with reference to a particular character, but does not show how the evolution has been accomplished.

Adaptation represents the bionomic aspect of evolution, speciation the taxonomic. Selection strengthens adaptations; isolation multiplies species; symbasis conducts evolution. Adaptation and speciation have appeared to many writers as causes of evolution, but in the kinetic or physiological interpretation they appear only as results, quite incidental to the true evolutionary process of progressive change in species.

RELATION BETWEEN HETERISM AND SPECIATION.

Recognition of the phenomena of heterism, the normal diversity of the interbreeding members of specific groups, is necessary, perhaps, to a full appreciation of the preceding distinctions between evolutionary change or vital motion and the subdivision or multiplication of species. Although commonly treated together, or even indiscriminately confused, these two processes are quite distinct. They may even run counter to each other, for evolutionary progress is not assisted by the subdivision of a subdivision of a species, but more likely to be hindered. The larger the number of interbreeding individuals the larger are the possibilities that desirable variations will appear, and the wider are the opportunities of a progressive utilization of a new feature. The group, as a whole, will advance more rapidly than if the range of transmission be narrowed by subdivision.

Segregation permits the subordinate groups to become differentiated, but it does not conduce to the advance of the whole series. The newly segregated groups become capable of taxonomic recognition as species, but this is a mere incident of evolution, not an actuating cause nor a necessary effect.

The recognition of heterism or diverse, alternative descent, and the frequent development of sexual and other specializations of heterism inside specific lines, shows that the subdivision of species is to a very small extent, if any, the direct result of evolutionary advance. Not only can diverse characteristics exist inside specific lines, but it is an advantage to maintain just such heterogeneity. The only condition in which heterism would directly conduce to the formation of a new species would be that of alternative characters which hindered interbreeding. It is conceivable, for example, that a species might contain at the same time variations both toward earlier and later flowering, and that, instead of counteracting each other, both tendencies might become gradually more accentuated. The incidental result would be that interbreeding would cease and two separate groups would become established.[1] In such a case it might well be claimed that evolution had directly resulted in the multiplication of species, but it would still be true that it had done so only by means of segregation, and would show only that evolution might result in segregation, not that segregation is a factor in evolution, as often supposed. Isolation is an important consideration in phylogeny or historical biology, which undertakes to tell why the species are in the places we find them. But isolation and species-subdivision have only a remote aud incidental connection with evolution; they do not cause the progressive change.

The confusion of evolution with speciation has greatly impeded the progress of evolutionary science by withdrawing attention from the real issues to relatively unimportant considerations. It has misled many students of evolution into the belief that isolation or segregation is an important factor of evolutionary progress, whereas its influence is negative rather than positive. The selection doctrine of Darwin and the mutation doctrine of De Vries are both theories of speciation rather than of evolution.

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[1] The hickory-borer (*Clytus pictus*) and the locust-borer (*Clytus robiniæ*) are very similar species, and the females are quite indistinguishable. The perfect insects of the former emerge however, in June, those of the latter in September. See Packard, A. S., 1880, Guide to the Study of Insects, p. 497.

They hold that new groups have to be isolated, that new species have to be made, in order to originate and preserve new characters.

"Each new variety or species, when formed, will generally take the place of, and thus exterminate its less well-fitted parent. This, I believe to be the origin of the classification and affinities of organic beings at all times; for organic beings always *seem* to branch and sub-branch like the limbs of a tree from a common trunk, the flourishing and diverging twigs destroying the less vigorous, the dead and lost branches rudely representing extinct genera and families."

Evolution, on this basis, would not be a process of transformation so much as of elimination and substitution. The parental type remains relatively stationary and unmodified until the new form can expand and replace it. The same is true of the mutation theory of De Vries, except that the new variations are supposed to be larger. The new character can persist only as it is able to crowd out its parent or neighbor and to conquer for itself a place in nature. Every new character which has been preserved, must, under these theories, be environmentally useful, which a very large proportion of the characters and differences of plants and animals are not, as even the most pronounced Darwinians like Professor Lankester now admit.

The kinetic theory does not encounter these difficulties and improbabilities. It recognizes speciation and evolution as entirely distinct problems, and does not require that a new species be made in order to preserve a new character, or even that characters must be useful. Characters may be preserved even when they are harmful, and may contribute to the extinction of the species. Evolution, in the kinetic theory, is definitely a process of transformation by the adoption and propagation of new variations in existing species. New variations are not segregated from the parental type, but interbreed freely with it, and thus bring about its evolutionary progress.

SELECTION EXPLAINED BY EVOLUTION.

As so often happens, the philosophical abstractions of logic have yielded very little assistance in the comprehension and description of the facts of evolution. Numerous attempts have been made to define the relations of selection and evolution by means of Aristotle's categories of causation. Perhaps the best example of this is by Professor Cattell:

"In discussions on the theory of evolution we find Neo-Darwinians saying that 'natural selection' is the cause of the origin of species, and Neo-Lamarckians saying that the environment and the movements of the animal are the causes of adaptations. Now in these cases the word 'cause' is used ambiguously, ignorance of the facts of evolution being concealed by the exhibition of ignorance of logic.

"I wonder how many men of science have read Aristotle, or understand his distinctions between material, efficient, formal and final causes. We are not here concerned with a formal cause, the idea or plan of a thing, nor with a final cause, the end for which it is made; but no student of organic evolution can afford to ignore the distinction between material and efficient causes, or between the occasion and the efficient cause of an event. The material cause is that of which a thing is made, one of the occasions or necessary conditions of its existence; the efficient cause is that which produces a thing and makes it what it is. When no qualification is used *cause* should mean efficient cause or *vera causa*.

"'Natural selection' is no cause of the origin of species, but may be the cause of the annihilation of unfit species. Whether or not the environment, or consciousness, or the movements of animals are causes of hereditary modifications are open questions. What is called the cause of an adaptation is, however, usually only its occasion."[1]

Selection is neither a formal, a final, a material nor an efficient cause of evolution. Evolution goes on without selection. This shows how poorly adapted the Aristotelian categories are for the expression of relations so complex as those of evolution. Those who depend upon systems of abstract formulation for the comprehension of biology can fit selection and evolution into these categories only by saying that evolution is the cause of

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[1] Cattell, J. McKeen, 1896. The Material and Efficient Causes of Evolution. Science, N. S., 3: 668.

selection. This, at least, would not wholly misrepresent the facts of nature, for evolution accomplishes the results which it has been customary to ascribe to selection.

Unless evolution were going on the selective effects would not appear. The older writers commonly made the confusion even worse by assuming that adaptation and evolution are the same. Adaptation is not evolution, but only a special kind or result of evolution. Selection aids evolution to produce adaptation. Translating again into scholastic language, evolution is the efficient cause of adaptations, while selection is the occasional cause or condition which conduces to adaptations. Adaptive characters are brought into existence in the same way as other characters, by the evolutionary motion of species. Adaptation can be said to be caused by selection only as a pure abstraction, when it refers merely to the deflection which environmental obstacles have induced in the normal motion of the species.

The confusion of ideas has not been limited to advocates of natural selection, but is shared even by its most active opponents. Thus Mivart, in a book written to show the inadequacy of the selective theory of evolution, admits for selection a power which it does not have:

" 'Natural Selection,' simply and by itself, is potent to explain the maintenance or the further extension and development of favorable variations, which are at once sufficiently considerable to be useful from the first to the individual possessing them. But Natural Selection utterly fails to account for the conservation and development of the minute and rudimentary beginnings, the slight and infinitesimal commencements of structures, however useful those structures may afterward become."[1]

As long as we fail to perceive that selection is not a cause of evolution the issue remains uncertain. If selection is able to cause even a little evolution it might, with time, cause much. The "slight individual differences" may suffice for the work, as Darwin claimed, and the practicability of a selective evolution appears to turn on such arguments as the amount of time estimated by geologists and physicists from considerations even more obscure than those of biology itself. Selection is not

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[1] Mivart, St. George, 1871. On the Genesis of Species, New York ed., p. 35.

merely inadequate as a cause of evolution; it is not an evolutionary cause at all, but only a test and an evidence of the efficiency of other causes which reside in the species and enable it to go forward with persistence, even when obliged to follow a narrow path between environmental obstacles.

Selection is potent to explain the further extension and development of favorable variations only by its ability to influence an evolution which is already in progress, and not in any sense which renders it a cause of evolution. The selective potency of the environment consists only in its ability to restrict evolution, not in any power to actuate or to carry forward the process of development. Selection may still be enumerated as an evolutionary factor, but it is wholly a negative factor, restrictive and not constructive.

DARWINIAN FORMULÆ OF EVOLUTION.

Evolution is a name for the process of gradual change by which the diversity of organic nature has come about. Darwin's theory of natural selection was based on the indication that some of the characters of plants and animals have been attained because individuals possessing these characters had an advantage in the struggle for existence. Many Darwinians "more Darwinian than Darwin" have made this proposition universal and say in effect that all characters of plants and animals have arisen because they give or have given their possessors advantages in the struggle for existence.

Darwin's original proposition points in the direction of an important truth, that plants and animals are specially adapted to their various environments. Great emphasis came to be placed on this point because the adjustment of species to their respective places in nature had been taken to prove the special creation of species, so that a theory of gradual development had to supply a solution for the problem of adaptation before it could expect to receive general credence or even the serious consideration of the scientific public.

In the course of the discussion which raged in the decades after the publication of the Origin of Species attention was principally directed to the phenomena of adaptation and speciation, and the Darwinian doctrines were crystallized into formulæ which were believed to demonstrate evolution from the facts of the struggle for existence and the survival of the fittest.

PROVED FACTS.	NECESSARY CONSEQUENCES.
Rapid Increase of Organisms. Total Number of Individuals Stationary.	Struggle for Existence.
Struggle for Existence. Heredity with Variation.	Survival of the Fittest.
Survival of the Fittest. Change of External Conditions.	Changes of Organic Form.

The earlier Darwinists were practical men and made the best use of the facts as they knew them. Whether the facts they regarded as proved would really be able to bring about evolution in normally stationary species is a question which might still be debated on philosophical grounds, like the fourth dimension of space and other hypothetical problems. But for practical purposes there is no need to reopen the discussion, since it is now apparent that formulæ like those quoted above leave out of account a very important part of the facts of nature, the very facts, as it happens, which are most potent in the development of organic types. The evolution, if any, which the formula would provide would certainly not be that found in nature.

Scientific progress, at least in biology, does not follow the lines of formal mathematics or logic, but depends on history and human nature, like political and economic movements. It could not be expected that the evidences of evolutionary processes would be carefully weighed and correctly appreciated at a time when the very idea of evolution was being assaulted as an immoral perversion of intellect.

The best that could be done at the time was to drive the piles of accepted inferences into the mud of ignorance. The structure reared on such a foundation could not be a permanent one, but it has served to shelter a generation of students of nature, and enabled them to prepare the foundations of a more secure edifice of evolutionary doctrine based directly on ascertained facts.

In popular discussions it often happens that the best and most important data are left in the background because the public is not ready to appreciate them. Thus Huxley, who rendered the most valiant service in the defense of Darwinism as a theory of environmentally caused evolution, also wrote this discriminating statement:

"It is in the recognition of a tendency to variation apart from the variation of what are ordinarily understood as external conditions that Darwin's view is such an advance on Lamarck."

To have secured popular appreciation for these nonenvironmental variations at that time was manifestly impracticable. Even after fifty years their existence is still generally unrecognized.

The credit of turning the scientific world to the study of evolution will always belong to Darwin and Huxley, but the fifty-years canvass which has now been given to the Darwinian theory of environmental action upon normally stable species has yielded nothing of moment. Huxley's appreciation of the advance of Darwin beyond Lamarck has not been shared by the evolutionary public, and the result has been a general reaction toward pre-Darwinian conceptions, and even to some which Darwin himself considered and dismissed.[1]

Perhaps the time has come to renew the consideration of the problem from the kinetic standpoint and to take into account again the normal diversity of descent and the normal interbreeding of the members of species. These facts have remained veritable stones of offense for the builders of static theories of environmental causation, but they can now be utilized as foundations of a new and more commodious structure of evolutionary thought.

4. MODES OF EVOLUTIONARY MOTION.

The law of evolution which declares that organic nature has come into existence through a connected and gradual process, and not through millions of separate creations of species, now commands the practically universal adherence of biologists, and

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[1] "And again, after mentioning the frequent, sudden appearances of domestic varieties he speaks of 'the false belief as to the similarity of natural species in this respect.'" See Mivart, 1871. Genesis of Species, 36.

has also been applied as a philosophical principle in the elucidation of many facts and problems outside the organic series. After being once adequately presented such an integration of knowledge could scarcely have failed to command respectful consideration, and its general acceptance has already become so much a matter of course that the word evolution is not uncommonly used in a much narrower sense and identified with one or the other of the theories which have been invented to explain the methods and immediate causes of the process of organic change, a subject upon which there is still no lack of differing opinions.

Although the doctrine of the independent creation of species has been set aside, it has proved much more difficult to eliminate, even from the minds of the biologists themselves, what may be called the static view of nature. It is not strange that the stability of species should have first impressed the scientific mind. When closely similar plants and animals, not distinguished by the popular intelligence, were found to differ in minute particulars which were, nevertheless, invariably transmitted to their offspring, a creative pre-arrangement seemed to be the only explanation, and the apparently gratuitous variety of organic forms was very naturally ascribed to causes outside the reach of human comprehension.

Later, when it was realized that in spite of the wonderful stability of species the component individuals are never identical in all particulars, but differ endlessly among themselves, and that even these minor differences tend to reproduce themselves, the theory of the gradual transformation and subdivision of species became a logical possibility, and the search at once began for a method by which variations of a certain kind could be accumulated instead of cancelling each other and disappearing in a stationary average.

The explanation of evolution is the biological task now receiving the widest and most earnest attention, and is the subject, directly or indirectly, of a literature so vast that even a casual reading of all the books and papers as they come from the press would be a formidable undertaking. Such multiplicity of publications betokens, of course, a corresponding diversity of opinions. Not only is there no common point of view from which evolutionary problems are studied; there is no agreement regarding the nature of the problem or the methods by which a solution is to be expected, nor even a general evolutionary language in which discussion may be made intelligible.

Explanations of such a process as evolution are of many different grades or categories. Literary demands were satisfied by a name and a definition; theologically it was sufficient to substitute the idea of a continuous for an intermittent creation. Philosophy was content with the predication of gradual transformations due to natural causes. Even among biologists there are those who appear to have rested content with similar generalities, though some have not failed to appreciate that when Darwin established the probability of biological evolution he opened a multitude of other questions regarding the nature, causes and significance of the process. Realizing at once the importance of his discovery and the difficulty of securing the confidence of either the scientific or the general public, he expended years of labor in the collection of facts and the contrivance of theories which should increase the plausibility of the main proposition, that plants and animals are variable, both in nature and in domestication, and that the diversity of organic nature was gradually attained through the medium of variations.

When the causes of a phenomenon are known the sequence of events can be predicted. Theory may then out-run and assist observation. On the other hand, if the causes are out of reach it is obvious that we can not even theorize to advantage without a correct conception of the externals. We must know what takes place before we are in a position to ask why it takes place. In some lines of thought the simple historical conception of continuous evolutionary change greatly assists in the causal explanation of events, but in biology, the home of the evolutionary conception, the sequence is still in doubt and we are still far from the causal stage of knowledge. It is needless, perhaps, to add that the application of false and fictitious biological analogies vitiates much philosophical and sociological literature.

Gravitation was not explained by Newton, its behavior was carefully studied and found to be consistent, and mathematically precise. "Natural laws" are working substitutes for causal explanations. When we understand the *why*, the 'law' of sequence becomes superfluous.

There is a frequent impression that the principal object and result of scientific study is generalization, but as a matter of fact the progress of science leads much more often to particularization, to the recognition of distinctions between things previously supposed to be alike. The powers, forces and principles which formed the subject of abstract discussions in the earlier history of science are being gradually relegated to the background, as our acquaintance with the facts improves and yields insight into the causal connection of events which formerly appeared mere sequences.

Evolution is not merely a law, but a process. In each species an evolution is going on, in a manner quite analogous to the processes of growth, locomotion and reproduction in the individual. Certain features of similarity there are, no doubt, in all evolutions, as there are in digestion and other general forms of vital activity. These general similarities can be collected, it may be, and formulated as laws if this method of expression be desired, though this would be, after all, only a special method of describing the processes. Laws themselves have to be explained by resolving them into processes. Only hopelessly metaphysical minds are satisfied with abstract statements, or able to imagine that generalizations are explanations.

Evolutionists agree that organisms change, but regarding the nature and causes of change great diversity of opinion still exists. The progress thus far is negative. We have learned that evolution is not a merely mechanical process, or due to merely environmental causes, and that it is not a merely cytological process, due to internal mechanisms of descent. It is a superorganic process accomplished through the association of organisms into large specific groups.

Evolution is, in short, a process of change in organisms, a kind of motion by which plants and animals have advanced from the simple and undifferentiated protoplasm of the lowest types to the highly specialized and complicated structures of the highest. For half a century this probability that the world of organism has come into existence through long series of changes has been the most prominent idea before the scientific public, but we have not yet accepted fully the simplest purport of the idea of evolution and asked ourselves the direct question: By what mode or manner of motion is evolution accomplished?

Some have assumed that the evolutionary causes are resident in the environment, and others that they exist in the organisms themselves. A third alternative is here considered, that evolution arises from the association of organisms into interbreeding groups, or species. Species, in this interpretation, appear to contain the causes of evolution, instead of evolution affording the explanation of species.[1]

The first result of Darwin's attempt at establishing the general idea of evolution on a basis of relation to concrete facts was a long and bitter controversy with those who clung to the older theory that the species of nature had arisen by separate creative acts. Biological science made good its escape from the house of theological bondage, but its controversial sins have condemned it to forty years of wandering in the wilderness of species-formation and environmental adjustments, desert regions often very interesting in themselves, but remote enough from the fertile fields of evolution.

It may well be doubted whether any student of nature, if asked the direct question, whether species are normally at rest or normally in motion, would definitely and dogmatically hold to the static assumption. This appears to have been made quite unconsciously, in the great majority of cases, or taken entirely for granted. Nevertheless, all the current theories and methods of investigating evolutionary problems are based on this assumption of normally stationary species. The influence of the doctrine of special creation was too strong to be overcome at once, even by biologists who were very active in opposing its theological implications.

The idea of environmental causation of evolution has com-

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[1] Cook, O. F., 1904. Evolution not the Origin of Species, Popular Science Monthly, for March. Reprinted with additions in the Smithsonian Report for 1904 under the title, The Evolutionary Significance of Species.

pletely pervaded all our forms of thought and expression; it has been the general base and background of evolutionary science. The average of biological opinion remains very nearly in the same place as Darwin's original announcement of a theory of environmental causes of evolution. The environment is supposed to bring about the variations and to select and preserve those having adaptive value, and thus to cause evolution. Though Darwin himself appreciated in later years the tentative character of this inference and sought in every direction for contributing agencies to strengthen and support it, some of his followers have had no such reluctance in crystallizing the idea of environmental causes into definite formulæ which are still the shibboleths of evolutionary orthodoxy. President David Starr Jordan not long ago quoted an interesting paragraph from the evolutionary creed of the late Dr. Eliot Coues:

"Every offspring tends to take on precisely the structure or form of its parents, as its natural physical heritage; and the principle involved, or the *law of heredity*, would, if nothing interfered, keep the descendants perfectly true to the physical characters of their progenitors; they would breed true and be exactly alike. But counter influences are incessantly operative, in consequence of constantly varying external conditions of environment; the plasticity of organization of all creatures rendering them more or less susceptible of modification by such means, they become *unlike* their ancestors in various ways and to different degrees. On a large scale is thus accomplished, by *natural selection* and other natural agencies, just what man does in a small way in producing and maintaining different breeds of domestic animals."[1]

It should be needless to say that this formula, like many statements of similar import which might be collected from biologists of a former generation, and even from those of the present day, involves a complete misrepresentation of the facts. No such species has been found in nature, and no species has been made uniform by any refinement of artificial conditions. It is possible through selective inbreeding to eliminate a large part of the normal individual diversity of organisms, but at the

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[1] The Popular Science Monthly, May, 1903.

expense of vitality, and at the ultimate cost of extinction, where-ever such experiments are continued for a sufficient period of time.

More recently still, a son of Charles Darwin, speaking as President of the British Association for the Advancement of Science, has reflected the conclusion which the scientific world has drawn from his father's doctrine of natural selection, that it is the cause of evolution.

" The fundamental idea in the theory of natural selection is the persistence of those types of life which are adapted to their surrounding conditions, and the elimination by extermination of the ill-adapted types. The struggle for life amongst forms possessing various degrees of adaptation to slowly varying conditions is held to explain the transmutation of species."[1]

It may be doubted whether Charles Darwin himself would ever have ventured upon so direct and so generalized a statement. He was anxious always that his readers should take a favorable view of the feasibility of evolution through natural selection, but at the same time he could not forget the immense improbability of the claim that all characters are adaptive and useful. This caution was not shared by Wallace, who has never hesitated to proclaim selection as the cause of evolution, alike efficient and sufficient. With Darwin, natural selection remained a theory, and he never ceased to seek additional evidence to support or supplement it, but with Wallace and many others it soon became an undoubted fact, or at least an unquestioned formula.

" Suffice it to say here that this theory of natural selection — meaning the elimination of the least fit and therefore the ultimate 'survival of the fittest' — has furnished a rational and precise explanation of the means of adaptation of all existing organisms to their conditions, and therefore of their transformation from the series of distinct but allied species which occupied the earth at some preceding epoch. In this sense it has actually demonstrated the 'origin of species,' and, by carrying back this process step by step into earlier and earlier geological times, we

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[1] Darwin, G. H., 1905. Address of President of the British Association for the Advancement of Science; Nature, 72 : 370. Science, N. S., 22 : 258.

are able mentally to follow out the evolution of all forms of life from one or a few primordial forms. Natural selection has thus supplied that motive power of change and adaptation that was wanting in all earlier attempts at explanation, and this has led to its very general acceptance both by naturalists and by the great majority of thinkers and men of science."[1]

But notwithstanding the categorical certitude of these and many similar statements which might be collected, it is still very doubtful whether any naturalist, that is, any careful and experienced student of plant or animal species in nature, would definitely claim or undertake to prove that isolation or natural selection is, or could be, a true, actuating cause of evolution. Nevertheless, many such students have permitted themselves to use expressions which can be so interpreted, and the philosophical, and especially the unbiological part of the scientific community, has not hesitated to repeat and elaborate this idea as though it were an ascertained and undeniable fact.

Primitive peoples are ever ready to personify nature and inanimate objects and to ascribe to them the ability to grow and to put forth other spontaneous actions. Modern science has gone to the other extreme. It has denied to the species of plants and animals the powers of development which they really possess, and has sought for the causes of organic evolution among the inanimate objects of the environment. It has done this quite gratuitously and as a matter of course, without taking the trouble to raise the question whether there might be any alternative worthy of consideration.

The primitive theory of a flat earth, with its various childish explanations of the sun's whereabouts during the night, endured for thousands of years, but finally gave place to the conception of a spherical earth, about which the luminary revolved continuously. Nevertheless, this improved doctrine, while adequate for the explanation of the phenomenon of days and nights, was also erroneous, and had to be replaced by a still broader interpretation of astronomical facts.

Astronomers of the Ptolemaic school saw no reason to doubt that the earth was stationary, and they were able to predict

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[1] Wallace, Alfred Russell, 1900. The History of the Nineteenth Century.

eclipses and planetary movements in spite of this fundamental misconception. Mysteries and discrepancies remained, however, until students of the heavenly bodies were willing to admit that the sun was the center of the system and that the earth revolved like her sister planets.

If adaptations were the only evolutionary phenomena in need of explanation, the doctrine of environmental causes might serve scientific purposes for as many centuries as the Ptolemaic astronomy, but it has become very apparent that many organic changes are going on which have no connection with adaptation, and which would not be explained by selection, even if everything claimed for it were to be admitted.

To think of species as normally in motion will be found very difficult, no doubt, by those who have been so long accustomed to take it for granted that they are normally at rest. The difficulties of readjustment are still further increased by the fact that the available technical language and customary forms of expression have been elaborated for the exposition of the static doctrine of environmental causation, and lend themselves only with difficulty to the presentation of the opposite doctrine, that species are normally in motion.[1] Many distinctions formerly considered of value now appear to have little significance. Many things are readily explainable which seemed utterly mysterious before, and many new problems can be approached which have hitherto appeared quite inaccessible.

Since the time of Darwin a long and varied series of amendments and supplements have been proposed for the doctrine of natural selection, and no end of diversity of individual opinion has existed among biologists regarding the adequacy and relative significance of the various factors and forms of selection. The kinetic theory enables us to look beyond all this cloud of discussion and to perceive that selection is not merely inadequate as the cause of evolution; it is not an evolutionary cause at all, in the concrete physiological sense; it does not set evolution in motion, nor keep it going.

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[1] Three classes of difficulties attend the progress of science, the concrete difficulties of ascertaining facts, the conceptual difficulties of interpreting them, and the philological difficulties of describing the new facts and the concepts in terms of general intelligibility. The problems of expression are often quite as serious as the others, and quite as worthy of scientific study.

The difficulties which attend the presentation of the kinetic theory arise, no doubt, largely from this fact, that it breaks with the Darwinian traditions and recants the whole doctrine of selection as the actuating cause or principle of evolution. It seeks for the laws and causes of evolution, not in the environment, nor in a "hereditary mechanism" of the organisms themselves, but in the association of organisms into specific groups of interbreeding individuals, which are the units of evolutionary motion. The reader is therefore duly warned that, unlike most of the suggestions made since the time of Darwin, kinetic evolution does not come as an amendment to natural selection.

Those who may wish to experiment with the new method of biological locomotion had best unload beforehand all their prepossessions regarding natural selection as an evolutionary cause. This does not mean that selection is to be permanently abandoned, but it can be taken up later, and put to a much more useful purpose than before. Indeed, the material analogy may be carried a step further by saying that the supposed evolutionary properties of selection have been due to an unsuspected admixture of kinetic implications, the selection idea in itself being quite inert, and incapable of actuating even a logical conception of evolutionary motion.

Theories which located the causes of evolution in natural selection or other forms of environmental reactions have considered the species normally stationary until acted upon by the external forces. Theories which located the causes inside the organisms have thought of evolutionary motion as proceeding in definite directions without regard to environmental influences, except as they might work the extermination of types poorly fitted to the conditions they happened to encounter. The kinetic theory, in appreciating the fact that the evolutionary change goes forward in a network of descent woven by the free interbreeding of the individual members of the specific group, reaches the conception of a highly composite, indeterminate motion carried along without any environmental causation, but at the same time capable of being deflected through selective influence into channels of adaptation.

Proc. Wash. Acad. Sci., January, 1907.

The most feasible way of presenting the kinetic interpretation and of comparing it with other alternative views has seemed to be that of canvassing further this question of the nature of the motion by which evolution is supposed to be accomplished in accord with the different doctrines. It may be that by so doing the issue can be made more direct and that there will be less risk of wandering into the unprofitable side-paths of aimless discussion. The fact already referred to, that the vocabulary of evolution has been constructed so largely for the explanation of static doctrines, makes it necessary to review briefly some of the primary terms and distinctions.

PHILOSOPHICAL USES OF EVOLUTIONARY MATERIALS.

Circles can be described through any three points, and new systems of philosophy can be elaborated out of a few primary distinctions. As geometry and other speculative sciences of number and space relations have been called upon to assist in the measuring of land, the building of machines, the navigation of the sea, and the exploration of the heavenly bodies, so have the methods of philosophy been applied to evolution. This is not only because philosophers have become interested in evolution, but because philosophical systems are the most available form of mental machinery for dealing with complex miscellaneous, hypermathematical problems, like evolution.

It has been the ambition of philosophers to frame general descriptions of the universe of thought in terms of logical consistency. Indeed, the tendency in philosophy has been to place by far the greater emphasis upon the logical consistency, each philosopher assuming the right to choose his own particular universe for descriptive purposes. Unfortunately for evolutionary philosophers, their systems are confronted, sooner or later, with the concrete facts of plant and animal life, and then no amount of logical consistency can atone for a biological oversight. Theories may be perfectly logical and yet be utterly inadequate. But even though not correct or final, philosophical theories of biology may still amply justify themselves by aiding in the discovery of relations which might have remained unsuspected and hence uninvestigated. The ungrateful facts may refuse to support the theory which has led to their discovery, but this does not render the facts of less value for practical purposes, nor even for use in other and better theories. It is as idle to condemn theories as to worship them; it is the old counsel of using and not abusing.

Theories of evolution have been made thus far from the facts of variation, the differences which exist among the members of the same species. In each of the different systems it has been assumed that a certain kind or group of variations represented steps in the evolutionary journey. The philosophical circles of doctrine have been described in different planes in accordance with the selection of particular lines of samples from the multitudinous facts of variation.

The theory of natural selection is supported by the facts of adaptation and geographical distribution. The theory of direct adaptation was based on variations of accommodation, on the fact that organisms are often able to adjust themselves to a considerable range of environmental conditions. Nägeli's determinant theory was based on the fact that the plants most carefully studied by him showed tendencies of variation in definite directions. The theory of mutation rests on facts of abrupt modifications in the form and structure.

The kinetic interpretation claims the consideration of believers in the other doctrines because it affords a larger outlook upon the facts of nature. Adaptation and mutation no longer appear as unconnected or contradictory phenomena, but are completely reconciled under one simple inference.

The kinetic theory differs from its predecessors not merely nor principally in dependence upon a different series of facts of variation, but also in the method of combining them. It is not merely a circle cut in one plane or described on one cross-section of data, but considers all three dimensions of space. It permits us to understand that variations are not all of the same character or of the same evolutionary significance. It also recognizes that as species are networks of descent and not mere aggregates of similar organisms, so evolution is not merely a summary or integration of variations, but is accomplished only through the normal extension of the specific reticulum.

In pre-evolutionary days there was no need to make special studies of variation, since it was freely admitted by the scientific public that the differences of varieties and even of species arose from environmental influences upon normally stationary types. The supposition was that genera had been created, rather than species, though Linnæus interfered with this view by combining many of the groups recognized by his predecessors as genera and by holding then that species also were specially created.

The significance of this history is that the two ideas, first, that of normally uniform and stationary species, and second, that of the environmental causation of variations, were inherited from the pre-evolutionary period and have continued to be used without scientifically critical warrant.

Moreover, the first quest for evolutionary causes was not made in the direction of more thorough study of the constitution of species, but was concerned rather with the exploration of the boundaries and the gaps between species. The issue raised by Darwin, and more especially by Huxley and other controversial biologists, was that of proving to the theological public that new species could be produced by evolution, instead of definitely investigating the means by which the evolutionary progress of species is accomplished. The chief interest was directed, not to evolution itself, but to the two results of evolution, speciation and adaptation, the generally admitted pre-Darwinian doctrine of environmental causation of variations serving all the immediate needs of the discussion.

TYPES OF EVOLUTIONARY THEORIES.

Static Theories. — According to the theory to which the name Darwinism is generally, though unjustly, limited, evolution is brought about by the influence of environment, which causes organisms to vary, preserves advantageous modifications, diminishes or eliminates the relatively unfit, and thus transforms or subdivides species.[1] Such theories may be called static because they assume that species are normally in a state of rest or

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[1] "Darwin has left the causes of variation and the question whether it is limited or directed by external conditions perfectly open." Huxley, Life and Letters, 2 : 205, 1901.

stable equilibrium, so that evolutionary motion appears as the result of forces external to the organism. Differences among the individuals of a species are ascribed to environmental causes; without such disturbing influences the species is thought to remain stationary and uniform. Darwin and many others have believed in spontaneous variations, but it has been argued that such must be 'swamped' in the general average by intercrossing, so that without the external influence of selection there could be no progressive change.

Darwin himself admitted that in the domestic animals 'man does not cause variability and cannot even prevent it,' but on the same page he made the contradictory statement that 'the initial variation is caused by slight changes in the conditions of life,' and this has served as the cardinal principle of those who have claimed to be Darwinists, while rejecting the wider perception cited above. Again in the same work (p. 79) Darwin is ready to admit that 'a somewhat complex, though apparently useless, structure may be suddenly developed without the result of selection.'[1]

Saltatory Theories. — That variations can be preserved by selection, and are frequently so preserved among domesticated animals and plants, cannot, of course, be doubted, but the difficulty of believing that natural conditions would provide the necessary selection or segregation at the right junctures has led many biologists to look with favor upon the idea that new species have not arisen by imperceptibly gradual changes, as Darwin supposed, but by a succession of leaps, as it were. This view is defended by reference to the so-called 'sports' or very pronounced variations occurring among domestic plants and animals.

Mr. Francis Galton has compared the organism to a polygonal body which comes to rest at a point considerably in advance of its former position when its equilibrium has been sufficiently disturbed. Professor De Vries has adopted the saltatory view, as a result of his studies of what he calls mutations, or pronounced and readily transmissible variations of domestic plants.

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[1] The Variation of Animals and Plants under Domestication, p. 3, New York, 1897.

Instead of slow or gradual changes of the characters of species there are supposed to occur at remote intervals in the life of a species relatively brief periods of mutation in which violently abrupt variations are given off in an explosive manner. Each of these discontinuous variations is considered as representing the production of a new species, there being no gradations between it and the parental type. Unfortunately, the wide application of this analogy is prevented by the fact that in many natural groups descent from a single individual is impossible. Moreover, the new types or sports studied by Professor De Vries are, like other closely inbred plants and animals, much less fertile than their wild progenitors, thus increasing the probability that the inbreeding or segregation necessary to secure and preserve these abnormalities would give them a fatal handicap in the struggle for existence. Finally, the wide distribution, among both plants and animals, of sexual differentiation and other expedients for securing cross-fertilization, seems a sufficient warrant for distrusting any theory which disregards this important group of evolutionary phenomena.

Determinant Theories.—The noninheritance of acquired characters led Nägeli and Weismann to formulate what may be termed determinant theories, under which the motion of species is not thought of as caused or directly influenced by the environment, but as the function of internal "mechanisms of descent." Nägeli believed that species did not vary in all directions indiscriminately, as Darwin had held, but that they kept, without selective influences, a definite direction. He therefore concluded that the organization of living matter contained what he called a "*Vervollkommungsprinzip*," or principle of perfection, which carried them ever upward along the road from simplicity to complexity.

Weismann sought in his doctrine of determinants to render this conception more concrete regarding the nature of the internal mechanism, and to provide a means of selective influence. Determinants may be described as biological atoms, resident in reproductive cells and able to determine in advance the character of the new organism, independent of its environmental relations. The environment also has no effect on the next generation, selection pertaining not to the characters themselves, but to the determinants which might repeat the characters in the next generation. Further elaboration of the doctrine of determinants has been made in the belief that the external conditions, while unable to act through the body of the organisms, might act directly upon the reproductive cells. Others assume conflicts or struggles between determinants (germinal selection) as possible factors in evolutionary motion.

As a suggestion that evolution might be the result of external influences, and as a means whereby characters imposed by the environment could be transmitted, Darwin invented the theory of pangenesis, to the effect that the germinal material carrying reproductive influences was assembled from all parts of the body of the parent organism. Direct evidence for this supposition has never been found; indeed, the contrary proposition, that acquired characters are not and cannot be inherited, has commanded the belief of Professor Weismann and his numerous followers. Having cut loose, as it were, from environment, which had been the chief resource of static theories, they have sought the explanation of the evolutionary problem in a so-called "hereditary mechanism," by which the characters of successive generations are held to be predetermined in the reproductive cells. The structure of the living cell has accordingly received the attention of many earnest investigators and a new science of cytology has been rapidly built up. But, as in the pursuit of her somewhat older sister, embryology, no general uniformity of structure or processes has been discovered. Biology has been enriched by the addition of a vast number of interesting facts, but the minute structure and internal organs of plants and animals, including the structure and organs of the component cells themselves, have been found to share the general diversity of nature, and to be as much in need of evolutionary explanation as the external characteristics of the various natural groups.

With an infinity of biological facts to draw upon, no theory need remain without support, real or apparent. An evolutionary inference warranted in one group may be quite false as a general law, and in this sense an inadequate theory may be more misleading than one which is actually erroneous. Thus each of these types of evolutionary theories may be said to rest upon certain groups of evolutionary facts which are more or less completely ignored by the others. The niceties of many adaptations to environment have led Darwin and his followers to almost exclusive reliance upon that factor. Saltatory theories provide larger variations, but require even more effective isolation. Determinant theories deny the influence of environment and must ascribe adaptations to accident or to pre-established harmony. All three theories antagonize the obvious fact that a very general tendency of organic development has been toward the increase of facilities for cross-fertilization. These have been interpreted as inimical to evolution because they interfere with the preservation of the abnormally close-bred variations which have been mistaken for true steps in the progress of organic series.

KINETIC OR SYMBASIC EVOLUTION.

Somewhat between the doctrines of selection and of determination, but distinct from both, is another conception of evolutionary motion, that it is caused neither by external environments nor by internal mechanisms, but goes forward as a necessary result of the normal specific constitution of living matter. It is observed that organisms normally exist and make evolutionary progress only in large groups of interbreeding individuals. Evolution is, in a word, symbasic; that is, organisms must travel together along the evolutionary pathway, and must be connected with each other by an intricate network of descent in the weaving of which the diversities of the members of a species have a definite physiological value. Without diversity of descent the cellular organization deteriorates. This being the case, it is easy to understand that new variations are prepotent, and that species make more rapid evolutionary progress in proportion to their numerical size. The larger and more widely distributed the species, the greater the opportunities of variation and of evolutionary progress.

Kinetic evolution is thus the reverse of many current theories, in that it recognizes a normal and necessary movement of change not caused by environment. It is the reverse of the selective theory of Darwin in holding evolution to be independent of natural selection. It reverses the panmixia doctrine of Professor Weismann, in that it treats the interbreeding of the numerous and diverse individuals of species as conducive of biological motion, instead of as hindering it. It is the reverse of the mutation theory of Professor De Vries, in that evolution is held to go forward normally in entire species, and not merely in individuals or in narrow lines of descent.

One of the chief weaknesses of all the static doctrines, both saltatory and selective, lay in the apparent necessity that new variations be isolated from their relatives in order to preserve their new characters and make evolutionary advance possible, for the fundamental concepts of the static doctrine are the normally stationary average and the swamping effects of intercrossing.

The kinetic theory differs fundamentally from all its predecessors in recognizing the fact that evolution is not a process of segregation, but of synthesis and integration. The transformation of species in nature is brought about by the sharing of individual variations through interbreeding. Conjugation and cross-fertilization do not hinder evolution, but are essential to the gradual building up of the intricate coordinations of characters through which adaptations and other desirable changes go forward. Selection, inbreeding, isolation and other forms of segregation, reduce the number of accessible variations, narrow the basis of the vital structure, and result in organic weakness, sterility and extinction. Selective isolation accentuates particular variations and has been utilized in the diversification of domestic varieties of plants and animals useful to man, but abnormal and weak from the evolutionary standpoint, and affording no complete analogy with the natural development of organic types. The sterility of many hybrids and the tendency of inbred varieties to produce relatively infertile sports may prove to be explainable by the same fact of inadequate fertilization. For want of better words it may be said that the vital tension of inbreeding is too little, while that of hybridity is too great; the normal course of biological evolution lies, obviously, between the two extremes. Evolution, or biological motion, appears to be necessary as well as universal. Free interbreeding between the members of large organic groups, or species, is the condition under which biological evolution is going forward in nature, and we have no reason to seek its cause in any aberration or specialization of structure or function.

The fundamental and truly dynamic causes of evolution still lie hidden in the equally unknown causes of genetic variation, but the evolutionary history of a group of organisms is a process which a kinetic theory adequately explains by supplying physiological reasons and methods.

The ultimate theory or stage of evolutionary explanation must await far more complete knowledge of the nature of the phenomena to which we commonly refer under such abstract terms as matter and force, expressions which we can neither describe nor define, except in a purely formal manner. Much is gained, however, by the recognition of the fact of normal evolutionary motion, by perceiving that organic development is a kinetic phenomenon, for the species no less than for the individual. Individuals and species are conditioned, but not caused, by their environments; they descend from other species and from other individuals in continuous series of ever-changing forms. There is an inside as well as an outside physiology of evolution, and it is idle to ignore either the one or the other.

To advance from the static to the kinetic point of view gives us ready and practical solutions for many problems which on the static basis bid fair to have required long periods of time and large expenditure of money. It brings also, as does every advance of science, a host of new questions which the static evolutionist could never have asked, such as the rapidity of evolutionary motion and the means of accelerating, retarding or deflecting it.

A kinetic theory of evolution does not need to explain variation any more than it needs to explain symbasis and environment; it accepts these three groups of biological facts, and correlates them as evolutionary factors. Conversely, a theory of variation is not necessarily a theory of evolution; the two questions may be viewed as quite distinct. The recognition of evolution as a kinetic process does not conflict with a dynamic explanation of variation, but contributes to such an achievement by rendering the problem more definite. It affords another conception of how evolution may be accomplished, but a conception more comprehensive than those which have gone before ; one which does not depend upon any theoretical or doubtful relation, but upon the well ascertained and universal fact that organisms exist everywhere in species—groups of diverse individuals freely interbreeding to form a complex network or fabric of descent.

To some there may appear to be no practical distinction between the static and the kinetic views. Not a few naturalists have entertained truly kinetic conceptions of the facts of organic nature, even while continuing to misrepresent them by the use of the static terminology. For descriptive purposes, such as the tracing of phylogenies, the differences are less important, but fundamental divergence is obvious in approaching the physiological questions of methods and causes. The probable truth of a theory does not depend merely upon the number of facts which can be assembled under it, but also upon the coherence and practical consistency of the relations alleged. Of two theories otherwise equal the more simple and direct should receive the greater confidence. The kinetic theory is not compelled to ascribe utility to all characters, and can explain useful and useless characters by reference to the same facts of organic diversity and association in species.

SUMMARY OF EVOLUTION THEORIES.

Static theories view the species as normally stationary, and ascribe evolutionary motion to environmental causes of adaptation. The static theory commonly called Darwinism (though avoided by Darwin himself) treats adaptations as caused indirectly through natural selection, by the survival of the fittest of the individual variations. The static theory of Lamarckism treats adaptations as direct results or responses to environmental influences.

Saltatory theories view the species as normally stationary except for rare intervals of sudden transformation or "mutation" caused either by the environment or by internal "forces" of unknown character. Selection can determine the survival of mutations adapted to environmental conditions, but exerts no direct adaptive influence.

Determinant theories view species as moving gradually in definite directions in obedience to internal "principles of perfection" or "mechanisms of descent." Adaptation depends on the coincidence between evolution and environment; selection exerts no direct influence.

Kinetic theories view species as normally in motion, but not in a single or definite direction, and not as a result of environmental causes. The normal evolutionary motion of the species may be restricted and deflected by the selective action of the environment, resulting in adaptation.

The adjacent tables may assist in showing the relations between these different types of evolutionary theories. Table I indicates the methods by which the various doctrines answer some of the principal questions regarding evolutionary motion. Table II brings these questions into relation with the conclusions reached in previous chapters. Discrepancies between different evolutionary doctrines are often explainable by the fact that some of them are in reality theories of adaptation or of speciation, rather than of evolution. Thus, as the table shows, interbreeding is a strongly negative factor in the multiplication of species (speciation), but at the same time it is a strongly positive factor in evolution. The chief factors in adaptation and speciation have only negative or restrictive effects upon evolution.

NORMAL CONDITION OF SPECIES.

The most fundamental diversity of opinion regarding the nature of evolutionary motion is that of the normal condition of species. Two assumptions are possible and have equal warrant for scientific consideration. Under theories of environmental and selective causation, it has been taken for granted that species are normally stationary and uniform unless acted upon by some disturbing external influence. The question of causes, on this assumption, is a simple one. The difficult problem is to explain how the external influences produce the organic results which have been ascribed to them. Fifty years of study have been

TABLE I.

OUTLINE COMPARISON OF TYPES OF EVOLUTION THEORIES.

	Static Selection. (Darwinism.)	Static Isolation. (Gulick.)	Static Direct Adaptation. (Lamarck.)	Saltatory. (De Vries.)	Determinant. (Nägeli, Weismann.)	Kinetic.
Normal condition of species.	Stationary, uniform.	Stationary, uniform.	Stationary, uniform.	Stationary, uniform.	Determinate change.	Indeterminate change.
Character of evolutionary motion.	Gradual.	Gradual.	Gradual.	Abruptly discontinuous.	Gradual.	Gradual.
Occurrence of motion.	Occasional.	Occasional.	Occasional.	Intermittent at rare intervals.	Continuous.	Continuous.
Principal agent of change.	Selection.	Isolation.	Environment.	Environment.	Hereditary mechanism.	Symbasic interbreeding.
Utility of new characters.	Requisite.	Unnecessary.	Requisite.	Unnecessary.	Unnecessary.	Unnecessary.
Methods of preserving new characters.	Selection.	Isolation.	Environment.	Isolation.	Germinal selection.	Interbreeding.
Natural selection as evolutionary factor.	Positive efficient.	Positive Inadequate.	Unnecessary.	Positive Inadequate.	Positive Inadequate.	Negative.
Interbreeding as an evolutionary factor.	Negative.	Negative.	Negative.	Negative.	Negative.	Positive.

TABLE II.

EVOLUTIONARY CONDITIONS, FACTORS AND RESULTS.

	Normal Interbreeding. (Symbasis.)	Selection.	Isolation.	Accommodation Differences. (Artism.)	Descent Differences. (Heterism.)	New Characters. (Neism.)
Evolution.	*Positive.*	Negative.	Negative.	Positive.	*Positive.*	*Positive.*
Adaptation.	Positive.	*Positive.*	Positive.	*Positive.*	Negative.	Positive.
Speciation.	*Negative.*	Positive.	*Positive.*	Negative.	Positive.	*Positive.*

expended on this phase of the problem, but with no direct results. For this reason, if for no other, the careful consideration of the alternative possibility would be justified.

The kinetic theory is not dependent, however, upon merely abstract or inferential justification, but is supported by the evidence of all observations and experiments which have a bearing upon the question. That groups of organic individuals become different whenever they have been isolated for any considerable periods of time, may be taken as proof that evolutionary change is a general and normal condition of the existence of species. It can be asserted, of course, that divergences between groups of common origin are due to differences of environment, but the inadequacy of this explanation is conclusively shown by the many instances where groups have preserved great similarity of habits and environmental conditions, but have attained, nevertheless, to a great diversity of form and structure, as in the conspicuous instance of the animals of the class Diplopoda, and of various classes of the lower plants, such as the mosses and hepaticæ.

Two modifications of the stationary assumption had been formulated, previous to the kinetic theory. Under the mutation theory of Professor De Vries, the normal condition of uniformity is supposed to give place at rare intervals to periods of mutation or sudden appearance of new species. In the determinant theory of Nägeli, species were held to be normally in motion, but the motion was supposed to follow a definite direction as the result of internal physical and chemical adjustments.

The changes predicated as normal for species under the kinetic theory are of an indeterminate and composite character. The species is not thought of as changing in one direction merely, but in many characters at once, the required result being a constructive coördination of changes which will increase the vita efficiency of the organism and enlarge its power of utilizing its environmental opportunities.

RAPIDITY OF EVOLUTIONARY MOTION.

Static theories, which have agreed in thinking of species as normally stationary, have also taken it for granted that evolutionary changes must be gradual, and some writers have dwelt upon the imperceptible slowness of evolutionary progress. The mutation theory of Professor De Vries adopts the other extreme, in holding that evolutionary motion is abruptly discontinuous, the individual organism leaping, as it were, from one species to another without any steps or gradations. From the kinetic standpoint, mutations like those studied by Professor De Vries are interpreted as abnormal and degenerative phenomena, but the fact is recognized that the individuals of many species in nature have very recognized differences, so that the steps of evolutionary progress may not always be infinitesimally gradual. There are indications that prepotent new characters may often transform a species or variety in a comparatively short period of time.

CONTINUITY OF EVOLUTIONARY MOTION.

Theories which ascribe organic changes to selection or to environmental causes imply that progress is limited to the characters which happen at the time to have environmental significance. In this view evolutionary motion, though gradual, must be described as occasional, rather than as continuous. After a period of selective development a species might cease, for a time, to be affected by selection and remain stationary, or might even retrograde, as claimed by Weismann and others.

In the mutation theory the idea of occasional change is carried still farther, so that evolutionary motion would need to be described as intermittent and occurring only at rare intervals. This is the type of evolutionary theory which comes nearest to the older doctrine of separate creation of species. It represents species as arising from single individuals, and denies gradual or continuous progress. It declares that evolutionary motion is saltatory or discontinuous; that there are sudden changes or jumps from one species into another. Such an evolution could not be described as taking place *in* species, but *between* them, the species themselves being essentially stationary except when acted upon by special "forces." Whether the forces are external or internal is a matter of opinion which subdivides saltatory evolutionists into two subordinate schools.

Saltatory evolution consists of a series of abrupt lateral displacements, each species remaining stationary and unchanged from the time of its origin by mutation. No forward progress of the members of interbreeding groups is provided. Motion takes place only in the individuals which give rise to the new groups. Selection would thus have no influence upon evolutionary motion in connection with the mutation theory. Its function would be limited to the determination of the survival of the new species which might prove to be adapted to their environments. Motion is conceived only in simple inflexible lines and not in a network of descent which can bend in adaptive directions when environmental obstacles are encountered.

Saltatory theorists do not deny that diversity exists among the members of species, but they ascribe this to the influence of external conditions or to a general principle of inconstancy or fluctuation, without any special evolutionary significance.

Saltatory theories stand in most direct contrast with those which ascribe continuity to the evolutionary motion of species, which are thought of not as advancing by leaps or sudden transformation of one species into another, but as going forward by gradual steps, larger or smaller. Natural selection by the environment is thought of as changing the average and hence as causing evolutionary motion. The higher groups of plants and animals have so many adaptive characters that evolution by natural selection has been accepted by many biologists as a demonstrated fact.

Determinant and kinetic theories agree in expecting evolution to be continuous, the one because the internal mechanisms would continue to act, the other because the interbreeding of the ever-diverse individuals of the species is being continued.

MUTATIONS DISTINGUISHED FROM NATURAL SPECIES.

There is a wide and fundamental difference between the kind of evolutionary motion shown by mutations of inbred domesticated species and that by which the progressive development of natural species has been brought about. The condition of inbreeding under which mutations appear has so far weakened the organism that the newly modified form is recessive, that is, it tends to disappear when crossed with unrelated groups. Such variations could not spread or propagate themselves in a normally symbasic species; each would need to be carefully isolated in order to be preserved. In the second place, very few, if any, of the thousands of mutations which have come under the eyes of planters and experimenters have proved to be more fertile, in the true reproductive sense, than the parental types. Nearly all of them are conspicuously deficient in this respect, and would thus struggle under a fatal selective handicap in competing with the parent form, if they were not at once wiped out by interbreeding. Mutations have very great agricultural importance, but their practical value will not be enhanced by overlooking this fact of deficient fertility which is fatal to the view that they represent a genuine condition of progressive evolution.

Mutations arise sideways, as Professor De Vries explains, but it does not follow that new species are formed in this manner. Mutations are frequent in domesticated plants because varieties in cultivation are separated by inbreeding from the normal forward progress of the whole interbreeding species. Each species when once formed is supposed, under the mutation theory, to remain stationary so that progress can be made only when new varieties become segregated from the mass.

There is, however, another and very different way in which variations can contribute to evolutionary progress. Instead of being recessive mutations, the variations which have practical evolutionary significance are prepotent, and can work one change after another in the gradually advancing group. The true evolutionary significance of mutations is not that species arise by mutation, but that the progressive steps, by which the evolution of species is gradually accomplished, are not imperceptibly small. There may be a very appreciable advance between two successive individuals.

Very acute selection or some other way of separating a new mutation from its unmodified parent stock must be imagined in order to account for its preservation, but plants and animals abound in characters which could scarcely have been perpetuated in this way. With self-fertilized plants a single individual

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can start a new race or variety, but with sexually differentiated animals this is much more difficult, since interbreeding is necessary for reproduction. An actual instance will illustrate the point. In all the millipedes of the world-wide order Merocheta the olfactory cones of the antennæ are four in number, arranged in a square, with the single exception of a series of closely related East African genera of the family Gomphodesmidæ,[1] which are unique in the possession of ten olfactory cones arranged in a circle. That the four cones in a square is the ancestral condition, is certain, because it is shared also by all the other orders of the very ancient class. Diplopoda, many members of which are known from the carboniferous period. That the number is invariable in the order Merocheta can not be claimed, since, obviously, it must have varied at least once, when the circle of ten cones came into existence. No variation has been recorded, however, either in the four-coned or the ten-coned genera, on the many thousands of specimens which have been examined.

Nor are there any indications that the ten-coned condition is an advantage which has gained any favors from natural or other forms of selection. The ten-coned genera as a group show no other conspicuous peculiarity and have contributed, apparently, only an average share to the evolutionary diversification and geographical distribution of the family. Moreover, the habits and environmental relations of the whole class Diplopoda are such as to reduce the influence of natural selection to a minimum.[2]

Under such circumstances the sidewise origination and preservation of a ten-coned new species as a mutation seems highly improbable, but there is, on the other hand, no reason why a genetic variation to ten cones should not spread through a species and be carried forward into the other species and genera into which the ten-coned group might afterward subdivide. If there had ever been millipedes with the intervening number of

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[1] Cook, O. F., 1899. African Diplopoda of the Family Gomphodesmidæ. Proc. U. S. National Museum. 21 : 677–739.

[2] Cook, O. F., 1902. Evolutionary Inferences from the Diplopoda. Proc. Entomological Society of Washington. 5 : 14.

cones we have every reason to expect that indications of them would remain, either in species with such numbers or in occasional individual variations. The facts of mutation may help us to be reconciled to the probability that millipedes with five, six, seven, eight or nine cones may never have existed, but they do not warrant the general inference that evolution goes forward by the origination of species sideways by mutation.

The difficulty is not that the mutations of domesticated plants and animals are not as different and as readily to be described and distinguished from each other as natural species. Nor is it impossible that some of the species named and described in formal botanical and zoölogical classifications represent mutative variations from narrowly segregated wild types. The differences are not formal or theoretical, but physiological and practical. The conditions under which the mutations of cultivated plants and animals arise are not those under which the constructive evolution of nature has gone forward, and the mutations are deficient in the primary requirements of vigor and fertility.

That discontinuous variations may contribute to the evolutionary progress of species in nature is no part of the mutation theory of De Vries, which definitely rejects and denies any gradual evolution, any continuous change and accumulation of characters. Species once formed by mutation are just as stationary and immutable, according to De Vries, as Linnaeus said they were. All the evidences of gradual evolutionary divergence of organic groups accumulated by Darwin and his successors are ignored in the mutation theory, because no evolutionary changes were detected in the original Œnotheras which Professor De Vries kept in his garden for eighteen years.

The kinetic theory is not thus at odds with the facts of science. It provides an evolution of species by a thoroughly gradual, continuous process, more broadly continuous, indeed, than any suggested before. It recognizes that new variations are prepotent, and are able to accumulate and to transform the species in which they appear. Species are normally in motion and do not depend upon the intermittent interference of selection, nor upon mutation, for the development of new characters. Instead of finding the motive power or active principle of evolution in natural selection or in mutation, the kinetic theory finds evolutionary causes in normal diversity and free interbreeding in specific networks of descent.

Both the selection theory and the mutation theory imply that new characters and new types have to be preserved by isolation. Under the kinetic theory it is clearly perceived that isolation explains only the multiplication of species, but is not an evolutionary factor, or even a necessary condition of evolution. The kinetic theory provides for the first time a consistent outline of a method of gradual and continuous evolution in normally extensive, freely interbreeding specific groups, the condition in which organisms everywhere exist in nature.

PRINCIPAL AGENT OF EVOLUTIONARY CHANGE.

At this point the various theories show, perhaps, their most obvious divergencies. The doctrine of pure selection, or Darwinism, holds that selection is the actual cause or principle of evolutionary advance, supporting this by various other assumptions, such as an environmental causation of variations or a correlation between useful and useless variations.[1]

The isolation theory of Gulick appreciates the inadequacy of selection and seeks for special conditions or behavior which can explain the evolutionary progress of groups of individuals which have merely been isolated from the parent species without having been placed in appreciably different environments. The Lamarckian doctrine of direct adaptation finds its greatest advantage here, in that the environment itself is supposed to cause the changes directly. Professor De Vries argues, in some of his writings, that mutations are due to environmental causes, though frankly admitting that the connection of events is unknown.

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[1] Belief in correlation of characters as an important adjunct to selective evolution has been reaffirmed very recently by Professor Lankester.

"For they [correlated characters] enable us to understand how it is that specific characters, those seen and noted on the surface by systematists, are not adaptations of selective value. They also open a wide vista of incipient and useless developments which may suddenly, in their turn, be seized upon by ever-watchful natural selection and raised to a high pitch of growth and function." See Lankester, E. Ray, 1906. Inaugural Address before the British Association for the Advancement of Science. Science, N. S., 24: 228.

It is commonly taken for granted by the advocates of the selection hypothesis that a certain constant of variation will be maintained by the species, so that the cutting off of the extremes on one side will cause a still greater development on the other, and thus actually move the species along.

This idea may never have been very definitely formulated, but it is obvious that many writers on selection have relied upon the unexpressed assumption as affording the means by which selection could produce evolutionary change in a normally stationary group of organisms.

The Darwinian doctrine of variation grafted upon the older idea of stationary species resulted in the conception of a species composed of variable individuals, but with a stationary specific average. Experiments with domesticated varieties had shown that selection could change the center of gravity or character-average of a group, and this idea applied to nature at large gave the hypothesis of evolution through selection.

In arguing the inadequacy of selection, Mivart, De Vries and others have taken the ground that selection could not carry the specific average beyond the boundary or limit of range of variation for the original group, and this is the logically correct inference, unless the idea of a constant of variability be included as a factor of the problem. But even this is inadequate to account for the general evolutionary results, for unless the further notion of a normal tendency to progressive change be added, the presumption would be that the selectively reduced species would attempt merely to reproduce its lost members, to regain its original size and cover again the field from which it has been excluded by selection.

It may be held, therefore, that both in logic and in fact the explanation of the ascertained and generally admitted data of selection depends upon the recognition of a normal and spontaneous tendency of species to evolutionary change. It is this tendency, this specific kinesis or law of motion, which carries species into close selective contacts with their environments. The species are travelling by their own motion, in spite of selective obstacles, and not because environmental selection is carrying them along.

The determinant theory of Nägeli, as already indicated, ascribed changes to an internal "principle of perfection" of heredity, which conducted the evolution of a species in a definite direction. There was no need, in this view, of showing any direct connection with the environment. Selection was applied to a species as a whole, to preserve or to eliminate, but it was not thought of as actuating evolution or as conducting it in adaptive directions.

The determinant theories of Weismann and his followers may be described as hybrids between the doctrines of Nägeli and those of Darwin and Lamarck. They predicated a cellular mechanism of heredity for conducting the process of evolution, but supposed that this mechanism could be actuated or affected by environmental influences and compelled in this way to carry the species in directions of adaptation.

Darwin, in his theory of pangenesis, assumed that all parts of the body of the parent contribute materials to the germ-cells and hoped thus to explain how characters acquired from the environment might be passed on to succeeding generations. Weismann denied the inheritance of acquired characters, but he nevertheless repeated Darwin's attempt at providing for the inheritance of environmental influences, because it appeared impossible without this to construct a theory of environmental causation and explain the facts of selection and adaptation.

Weismann was well aware that his theory of determinants was so complex as to appear improbable, but he defended it with persistence on the ground that it was the only way in which heredity could be understood. Unfortunately, the vast complexity of ideas does not explain the facts of organic descent, but only adds to them an even more mysterious hypothetical field. Moreover, the data of environmental relations do not accord any better with the Weismannian than with the Darwinian hypothesis. Experiments have not shown that there is any close, constant or definite relations between environment and heredity. The most that can be claimed is that the environment, in some manner still quite unexplained, may sometimes induce an instability, or tendency to stumble and fall from the normal hereditary pathway of the type.

The theory of determinants afforded, at most, a method of thinking about the process of organic succession, but it does not appear that this way of thinking is either correct or necessary. It assumes a complete diversity of nature between germinal and somatic cells, which the facts do not warrant, especially among plants, and it assumes further that there are definite mechanical directive relations between the germ-cells and the resulting organisms, which the facts also refuse to indicate. Of the real nature of heredity we know, as yet, absolutely nothing, any more than of analogous phenomena, instinct and memory. Speculations, even of purely hypothetical character, may sometimes be of service in the treatment of scientific problems, but no speculation should be cherished which hides or even casts a shadow over facts.

Under kinetic evolution the symbasic interbreeding of the diverse individuals of the species is held to be the principal agent of evolutionary change, since it is in this manner that the prepotent variations which appear among the component individuals are transmitted and combined into the complex organic result. Interbreeding is held to effect an integration of individual variations inside the species, instead of each variation being considered a new species, as in the mutation theory.

Symbasis is one of the general conditions of organic existence, but under static theories its evolutionary significance was so completely overlooked that no term was provided by which it could be directly and definitely symbolized. The word interbreeding, if used alone, would generally be misunderstood in one of two opposite and equally unfortunate senses. Some writers use interbreeding as synonymous with inbreeding or close-breeding, and some for wide cross-breeding, which are exactly the conditions to be avoided in the discussion of normal specific relations. Another term being indispensable, symbasis was introduced, in allusion to the fact that the individual members of species are normally associated in groups. The expression also lends itself most conveniently to the description of kinetic interpretations, in view of the fact that the association of organisms into symbasic groups is looked upon as one of the principal agencies of evolutionary progress.

The introduction of a new term is always to be deprecated, and may help very little, after all, in the explanation of a new distinction. The word has to be explained, as well as the idea. Nevertheless, there are occasions like the present, where progress in expression is likely to be permanently hampered unless we can be permitted to place definite labels upon our phenomena and refer to them by unequivocal word-symbols.

Symbasis, more properly than any other ascertained fact, can be called a cause of evolution. It may not cause variation, but it does enable variations to be combined into a general evolutionary change of type.

UTILITY OF NEW CHARACTERS.

New characters, as mere fortuitous variations, might or might not be useful, but if selection were the only cause of evolution, progress would be limited to characters of definite utility. Every character, therefore, which has attained to any considerable degree of expression would have a definite use, or would have had use at some former time in the evolution of the species. This logical necessity of predicating the utility of all characters is the most obvious weakness of the theory of selection, for there are large numbers of character differences between species which are not only obviously useless at present but which were probably equally useless in the past.

Gulick's isolation theory does not insist on the utility of specific differences, nor do the mutations of De Vries or the determinate changes of Nägeli and Weismann follow, of necessity, the course of environmental utility. Selection would explain the disappearance of types too far lacking in fitness, but adaptation would remain a mere coincidence, depending on whether adaptive variations happen to appear.

Under the kinetic theory it is possible to admit that useful and useless characters have equal possibilities of appearing and evolving, as long as they do not become actually detrimental, but at the same time selection is admitted to have a definite and practical evolutionary function, since the rejection of harmful tendencies has the power of enforcing more rapid specialization in useful directions. Selection is, indeed, more effective for inducing adaptation under the kinetic theory than under the purely selective doctrine of Darwinism, because in kinetic evolution a much wider range of characters can be expected to reach a sufficient development to render them of selective importance. Under a logical static theory, only those characters could be developed which have selective value from their first inception.

METHODS OF PRESERVING NEW CHARACTERS.

The great weight given to the various forms of selection, isolation, and environmental influence as factors of evolution have been determined largely by the belief that new characters or variations could not be preserved unless they were in some way separated from the unmodified parental type. This opinion has been supported largely by the fact that many of the variations which have been taken for examples of normal evolutionary motion have been in reality more or less abnormal results of the condition of inbreeding common in our domesticated varieties of plants and animals. The prepotency of the unselected wild type has been insisted upon, as well as the swamping effects of intercrossing, when the characters of the carefully selected variety fade away into those of the unspecialized parental form without leaving any apparent result. Nevertheless, the fact seems to be that new characters are prepotent, not of necessity over the whole taxonomic species to which the individual may belong, but at least in the particular variety or group and in the particular stage of interbreeding in which the variation appears. The recognition of the prepotency of new variations makes it obvious that the preservation and continued evolution of new characters does not involve the necessity of isolating the new form or the extinction of the old, after a period of struggle for existence.

Mechanical theories of evolution have centered largely about this question of acquiring characters, but it is still more important to know how characters are preserved after having been acquired. Organisms appear to acquire some characters from the environment, but it does not follow that the characters are also preserved by the environment, or even that the characters acquired from the environment are those which contribute in a definite manner to evolution. The kinetic interpretation enables us to understand the probability that a character is preserved for the same reason for which it appears in the first place.

The name Darwinism is commonly, though rather unjustly, limited to the gradual or selective theory under which variations gained genetic significance only when they were favored by partial or complete isolation, brought about either by the elimination of the less efficient parental form during the struggle for existence, or through geographical or other accidents preventing the swamping effects of intercrossing. This meant that variations did not tend to be preserved, that they tended only to continue their fluctuations around the stationary specific average. This conception was based, as already indicated, on the choice of the fluctuating variations or unspecialized heterism and artism as representing the variations on which evolution proceeds.

Under the assumption that organisms are normally stationary it was natural to ascribe variations to new conditions. It may be found, however, that the facts can be accommodated as well or better by supposing that new conditions of nutrition and growth afford more facilities for variation. Variations, once produced, tend to repeat themselves; not, it may be, in all of the offspring, but at least in some of them. The object of variations, the value of variations for the species, lies not so much in giving them new characters as in giving them a diversity of characters. Variations which appear in a part of the offspring, but not in all, serve most efficiently the purposes of increasing and maintaining heterism, and of insuring diversity of descent, after the manner of the many secondary sexual characters which appear to be quite useless except for this physiological purpose.

The kinetic theory differs from all its predecessors in recognizing physiological reasons for holding that new characters are prepotent. From the fact that they afford opportunity for organic readjustment, they enjoy an advantage over the unmodified type both in accentuation of characters and in vitality and fecundity of offspring. The evolutionary possibilities of a new character may depend as much or more upon its fitting into and supplementing the complex of existing characters as upon any direct utility from the environmental standpoint. Evolution, in other words, may be viewed as an aspect of the physiological process of interbreeding by which the vitality of organisms is sustained.

NATURAL SELECTION AS AN EVOLUTIONARY FACTOR.

The preponderance attained by the selection theory has probably been due, in large measure, to its logical simplicity and consistency in holding that selection is the positive, efficient factor or actuating principle of evolution. The unbiological public has accepted this interpretation of the causes of evolutionary motion with practical unanimity, but among biologists themselves there has always been a wide appreciation that the facts did not warrant the definite generalization which Darwin himself carefully avoided, but which his friends made for him and christened with his name.

All other suggestions of methods of evolution are the result of more or less definite perceptions of the inadequacy of natural selection as an evolutionary cause. No amendment of natural selection has the logical consistency of the original, nor has any gained a comparable popularity in the scientific world. The mistake has been made, if the present diagnosis is correct, in attempting to modify or repair the hypothesis of selection as an evolutionary cause.

Under the kinetic theory selection appears as a negative factor only; its power is to inhibit motion, not to cause it. It is not improbable that selection, by closing other avenues of change, can induce more rapid progress in a particular direction, but such an effect of accleration would not prove that selection can cause evolutionary motion; it would indicate that a certain amount of change necessarily takes place as the result of causes inherent in the species. A variation eliminated by selection does not help to maintain the needful diversity of descent, and this may make the surviving variations the more effective for inducing adaptive specializations. Selection, by thus restricting the field of change, may be able to focus the evolution upon one variation, but a condenser is not to be reckoned as a source of light.

The kinetic theory therefore definitely abandons selection as a cause or positive factor, and perceives that the influence of selection, powerful though it be in many cases, is of a negative and restrictive character — an influence which could not be exerted if the species were not already in motion.

The kinetic theory, though departing radically from the doctrine of selection as an evolutionary cause, is, in a practical sense, much nearer to Darwinism than are many other suggestions which, though intended to supplement the selection hypothesis, would in reality completely nullify it, by denying to selection any true power to influence the course of evolutionary progress. The kinetic theory, though denying that selection is in any proper sense an evolutionary cause, ascribes to it a definite evolutionary function. The environment does not carry the species into adaptive specialization, it only deflects the normal specific motion. The evolution is in the species, the power of deflection in the environment.

Professor De Vries clearly recognizes that the function of selection is regulative and not active, though he still refers to it as a cause of evolution.

"Notwithstanding all these apparently unsurmountable difficulties, Darwin discovered the great principle which rules the evolution of organisms. It is the principle of natural selection. It is the sifting out of all organisms of minor worth through the struggle for life. It is only a sieve, and not a force of nature, no direct cause of improvement, as many of Darwin's adversaries, and unfortunately many of his followers also, have so often asserted. It is only a sieve, which decides which is to live, and what is to die. But evolutionary lines are of great length, and the evolution of a flower, or of an insectivorous plant is a way with many sidepaths. It is the sieve that keeps evolution on the main line, killing all, or nearly all that try to go in other directions. By this means natural selection is the one directing cause of the broad lines of evolution."

"Of course, with the single steps of evolution it has nothing to do. Only after the step has been taken, the sieve acts, eliminating the unfit. The problem, as to how the individual steps are brought about, is quite another side of the question."[1]

This is in notable contrast with the previously quoted dictum of Professor Lankester, regarding an "ever-watchful natural selection" by which characters are "seized upon" and "raised to a high pitch of growth and function."

INTERBREEDING AS AN EVOLUTIONARY FACTOR.

In full accord with the idea that evolutionary change or motion is caused by selection or environmental influence, are the opinions, already emphasized, that isolation is necessary to preserve new characters, and that the sexual phenomena of interbreeding stand in the way of evolutionary progress by hindering the perpetuation of new characters. These corollaries of the selection hypothesis find no place in the kinetic theory. Interbreeding and other phenomena of sexuality have been reckoned in the present discussion as positive factors in evolutionary motion.

Evolution, in the kinetic interpretation, represents the workings of no special force, principle or mechanism; it is carried forward by the symbasic interbreeding of the diverse individuals of which species are composed. The final and ultimate explanation of evolution must await an understanding of the constitution of living matter. We must learn why the prepotent genetic variations occur, and why the interbreeding is necessary. But having once appreciated the variations and the interbreeding as ever-present facts, evolution is no longer mysterious; it follows as a natural and obvious consequence.

THE KINETIC FIGURE OF EVOLUNTIONARY MOTION.

It will be apparent from the preceding chapters that the evolutionary motion predicated under the kinetic theory differs from that of previous doctrines in important respects. In the first place, it is a highly complex or compound motion instead of a simple one, not to be typified by a push from the environment, by a pull by natural selection, by an occasional mutative leap, nor even by the onward transportation of a determining

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[1] DeVries, H., 1905. Species and Varieties, p. 6.

"hereditary mechanism." The figure of developmental progress under the kinetic theory is that of the advance of a huge and intricate network or trestle, built and supported by the intergrafting of the lines of descent throughout the species. Environmental obstacles can compel the progressive advance of this specific structure to be accomplished by many lateral bendings, but these deviations and displacements need no longer be mistaken for examples of normal evolutionary motion. That individual organisms can step aside, or even fall out of the ranks, proves, at the most, only that such transverse motions are possible; it does not show that they represent the method or the conditions by which the constructive evolutions of natural species go forward. The environmental reactions and mutations are made suddenly and can be readily demonstrated to our impatient eyes, but the coherent advance of the whole specific network has to be inferred from the relations of species as we find them in nature.

Some are inclined to distrust the results of the cosmic labora tory and to prefer to explain evolution by the lateral diversions which can be demonstrated in their own experimental cages and gardens. After keeping Lamarck's evening primroses in his garden for eighteen years without detecting any change, Professor De Vries has concluded that the species is constant and stationary and that further evolution is accomplished only by mutative variations, like those which appeared during this interval.

"There is neither a gradual modification nor a common change of all the individuals. On the contrary, the main group remains wholly unaffected by the production of new species. After eighteen years it is absolutely the same as at the beginning, and even the same as is found elsewhere in localities where no mutability has been observed. It neither disappears nor dies out, nor is it ever diminished or changed in the slightest degree.

. . . "My evening primrose, however, produces in the same locality, and at the same time, from the same group of plants, quite a number of new forms, diverging from their prototype in different directions.

"Thence we must conclude that new species are produced sideways by other forms, and that this change only affects the product, and not the producer. The same original form can in this way give birth to numerous others, and this single fact at once gives an explanation of all those cases in which species comprise numbers of subspecies, or genera large series of nearly allied forms."[1]

These inferences were made, of course, without reference to the kinetic conception of evolutionary motion as a specific structure or network of descent. Nor is the possibility considered that a small group of individuals isolated and inbred in a foreign land might behave in an abnormal manner, or at least in a manner that would afford small indication of the normal mode of evolutionary motion. Other parallel cases observed in coffee, cotton, capsicum, tea and other plants, indicate that mutative variations like those of the evening primrose are the regular results of the treatment to which the plants have been subjected in domestication. Instead of illustrating the method by which evolutionary advance is accomplished, mutations appear to represent a stage in the degeneration of organisms which have been removed from the vital fabric of specific descent; they do not show how the evolutionary network is woven, but how the strands can be unraveled. Conditions of uniformity like those of inbred domesticated varieties are to be found in nature only exceptionally, in the relatively few degenerating types which have become regularly addicted to self-fertilization or to vegetative propagation. Nor do we find under normal evolutionary conditions of symbasic interbreeding and individual diversity these violent mutative departures from the parental types. There is a vastly greater range and flexibility of characters and character-combinations. Nevertheless, it is very doubtful whether a species as a whole would make an appreciable evolutionary advance in eighteen years. In any event, the fact could hardly be determined from a few specimens in a foreign garden.

All kinds of variations can be described as having been pro-

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[1] De Vries, H., 1905. The Evidence of Evolution. Smithsonian Report for 1904, p. 396.

duced sideways. The doctrine of selection, like that of mutation, looks upon lateral or transverse displacements as the steps by which evolution is accomplished. From the kinetic standpoint it appears obvious that only those lateral movements really contribute to the evolution of the species which make a lasting addition to the internal diversity of the species and broaden and strengthen the structural network of descent. Mutations which arise under conditions of inbreeding do not serve this purpose. They are loose loups or free ends of the fabric of descent, torn out by the disarrangement of the tensions of the specific machinery of development. They do not affect the species, of course, if they remain isolated from it. On the other hand, mutations which are allowed to interbreed freely with the wild type, or even with each other, loose their distinctive peculiarities and are merged back toward the ancestral form, and toward the more normal condition of promiscuous individual diversity.

As evolutionary phenomena the mutations described by Professor De Vries have not less of interest and significance than the facts of adaptation and environmental adjustment which served as the basis of earlier theories of evolution. And like the data of the earlier theories, the facts of mutation are capable of being interpreted in a very different relation to the evolutionary motion of specific groups of organisms. Since constructive evolution is accomplished, as far as we know, only in these large groups of freely interbreeding individuals, we may well be cautious in the acceptance of any doctrines which do not take into account the normal constitution of species, and the nature of the motion by which their evolutionary progress is accomplished.

A species is not a merely arbitrary collection or aggregate of organisms; it is itself an organization by which organic existence is maintained and organic evolution is accomplished. It is customary to think of the higher types of organisms as having been made possible by the association of greater and greater numbers of cells, but this association and specialization of cells into tissues and organs has not been accomplished without the meeting of another evolutionary requirement, the association of the organisms into large interbreeding groups, or species.

Organic energy is primarily an integration of cellular energy, and the energy of cellular development has to be readjusted and renewed by conjugations between cells of diverse descent. The answer to the question why this is so must come from a new department of science, a general cellular biology which shall study the problems of cellular organization and association. It is here, if anywhere, that we must learn why organisms are normally diverse, why interbreeding is necessary and why evolution follows as a universal consequence. A species, viewed as a protoplasmic fabric of interwoven lines of descent, is different from any other object in nature, but its properties and potentialities are no less peculiar than its structure and its modes of motion.

5. THE HEREDITY CONCEPT MODIFIED BY HETERISM.

Questions are debated with the most persistence and the least profit when diverse opinions are being expressed by means of the same words. The term heredity has figured largely in evolutionary discussions ever since the time of Darwin, and yet the ideas which it represents are by no means the same in the minds of the many investigators who use it. The meanings do not vary merely in the extent of their application to related ideas. They differ fundamentally in their standpoints, and in their conceptions of the nature of the causes of evolution.

The traditional concept of heredity, the supposed production of like by like, also enters largely into the composition of the various philosophical systems of evolution, so largely, in fact, that evolution, descent and heredity are often treated as synonymous terms. Indeed, the whole subject of evolution is often summarized and crystallized into heredity, so that no further thinking is possible which does not definitely adopt or as definitely reject the heredity conceptions of the various schools of evolutionary study. The extreme views are very widely divergent, and perhaps equally remote from the truth.

On the one side is the hypothesis of environmental causation, or a direct impression or moulding of characters by external conditions; on the other side is the hypothesis of prefiguration or definite predetermination of characters by internal character-unit mechanisms of descent. Some regard heredity as a summary of environmental influences, and some as the result of an intracellular mechanism of predetermination, having no relation to the environment.

The environment does not form organisms, but neither can organisms be thought of correctly without bearing in mind their normal diversities and powers of individual accommodation to different external conditions, powers which are as incompatible with ideas of complete predetermination from within as they are with ideas of direct causation from without. Heredity, as signifying the succession of organisms in continuous lines of descent, is an actual fact, though as yet quite unexplained. Heredity, in the sense of a normal uniformity of organisms in species, does not exist. Instead of like producing like, the rule of heredity is that unlike produces unlike. To assist in an understanding of evolution and of the processes of descent the conception of heredity must be modified, and for some purposes entirely replaced, by a recognition of the facts of heterism, the normal inherent diversity shown by the individuals, castes and sexes of the same species. It is only when the members of a species are compared with the members of other species that they can be said to be alike. Compared with the members of their own species, all organisms are different.

Heredity and variation are not uncommonly personified as two opposing agents or "forces," the one striving to make organisms alike, the other to make them different. The late Professor Hyatt and others have even gone so far as to definitely locate all the heredity *inside* the organism and all the variation *outside*, holding that the organisms would be identical in form and structure were it not for variable external influences. The conception of heredity as an ideal uniformity is more applicable to some species than to others, but is not completely true of any. Experiment has everywhere shown that the members of the species and varieties are alike — as far as they are alike — because they breed together, not because they live in the same environments or because their form is definitely predetermined by an internal mechanism. The network of descent is a part of the mechanism of heredity, quite as truly as any character-unit particles can be.

The character-unit hypothesis of heredity is one of the corollaries of the environmental causation hypothesis of evolution. It seemed necessary to predicate something in addition to the observed methods and sequences of organic existence, in order to explain the evolutionary progress of species. How could the environment change the characters of organisms, and how could the changes of the characters be inherited and bring about the transformation of the characters of the species? These are the questions which Darwin sought to answer by his hypothesis of pangenesis, a migration of determinant particles from all parts of the body of the parent to the reproductive cells, so as to repeat in the offspring the modifications which the parent organism had experienced. The doctrine of pangenesis never found any support or justification in fact, since it could not be ascertained that characters caused by the environment are inherited by pangenesis or otherwise. Nevertheless, the doctrine of determinant character-unit particles has been kept alive by the speculations of Nägeli, Weismann, and many other mathematically inclined students of evolutionary problems.

The kinetic theory does not approach the problem from this standpoint, for it finds causes of evolution in the facts of symbasic interbreeding and normal intraspecific diversity. The first significant fact in the direction of an explanation of evolution is the method of interweaving of the network of descent in which evolutionary progress is carried forward. In place of the assumption by static theories of a hypothetical mechanism of character-determination, with an equally hypothetical result of ideal uniformity, the kinetic theory presents for our study conjunctions of lines of diverse descent and results of continued diversity of offspring.

HEREDITY IN CELL SPECIALIZATION.

The fact that the germ-cells of the higher plants and animals are so different from those of which the various tissues and organs of the adult body are composed, has been taken to mean that they have some special function of heredity. A long series of exceedingly difficult and detailed investigations have been made in the hope of discovering these causes of development which were supposed to lie hidden inside the nuclei of the reproductive cells.

If we trace back the organic series to their more simple representatives we not only find that the body cells become more like each other, but that the distinction between somatic or body cells and reproductive cells quite fades out. When the unicellular stage is reached, the problem of heredity seems largely eliminated, for here reproduction consists merely in the repeated division of cells into two equal parts, the close similarity of which appears in no way mysterious. The difference between the higher plants and animals and the lower lies in the fact that in the former the cells do not repeat indefinitely the same size, shape and structure, but are greatly diversified, though remaining joined together in colonies or compound individual organisms. Viewed in this manner it becomes apparent that there is no particular point at which this mechanical idea of heredity becomes necessary, no definite stage where the similarity of parts of a divided cell ceases to explain the facts of organic structure.

Reproduction and growth frequently figure merely as two names for the same process. Division of cells, which is reproduction among the lowest organisms, means growth in the higher. The process of conjugation of cells commonly termed sexual reproduction, need not be allowed to complicate the question of heredity, since the same stages of gradual differentiation can be traced among double- or conjugate-celled organisms as among simple-celled. Organisms which have conjugated recently do not divide differently from those which have not, though they may not be able to continue to divide indefinitely without conjugation. Among the higher compound organisms, conjugation takes place only at the unicellular stage. All the cell divisions necessary to the building up of the plant or animal body must be carried on without any readjustments of conjugate relations. To this limitation is doubtless due the fact that as organisms increase in complexity and in specialization of tissues, conjugation becomes a more and more indispensable preliminary to the reproduction of each new cell colony, or compound individual. If, for example, there could be one hundred divisions between each conjugation, this would suffice for one hundred generations of unicellular organisms but might provide only one compound individual. Plants and lower animals can be grown from cuttings or will regenerate lost parts, but among the higher animals these powers of asexual reproduction gradually disappear.

Divergence from the normal may occur at any stage in the development of the individual, which also varies continuously, and not merely in the germ-cell. If the life-history of a very simple animal or plant be considered, the concentration of interest on one point tends to disappear. The processes of growth and the preparation for spore-formation in such an organism as *Spirogyra* do not appear less interesting or less fundamental from the biological standpoint than conjugation and reproduction. Moreover, we now know that adaptations arise inside of cells as well as outside. The chromosomes and centrosomes, no less than the larval stages of insects, may prove to be resultant phenomena of evolution, rather than causal or truly primitive.

It is easy to understand how those who have approached evolution through the study of complex and specialized higher groups should be led to think of heredity as a mechanism, but if we take our standpoint at the other end of the organic creation it becomes apparent that heredity is merely a name for the fact that cell divisions by which organisms are built up follow closely similar lines in each successive generation. Organisms are not different merely because they are built of different kinds of cells, nor merely by reason of different arrangements of the same kinds of cells. Both causes of difference are present together in all the higher groups. Both kinds of differentiation have gone forward simultaneously and it need not be thought more wonderful that the cells of the same compound individual are different than that different species should be found among unicellular organisms. Indeed, heredity is most perfect when the cells formed by successive divisions are all alike. It may be deemed a departure from strict heredity when they become diversified, as in higher organisms. But whether the individual consists of a single cell or of a colony formed by many cell divisions, we are still dealing with the same fact of organic repetition, and have no more reason in the one case than in the other to view heredity as the function of any special organ. We may define heredity as the property of organisms with as much propriety as the chemist treats crystallization as a property of sugar. The cells know, as it were, how to arrange themselves repeatedly into similar colonies or compound individuals, just as the molecules of a chemical compound take repeatedly the same crystal form.

The causes of crystallization and of heredity are equally unknown; we can merely expect for the future that to which the past has accustomed us. We have no better reasons for expecting to find that the adult is definitely prefigured in the germ-cell that we have for supposing that the crystallographic forms or other properties of inorganic materials can be determined by microscopical examinations of the substances in solutions or in amorphous states. The germ-cells with their chromosomes and other internal organs do indeed carry the organic sequence from one generation to another, but this fact gives us no warrant that they contain any parts or particles which will afford a general explanation of evolution. And even if the germ-cells do contain some feature of special bearing upon heredity, it does not alter the probability that the results of the agencies operating in the germ-cells are shown to best advantage in the completed organisms. Sperms and egg-cells are themselves organisms, quite as truly as the elephants and whales, but their infinitesimal size, which kept them unknown and mysterious so long, does not warrant us in ascribing to them any gratuitous mysteries, nor in failing to appreciate that evolution is a motion of the specific network of descent.

Whatever the nature and functions of nuclear organs may be in different groups of animals and plants, we may expect that these organs and functions will find their primary explanation and relations in the evolutionary network of descent, rather than as affording an independent basis for theories of heredity. Neither the relations of individual organisms to environment, nor the possibility that germ-cells have predetermining relations to adults, will justify us in leaving out of account the network of descent in which the evolution of species goes forward.

HEREDITY AS A RESULT OF ENVIRONMENT.

The strength of the predisposition toward theories of environmental causes of evolution finds many illustrations in the controversies which have raged about the Lamarckian doctrine of direct environmental influences. Thus Professor Lankester, even when opposing Lamarck, assumes environmental influences of a character which the facts may not justify. It is shown that Lamarck was illogical in supposing that new environmental characters could be preserved by heredity and thus replace at once the effects of the "long-continued response to the earlier normal specific conditions," but it becomes evident, even while this excellent chronological distinction is being drawn, that it rests on a conception of heredity only slightly less objectionable than that of Lamarck himself. Though making no direct reference to mechanical theories of heredity, these assumptions are such as to suggest and to justify such interpretations.

"Normal conditions of environment have for many thousands of generations moulded the individuals of a given species of organism, and determined as each individual developed and grew 'responsive' quantities in its parts (characters); yet, as Lamarck tells us, and as we know, there is in every individual born a potentiality which has not been extinguished. Change the normal conditions of the species in the case of a young individual taken to-day from the site where for thousands of generations its ancestors have responded in a perfectly defined way to the normal and defined conditions of environment, reduce the daily or seasonal amount of solar radiation to which the individual is exposed; or remove the aqueous vapor from the atmosphere; or alter the chemical composition of the pabulum accessible; or force the individual to previously unaccustomed muscular effort or to new pressures and strains; and (as Lamarck bids us observe), in spite of all the long-continued response to the earlier normal specific conditions, the innate congenital potentiality shows itself. The individual under the new quantities of environing agencies shows new responsive quantities in those parts of its structure concerned, new or acquired characters."[1]

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[1] Lankester, E. Ray, 1906. Inaugural Address before the British Association for the Advancement of Science. Nature, 74 : 330. Science, N. S., 24 : 607.

If the environments controlled the character-units and thus moulded the characters of organisms we should expect to find that each environment would have its own organisms, or that all the individuals of the same species in the same environment would be alike, or at least more alike than individuals from different environments, but these results have not been attained. Sexual and other analogous differences which have been developed among the members of the same species in the same environments are vastly greater than any of the diversities which differences of environments can cause or induce. Moreover, there are nowhere in nature any constant environments which suppress or tend to extinguish the potential of adjustment. Vicissitudes are ever at hand, ready to make selections in directions of adjustability. The highest types of organic life, those which have been able to travel farthest on the evolutionary road, are those which have responded most effectively to their opportunities for learning the arts of adjustment. Neither are these responses mere passive mouldings; the powers of individual adjustment, no less than the general adaptive characters of the species have been attained by the putting forth of variations, the steps by which species travel.

Heredity, the name we have given to the mysterious power of plants and animals to follow accurately the developmental pathway of the species, and even to repeat the individual peculiarities of the parents, is more similar to memory than to any other biological phenomenon. Professor Lankester's conception of the facts implies that the hereditary memory is imposed from without, that it is stamped or moulded upon the species by the environment, and that its strength is, or should be, proportional to the time during which the environmental impression is continued. It is true that new or recent environmental reactions, or direct adaptations, are not inherited, and do not replace the older responsive characters of the species, but this fact lends no support to the doctrine of environmentally moulded heredity, for other character-modifications do appear suddenly, and do immediately and definitely replace the earlier type of the species, as shown in numerous and well established instances of genetic variation and mutation. These modifications of heredity have no doubt adequate physiological causes resident in the species, but as far as the environment is concerned they seem to be thoroughly spontaneous and fortuitous. They appear without notice and bring their own new and complete heredity with them; their very appearance signifies and consists in an abrupt modification of heredity. The environment may reject the new character and extinguish all the individuals with the modified system of heredity; it may limit heredity through selection, but it does not mould or modify heredity.

Heredity has been defined, in accordance with Professor Lankester's view, as the sum of past environments, but this statement, as usually understood, is only partial and misleading. It is true only to the extent that it means that the heredity of a species is a summary of the variations which the environments have permitted it to retain. The idea, for example, that improved environments will change the inherent characters of backward races of mankind or of the deficient and criminal classes of our populations, as often stated by philanthropists, is founded on teleological inferences, and not on concrete observations. New environments may permit new and desirable characters to be put forth which the selection of adverse conditions has forbidden hitherto, but humanitarians seldom have patience with such time-consuming methods of improvement. Moreover, if they were to view the subject from a biological standpoint they would soon appreciate the desirability of selecting the good stocks for further amelioration instead of wasting their efforts, relatively, at least, upon unworthy materials, in the vain hope of realizing an unnatural ideal of equality. Ethical considerations which concern only the relations of individuals and organized social bodies are often applied to racial and other questions as purely biological as those of the relations of species and subspecies in any other department of nature. Our chief duty with reference to the really backward and deficient races is to keep them from bringing about the deterioration of our own, as almost inevitably occurs when a higher race comes in contact with a lower. The qualities and standards which conduce to fitness in a higher civilization are of little or no significance in a lower, and rapidly deteriorate. This does not prove that the higher qualities are caused by the environment, but only that they require certain conditions in which to develop and maintain themselves.

Environment is of the first importance to individual organisms, but the inference so widely drawn in scientific and general literature, that the environment causes and controls evolution, is essentially fallacious. It controls, in a measure, by limiting some of the avenues of advance, or by setting higher and higher requirements for continued progress, but life finds millions of different ways to solve its environmental problems. Given a particular environment and a particular selection of individuals with their hereditary qualities and habits known, and we may with confidence expect a fairly definite reaction in line with previous experiments of the same kind. But this does not mean that evolution is an environmental *cul de sac.* Changes are not passive merely, but kinetic. The environmental possibilities are persistently tested by many variations. Species have retained in this way the power of ameboid motion, and have thus crept over the whole face of nature, and into all the crevices.

The progress possible in a single life-time or generation may be small, but the lesson is plain. The largest, most practical, and most precious factors of amelioration for plants, animals and men, lie in the discovery and preservation of those individuals which are in the line of evolutionary advancement for the breed — those possessing the qualities required by the environment, and which at the same time strengthen the species and help to maintain the necessary vital motion in courses of beneficial change.

THE PURITY OF GERM-CELLS AND CHROMOSOMES.

In the search for causes of natural phenomena an important step appears to have been taken when definite quantitative relations have been established. It is not strange, therefore, that the discovery of Mendelian or "disjunctive" hybrids should have aroused much interest, and even a certain amount of excitement, among biologists. Mathematical considerations have been allowed to obscure biological facts, and Mendel's "principles of inheritance" have been declared to be as fundamental and significant for biology as Dalton's law of definite proportions for chemistry. Deductions from Mendelism followed in rapid succession, such as the purity of germ-cells, inheritance by character-units, and the localization of these in chromosomes.

Mendelism as a phenomonon is both interesting and suggestive, but it lacks warrant as a generalization, because the conditions imposed by the experiments are as likely to be the cause of the results as the general principles of heredity alleged to have been revealed. There are, in fact, many reasons for believing that the inbreeding which is deemed an essential preliminary to experiments in Mendelism, induces the "disjunction" of the hybrids, instead of the purity of the germ-cells or the antagonism of "dominant" and "recessive" character-units. It is, perhaps, to be expected that Mendelism can be found whenever the conditions of the experiment can be met, but this does not prove that the phenomenon is a normal one. Still less has it been shown that Mendelism has been a contributing factor in evolution, since in Mendelian hybrids the more recently derived characters are held not to be dominant, but recessive, and would thus have the less chance of being preserved under natural conditions of unrestricted crossing.

Some writers have claimed for Mendelism a practical utility as determining the methods of procedure in breeding, and many plants and animals are being bred to learn which characters are dominant and which recessive, it being taken for granted that such facts have a fixed and definite value for each species or variety, thus enabling the results of breeding combinations to be known in advance. The utility of such knowledge is, nevertheless, negative rather than positive; it may keep the breeder from attempting the impossible, but it seldom gives him new leverage in attacking practical problems. The danger is rather that the acceptance of erroneous theories of heredity may delay his perception of facts and discourage his efforts.

It seems to be agreed by several experimental evolutionists that white fur or feathers is a recessive character; but no attempt has been made to test the general basis of this assumption by comparing interbred white mice with inbred gray mice. Albinism is one of many mutations induced by inbreeding, and this debilitating process has been continued with white mice ever since the original specimens were caged, while gray mice have mostly remained at liberty until needed for breeding experiments. To overlook these historical differences is to neglect factors of known significance for those of purely hypothetical meaning.

A second series of pertinent facts commonly ignored is the frequent and perhaps general dominance or prepotency of mutations when bred upon their own immediate blood-relations. Commercial white mice are a long standing breed, with no close and equally inbred gray relatives. To test prepotency fairly a new mutation would be required. There are numerous instances in literature, but experimenters naturally attach special importance to what happens in their own cages.

For a third experiment which might afford conclusive evidence on the pure germ-cell theory, some of the more recently developed varieties of mice might serve. If two varieties of independent origin which had been crossed separately with mice of the ancestral type and found to mendelize, were then crossed with each other and found to revert to the parental type, experimentalists might admit that the doctrine of pure germ-cells had been definitely disproven. The mice which in the Mendel experiments had produced pure white, yellow or black germ-cells would later have produced gray germ-cells. And yet this possibility in crosses of selected domesticated varieties has been known since the time of Darwin's experiments with pigeons.

The arrangement of the chromatin granules into chromosomes, to which so much importance is ascribed, is a very temporary phenomenon. The chromosomes do not appear to retain their separate identity either during sexual fusion (mitapsis) or during vegetative growth, when the activities of the cells are bringing to expression the qualities which have been transmitted through the gametes. The diversity in number of chromosomes in closely allied species, or even in the same species, also tends to weaken our faith in the idea that chromosomes as such, or as character groups, play a very definite or determining part as governors of the form of the organic structure of the individual plant or animal. The chromosomes may prove, after all, to be merely crowds of chromatin granules which are being assembled from the vegetative nucleus for mitapsis, and redistributed after mitapsis to resume the functions of control over vegetative growth.

Adult organisms, with their various characters, do develop out of germ-cells, but until we know something more of the nature of protoplasm, there can be no certainty that the individual characters of the adult are in the germ-cell in any such form that we can look in and find them. As well might we undertake to find in human embryos or infants the mental and moral characters of adult persons. All that we can be sure of is that the potentialities are there, but the nature, form and residence of these potentialities can be discussed only by means of abstract inferences, and are not yet accessible to the concrete imagination. This explains why the theories of hereditary mechanisms are merely philosophical or mathematical, not biological. Even if the conception were correct and it were possible to ascertain by some extension of microscopic vision that chromosomes or granules are prefigurations of adult organisms, the fact would still have little use as an explanation of heredity, or even as a working hypothesis, until we could learn, or at least imagine, how the models could build the structures. It is as though some barbarous tribe, on being visited for the first time by a modern man-of-war, should think to explain the structure by finding a small model of the ship in a glass case in the saloon. There would simply be two ships to explain, instead of one. Indeed, the discovery of the character-unit mechanism has been so long and so vividly anticipated that it is not altogether unjust to mention the fact that no very definite uses for such a contrivance have been suggested.

The studies of Boveri tend to show that in one group, at least, there is a definite necessity for the presence of one full series of chromosomes to make normal development possible, but this is still very far from showing that individual chromosomes or granules correspond to different parts of the animal. A mutilation or disarrangement of the organs of the germ-cells might well interfere with their development into normal individuals, even if the adult organism were not prefigured, preformed, or prefixed, inside the reproductive cell. It is highly important, of course, that the nature and extent of all determinative relations be known, but until the nexus, the *modus operandi* of the process has been learned, predetermination by material particles has no special standing as a theory, especially where the resulting concept of heredity fails to accord with concrete facts, such as the need of normal heterism and free interbreeding.

To those who view the matter from the mathematical side only, it is still impossible to *prove* that essential changes occur in mitapsis which make the chromomeres and chromosome aggregates different from what they were before the fusion took place. Nevertheless, there are three facts of nature, universal and much accentuated among all the higher plants and animals, which these theories of construction of organisms by character-unit mechanisms leave entirely out of account, without physiological meaning or explanation, (1) the diversity of the individual members of species, (2) the elaborate adaptations for interbreeding, and (3) the conjugation of the granules in mitapsis. The different assortments of chromosomes or granules might explain the diversity, but they show no use or reason in it. They may cause, too, the adaptive characters of interbreeding, but still for no purpose. Finally, they perform the elaborate evolutions of mitapsis, but all without result, according to these hypotheses of purity of germ-cells or of chromosomes.

For numerical purposes it may be that all these complexities of symbasis are useless and unnecessary. The diversity of genera and species, and of the individuals inside the species, could all be worked out arithmetically if we could be provided beforehand with the determinant mechanisms and a system of permutations for combining them. But from the biological standpoint it seems equally clear that this is not the way the organisms were developed in nature. The character-unit plan might have avoided all these unexplained and apparently unnecessary complications of heterism and symbasis. The difficulty is that, like its progenitor, the static theory of evolution by environmental causes, it seems not to be followed in the organic creation. Organisms are not naturally uniform and they do not tend to stay uniform. Organisms are not naturally pure-bred, and their tendencies are ever to be mixed more and more. This is the overwhelming testimony of the facts of nature, which the inventors of character-unit mechanisms would do well to canvass before entering upon their labors.

Chromosomes and granules as parts of cells are morphological entities, in the sense that they exist and can be made visible by microscopical technique. It does not follow, however, that they are biological or evolutionary entities, or that they can properly be thought of as having any general evolutionary significance, except as parts or organs of cells or of organisms, which are the units of life. Moreover, as already indicated from other considerations, not even organisms can be considered units of evolution, which requires the coherent network of descent of a normally diverse, interbreeding species.

CONTACTS BETWEEN LINES OF DESCENT.

The fact that the lines of descent are joined only in reproductive cells should not be taken to mean that there is merely a single or casual contact between them, nor prevent our recognizing the possibility that the functions of the chromatin granules may be physiological rather than morphological. It is through them, evidently, that the reorganization of the protoplasm of the cells is accomplished. They represent the citadels of life, the most vital points of the cell substance. The final stage and apparent purpose of the process of conjugation is to bring them into contact with other granules from other lines of descent. The nature of this contact, whether the granules exchange particles, or renew their vital energy by molecular or other adjustments, is still unknown.

The most recent results of cytological investigation are in accord with the supposition that the ability of the higher plants and animals to lessen the number of conjugations and prolong the intervals of vegetative growth, has been attained by the development of more and more efficient methods of conjugation. A few years ago the opinion was held that the process of synapsis involved only a fusion and reduction of the number of the chromosomes; it now appears that the chromosomes are not the ultimate units of the nuclear structure, but are merely aggregates of granules of chromatin. In the final stage of conjugation (mitapsis) the chromosome aggregates no longer appear distinct, but are subdivided into small clusters of granules called chromomeres. The chromomeres are strung out like beads in single file along two slender, protoplasmic threads which finally lie parallel and close together, so that the individual chromomeres can be paired off and fused with each other. Instead, therefore, of thinking of conjugation as a simple bulk fusion of protoplasm or of nuclei, we must view it as involving a long line of many scores, hundreds, or even thousands, of contacts or combinations between the much smaller granule-groups or chromomeres. Chromomeres appear, therefore, to have important physiological functions as specialized contact points in the fusion and reorganization of the protoplasm, and do not need to be thought of as bearers of hereditary character-units.

There remains one other stage of elaboration of mathematical hypotheses of heredity, to treat the chromomeres as permanent entities of descent and deduce the infinitely multifarious diversities of individuals in nature from the infinity of combinations and rearrangements of which the chromomeres may be capable. This theory is complete and unimpeachable mathematically, but is as indefensible biologically as its predecessors; for like them it rests on the assumption that the bringing of the chromatin granules into contact in mitapsis has no significance in descent. It takes for granted that nothing of importance occurs when the granules appear to fuse, and that they separate again without mixture, interpenetration, or combination, of the granular or fluid constituents of the protoplasm.

The character-unit assumption requires us to imagine some way in which the particular granules could create or bring about the existence or the accentuation of the particular character, whereas the other interpretation, by lines of descent, does not needlessly destroy the unity of the problem of heredity. It avoids the necessity of elaborate and gratuitous hypotheses in a field which science is scarcely prepared to enter. As in the adjoining regions of instinct and memory, it is easy to ascribe the phenomena to positional or other relations of molecules or atoms of the cerebral tissues, but impossible to imagine an adequate nexus of association with the concrete facts, actions or functions. The opinion has already been recorded in another place that truly mechanical solutions of this series of problems are likely to await the recognition of additional properties of matter, which physical researches are now revealing with such startling rapidity.[1] As clearly perceived and definitely stated by Lord Kelvin, the current conceptions of physics are not adequate for the treatment of the problems of biological evolution.

The wonderful and altogether unexpected results of studies of the internal structures of cells are but poorly appreciated by those whose hopes have dwelt on the discovery of mechanisms of heredity. From the morphological standpoint it may appear that little has been obtained except to open another chapter in the vast complexity of nature. The internal organs and processes of cells have their multifarious similarities and diversities, like all other phases of organic existence. Reproduction is carried on by as many different methods as assimilation, respiration or locomotion. The great and surprising result of cytological investigation is not in learning that such diversity exists, which might have been anticipated, but in ascertaining that the evolution of the large and complex bodies of the higher plants and animals has been made possible by the evolution of superior methods of reproduction. Mechanical theorists have been so intent on finding a mechanism of heredity that they have failed to recognize the physiological significance of an improved process of conjugation.

The older idea was that reproduction, that is, the production of a new individual plant or animal, followed the conjugation or complete union of the parental germ-cells, but it has been found that this is not true of any of the higher types of life. What has been considered conjugation among the higher groups, that is, the process in which the characters of the new organism are determined — as far as they are determined in the germs — is not a complete conjugation of the germ-cells, but only the beginning of a conjugation which continues throughout the life of the new individual.

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[1] Cook, O. F., 1904. Evolution and Physics. Science, N. S., 20: 87.

This fact has bearing upon the conception of heredity, for it takes us another step away from the older idea of a mechanism in the cell, and shows us that the intracellular organs, which some look upon as the mechanisms of heredity, are capable of change and adaptation like other parts of organisms, and that the problem of evolution is not to be solved by the supposition that evolution is determined in advance by mechanisms of heredity.

In the lower groups the union of the gametes is completed before vegetative growth is resumed, or before the new generation begins. But in the remote ancestors of the higher groups this procedure was abandoned, and the completion of conjugation was deferred. Vegetative growth began to be carried on while the cells were still in the double, conjugating condition. If the form of the adult were strictly predetermined by the internal organs of the cell, the double-celled organisms could have existed only as monstrous doubles of the simple-celled organisms which are built up after conjugation is completed. But, as a matter of fact, the structures which were built up from these double, conjugating cells proved to be entirely different from those which had been built previously from simple cells. New evolutions began on entirely independent lines, without reference to the character-units or other equipment of heredity resident in the cells of which the new structures were built. Moreover, the old form of heredity continued to be transmitted, even after new and higher types of organic structures had been intercalated into the life-history of the primitive organism.

All the liverworts, mosses and ferns continue to build up the two different kinds of cellular structures, one during conjugation and the other after or between conjugations. The two kinds of heredity, the conjugate and the post-conjugate, continue to run peaceably along the same lines of descent, like multiple telegraphic messages on the same wire.

Such complications do not, of course, dismay the inventors of hereditary mechanisms. Difficulty only adds zest to their ingenuity. Having invented one set of determinants, it is easy to invent another and have them working by turns, as Weismann gravely proposed in explaining the alternative heredity of sexes. For the bees and ants three kinds of mechanisms were provided, and for the termites four kinds, though in reality upwards of a dozen sorts would be needed to account for the strange diversity of types found in some of the African species. And the most curious thing about the ants and termites is that the animals which exhibit the supposed results of these diverse kinds of mechanisms do not transmit them at all, but are descended independently in each generation from sexual insects. Here again it is apparent that new methods of development have been entered upon without requiring any change or displacement of the old. With the bees, at least, the heredity is not determined when the egg is laid, or even when it hatches. It is still possible for two or three days to induce the young larva to develop either into a queen or into a worker, by varying the nature and amount of food. The environment determines, evidently, which of the mechanisms shall continue in play and which retire into desuetude.

There is no need, of course, to continue the discussion in this direction; doubtless it is too long already. There are those who think only in relations of numbers and spaces; and for these mechanical forms are a necessity. But for those who approach from the biological side, who are curious to understand nature, and yet not so impatient as to accept even scientific fiction at the expense of ascertainable fact, these character-unit mechanisms of heredity do not appear to help, but rather to hinder, clear perception and exposition.

ALTERNATIVE OR POLARIZED HEREDITY.

From the standpoint of the kinetic theory it appears possible to reconcile the proposed character-unit phenomena of Mendelism with other facts of alternative descent, without invoking the hypothesis of character-units and pure germ-cells. The phenomena of heterism and symbasis, that is, normal diversity and broad-breeding in specific groups, do not necessitate the character-block assumption. They only require us to suppose that diversity of descent affords a certain amount of molecular tension or attraction, a polarity, as it were, between protoplasmic elements derived from the different lines of descent.

There also appears to be a complete series of stages of accentuation of this polarity of descent. The most primitive condition is that of indiscriminate or unspecialized heterism, in which a character shows all degrees of expression from the lowest minimum to the highest maximum, with a preponderance at some intermediate or optimum point.

The physiological advantages of diversity of descent not only prevent the species from concentrating or stagnating on a central average or optimum point, but they often favor the development of two optima. The connecting series of character-stages may weaken, or it may entirely disappear, except for rare abnormalities, the normal form of the species being represented by the two separated extremes. The typical and most familiar instances of specialized heterism is to be found, of course, in the phenomena of sex. The primary sexual characters are now so intricately involved with the functions of reproduction that their significance as specializations of heterism is much obscured, but large numbers of secondary sexual characters are quite functionless for any purpose thus far detected, except this of increasing the diversity of descent inside the species.

When once a species has reached the stage of sex-differentiation, and has thus established a polarity of descent, the tendency seems to be for other specializations of heterism to group themselves with sex. The result is to give each generation the benefit of full diversity of descent, instead of losing this advantage in cases where similar individuals might breed together. No doubt it is easier, too, for a new character to join with and accentuate an already established polarity than to establish a new one for itself. Even among the plants which have not attained differentiation into separate sexes there are definitely alternative characters, and sometimes there are not merely two alternatives, or two groups, but several, and in a variety of combinations, as in the genus *Lythrum*. In insects the phenomena of alternative descent reach their highest accentuation and complexity, for there they are superposed upon the sex-differentiation. There may be two distinct forms of one of the sexes, as among the bees. In some species of termites both sexes are capable of specialization in several different directions, so that more than a dozen different and distinct types of individuals may be found in the same colony, and no intermediate forms.

The equal sharing of the two sexes in these wonderful specializations of the termites is a reminder of the general fact of numerical equality between the sexes. Among the bees where the male sex is completely useless in the social economy and environmental relations of the colony, the reduction of the number of males has been accomplished only by the very remarkable specialization of the reproductive process. The sex is no longer determined by a polarity or other simple relation which would give equality of sexes, but by the queen herself, who has the power of laying at will either fertilized or unfertilized eggs, the former developing into females, the latter into males. This arrangement appears peculiar because it constitutes so radical an exception to the general rule of equality in the choice by individuals of one or the other of the two routes of development possible in all sexually differentiated species. If these relations depended upon merely mechanical arrangements or upon the relative numbers of different kinds of pure germ-cells, we should expect the frequent occurrence of many definite deviations from equality of sexes.

Experiments have shown that in some groups of animals and even in plants the sex-determination may be influenced by the conditions of existence, and particularly by nutrition and temperature. The changes are supposed, however, to occur in continuous series of gradations, as though brought about by general influences upon the constitution of the organism, rather than by the abrupt changes of adjustment which might be expected to result from the action of character-unit devices.

The phenomena of Mendelism constitute an extension of the facts of alternative descent; for they show that this is not limited merely to secondary sexual characters and to the form differences of polymorphic species, but that closely similar effects can be obtained in a somewhat artificial manner, by combining domesticated varieties with properly opposed characters. Instead of producing merely averages or miscellaneous gradations of intermediates, well established and contrasted differences are preserved separately, like alternative sexual differences. Instead, therefore, of considering that Mendel's Laws explain sexuality, it seems more reasonable to assimilate the Mendelian phenomena with those of normal alternative descent as shown generally in sex-inheritance.

If the principle of alternative or polar heredity applies to Mendelism, the earlier explanations by the special character-units, segregated in different germ-cells, will be superfluous. The phenomena would still be abnormal, as are the conditions under which they appear, but they would no longer need to be associated with the phenomena of incompatability of chromatin, described by Guyer in sterile hybrids between diverse species.

"When germ-cells are to be matured, before the real reduction, there is in most forms a so-called false reduction, in which the chromosomes fuse in pairs so that there appears to be only half the normal number present, though in reality each is double (bivalent) and equivalent to two of the simple (univalent) type. The doubling of chromosomes which normally occurs at such times is frequently incomplete, or lacking, in hybrids. This is especially true if the hybrids are from widely separated species. Instead of a normal spindle bearing the usual number of bivalent chromosomes, multipolar spindles, or two separate spindles may appear, thus apparently permitting the two kinds of parental chromatin to remain apart. In the most extreme cases a complete separation may occur subsequently, the entire chromatin of one parent occupying one cell, that of the other a different cell. Such visible separations, however, only occur extensively in sterile hybrids from markedly different parent species. Fertile hybrids from closely related forms, for the most part, display spindles normal in appearance. . . .

"In the case of these milder fertile crosses, then, where reversions follow the Mendelian law, the germinal incompatibilities must be narrowed down to the qualities themselves rather than confined to the respective germ-plasms as a whole. These qualities must separate and each take up its abode in a different germ-cell irrespective of whether the other qualities of that particular germ-cell are of a different parentage or not. The cases in which the entire plasmas are segregated are then probably but magnified images of what occurs among the specific qualities of the milder crosses. The interesting possibility arises that if fertile hybrids can be secured from widely different species the plasmas of which must be more incompatible than those of nearly related forms, such hybrids will give rise to offspring in which there is reversion, not only of one character, but of many or all characters in the same individual, due to a more thorough segregation of the parental germ-plasm as a whole. In other words, the farther apart the parent species are, the more complete will be the return in any given offspring which shows reversion."[1]

Instead of representing germinal incompatibility, the Mendelian phenomena may prove to be merely examples of the preservation of welcome and desirable contrasts. Nor is it unreasonable to suppose that the polarity or other form of alternative reaction is rendered more definite and intense by the process of inbreeding which is considered a necessary preliminary for the exhibition of the Mendelian phenomena. Contrary to Dr. Guyer's supposition, the "disjunction" of characters does not appear to depend upon the extent of diversity, but upon conditions of inbreeding. Experiments with Mendelism seem to succeed only with closely inbred domesticated varieties, not with wild species. Indeed, it is only among narrow-bred domesticated varieties that materials for such experiments can be found, that is, definitely contrasted pairs or small groups of uniform characters.

SEXUALITY OF CONJUGATE ORGANISMS.

The sexual differentiation of the higher plants and animals affords another fairly definite indication that sexual and other alternative characters are determined by some such general principle as polarity, rather than by specialized character-unit mechanisms of the reproductive cells. It is now known that the bodies of higher plants and animals are not the result of a completed conjugation of the parental sex-cells, but are formed be-

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[1] Guyer, M. F., 1903. The Germ Cells and the Results of Mendel. Cincinnati Lancet-Clinic, May 9.

fore the conjugation is completed, and are thus a joint or conjugate product of the two germ-cells.

The sexuality of the higher plants, known to the ancients, and to the aborigines of tropical America, reasserted by Bacon, rediscovered by Sprengel and substantiated by Müller and Darwin, has been denied on technical grounds by recent botanical writers, as a result of the prevalence of certain morphological theories of alternation of generations. This doctrine has led to the inference that the bodies of our higher flowering plants represent an "asexual generation," and it is held to be absurd to ascribe to such organisms the qualities and specializations of sexuality.

Some botanists accordingly refuse to call the stamens and pistils sexual structures, or the staminate and pistillate plants male and female, because they do not represent the same kind or stage of sexual differentiation as that shown in male and female moss-plants or male and female fern-prothallia. The fact remains, however, that the sexuality of such a plant as the date palm is completely analogous to the sexuality of the higher animals and of man himself. In other words, it has been proposed to deny sexuality to exactly that form of sex-differentiation to which the word was originally applied.

The significant fact is that the sexual differentiation of organisms should have taken place on the two different planes of structural organization, both in the simple-celled lower types and in the conjugate-celled higher types. Indeed, there are three grades or stages of development where sexual diversification has taken place.

1. Sexual differences of the single gametic cells, as of the sperms and ova, or the pollen-grains and the egg-cells.

2. Sexual differences of simple-celled gamete-bearing structures, as of the male and female thalli of liverworts, the male and female plants of mosses, and the male and female prothallia of ferns, *Isoetes*, *Selaginella* and *Equisetum*.

3. Sexual differences of double-celled or conjugate structures, as of the male and female individuals of the higher plants and animals.

Nor does the reckoning end here, for the separation and diversification of the sexes has not taken place twice only among the plants, but probably hundreds of times, independently, and in different and unrelated natural groups, the ancestors of which were bisexual. Separate sexes, though well-nigh universal among the higher animals, both arthropods and vertebrates, show, nevertheless, numberless independent specializations. In short, no tendency of evolution has been so definite and so general as that leading toward the accentuation of sexual differences. This can hardly mean anything less than that diversity of descent, to which sexuality ministers, has a general physiological importance and is not merely incidental to fortuitous collocations of character-units. No doubt it will be found that the details of sex-determination differ much in the different groups of animals and plants, but this will not diminish the general significance of the phenomenon.

Sex-determination by purely mechanical means might still serve the purposes of symbasic interbreeding, but the heredity which might be due to the existence and operations of such mechanisms would not afford the basis of a complete theory of evolution. It would still be in need of an evolutionary explanation.

VEGETATIVE MODIFICATIONS OF HEREDITY.

Further reasons for preferring this idea of polar or positional relations of the ancestral hereditary elements to that of character units or determinants, is to be found in the fact that the hereditary attributes of form and structure are apparently capable of change at any time in the life-history of the organism, and not merely at the time of conjugation when under the more mechanical theory the nature of the individual should be determined, once for all.

As a matter of fact, plants do make extensive and permanent alterations of their characters during the vegetative period. Such cases, though relatively rare, are numerous in the aggregate. The best known instances are those of bud variations or "sports," as the gardeners call them, where a single bud produces a branch as different from the others as seed-grown individuals, or more so. A bud mutation of coffee found in Guatemala in 1904 showed characters often approached by seedling mutations, but somewhat more accentuated than any of the similar mutations which have been raised from seedlings.

Fasciation is, perhaps, to be looked upon as a form of bud variation, but it must rise in some instances, at least, through a derangement of the apical cells, rather than as a mutating adventitious bud. This has been observed very frequently in fasciations of asexually propagated plants like *Dioscorea* and *Ipomœa*. A normally round stem broadens gradually to several times its normal width, but retains its original thickness or even becomes thinner than before.

Another instance in which heredity, in the usual sense of the word, is suspended or set aside during vegetative growth, may be found in the familiar phenomenon of galls, where the presence of the insect parasite or the substances secreted by it, is able to cause the formation of complicated and highly specialized structures, as though new ingredients of heredity had been added.

The mutations which often occur in the first generation of plants when grown in new regions are also to be reckoned as post-reproductive changes of the hereditary type, for while we could not be certain in any individual case, that the mutation could not have occurred if the seed had not been transferred, the very great difference in the percentage and the range of mutations which can be secured from the same stock of seed will prove that the new conditions have been an inducing cause, able to act after the planting of the seed and long after the nuclear elements have been arranged on a basis which would normally have persisted throughout the life of the individual.

The fourth type of interference with heredity during the vegetative period is that of graft hybridism. The extent to which this takes place with normal plants has not been ascertained, but the power of communicating diseased conditions has been well established in a variety of instances ranging from peach-yellows, peach-rosette, and the mosaic disease of tobacco, to the only slightly abnormal variegations. Mr. Luther Burbank relates also an instance in which a graft of a red-foliaged variety of *Prunus* influenced the foliage and the progeny of the stock.

RELATION OF HEREDITY TO HETERISM.

The recognition of normal diversity inside the species necessitates a modification of the older view of heredity which predicated an exact likeness among the members of a species. The uniformity which the older authors had chiefly in mind was that of the members of one species compared with those of another species. This is indeed a wonderful phenomenon, and it is not surprising that mechanical explanations were suggested. It was also quite to be expected that when the idea of internal "mechanisms of heredity" had arisen it should have seemed necessary to predicate a complete uniformity of individuals as the normal result of the workings of such a device. The mechanical inference was carried even to the extent of suggesting that the diagnostic characters like those enumerated in systematic manuals are each represented by one of the chromosomes or minute masses of infinitesimal granules found in the nuclei of reproductive cells.

As a matter of fact, natural species do not differ merely by six or seven formally expressed characters. They are different throughout, and the diversity does not end with the distinctions between the species, but extends to the individuals of each of the groups. Appreciating the necessity of greater flexibility for the mechanisms of descent, Mr. Walter T. Swingle suggested several years ago that the expression of characters might not depend directly or entirely upon the chromosomes or granules themselves, but upon their positional relations. This suggestion avoids all occasion of resorting to the character-unit hypothesis, and may afford a clue to a cytological explanation of the phenomena of heterism.[1]

It is not necessary to think that the granules determine the characters as such; they need be considered only as representing the characteristics of the ancestral lines of descent. It is then

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[1] Mr. Swingle also calls my attention to the very pertinent fact that the narrowly mechanical character-unit hypotheses, to which objection is taken in the present paper, have not been proposed or defended by those who have made the truly important contributions to the science of cytology. Indeed, it is exactly these investigators with first-hand knowledge of the anatomy of cells who appreciate most keenly the wholly hypothetical nature of the character-unit speculations.

possible to suppose that if the granules derived from a given ancestor secure a favorable position the characters of that ancestor will predominate in the new individual. In this way the characters of different ancestors might assert themselves in endlessly varied degrees, even in the offspring of the same parents, as they often do. This theory has the advantage of affording a thinkable connection between facts which otherwise appear completely mysterious. Two collateral circumstances increase the warrant for applying the suggestion to the phenomena of heterism.

It has been indicated by several observers, but most directly by Prowazek[1] that the granules of chromatin, which compose the chromosomes at the period of the conjugation, migrate, during vegetative growth, to positions at the knots of the nuclear network, as though to direct the processes of assimilation and growth. It was found by Maupas in his experiments with infusoria that continual inbreeding causes the gradual deterioration and diminution of the nucleus, as though diversity of descent were necessary to maintain the nuclear network, either by keeping up the number of granules or by enabling them to stay at the right distance apart. Such a relation would explain the known facts, to the extent of indicating a reason for heterism and a means for bringing it about.[2]

It is also easier to conceive of the possibility of bud-variations under the supposition that the influences exerted by the chromatin depend upon position, rather than upon the origination of new units or upon the making of different combinations. Modifications of hereditary forms and methods of growth do occur during the vegetative period, as already stated, and may be quite as pronounced as the mutations obtained from seed. Changes capable of accounting for bud-variations would also be adequate for the explanation of mutative variations.

Those who begin with the assumption that evolutionary progress is actuated by external causes are compelled to argue that the diversities of individual organisms arise through varied

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[1] Prowazek, J., 1904. Keimveränderungen in Myxomycetenplasmodium. Oesterreich. Bot. Zeitsch., 54: 278.

[2] Cook, O. F. and Swingle, W. T., 1905. Evolution of Cellular Structures. Bul. 81, Bureau of Plant Industry, U. S. Dept. of Agriculture.

environmental experiences, but the inadequacy of this conjecture is made plain by the fact that the greatest of these intraspecific divergencies, those of sexes, castes and alternating generations are obviously not subject to such an explanation. Protoplasmic arrangement, and the specializations of the organs and processes of reproductive cells, were not, of themselves, effective for the problems of advancing organization. There had to be differences, vital tensions, as it were, between the protoplasms, if organic progress were to be maintained, and conjugation were to become adequate for the building up of large, complex and long-lived organisms.

As fission suffices for the reproduction of only the simplest types, and haplogamy, apaulogamy and finally paragamy, have proved necessary to continue the propagation of organisms of successively higher degrees of complexity, so, for the very highest, sexual diversity and continuously maintained symbasis are requisite. The effect of prolonging the process of conjugation is to double in each organism the threads of the vital network. The separation of a species into sexes is a still more advanced category of specialized descent, since it doubles the whole specific network, permits accumulation of two sets of variations, and insures that each individual be descended from two diverse parents.

But even this provision of interbreeding does not suffice to maintain the perfection of organic excellence found in man himself, where the requirement of diverse descent is so acute as to forbid, on pain of degenerate offspring, the union of individuals separated by less than four or five generations, or by two or three strains of alien blood. Human descent is so difficult and precarious a fabric that the double network cannot be held in place merely by the joining of adjacent knots. The structure is likely to totter or fall if the lines of descent which join in the building of each new individual are not well braced by meeting each other at broad angles. Neighboring parallel or only slightly divergent lines do not afford the necessary stability of contrast, the vital tension which enables the conjugate cells to build a well-knit body. The intricacies of relationships which fascinate the genealogist are not gratuitous or accidental, but are a biological necessity in the elaboration of the framework of symbasic descent which sustains the organic vigor of the species.

In cytology, no less than in the more general fields of study, it is the physiological values which need first to be ascertained, before the morphological considerations can be correctly appreciated. Germ-cells can indeed be viewed as mechanisms of descent, but speculations regarding them should not be made the basis of evolutionary thought nor the test of orthodoxy, to the exclusion of more definite and concrete indications of the nature of evolutionary processes.

The kinetic theory finds significance and confirmation in the now rapidly accumulating indications of an extensive series of fusions between the individual granules of chromatin, which previous cytological interpretations, based on static views of evolution, have denied. From the kinetic point of view the fusions of the chromatin are an important and altogether accordant part of the whole system of evolution; they are the actual knots and junctions of the fabric of descent. Static theories of cellular determinants, on the other hand, can see in these evidences of fusion only an elaborate deception, an unnecessary complexity of the process of reproduction, just as it was formerly held that sexual reproduction itself stood in the way of evolution, because it interfered with the subdivision of species and the isolation of new variations.

The traditional concept of heredity, the ideal of uniformity in descent, has furnished the basis of all preceding doctrines of evolution. Conditions of isolation or of restricted descent have accordingly been considered typical for evolution, because it was only in narrow bred groups that the ideal of uniformity could be approximated in nature. The kinetic theory breaks with all these traditions, and seeks to substitute for the abstract conception of a uniform, definite or mechanical heredity, a recognition of the concrete fact of normal diversity, inside the species.

6. THE CONSTITUTION OF SPECIES.

Astronomy is reckoned as queen among the sciences because it has demonstrated that definite and orderly relations exist amidst the apparently hopeless disorder of the stars. The ancients, grouped the stars into constellations, but modern science shows us systems ruled by laws of mathematical precision.

Biology has remained longer in the constellation stage. Species are still discussed, even by evolutionists, as though they were mere chance aggregates of organisms, at once too familiar and too diverse to be formally defined.

It may well be that no coherent definition can be made for species as mere aggregations or constellations of organisms; the idea itself is vague and essentially unscientific. The primary error was that of treating the species as a morphological group, whereas the true evolutionary species is a physiological system. Like a stellar system, it may contain a large number of different individual members, and even different kinds of members. The unity of the species does not depend upon the organisms being all alike. It is necessary only that they remain within range of mutual influence through interbreeding, which is the biological analogue of gravitation.

A species, that is, a normal, natural, evolutionary species, is a large, coherent group of freely interbreeding organisms. But with species, as with stars, all systems are not alike. There are suns, satellites, planets, asteroids, nebulæ, variable stars, doubles and comets, in vast diversity of sizes and combinations.

In biology, as in astronomy, the most familiar things have proved very deceptive. The sun, moon and stars appear alike to revolve around the earth, from east to west. It was at first an extremely heterodox idea that the earth revolves around the sun. Moreover, neither of the apparent motions gave any intimation of the third order of motion, that of the system as a whole. In a similar way we have taken it for granted that the evolution of species could be explained by the motions we have been able to detect among our domesticated plants and animals. We are now learning that these types of life are not reliable examples of evolutionary systems, that their motions are often retrograde or degenerative instead of progressive and constructive. Nor are abnormal evolutionary conditions entirely confined to domesticated organisms. Among the millions of biological systems many have wandered from the path of progressive evolution and are on the way to extinction. As with the motions of the heavenly bodies, nature herself has deceived us, or rather she has given us new riddles to read.

The motion of species is not like that of the stars, in simple geometrical figures. The evolutionary progress of species is accomplished by the weaving of an intricate fabric of lines of descent through the free interbreeding of the component organisms. The simple, normal and typical constitution of a species may be thought of as a huge but simple network of uniform texture. All the organisms are diverse, but the diversity is merely individual and indiscriminate, so that the network has a uniform texture.

THE SPECIFIC CONSTITUTION OF LIVING MATTER.

Inorganic matter exists in a variety of conditions or physical states, gaseous, liquid, colloidal, crystalline, granular or amorphous. The properties of matter depend upon these conditions or states quite as much or more than upon the chemical composition or ultimate nature of the materials of which they are composed. There are laws of gases, liquids and crystals because the different substances behave very much alike in the same physical states. Indeed, the same physical states of different substances are generally very much more alike than the different physical states of the same substance.

In a similar manner the qualities of living matter are to be associated and described with reference to its various states or conditions. Chemically it is a mixture of water and of small quantities of numerous substances and compounds. Physically it is a jelly or colloid. Biologically it manifests such powers as growth, digestion, motion and reproduction. Morphologically it consists of cells or protoplasmic units with a more or less differentiated internal structure, and a power to combine or associate into organisms.

For evolutionary purposes the chemical, physical and organic points of view do not suffice. It is necessary to recognize that living matter shows still another unique property, another kind of constitution, the specific. A species is quite as concrete a phenomenon as a crystal. Both are collections or aggregates of smaller units, and the units have in both cases definite and necessary relations to each other on which the existence and further development of the crystal or the species depend.

It is true that many valuable evolutionary data have been secured from captive or domesticated plants and animals, but the results of this whole class of experiments indicate very definitely that evolutionary phenomena under these conditions are degenerative and not constructive. We are driven back to study the constitution of species in nature, to gain a clear understanding of the organic conditions which make possible genuine developmental progress, a true organic evolution.

No theory or evolutionary interpretation can hope for permanence which leaves out of account this primary fact that organisms normally exist in large groups of freely interbreeding individuals, the groups commonly called species. Domesticated varieties of plants exist without interbreeding and a few species in nature are supposed to propagate only by vegetative methods, by parthenogenesis or by self-fertilization, but no genus, family or order appears ever to have developed without the association of the individual organisms into interbreeding groups or species. The only exceptions, if any, are among the bacteria and other extremely simple forms of life which have failed to develop either a specialized nuclear structure in the cells themselves or an ability to associate and differentiate to form compound cellular organisms.

The reigning popularity of laboratory methods of research may permit small welcome for the suggestion of a method of evolution which requires the extensive equipment of nature and can not be demonstrated in cages or gardens, except by negative results, like those already well known. This disappointment need not continue, however, any longer than may be necessary to perceive that while experiments with domesticated species lose in apparent general significance under the new interpretation, they gain greatly in definiteness. If they do not show us how the fabric of normal evolutionary descent is woven, they at least teach us how it may be unravelled. This knowledge is of great value, not only to help breeders in the making of useful domestic types, but also to students of the general problem.

Domesticated plants and animals furnished the most effective arguments for the theory of organic evolution, for although the ancestral wild types of many cultural species are still unknown, and may have become extinct, there can be no doubt that thousands of their varieties have originated in domestication, and that similar varieties continue to arise under the eyes of the cultivator and breeder. Domesticated plants and animals have supplied, too, nearly all the materials for evolutionary experiments, and it is also with them that evolutionary theories must find, ultimately, their practical application.

A false or inadequate theory, though avowedly based on studies of domesticated species, may be quite as injurious to agricultural progress as another drawn from facts ascertained from useless wild species. Any idea worthy of general credence will bear the test of application to both classes of phenomena. A theory is merely a way of thinking about things, and is useful if it enables us to see, or even to suspect, causal connection between facts previously unassociated. One theory is better than another if it brings important facts into relation, and is considered established as a law or doctrine when it accomodates all the facts of the field it was designed to cover. The distinction frequently attempted between "theoretical" and "practical" investigations of evolution is quite fictitious, as in other fields of knowledge.

By a curious perversity of language the designation "pure science" is often applied to accumulations of knowledge not yet refined enough to be useful for practical purposes. The talk of discrepancies between theory and practice amounts to a kind of fiction, a euphemistic way of saying that an inadequate theory may not be wholly worthless as an indication of relations not yet adequately understood.

For establishing the general fact of variation and thus demonstrating the possibility of an evolutionary and continuous creation, the variations which have arisen under domestication afforded the most pertinent and convincing testimony. No biologist now doubts that evolution has taken place and still continues, but there is, nevertheless, a very wide and very practical divergence of opinion regarding the nature and causes of the evolutionary process. In the study of this question it becomes important to realize that the evolutionary condition of cultural species differs from that of wild types because of the much greater degree of inbreeding to which the former are commonly subjected.

The constitution of species has a practical bearing upon agriculture, not because the domesticated plants and animals have not been studied from an evolutionary standpoint, but for the very opposite reason, that they have been considered too exclusively, so that the important differences existing between them and wild species have been overlooked. Ideas drawn from domesticated varieties have been projected into nature at large, and this made it only the more impossible to appreciate the fact that grave differences exist between wild and domesticated groups of organisms.

Evolutionary science has gained much from the study of domesticated plants and animals, and may gain still more in the future. The objection is only to the use of such studies and results as an exclusive basis of interpretation of the facts of nature. All that happens in domestication may also happen in nature, for domestication is, after all, only a department of nature. It does not follow, however, that nature is fully mirrored in domestication; the mirror is too small. It shows us only the conditions in which constructive evolution does not take place, even in nature.

The recognition of the fact that evolution is a phenomenon depending upon the specific constitution of living matter has been delayed, no doubt, by the difficulties which have been encountered in the field of taxonomy. In the recent decades naturalists have faltered in the task of nomenclature set by Linnæus. To merely describe and give names to the millions of evolutionary unit groups of organisms which occupy the surface of our planet is a work much too vast for the present resources of science. The temptation of weariness has been to shorten it by passing over the apparently useless redundancy of slightly different groups, or by declaring that all is vanity of merely abstract conception, that species do not exist, and can not be defined.[1]

Those who have not persevered beyond this stage of skepticism and satisfied themselves of the existence of species in nature, can have little use for an interpretation based on the recognition of species as definite entities, consisting not merely of aggregates of individual organisms, but also of fabrics of interwoven lines of descent.

The difficulty in defining species is the lack of clear perceptions, not only of the nature and constitution of species, but also of the fact that several diverse types of phenomena are being covered by the word. Under such circumstances a general definition of species, however framed, could afford only a fictitious unification of expression, the ideas and implications covered by the term remaining essentially diverse and often quite contradictory. This confusion affords, however, no justification of a failure to use the term in one or another of the explicit senses of which it is capable, nor of a refusal to define the usage of the term in any particular connection.

The difficulty of defining the term species has arisen mostly from the fact that the phenomenon is a physiological one, whereas the general supposition has been that it is morphological. The idea that species are "founded on identity of form and structure," as the dictionaries say, is still widely prevalent, and is one of the tenets of evolutionary belief upon which Professor De Vries especially insists.

The impracticability of a morphological definition of species arises from the fact that it is impossible to set definite limits to the extent of the variability or diversity which is to be permitted in the species. Identity of form and structure makes an excellent definition; the objection to it is that no such species seem to exist in nature, or as Professor De Vries says, "* * * purely uniform species seem to be relatively rare."[2] In some groups

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[1] Thus a recent defender of the mutation theory of De Vries has declared: "If it is really true that De Vries does not know what constitutes a species, then, indeed, we find our faith in his work thereby increased. Who, indeed, except the makers of dictionaries, does 'know what constitutes a species'?"

This method of reasoning was very popular in mediæval times and was then, reduced to the neatly pious formula: "*Credo quia absurdum.*"

[2] De Vries, H., 1905. Species and Varieties, 64.

all the members of the species are closely similar, but in others they may be extremely unlike, as when the specializations of sex and polymorphism have been developed. There is no need, however, that we define species as a morphological term, since species are not caused nor constituted by the likeness or unlikeness of the component organisms. Indeed, it is unlikeness rather than likeness that conduces to the prosperity of the species.

The species in nature is constituted by the fact that the component individuals breed together. For evolutionary purposes a species is a group of interbreeding organisms; nothing more is required, nothing less will suffice. Species are units of organic evolution; organisms continue to exist and to make evolutionary progress only in large groups of freely interbreeding individuals. Groups of organisms which do not interbreed are no longer species; they no longer have the typical and essential evolutionary constitution of living matter.

Whether the individuals are alike or different does not in the least affect the specific unity of a group if the organisms are associated in nature on a basis of free interbreeding. If the groups have ceased to interbreed, whether by reason of geographical barriers, or of structural or instinctive incompatibility, they are no longer a unit of evolution, no matter how close the external similarity may appear.

Natural species are not the only groups of organisms to which the name is applied, but since all other so-called species are mere parts or fragments of natural species, a recognition of natural species must precede a true appreciation of the more or less artificial subdivisions of species.

These evolutionary facts are quite independent of the old taxonomic idea that the limits of species could be determined by ascertaining whether the animals or plants *can* interbreed. The evolutionary question is whether they *do* interbreed. Groups able to interbreed perfectly will still follow divergent courses of evolution, if kept apart. On the other hand, the failure of the extreme members of the same species to interbreed would not destroy the unity and coherence of the group.[1]

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[1] Cook, O. F., 1905. The Evolutionary Significance of Species. Smithsonian Report for 1904.

The exclusion of the domesticated plants and animals from use as illustrations of the true methods of evolution may appear to withdraw the subject from the consideration of all who do not have intimate acquaintance with species in nature. There remains, however, an excellent and very familiar example of evolutionary conditions, that of man himself. The genus *Homo* has achieved in a relatively brief period a wide divergence from its simian relatives. This progress in development has been coincident with the achievement of a world-wide distribution and with free interbreeding throughout the area of distribution, except as hindered by geographical barriers. Moreover, a further close analogy is to be found in the development of the human individual personality by a complex network of contacts with other members of a social group. Without such social contacts the intellectual development was limited to automatic instincts; with socialization new lines of evolution became possible, just as conjugation opened the road to the development of compound organisms, and the further various stages of advance in prolonged conjugation made possible higher and higher types of cellular structures.

LONGITUDINAL AND TRANSVERSE SECTIONS OF SPECIES.

Longitudinal sections of species show differences along lines of descent. They include what are commonly called life-histories, based on studies of the progressive changes of form and of methods of existence by which individual organisms follow each other in lines of descent.

Transverse sections of species show differences and relations *between* lines of descent, that is, the internal bionomy of the species. The objects of study are not the methods of development or the physiology of individuals as such, but the nature and relations of the different kinds of individuals which exist in the species. The individuals of a species which are alive at any one time may be thought of as affording a cross-section or end view of the network of descent.

Some of the facts of the constitution of species can be understood best from longitudinal sections, some from cross-sections, and many can be best thought of by keeping both aspects of the network in mind.

DIVERSITY IN LENGTHS OF CONJUGATE PERIODS.

The patterns of longitudinal sections of the networks of descent of different species are determined by the longevity of the individual organisms. In popular language it might be said that the generations of some species overlap while those of other species do not. Many species, both of animals and of plants, are strictly annual. All of the adults die in the fall, and the species exists in the winter only in the form of eggs, spores or seeds. These hatch or germinate in the spring and all the new individuals grow to a simultaneous sexual maturity, interbreed, reproduce and die. All the members of the species are in nearly the same condition at the same time and the figure of descent is simple and regular.

A few species, such as the bamboos among the plants, preserve this complete simultaneity, although living through a considerable series of years. Flowers and fruits may be produced only at rare intervals of two or three decades. All the plants of the species reproduce at the same time and then die. But in nearly all groups the lengthening of the life of the individual organism means the overlapping of the generations and the simultaneous existence of many different forms or stages of the species.

Such a statement is not adequate, however, for a scientific description of the complexities of overlapping descent; for the word generation has been used with a great diversity of meanings. In the lowest unicellular organisms each independent cell-individual is a generation. In the next stage, where the cells are joined into simple and relatively undifferentiated structures, the word generation may well denote the interval between two successive conjugations, or rather the structure which is built up between the ending of one conjugation and the ending of the next. But even this definition fails us as we go higher in the scale of existence and find plants and animals which build two or more organic structures between successive conjugations.

In some cases there is a succession of two kinds of cellular structures, one structure being built up before the formation of the sex-cells, before conjugation commences, and another structure after conjugation has commenced. The former is built of simple nonconjugate cells, the latter of double or conjugate cells. The nonconjugate structure corresponds to the "generation" of the simpler types of organization. The conjugate structure is a new feature intercalated into the previous life-cycle, which it often completely overshadows. The conjugation period of many organisms, and especially of the highest groups, both of animals and of plants, is now very much longer than the part of their life history which corresponds to a whole generation in the lower groups. For tracing homologies between the higher and the lower groups it is still possible to talk of the period between conjugations as a generation, but most of the generation is now occupied by the conjugation period, the life-time of the double-celled phase of organization. This corresponds merely to the fertilized egg-cell or oospore of the lower algæ which do not build up any structures of conjugate cells.

In other cases, which are properly to be called alternation of generations, the diversity of the two interconjugational forms has been brought about by vegetative propagation, which replaces or supplements the sexual reproduction of the species. Alternation of generations, that is, of two forms of organic individuals in the same species, may take place either in the conjugate or in the simple or nonconjugate period of the "generation." Thus in the mosses and liverworts vegetative propagation is frequent in the simple-celled phase, while in the ferns and flowering plants it appears in the conjugate period. Vegetative propagation is often described as a purely asexual process, but this is not true of the higher plants, since the conjugate phase is wholly a sexual phenomenon, a part of the sexual process of conjugation.

It may therefore be held that the term generation, as popularly used with reference to the higher plants and animals, does not correspond to what is meant by generations among the lower groups. The period of the life-history which constitutes a generation among the more primitive types of life is so brief as to remain practically unnoticed among the highest. Conversely, the conjugate period which is so short and unimportant as not to complicate the question of generations in the lower groups is lengthened to cover nearly all the activities of the species in higher types of life.

Among the lower groups the overlapping of the generations appears to be a mere coincidence and serves no important evolutionary purpose, but among the higher types it is a condition of the utmost significance, since it has permitted the development of parental instincts and of the numberless devices and habits by which the eggs or seeds or the young individuals are protected and nourished through periods of helplessness. The lengthening of the embryonic and juvenile periods has been necessary to permit the development of large and highly specialized organisms. The overlapping of the generations is also a prerequisite for the development of social habits and instincts, and especially in the transmission of the postnatal inheritance on which the development of human culture and civilization depends. Civilization has been developed and has persisted only among those races in which the family unit of social organization was maintained, so that the children secured the advantage of long and intimate contact with their parents and were thus able to acquire, transmit and accumulate in the race the collective experience and progress of the component individuals and families. Thus the aborigines of tropical America who live mostly in separate and isolated families have built up numerous primitive civilizations, while the natives of tropical Africa who live only in villages have never developed civilizations. Indian children are the constant associates and helpers of their parents while the children of an African village are herded among themselves in little troops or squads like the street waifs of our slums. Even our highly developed systems of formal education have this serious defect and danger, that they tend to disconnect the generations, and to throw the young into premature and reactionary forms of social organization instead of permitting them to grow gradually into their normal places in the general fabric of the community.

DIFFERENT TYPES OF CELLULAR ORGANIZATION.

The complexity of the constitution of species can not be fully appreciated unless it be kept in mind that each individual of all the higher types of life is itself a compact system or colony of cellular organisms, and that these compound units are not only different as to the aggregate cell-individuals, but there are different kinds of cellular organizations. Not only does endless diversity exist among the unicellular or single-celled types of life; there are also different manners and degrees of cell-association to make up the multicellular types. If the cells of the colony-individuals are alike, the organism is called isocytic, if unlike heterocytic.

If the cells which associate have no separating cell-walls the organism may be described as plasmodial, as in the Myxomycetes and in such algæ as *Caulerpa* and *Acetabularia*. If the cells have the form of long slender filaments the organism is described as hyphal, as in the fungi; if built of definite cell blocks it is called cellular, in the strict sense. The fourth or highest type, found in the animals, combines the other three. Some cells remain quite free and unattached, like the red and white blood corpuscles; some tissues are still plasmodial, others hyphal, while still others, and these in the majority, have definite cellular structure.

Finally, the colony-individuals differ in being built of cells which are not conjugating (agamic cell-structures) or of those which are in conjugation (conjugate cell-structures). Of the latter there are two types, the first is that shown by the higher fungi which build colony-individuals of binucleate cells, formed before the nuclei have fused in conjugation (apaulogamic cell-structures). The second type of conjugate structure is that of the higher plants and animals whose bodies are built up of cells with the nuclei fused, but with a double number of chromosomes (paragamic cell-structures).

These facts are capable of a very definite graphic representation in our ideal longitudinal sections of specific networks of descent. Double-celled structures are the conjugate product of two lines of descent and their existence is to be shown in our diagram by double, closely parallel lines. The network which represents the method of descent of intermediate groups, such as the archegoniate plants (liverworts, mosses and ferns), may show single and double lines in almost equal proportions. Primitive groups may show only single lines, higher groups only double lines, except at the actual points of junction where conjugation takes place.[1]

In alternation of generation and metamorphosis the organism changes its external form without altering the figure of descent. Alternation of generations, like the differentiation of separate sexes, exists in simple-celled as well as in double-celled organisms. The phenomena are of an entirely different and minor order of significance compared with the diversities of the different types of cellular structure. Wonderful as the changes are, they are still of a merely morphological and adaptive character and do not indicate new evolutionary departures of the scope of the double-celled structures.

SPECIFIC CONSTITUTIONS MODIFIED BY SPECIALIZED HETERISM.

There are two principal groups or kinds of specific constitutions which can be studied or thought of as cross-sections of the networks of descent. These two series of special types of species arise through two forms of specialization of methods of descent. Instead of remaining uniform or homogeneous throughout, the network of descent becomes variously subdivided or separated into subspecific strands.

The first form of subspecific differentiation consists in specializations of heterism, that is, the establishment within the species of definite forms of diversity of descent, so that individuals are not merely different individually, but fall into two or more groups regularly distinguishable by definite characters. These groups are not formed by isolation, and their existence does not interfere with interbreeding, but usually has the contrary effect of encouraging or compelling interbreeding, since the members of the same group may be unable to interbreed with each other, but are specially adapted for interbreeding with the members of the other group or groups of which the species is composed.

SPECIES WITHOUT SPECIALIZATION OF HETERISM (ARROPIC).

The diversity of normal symbasic descent remains miscellaneous and unspecialized. The individuals may be more or less

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[1] Diagrams of networks of descent in the various types of double-celled structures have been given in another place. Bulletin 81, Bureau of Plant Industry, U. S. Department of Agriculture.

obviously different, but the differences are fluctuating or completely intergraded, so that no definite alternatives of descent appear, and no distinct subspecific groups are indicated.

Individuals are all similar, equivalent and bisexual or hermaphrodite. None of the vertebrate or arthropod animals show this condition, but it appears to be very common among the lower animals and among plants. Species in which there are no specializations of heterism, no differentiated paths of alternative descent, may be called *arropic species.*

The arropic condition is not merely synonymous with hermaphroditism, through all arropic species are bisexual. The hermaphroditism of the lower groups of animals and of plants is a normal condition incidental to their more primitive organization. Among the higher groups which have attained sexual differentiation hermaphroditism has reference more definitely to abnormal cases of bisexuality. The arropic condition is also more definite and restricted than bisexuality, since organisms may be bisexual and still manifest some of the following forms of alternative heterism.

SPECIES WITH SPECIALIZATIONS OF HETERISM (ROPIC).

Specializations of heterism exist, and definitely alternative routes of descent are followed by different individuals. The individual members of species fall into distinct groups, but not as the result of segregation or of differences of environmental conditions. The group differences are usually such as to facilitate or to compel interbreeding between the groups.

The attainment of the ropic condition marks an important stage in the evolution of a species, very favorable, apparently, to its further development and to the greater and greater extension of the heteric specializations. The distinction is entirely concrete and practical, but there seems to be no suitable and convenient English word by which to designate it. The expressions alternation and alternative have been used too widely already, and would increase the confusion now existing as the result of identifying alternation of generations with phenomena of entirely distinct nature, such as the different kinds of cellular structures.

Subsexual Species. — A species consisting of bisexual organisms divided into subsexes, that is, into groups differing in one or more characters, but not showing special adaptations to secure cross-fertilization.

The first stage of specialized heterism is represented by species which include two or more types or forms, merely for the sake of the diversity, as it were, and with no sexual diversification, that is, no adaptations, for securing cross-fertilization between the two forms. The differences appear to be of the same nature and to have the same symbasic utility as secondary sexual characters, but the utilization of them is still left to chance. Examples of subsexes are probably to be found in such species as *Verbascum blattaria*, *Viola bicolor*, and others in which plants of different castes live together indiscriminately. Antidromous or right-and-left-handed plants like cotton and *Castilla*, might also be recognized as affording instances of subsexual differentiation.

It often happens in zoology that the sexes of the same animals are at first described and named as two distinct species, but after their true relations have been ascertained one of the supposed species is, of course, rejected, no matter how diverse the sexes may be. Similarly, these subsexual forms need to be taken into account by the taxonomist. The criteria commonly applied to determine specific distinctness are not adequate, since it is possible for constant differences unconnected with sexual diversity, to exist inside the same species without in any way justifying the taxonomic subdivision of the group on the usual basis. There is, however, no reason why any established type of diversity like these subsexes should not be named and described separately, just as the sexes are treated separately when their characters are different.

Botanists are acquainted with numerous instances of diversity among the members of species which may prove to be subsexes; though it is also possible that the differences may belong to species which closer study may distinguish. Thus there are species of *Actæa* which have the berries either waxy white or crimson, and in about equal quantities. Numerous species of *Delphinium* have the flowers either pink or blue. In species of *Aconitum* purple and creamy or greenish white flowers are described. Pink flowers also appear occasionally as definite variants of white-flowered species of *Achillæa*.

Semisexual Species. — A species consisting of bisexual organisms divided into semisexes, that is, into groups differing in characters which conduce to interbreeding between the groups.

This is the condition reached by many species in which the individuals are all bisexual, but differ among themselves in characters which insure, or at least facilitate, cross-fertilization. In the well known instance of *Lythrum* there are three castes of plants with short, medium, and long styles and filaments, and three different kinds of pollen grains and stigmatic papillæ. A long-styled plant produces only short and medium stamens, and must be fertilized by pollen from long stamens, to be found only on other plants. The semisexes of the primrose were described by Darwin. Similar conditions are known in *Oxalis*, *Houstonia*, and many other genera.

Among plants, at least, it might appear that semisexual conditions are more advantageous than the next stage of completely differentiated sexes. Cross-fertilization is secured, but at the same time all individuals may produce seed, and not merely half of them. That complete sexual differentiation has been attained notwithstanding, and in so many different groups, affords an intimation of the importance of symbasic heterism in the structural economy of organisms. The fact loses none of its significance if we reflect that the complete separation of the sexes in plants reduces by half the facilities of the species for producing seeds. All individuals being stationary, the males can contribute to the welfare of species by none of the accessory habits which have been so richly developed among the animals. Indeed, it is by no means unlikely that the tendency of selective influence on many plants has been to keep them in the semisexual condition, sexually differentiated only far enough to secure cross-fertilization, but not far enough to preclude the production of seeds by all individuals.

Sexual Species. — A species consisting of unisexual organisms, or divided into two sexes, male and female, so that interbreeding between the sexes is necessary to reproduction.

The complete separation of species into two sexes is the condition obtaining in all the higher animals, both vertebrates and arthropods, as well as in many of the lower animals, and in numerous plants. It has been found recently that even among the moulds and other lower fungi the plant body, or mycelium, is of two kinds, and that spores are produced only when these are brought together.

Secondary sexual characters are of two kinds, or may be so considered: (1) Those which are accessory to reproductive processes, or assist in caring for the seeds, eggs, or young, such as the mammæ of the higher animals; (2) those which are merely the result of accumulation of differences which add to the heterism or internal diversity of the species, such as the manes, beards, tail-feathers or sexual differences of color or form which are of no use in reproduction or in the environmental relations of the species.

The environmental uselessness of many sexual differences is an obvious and well known fact. Not only do the two sexes generally occupy exactly the same environment with equal success, but the presence or absence of many sexual characteristics may have no practical significance for the individual. Some varieties of mankind are beardless; some have beards only late in life, and some have beards in early manhood, but cut them off without appreciable detriment. The uselessness of such characters is shown even more strikingly in certain species of beetles. Some of the males are scarcely distinguishable externally from the females, while others have the head or thorax fantastically modified by the growth of long, heavy, antler-like processes. It is easy to understand that for all the males to be thus encumbered might be a serious handicap to the species.

It may be that selection will help to explain why such features commonly pertain to the male sex. Great diversity among the females would interfere with recognition by males unless their instincts were modified in a corresponding manner. Moreover, variation is the more practicable in the male sex because the extent of the coordination necessary among the bodily organs is not so great. Variation, which in the females might have occasioned serious functional derangements or might have too greatly increased the difficulties of existence, can be tolerated by the males without injury to the species.

That secondary sexual characters are often so completely without function, in the ordinary sense of the word, does not mean that they are of no value to the organism. With reference to the environment they are often worse than useless, but in the physiology of descent they may have an important function. The existence of two sexes doubles, as it were, the symbasic effect of cross-fertilization, by permitting the accumulation of two sets of variations, a second reason for the more rapid progress made by sexually diversified organisms.

What has been called organic evolution has been thought of too exclusively from the environmental side. Evolution has an internal as well as an external function; it has a bearing upon the quality of organisms, as well as upon quantity. Species are advantaged not only by characters which give them a wide range and permit the propagation of large numbers, but it is of equal importance that the vitality of the species be maintained through the provision of adequate diversity of descent, as assured by sexual specialization and by the access of new variations.

The doctrine of sexual selection was invented by Darwin to explain the so-called secondary characters, differences admittedly useless from the environmental standpoint, the two sexes of a species being subject, generally, to identical external conditions. And yet there is everywhere manifest a tendency to the further accentuation of sexual diversities, which are by no means confined to man, or to the higher animals in which esthetic instincts have been attained.

Viewed as specializations of heterism, secondary sexual characters have an obvious and general utility, though of an internal nature. A species with two separated sexes is the stronger because it can accumulate two lines of variations. Symbasic interbreeding becomes, as it were, doubly effective, and the stimulus of diversity can be utilized for a much longer period than if the character were to spread to all the members of the species.

If the present interpretation of the facts be correct, we have in the familiar phenomenon of sex an example of a fundamental evolutionary principle which has thus far escaped formal recognition. Heterism is a concrete property or requirement for constructive evolution, though left quite out of account in theories which have thought to explain organic development by external influences of environment, or by internal "mechanisms of heredity."

Sex specialization in species corresponds to paragamy in cells; the sustained diversity of the associated sexes is curiously analogous to the prolonged separation of the parental chromosomes. Sexuality supplements paragamy, and both serve the same purpose of increasing the vitality of the individual organisms and the coherence of the specific networks of descent.

Supersexual Species. — A species consisting of organisms of two sexes, but with one or both sexes again subdivided into two or more kinds of individuals.

That the uses of the diversities of the sexes are not limited merely to the reproductive functions, is well shown by the fact that specializations of heterism are sometimes carried beyond the stage of definite sexuality. Thus there are, among the sexually differentiated higher animals and birds, numerous instances of the existence of two color-forms, indifferently intermingled, but not intergraded. It has been found, for example, that there are in eastern North America two kinds of screech-owls, red and gray, which are not separated geographically or in breeding.

The following reference to the occurrence of leopards of two colors in the Malay region may serve as a sample of many similar observations among the mammals.

"Many of the hunters I have met, and some of the authors I have read, appear to consider the black leopard a distinct species, but it is simply a freak of the ordinary spotted leopard, just as the silver and the black fox are freaks from the common red. In a litter from a red vixen I have seen a silver among red pups; and I met a man in the jungle where lower Siam meets the Malay Peninsula who had found a black among the spotted leopard's cubs, upon which, however, the spots, of course, are not very clearly defined until they become older."

. . . "I noticed after I got its pelt off, that in the sun it had a kind of watered silk appearance, as a result of the deeper black of the spots, which, though invisible, were really there just the same."[1]

In a similar case of supersexual dichromatism in a chrysomelid beetle experiments showed that the two color-forms could be separated and established as uniform varieties by selective breeding.[2] The mating of black individuals produced only black offspring in the first generation, while matings of spotted individuals continued to give a proportion of black offspring until the third generation.

SPECIFIC CONSTITUTIONS MODIFIED BY RESTRICTED DESCENT.

This is the second form of diversity of constitutions revealed by cross-sections of networks of descent. Unlike the specializations of heterism, the members of groups formed by restricted descent do not, of course, breed together, for it is in this that the restriction of descent consists. The specializations of heterism are in accord with the evolutionary advancement of the species, but the groups formed by restricted descent are removed from the conditions of free interbreeding and of normal evolutionary progress. They represent, instead, the different stages of a process of deterioration.

Symbasic Species. — Species with descent unrestricted, consisting of large numbers of diverse individuals freely interbreeding in a broad, continuous and regular network of descent.

A species is not merely an aggregation of organisms, whether alike or different; the organisms are connected by a completely interwoven fabric of lines of descent. Such plants as *Portulaca oleracea*, *Poa pratensis* and *Ceratodon purpureus*, may serve as examples of very widely distributed symbasic species.

Porric Species. — Species made up of partially segregated subspecies. The cross-section of the network of descent, instead of showing a rounded or regular form,is irregular, or partially subdivided into arms or branches.

Widely distributed species, but locally diversified, like the

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[1] Whitney, Caspar, 1904. Outing for April, p. 14.

[2] McCracken, I., 1905. A study of the Inheritance of Dichromatism in Lina Lapponica. Journal of Experimental Zoology, 2 : 117.

European *Helix hortensis*, afford the best examples of this type of intraspecific diversity. The quail, or Virginia partridge, a non-migratory bird widely distributed through eastern North America from New England to Guatamala, shows many local subspecies connected by series of imperceptible gradations. The sugar maple of eastern North America has several geographical subspecies.

Stenic Species. — Species consisting of stens, that is, of narrowly segregated subspecies, domesticated varieties, or breeds, propagated by sexual reproduction.

As a result of propagation by narrow breeding, the individual members of a sten are much more nearly uniform than those of normal symbasic species, or even than those of geographical subspecies. As purely stenic species may be mentioned those which do not exist any longer in the wild state, but are made up of many local domesticated varieties. The domesticated animals fall here, except as they may represent hybrids of different wild species. Of domesticated plants the Indian corn or maize is the best example, since it has retained a complete system of cross-fertilization, which many domesticated plants have lost.

Very small, closely localized natural species, like the remarkable Hawaiian land-snails upon which Gulick has based his theory of evolution by isolation, represent essentially the same condition of restricted descent as domesticated stenic varieties.

Linic Species. — Species composed of separate, parallel or slightly diverging lines of descent, propagated by autogamy or parthenogenesis, and not united into a network.

Wheat and barley are perhaps the most conspicuous examples of linic species among domesticated plants, though many other species are autogamous, with more or less consistency. Strict line breeding is not possible, of course, among the sexually differentiated higher animals, but is sometimes approached by what is called in-and-in breeding of closely related individuals.

Line-bred organisms are extremely uniform, even more so than stens. Self-fertilization involves only the combination of gametes of the same origin and probably of very nearly identical nuclear configuration; at least there is even less variation. Linic species occur in nature as in the well-known instances of *Hieracium* upon which Nägeli based his theory of evolution in a definite direction. The persistence by parthenogenesis of the individual differences of transplanted specimens was accepted as proving that variation held to definite directions.

Likewise De Vries has made use of linic autogamous species of *Draba* to illustrate his conception of elementary species. The uniformity and stability of the line-bred plants has been taken to represent the normal condition of species, and the inference has been made that the species recognized in nature by taxonomists are generally composed of similar independent units, the effect of the method of propagation, to resolve the species into separate lines of descent, being left out of consideration.

Clonic Species. — Species consisting of separate lines of descent continued by vegetative propagation alone.

Clones, like lines, are propagated from single individuals, but by vegetative processes only, so that variation is almost completely avoided. Nevertheless, even vegetatively propagated plants are not completely uniform. Clonic groups of the same origin often show fine gradations of diversity, and occasional mutative variations are known.

Clones do not exist, of course, among the higher animals, but they areexceedingly numerous among plants. Several domesticated species now exist, as far as known, only in this form. The horse-raddish, sweet-potato, banana, arracacha, yautia and taro may be mentioned as seedless plants, but large numbers of others are nearly seedless or have varieties which are seedless.

THEORIES OF EVOLUTION BY RESTRICTED DESCENT.

It is a noteworthy fact that the earlier theories of evolution, including those of Darwin, Nägeli, Gulick and De Vries, have been based upon one or another condition of restricted descent. The kinetic theory is the only suggestion of a method of evolution applicable to conditions of unrestricted descent. The predisposition to see in restricted descent ideal conditions of evolution has been strengthened, if it has not been wholly supported, by the fact that it is only in restricted descent that the traditional ideal of heredity can be applied. Only narrow-bred organisms afford even an approximate identity of form and structure.

De Vries, Gulick and Nägeli have given their chief attention to extreme forms of restriction, like those of *Draba*, *Achatinella* and *Hieracium*. Darwin kept much nearer to the consideration of natural conditions, though his doctrine of selection implies that evolutionary progress depends entirely upon the plan of causing species to change by restricting the descent of the component individuals. In the kinetic theory, it need scarcely be repeated, the result of selective restriction is not evolution, but specialization. The evolutionary motion would still take place if the selective restrictions of descent were not imposed.

COMBINED FORMS OF SUBSPECIFIC DIVERSITY.

Modifications of the constitution of species by specializations of heterism do not interfere with the attainment of the other form of diversity by restricted descent. Thus a sexual species may be partially segregated into geographical subspecies or may be narrowed still further into the stenic condition of domesticated varieties and breeds. Linic and clonic subdivisions of sexually differentiated species do not occur, of course, among the higher animals, being limited to the lower groups and to plants which have the power of sexual propagation or of parthenogenetic development. But even among the cultivated plants it does not appear that any sexually differentiated species has been resolved completely into the clonic condition. There are large numbers of clonic female varieties of figs and date-palms, but the male trees are usually recruited from chance seedlings, so that the network of descent is not entirely destroyed. The female half of the species is represented by vegetatively propagated clones, but on the male side miscellaneous individual diversity remains.

The existence of restricted subspecific groups may not interfere in the least with the maintenance of a normal specific network of descent. A widely distributed symbasic species may have a few porric subspecies as a result of the partial isolation of particular localities. Special conditions, such as an alpine climate, might restrict a part of a species to linic or clonic propagation while the remainder retained fully symbasic conditions of descent. Through the fabric of broadly diversified descent there may run narrowly compact strands composed of linic or clonic individuals, which no longer share the symbasic interbreeding of the group and afford no true criterion of the conditions under which evolution goes forward. Just as most planets are attended by satellites, so species are sometimes found to be supplemented by small subspecific adjuncts, little species-like groups of organisms which some have taken for new or incipient species, but which stand in a permanently subordinate or retrograde relation to the evolutionary part of the species.

LIMITATIONS OF CLONIC PROPAGATION.

Vegetative propagation, whether in nature or in domestication, appears to conduce always to seedlessness. Some have thought to explain this fact by reference to the superiority of the asexual over the sexual propagation. This reasoning is scarcely adequate, in view of the fact that much larger numbers of species have retained their capacity of producing seeds, though regularly supplementing the sexual by the vegetative propagation. The greater probability is that the decline of sexual fertility in vegetatively propagated types is a symptom of deterioration, just as sterility is a frequent characteristic of abnormal variations or of hybrids.

The formation of the sex-cells, as we now know, is a highly specialized and complicated process, and it is easy to understand why it should be the first of the physiological functions to become deranged and inefficient. It is known also, from the behavior of hybrids and mutations, that vegetative vigor has no direct relation or apparent connection with reproductive vigor. Indeed, sterile hybrids and mutations often show great and notably superior strength and longevity, due, we may suppose, to the stimulation which attends new variations. This consideration may also explain why clonic and linic species usually appear to consist of definite groups of closely similar individuals. These groups may have originated by individual mutative variations of notable vegetative vigor, which have on this account survived or crowded out the weakening survivors of the original symbasic species or other variations less recent or less vigorous.

The disastrous effects of inbreeding among the higher animals have been known for centuries, and are taken into account by all breeders. That the same principles apply to plants, has remained in doubt for two reasons: (1) The much less complex organization and less specialized tissues of plants render many of them less acutely dependent upon cross-fertilization. (2) The plants which have been longest under cultivation are not grown for their seeds and are propagated asexually, so that their decline in reproductive fertility has not diminished their economic value. No plant valued for its seeds has been propagated other than from seeds for any considerable period.[1] Numerous tropical root-crops and fruits, such as the sweet-potato, yam, agave, sugar-cane, banana, pine-apple, and bread-fruit have been grown for thousands of years from cuttings, probably without the interposition of a single seedling generation. In a sexually propagated species inbreeding would have led long since to extinction, but these clonic varieties are still extremely vigorous. Nevertheless, such species do not form a real exception to the rule of deterioration under inbreeding, since a very large proportion of them, belonging to many and very diverse families, have shown this tendency towards seedlessness.

The reduction or elimination of the reproductive parts has been ascribed by some to selection, and by others to a supposed biological law of paucity which causes useless parts to disappear. No basis of fact has been shown, however, for either of these explanations; unassisted nature supplies us with instances like *Sphagnum* and *Lunularia* to which neither would logically apply, but which would be well accommodated in the view that continued asexual propagation, like other forms of isolation, weakens the reproductive powers. This law would also explain why the absence of sexual reproduction appears only as the character of aberrant species or genera, and has not been able to persist for a period long enough to permit the differentiation of organic groups of higher systematic rank. Botanists seem not to have ascertained the existence of any wild phanerogamous plant which is always and everywhere seedless.

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[1] Apparent exceptions to this rule appear only among trees, such as the almond and the pistache, where the normal long life of the individual may be thought of as lessening the period of vegetative propagation, if counted by generations.

The opinion has long existed among horticulturists that varieties of fruit trees tend to deteriorate, but a biological explanation has been lacking thus far. The most prominent horticultural writer to defend such a view is Burbidge, who holds that budding and grafting are artificial and unnatural processes, for which propagation by rooted cuttings should be substituted. The analogy of the seedless tropical root-crops indicates that the use of cuttings would afford no protection against the gradual reduction of fertility, though the suppression of seeds in fruit trees may not be an undesirable symptom, except when it is accompanied by a deterioration in quality. Only a few horticultural varieties have been propagated as clones for more than a century, but the advance of sterility has already become appreciable to nurserymen, who are careful to plant seeds from seedling trees, in the belief that these germinate better and produce more vigorous stocks than the fruit of grafted clonic varieties.

That superior varieties are commonly deficient in vigor is thus explainable without reference to any special perversity of nature ; such varieties may owe their reproductive debility to the fact that they have been more carefully and persistently propagated without crossing. Some varieties of peaches, for example, yield a very small percentage of viable seed. In France many attempts to secure seedlings of the "Alexander" have failed. This variety and the very similar "Amsden" appeared about the same time and are supposed to be seedlings of "Hale's Early," a variety also notably deficient in reproductive fertility, since only about ten per cent. of the seeds germinate. The seedlings of "Hale's Early" are also, as a general rule, very diverse, without close resemblance to the parent or to each other. The variety called "Hill's Chili" affords an instructive contrast, in that practically all the seeds germinate and about ninety per cent. of the seedlings come true to the parental type, leaving about ten per cent. of variations.[1]

Obviously, the evolutionary status of these two varieties is very different; one is entering upon the stage of mutative aber-

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[1] For these interesting facts I am indebted to Mr. William A. Taylor, of the United States Department of Agriculture.

ration, while the other is approaching that of complete sterility. Horticulturists have not uncommonly believed that the longer the succession of " grafted generations " of tree fruits the greater the likelihood of deviations from the type of the original seedling, but this idea seems not to have received scientific consideration or support, perhaps because it appeared to contradict the opinion of Darwin[1] and many other evolutionary writers who have held that characters can be permanently " fixed " by inbreeding, or close selective segregation, of which propagation by cuttings may be taken to be the extreme form. The kinetic theory of evolution permits us to understand, however, that the " fixity " to be secured either by inbreeding or by asexual propagation is only relative, and that its result in both cases is to predispose the organism to abrupt variations and reproductive debility.

ORIGIN OF LINIC AND CLONIC CONDITIONS.

The occurrence of self-fertilization, parthenogenesis, and vegetative propagation in nature has undoubtedly caused many writers to suppose that these methods of descent represent truly normal evolutionary conditions. Indeed, no abnormality need be charged in the many cases where the species maintains at the same time the normal network of descent by sexual reproduction with free interbreeding. The abnormal condition supervenes when the species loses its network of symbasic descent and is resolved into disconnected lines. Such a condition may result whenever the normally sexual and symbasic reproduction becomes less effective than autogamous or purely vegetative methods of propagation. Thus, in such little plants as *Draba* and *Viola*, which have to avoid the competition of larger neighbors by blossoming early in the spring, the non-symbasic methods of propagation take on great importance, for insects are scarce and the weather often so inclement as to completely prevent the transfer of pollen.

Similarly, in alpine and arctic conditions, vegetative propagation is much safer, and usually much more successful than sexual reproduction. The short and treacherous seasons often prevent the ripening of seed. The formation of apogamic bulblets

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[1] The Effects of Cross and Self-Fertilization in the Vegetable Kingdom, p. 27.

instead of flowers is frequent among the saxifrages and other Arctic plants, though many similar instances are known in natives of temperate and tropical regions.

Wheat and barley, and to a less degree several other domesticated plants, have been unconsciously selected towards autogamy in a similar manner, by being cultivated far to the north of their original habitats. In unfavorable seasons only the autogamously fertilized seeds would ripen. The wild relatives of all these plants, so far as known, have facilities for cross-fertilization.

That autogamy and other forms of restricted descent conduce to the breaking up of species into small subspecific groups, is well shown among the cereals. The rye plant has retained and even accentuated its provisions for cross-fertilization, and has kept its position as a relatively normal coherent species, instead of falling apart into distinct varieties. Cross-fertilization has also been fully maintained in the corn plant, but here the large size of the seeds and their compact grouping on the ears greatly facilitate selection, and have favored the establishment of many local varieties.

RELATION OF LINIC TO CLONIC PROPAGATION.

The fact that reproductive fertility deteriorates more rapidly than vegetative vigor, when organisms are placed under conditions of restricted descent, is to be correlated with another phenomenon, discovered by Darwin, that autogamous fertilization is sometimes superior to more miscellaneous methods of narrow inbreeding. This fact has been generally accepted to mean that autogamy and heterogamy are both normal evolutionary conditions. In the kinetic interpretation it does not appear that autogamy is a truly normal and progressive state. The superiority of strict autogamy over more miscellaneous inbreeding appears explainable by analogy with parthenogenesis and vegetative propagation. All three processes can be viewed as methods of postponing deterioration from restricted descent, by omitting the nuclear readjustments which are required in normal sexual reproduction. When diversity of descent is no longer sufficient for normal readjustments, degeneration begins, in the form of mutative variations. These usually fall below the parental standards, or at least diverge from them so seriously as to injure the commercial value of the crop, as strikingly shown in the tobacco varieties studied by Mr. A. D. Shamel.[1]

Seed produced by autogamous fertilization yields plants of very much greater uniformity, and it is in this fact that their superiority lies. The plants were not better, as individuals, than some of those produced by the more miscellaneous breeding, but the tendency to degenerate variation had been avoided, or at least postponed.

Such facts do not appear to warrant any general contrast between cross-fertilization and self-fertilization, but only between narrow breeding and line breeding, and of these the line breeding appears to be superior because it constitutes an approximation to vegetative propagation and avoids the need of nuclear readjustments with inadequate diversity of descent. The union of two nuclei which are the autogamous progeny of the same individual organism, can hardly require any new adjustments to be made. The formalities of sexual reproduction are observed, but diversity of descent, which gives physiological value and evolutionary significance to the process, has been eliminated. Self-fertility and parthenogenesis, like vegetative propagation, have value only as means of avoiding, for a time, the normal results of restriction of descent, not because they represent normal evolutionary methods of organic succession.

DIVERSITY REACTIONS IN RESTRICTED DESCENT.

Efforts toward the selective improvement of domesticated plants and animals have been accompanied everywhere by the narrowing of the lines of descent, and often by close inbreeding. How far this abnormal condition is responsible for the results of experiments with domesticated species, and how far these results are of general evolutionary significance, remains to be considered. Most of our important food-plants were domesticated long before the period covered by human history or tradition, so that the general claim of selective improvement through thousands of years could not be denied, and has

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[1] Shamel, A. D., 1906. The Effect of Inbreeding in Plants. Yearbook of U. S. Department Agriculture for 1905, p. 386.

continued to be accepted as a sufficient cause of the extensive modifications which have taken place.

The question has been debated at length on theoretical grounds, but without decisive results, since it appeared to lie outside the range of experimental determination, owing to the vast periods of time which have figured in the calculation. Fortunately, all plant cultures are not the same in method or in history, and the so-called Arabian coffee furnishes an instructive contrast with other domesticated species. Coffee has probably not been in cultivation much more than a thousand years, and has existed but a few centuries, or often only a few decades, in its present centers of production. It is not an annual, but a shrub, or small tree, the selective improvement of which would require more years than planters generally expect to give to the business. Plantations are generally large, and experiments with individual trees are difficult and time-consuming, so that it is only within recent years that the securing of improved varieties of coffee has received serious attention. The evolutionary factors of selection and of long periods of local influences of soils and climates are thus alike absent, and yet there is no lack of coffee varieties with abundant diversity in form, habit and color. Their general similarity consists only in being inferior in fertility to the parent type.

So much has been written upon the improvement of plants by domestication and selection that this inferiority of coffee varieties may seem exceptional, but the apparent anomaly disappears if we reflect that fruit trees and other horticultural plants supposed to have been greatly improved in domestication are not grown for the seeds, and hence complete fertility in the sexually reproductive sense has been a minor consideration or even a positive disadvantage; indeed, with many plants it has been one of the direct objects of selection to reduce the number of seeds or to eliminate them completely. More or less seedless abnormalities are valuable, for example, among the grapes, plums, and oranges. If coffee were cultivated as an edible fruit the new sorts would be of use, since thicker pulp and smaller seeds are frequent characteristics of the berries; indeed, a coffee which did not produce any normally developed seeds was found in 1903 in Costa Rica. As ornamentals, some variations offer new colors and greater abundance of flowers, and the foliage and habit of the trees sometimes deviate strikingly from the normal or parent form. Unfortunately, the planters would find an advantage only in the direction of increasing the number, size, or weight of the seeds themselves, and they accordingly pronounce the new varieties worthless.

Similar abrupt variations of many cultivated plants and animals were studied and described by Darwin as "sports," but it was also known to him that such variations are relatively infertile and do not persist in the presence of the normal or less closely inbred types, so that it has remained for Professor De Vries to base upon such variations a general theory of evolution. The variations, or sports, chiefly studied by Professor De Vries are those of an evening primrose native in North America and escaped from cultivation in Holland, and thus accidentally segregated from the wild stock of its species. It belongs, like the coffee, to a family in which there are specialized provisions to assist cross-fertilization, so that the early manifestation of the effects of inbreeding might be expected.

The variations of *Œnothera* described by Professor De Vries seem to be closely parallel to those of coffee; most of them are conspicuously deficient in reproductive fertility, and some are quite sterile. This relative or complete sterility of sports, or variations secured by inbreeding, warns us that evolutionary inferences founded on this class of facts must be carefully revised, since it is obvious that organisms notably deficient in the power of reproduction can not be expected to have played a large rôle in the process of organic evolution. Nature, like the coffee-planters, requires seeds; reproductive efficiency is the first requisite of survival.

A general evolutionary significance of the phenomena of mutations becomes apparent when the facts are interpreted from the standpoint of normal heterism, that is, as reactions from the abnormal uniformity which is the first result of restricted descent. The diversity of mutations is greater than the diversity of normal heterism, but this is in entire accord with what we know of other physiological reactions of organisms. Mutations are at once degenerative and reconstructive, just as the high temperature which attends many diseases of the human organism is at once an evidence of illness and an indication of constructive systemic reaction. Indiscriminate crossing of mutative varieties tends to restore the wild type of the species. Mongrel dogs are wolfish ; mongrel pigeons, even of white ancestry, are blue; mongrel roosters become red in approximating the primitive game breeds; mongrel flowers are single and small.

Stronger evidence could scarcely be demanded for proving that the interbreeding of the members of a species is a measure of organic stability, not a stationary or uniform stability, but a stability of coherent symbasic motion.

EXAGGERATED HETERISM OF CLONIC HYBRIDS.

Further evidence that mutations are reactions from abnormally restricted descent may be drawn from the results of sexual reproduction among clonic varieties. The sexual offspring of plants which have been subjected to considerable periods of vegetative propagation always show a very large amount of individual diversity. This has caused them to be reckoned as hybrids, though in reality they represent a very distinct type of evolutionary phenomena. Each clonic variety is, after all, only an individual member of its species, and as such varieties have not been selected or bred to uniformity, in the sense of coming true to seed, they and their offspring might be expected to retain the original amount of heterism or normal individual diversity of the wild type of the species. As a matter of fact the sexual offspring of clones have an individual diversity of the order of mutations. The only difference appears to be that all the individuals may be mutants, instead of the relatively small percentages usually appearing in species which have been subjected to courses of selective inbreeding for the elimination of heterism.

DIVERSITY RELATIONS BETWEEN SUBSPECIES WITH RESTRICTED DESCENT.

As long as the diversity of the members of species appears either as the merely accidental or arbitrary result of environmental influence or of mechanisms of heredity, both the theory and practice of evolution remain mysterious and contradictory. It is only after the physiological value of diversity in the constitution of species has been recognized that we begin to gain a definite appreciation of the practical bearings of evolutionary facts. With nature wrongly interpreted, the results of domestication and breeding were likewise obscured and distorted. As long as our reckoning was based on the false ideal of uniformity and stability of species, it was not possible to gain an orderly concept of even the simplest of evolutionary relations, or to escape from the confusion and contraditions which have left even the most concrete investigators in hopeless disaccord.

Among breeders of plants there exists the greatest possible diversity of opinion regarding the value of hybridizing as a means of securing new organic forms of superior agricultural utility. Some breeders have secured very valuable hybrids, while others have found hybrids of no use at all as a means of increasing the desirable characters of the species which they were seeking to ameliorate. To explain and reconcile this apparent contradiction is not only a matter of scientific interest in its bearing upon the general subject of evolution ; it is also of much practical importance to be able to distinguish between the different kinds and combinations of subspecific groups and to avoid a waste of efforts upon methods and materials which do not promise useful results.

The time has not yet come for the establishment of absolute standards and criteria, if indeed such a time is ever to come. There are unforseen accidents, not only in the best regulated families, but in nature as well. It is the rarely unusual circumstance, the exception to all known rules, which may have great interest and potential value. The sterility of mules is one of the most invariable of the phenomena of hybridization, and yet fertile mules are not altogether unknown, nor is it certain that such an animal might not be a means of securing new and desirable variations of our equine stocks. Hybrids between the different species of bovine animals are generally fertile and readily made, but the establishment of a breed combining the blood of the buffalo and the domestic cow has proved difficult.

For the practical breeder, as for the scientific investigator, nothing should be taken for granted until verified by actual experiment, but it is, nevertheless, useful to have, if possible, a system of interpretation by which results once attained can be understood, and proper discrimination made between the relative prospects of alternative fields of investigation. Selections, mutations, crosses and hybrids, have entirely different importance in different groups, depending upon the nature of the characters which it is desired to secure, and upon the adaptability of the species to different methods of propagation. In the amelioration of coffee, for example, mutations promise little because of their smaller production of seeds, but if the flowers or pulp of the berries were the valuable part, mutations would be as valuable as among other horticultural species.

Selection and hybridization have been thought of as two alternative methods by which evolution might be brought about, and the debate has continued as to which is the better. The question could never be answered in this form, for the assumption on which it is asked is a false one. The normal species, the unit of evolution, is neither stationary nor uniform. It not only makes a slow and gradual advance, as a whole, but it manifests all the time a vast diversity among the different individuals. Some of this diversity is induced by the environment, but much of it is quite spontaneous and continues to appear even in a uniform environment.

The value of selection does not lie in any power to cause these inherent differences; it can only preserve them and prevent, as it were, the swinging back of the pendulum of normal diversity. The alert breeder seeks to catch it at its highest and to hold it steadily there. It cannot be held forever, as is now generally recognized. Sooner or later the selected type deteriorates, and shows itself inferior to some more recent selection which has lost less of the normal vigor of the species.

To hybridize selected varieties may serve merely to release the pendulum and allow it to swing back along the curve of normal diversity. The vast majority of the progeny are likely to be inferior to the parents in the special qualities which have made them valuable. Some of them may approach the standard, but they seldom or never surpass it. The breeder concludes that hybridizing is a mistake and finds that much more can be accomplished by selection. This conclusion is quite correct if he is dealing only with long-domesticated strains of plants and animals, and if he wishes to obtain from them the greater accentuation of some character already specialized by selection. If the varieties are not too unlike, or too long selected, the result of crossing will be to restore the more normal but less desirable diversity. If the varieties crossed are somewhat more remote, the diversities may balance each other into a somewhat uniform intermediate average. Still longer selection may establish the specialized characters as definitely alternative, in the Mendelian sense, so that they do not combine again into a single hereditary pattern, but separate regularly into the two original components, as in the pea hybrids studied by Mendel, and the many other instances discovered by more recent investigators.

In none of these three cases or types of hybrids is there any reason to expect an increase of characters beyond the range of accentuation to be reached by selection ; they all involve, instead, a lessening of the amplitude of diversity obtainable through selection. If the selective specialization of characters of a variety were a true step in the evolution of the species, these kinds of hybrids could be called reversions or retrogressions, since they appear to go backward and undo the results of selection. To call them reversions is very misleading, however, from the evolutionary standpoint, since the closely selected type, however useful, represents only a temporary and abnormal phenomenon, a holding of the pendulum of variation to one side, instead of permitting it to describe its normal vibrations, or to change its general position and point of support.

The simple analogy of the pendulum proves entirely inadequate as a means of illustrating the normal conditions and requirements of true evolutionary advances of specific groups, for we are not dealing then with vibrations of single characters, but with a complicated network, a veritable fabric of descent and of character-combinations. The pendulum analogy is appropriate only for the single lines or narrow strands of descent which selection separates from the web of the species, and holds for a time at a point of high expression a character which averages much lower in the species at large.

MUTATIVE VARIATION OF SELECTED VARIETIES.

The only way in which the accentuation of such a narrowly selected character can be still further increased, beyond the range of normal variation of the species, is by abnormal variation; that is, by mutation. The narrow selection may be said to induce the mutations because it weakens and unbalances the hereditary tendencies of the variety, but the mutations are by no means limited to the character or quality for which the variety has been selected; they are likely to take any or all directions. Some of them are generally found to carry the breeder along the lines he desires to follow.

Are hybrids between selected varieties of the same plant or animal of no practical breeding utility? Yes, if it is desired to preserve or strengthen the vitality of the organism or to secure intermediate characters, or new combinations of characters already existing.

The general answer must be negative, if the purpose is to obtain new characters, or higher degrees for accentuation of characters already specialized by selection. Instead of securing a larger range of diversity, the contrary results are much more likely to be reached. It may even happen, if the varieties have been subjected to narrow selection, that the hybrid offspring, instead of being more variable than their parents, will actually be more uniform, the hybridization bringing them back, as it were, to the hereditary road from which they were beginning to wander towards mutative degeneration.

The mutations are as abnormal, of course, in the strictly evolutionary sense, as the narrow descent which induces them, but for agricultural purposes they may be very valuable, and often the abrupt change of form seems to lend them a remarkable vegetative vigor which greatly increases their productive capacity. This is notably the case among plants, and especially among those cultivated for their vegetative parts instead of for their seeds.[1]

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[1] Cook, O. F., 1904. The Vegetative Vigor of Hybrids and Mutations. Proc. Biological Society of Washington, 17: 83.

The facility with which many plants can be propagated from cuttings or by grafting often permits sterile mutations and crosses to be preserved and utilized for long periods of time. Among animals, on the other hand, mutations are of relatively small value. The higher organization of animals renders them liable to earlier and more serious deterioration from inbreeding, though there is great difference in the susceptibility of different kinds of animals.

BEHAVIOR OF DISCRIMINATE MUTATIONS.

When mutations are crossed with other members of their own immediate group of related individuals they are generally prepotent. They do not tend to average away and disappear, but are repeated, or even accentuated, in a considerable proportion of each successive generation, and sometimes in all of them. Plant mutations which can be propagated by self-fertilization are often constant from the first, and have been thought by some to represent the formation of genuine new species.

When mutations are bred outside of their own group, and especially when they are crossed with the wild type of the species or with the variety which has not been long or closely selected, they are not prepotent, but recessive. The new mutative characters appear weaker than the others and may fade out and disappear entirely. The same result may be reached by indiscriminate interbreeding among the representative of two or more mutations or selective varieties. The ancestral characters of the wild type of the species reassert themselves, and may even reappear in crosses between varieties from which they have long been lost.

All these and other similar phenomena can be understood, or at least brought into rational relations, if we keep in mind the fact that crosses between the narrowly selected varieties or mutations of the same species tend to restore the original and normal conditions of free interbreeding. They tend, in other words, to repair and reconstruct the normal fabric of symbasic descent, and to reduce the strains and deteriorations caused by too close segregation, too little diversity, and too much inbreeding.

Instead of being monstrous or unnatural, these crosses are more normal, more vigorous, and more fertile, than their parents. Why, then, are they called hybrids? Because we have been led astray by the theory of normally uniform and stationary species, in which it was made to appear that anything which interfered with identity of form and structure was essentially unnatural, like a cross between members of species which do not normally breed together, and which produce, when so bred, abnormal progeny. There are many groups in nature which are reckoned as species, but which are no farther apart than some of the varieties of cultivated plants, and which can breed together without difficulty or abnormality. For systematic purposes it is desirable to recognize each separate natural group of organisms as a species, and this can also be justified from evolutionary standpoints, for segregated groups are able to make evolutionary progress on distinct lines, and eventually to become different from other groups of common origin.

It often happens, however, that evolutionary progress is not consistent in the vegetative and reproductive parts of the organisms. Species which appear very distinct externally may, when brought together, breed freely and normally, while others whose bodily differences are difficult to detect may refuse to mingle or may produce only sterile or otherwise abnormal hybrids. While it is thus difficult or, it may be, impossible, to draw an absolute line of definition, or to restore the old distinction between hybrids and crosses, this does not justify us in ignoring the very wide and very practical differences between the extreme conditions of this series of phenomena.

ANALOGIES OF HYBRIDS AND MUTATIONS.

The phenomena which have the nearest and most genuine relations with hybrids are not crosses, but mutations. Hybrids and mutations can both be described in the same words, as aberrations from normal heredity. Both are due to the same cause, inadequate fertilization, which unbalances the organic equilibrium and gives rise to abrupt variation, usually in many directions at once. Mutations and hybrids show also a general deficiency of fertility. This is carried, very often, to the extreme of complete sterility, though there may be present at the same time unusual vegetative vigor, analogous, in all probability, to the stimulation of energy of growth which appears in normal crosses and in prepotent new variations. Though no experiments are known to have been made with the idea of such a test directly in mind, the indications are that results of mutation and hybridization might prove in the same species almost identical, for many so-called false hybrids do not appear to be the results of a genuine and effective interbreeding, but seem rather to involve an approach to the phenomenon of artificial parthenogenesis, somewhat similar to the parthenogenetic development through chemical and mechanical stimuli, described by Loeb and others. The two nuclei of the supposed parents of the false hybrid do not appear to have united and combined the parental qualities, since the progeny shows no definite indication of the traits of one of the supposed parents, either in the first or in subsequent generations. The facts discovered by Guyer in sterile hybrid pigeons, that the parental chromatin elements remain separate and do not undergo a normal mitapsis, illustrates the possibility of false hybrids, especially in plants and in lower types of animals where parthenogenesis can take place. Such an abnormal and inadequate method of fertilization would explain extensive variations of the progeny, which well deserve to be called false hybrids. Nor is it unlikely that the same explanation may be found to apply to variable hybrids, even when they share the characters of the parents. The indications are that in different cases there are all possible gradations in the extent and efficiency of the combination of the parental elements, from that which affords mere stimulation to that which gives a fully intermediate result.

It does not follow, however, that the combination is normal or complete when the first generation is intermediate. The first generation may be intermediate under two nearly opposite conditions, as already noted. Crosses are intermediate when the parental elements are thoroughly congruous. Their combination merely restores a normal condition of symbasis, that is, provides a normal amount of diversity of descent. The first generation of hybrids is also intermediate when the parental elements are very diverse and antagonistic. Hybrids which appear quite uniformly intermediate in the first generation may prove, nevertheless, to be completely sterile, as in the mule, whereas intermediate crosses between narrow varieties are always completely fertile, more so, it may be, than their more inbred parents. No distinction is to be drawn between crosses and hybrids which are uniformly intermediate and at the same time fertile, but there is a wide range of phenomena between an intermediate, fertile cross between narrow varieties and an intermediate sterile hybrid between diverse species. Next to the hybrids which are intermediate, but sterile, are those which are intermediate and fertile, but show diversity and partial sterility in the second generation, proving that the parental elements did not combine in a manner to afford a stable equilibrium of heredity. In another stage of hybridity, with less diversity of parents, the first generation is variable, which may be taken to mean that the parental elements are sufficiently similar to influence each other, instead of exerting a uniform degree of repulsion. Nevertheless, they do not combine readily, but form uncertain and extremely varied combinations.

The purpose of this enumeration is to show that with hybrids, as with crosses, there is a series of phenomena which can be described and interpreted in terms of diversity, using as a standard the normal diversity of the individuals of species in nature. In this way it is possible to avoid the ambiguities which have attended the use of the false and artificial standard of uniformity. From normal diversity there may be departures on either side, on the one to abnormal uniformity, on the other to abnormal diversity, and both of these can be reached, as we have seen, in several ways. Uniformity appears:

1. In closely selected varieties (stens).
2. In varieties or individuals propagated from cuttings or by other asexual methods (clones).
3. In the progeny of inbred saltatory variations (mutations).
4. In crosses between moderately inbred stenic varieties.
5. In first generation hybrids between species so remote as to combine with difficulty.

Likewise diversity greater than the normal may appear:

1. Among mutations from narrowly inbred varieties.

2. Among crosses between individual clonic types, long subjected to vegetative propagation.

3. In a species or variety which has been placed in new and unwonted conditions (neotopic mutations).

4. Among crosses between narrowly inbred varieties (Mendelian hybrids).

5. Among hybrids between species not too remote to combine at all, but not sufficiently related to combine in a regular and uniform manner.

THE NATURE OF STERILE HYBRIDS.

A further distinction of fundamental significance remains to be added to the preceding, before the full range of the phenomena of interbreeding can be made apparent. The general impression has been that the development of a new individual represented the result of a combination of the two parental sex-cells, but this is only partially true, especially among the higher plants and animals. The fusion of the parental sex-cells is carried through only two of the three stages of conjugation. Fertilization unites the outer, unspecialized protoplasms (plasmapsis) and also the nuclei (karyapsis), but the chromatin, the most highly specialized cell-substance, the citadel, as it were, of the life of the cells, remains distinct until after the new individual has developed, so that the body is not composed of simple, post-conjugational cells, but of double cells in a condition of prolonged conjugation.

The fusion of the chromatin granules, or ultimate sex-elements (mitapsis), may not take place until the new individual is mature and about to form new sex-cells of its own. The other cells of the body never reach mitapsis. The sterility of hybrids arises, it is now believed, from the inability of the sex-elements to pass this third and final stage of conjugation. It was always mysterious that hybrid combinations which could be made for one generation could not continue for a second or a third generation. This new appreciation of the nature of the process of conjugation makes it apparent, however, that hybrids are sterile because the parental elements do not make even one complete conjugation. There is thus a definite difference between a sterile hybrid and a fertile combination, one which might have restricted the use of the term hybrid to the former. Sterile hybrids, like false hybrids, are scarcely to be reckoned as forms of conjugation. They are rather to be looked upon as more nearly allied to parthenogenesis, a development through stimulation merely, but without the possibility of forming new relations of heredity or of making new combinations of characters. Sometimes there is not even enough coöperation between the mismated partners of the cell-units to carry the organism through even the normal cycle of individual existence. Hybrids often refuse to grow up, or they may die suddenly and without apparent external cause.

The building up of each cellular organism involves a continued coöperation between the parental sex-elements, which may be thought of as persisting in all the cells of which the body is composed. Whenever this coöperation breaks down, or proves inadequate, the further development of the conjugate organism becomes impossible.

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PROCEEDINGS

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AGE OF THE PRE-VOLCANIC AURIFEROUS GRAVELS IN CALIFORNIA.

BY J. S. DILLER.

GENERAL STATEMENT.

The age of the auriferous gravels of the Sierra Nevada in California is generally given as late Miocene or Pliocene and is based chiefly on fossil plants and a few animal forms. The auriferous gravel period in all probability was a long one and no considerable part of its flora has yet been connected directly with its contemporaneous marine fauna of the same region.

On physiographic and stratigraphic grounds and the general relations of the Sierra Nevada to sedimentation, it has long been supposed by some geologists that the oldest auriferous gravels, the deep gravels of Lindgren, are probably Eocene, but the evidence assigned is problematic rather then positive.

EOCENE FLORA OF SOUTHWEST OREGON

While studying the Eocene deposits of the Roseburg, Coos Bay, and Riddles quadrangles in Oregon, fossil leaves were found in the same strata with marine shells, thus affording an opportunity definitely to connect the land flora with its contemporaneous marine fauna.

The following list of ten species embraces the Eocene plants identified by Dr. F. H. Knowlton with more or less certainty from a number of localities within the area noted above:

Magnolia lanceolata Lesq.
Magnolia californica ? Lesq.
Laurus californica ? Lesq.
Sabalites californicus ? Lesq.
Aralia whitneyi Lesq.

Populus zaddachi Heer.
Aralia angustiloba ? Lesq.
Juglans californica ? Lesq.
Ulmus californica Lesq.
Ficus tiliæfolia ? Al Branner.

Among the shells found with or very near the fossil leaves, Dr. Wm. H. Dall has recognized over 20 genera, and remarks: "The fossils are Eocene. They contain a number of interesting things, particularly the Orbitolites, which is usually characteristic of the Oligocene on the Atlantic coast and is now for the first time recognized from the Pacific coast."

The fossil leaves were found near the southeast border of the Eocene where shells are not abundant, but a short distance farther northeast they become very abundant locally with such characteristic forms as *Venericardia planicosta* and *Turritella uvasana*, and there is no doubt concerning the Eocene age of the strata containing the fossil leaves.

Of the 10 species of plants identified seven are somewhat in doubt, but three, *Magnolia lanceolata*, *Aralia whitneyi*, and *Populus zaddachi*, are completely satisfactory. They all occur in the auriferous gravels of Independence Hill, on the western slope of the Sierra Nevada, as well as on the summit of the northern end of the range, 7½ miles southwest of Susanville. The last species occurs at many other localities among which may be mentioned the Ione formation of Kosk Creek and Little Cow Creek of Shasta County, Cal., and the auriferous gravels of Moonlight, Chalk Bluff, and Volcanic Hill.

Eight of the 10 species reported from the Eocene of Oregon, occur, according to Mr. Lindgren, in the "bench gravels" of Independence Hill, in California. It seems probable therefore that not only the "deep gravels" but also the "bench gravels," both of which belong to the pre-volcanic gravels, may be of Eocene age.

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AERIAL LOCOMOTION.

WITH A FEW NOTES OF PROGRESS IN THE CONSTRUCTION OF AN AERODROME.[1]

BY ALEXANDER GRAHAM BELL.

THE history of aerial locomotion is full of tragedies; and this is specially true where flying machines are concerned. Men have gone up in balloons and most of them have come down safely. Men have launched themselves into the air on wings, and most have met with disaster to life or limb. There have been centuries of effort to produce a machine that should fly like a bird, and carry a man whithersoever he willed through the air; and previously to 1783, the year sacred to the memory of the brothers Montgolfier, all experiments at aerial locomotion had this end exclusively in view.

Then came a period when the conquest of the air was sought through the agency of balloons. For more than one hundred years the efforts of experimenters were chiefly directed to the problem of rendering the balloon dirigible; and the earlier experiments with gliding machines, and artificial wings — and the projects of men to drive heavy bodies through the air by means of propellers, were largerly forgotten. The balloon was changed from its original spherical form to a shape better adapted for propulsion; and at last through the efforts of Santos Dumont we have arrived at the dirigible balloon of to-day. But in spite of the dirigibility of the modern balloon, it has so

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[1] An address presented before the Washington Academy of Sciences, December 13, 1906.

far been found impracticable to impart to this frail structure a velocity sufficient to enable it to make headway against anything but the mildest sort of wind. The character of the balloon problem has therefore changed. Velocity of propulsion rather than dirigibility is now the chief object of research.[1]

It has long been recognized by a growing school of thinkers, that an aerial vehicle, in order to cope with the wind, should be specifically heavier than the air through which it moves. This position is supported by the fact that all of Nature's flying models, from the smallest insect to the largest bird, are specifically heavier than the air in which they fly, most of them many hundreds of times heavier, and that none of them adopts the balloon principle in flight. It is also significant in this connection that some of Santos Dumont's most celebrated exploits were accomplished with quite a small balloon so ballasted as to sink in the air instead of rise. He was then enabled, under the influence of his motive power, to steer his balloon upwards without the expenditure of ballast, and to descend without the loss of gas. This probably typifies — for the balloon — the direction of change in the future. A reduction in the volume of gas, coincidently with an increase in motive power, will lead to greater velocity of propulsion — now the main desideratum. Then, dependence upon velocity for support rather than gas, may gradually lead to the elimination of the gas-bag altogether: in which case the balloon will give birth to a flying machine of the heavier-than-air type.

However this may be it is certainly the case that the tendency of aerial research is to-day reverting more and more to the old lines of investigation that were pursued for hundreds of years before the invention of the balloon diverted attention from the subject. The old devices have been reinvented. The old experiments have been tried once more. Again the birds are recognized as the true models of flight; and again men have put on wings — but this time with more promise of success.

Lilienthal boldly launched himself into the air in an apparatus of his own construction having wings like a bird and a tail for a rudder. Without any motor he ran down hill against the wind.

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[1] Some of the latest forms of dirigible balloon are shown in Plates XIX and XX.

Then, upon jumping into the air, he found himself supported by his apparatus, and glided down hill at an elevation of a few feet from the ground, landing safely at a considerable distance from his point of departure. This exhibition of gliding flight fairly startled the world, and henceforth the experiments of Lilienthal were conducted in the public eye. He made hundreds of successful flights with his gliding machine, varying its construction from time to time, and communicating to the world the results of his experiments with practical directions how to manage the machine under circumstances of difficulty. So that, when at last he met with the usual fate of his predecessors in this line, the experiments were not abandoned. They were continued in America by Chanute of Chicago, Herring, and other Americans, including the Wright brothers of Dayton, Ohio. (See Plate IX.)

Hargrave, of Australia, attacked the flying machine problem from the standpoint of a kite, communicating his results to the Royal Society of New South Wales. It is to him we owe the modern form of kite known as the "Hargrave Box Kite," which surpasses in stability all previous forms of kites. He also constructed successful flying machine models on a small scale using a store of compressed air as his motive power. He did not attempt to construct a large sized apparatus, or to go up into the air himself — so he still lives, to carry on researches that are of interest and value to the world.

No one has contributed more to the modern revival of interest in flying machines of the heavier-than-air type than our own Professor Langley, the late Secretary of the Smithsonian Institution. The constant failures and disasters of the past had brought into disrepute the whole subject of aerial flight by man; and the would-be inventor, or experimenter, had to face — not only the natural difficulties of his subject, but the ridicule of a sceptical world. To Professor Langley is due the chief credit of placing this subject upon a scientific basis, and of practically originating what he termed the art of "Aerodromics." In his epoch-making work on "Experiments in Aerodynamics," published in 1891 among the Smithsonian Contributions to Knowledge, he prepared the world for the recent advances in this art by announcing that: "The mechanical sustention of heavy bodies in the air, combined with very great speeds, is not only possible, but within reach of mechanical means we actually possess."

He also attempted to reduce his principles to practice, by the construction of a large model of an aerodrome driven through the air by a steam engine under the action of its own propellers. I was myself a witness of the memorable experiments made by Professor Langley on the 6th of May, 1896, with this large sized model, which had a spread of wing of about 14 feet. No one who witnessed the extraordinary spectacle of a steam engine flying with wings in the air, like a great soaring bird, could doubt for one moment the practicability of mechanical flight. I was fortunate in securing a photograph of this machine in full flight in the air, so that an automatic record of the achievement exists. (See Plate X). The experiment realized the utmost hopes and wishes of Professor Langley at that time: "I have brought to a close," he says, "the portion of the work which seemed to be specially mine — the demonstration of the practicability of mechanical flight; and for the next stage, which is the commercial and practical development of the idea, it is probable that the world may look to others. The world, indeed, will be supine if it does not realize that a new possibility has come to it, and that the great universal highway over-head is now soon to be opened."

But the world was not satisfied with this position. It looked to Professor Langley himself to carry on the experiments to the point of actually transporting a human being through the air on an aerodrome like his model; and so, with the aid of an appropriation from the War Department of the United States, Professor Langley actually constructed a full sized aerodrome, and found a man brave enough to risk his life in the apparatus — Mr. Manly, of Washington, D. C.

Great public interest was aroused; but Professor Langley did not feel justified in giving information to the public, and therefore to foreign nations, concerning experiments undertaken in the interests of the War Department. His own dislike to premature publicity coöperated with his conscientious scruples, to lead him to deny the newspapers the opportunity of witnessing the experiments. But the newspapers insisted upon being represented. The correspondents flocked to the scene, and camped there for weeks at considerable expense to their papers. They watched the house-boat containing the aerodrome by day and by night; and, upon the least indication of activity within, newspaper reporters were on hand in boats. After long delay in hopes of securing privacy it was at last decided to try the apparatus; but the newspaper representatives, embittered by the attempts to exclude them, were bringing the experiments into public contempt. They nicknamed the apparatus "The Buzzard," and were all ready to presage defeat.

Two experiments were made; but on both occasions the apparatus caught in the launching ways, and was precipitated into the water without having a chance to show what it could do in the air. The newspapers immediately announced to the world the failure of Professor Langley's machine, and ridiculed his efforts. The fact of the matter is, that the machine was never tried; and that there was no more reason for declaring it a failure than for deciding that a ship would not float that has never been launched. After having witnessed the successful flight of the large sized model of 1896, I have no doubt that Professor Langley's full sized aerodrome would have flown had it been safely launched into the air. (See Plate XI.)

When the machine was for the second time precipitated into the water it was not much damaged by the accident. Professor Langley, of course, was more anxious about the fate of his intrepid assistant than of his machine, and followed Mr. Manly into the house-boat to ascertain his condition. During this temporary withdrawal from the scene of the catastrophe, the crew of a tug-boat grappled the frail framework of the submerged aerodrome; and in the absence of any one competent to direct their efforts, they broke the machine to pieces, thus ending the possibility of further experiments without the expenditure of much capital. The ridicule of the newspapers however effectually prevented Professor Langley from securing further financial aid; and, indeed, broke his heart. There can be little doubt that the unjust treatment to which he was exposed contributed materially to the production of the illness that caused his death.

He lived long enough however to know of the complete fruition of his hopes by others; and, only two days before his death, he had the gratification of receiving a communication from the newly formed Aero Club of America, recognizing and appreciating his efforts to promote mechanical flight. This communication read as follows:

RESOLUTIONS OF THE AERO CLUB OF AMERICA, ADOPTED JANUARY 20, 1906.

"WHEREAS, Our esteemed colleague, Dr. S. P. Langley, Secretary of the Smithsonian Institution, met with an accident in launching his aerodrome, thereby missing a decisive test of the capabilities of this man-carrying machine, built after his models which flew successfully many times; and

"WHEREAS, In that difficult experiment, he was entitled to fair judgment and distinguished consideration because of his important achievements in investigating the laws of dynamic flight, and in the construction of a variety of successful flying models: Therefore be it

"*Resolved*, That the Aero Club of America, holding in high estimation the contributions of Dr. Langley to the science of Aerial Locomotion, hereby expresses to him its sincerest appreciation of his labors as a pioneer in this important and complex science; and

"*Be it further resolved*, That a copy of these resolutions be sent to the Board of Regents of the Smithsonian Institution, and to Dr. Langley."

Professor Langley was on his death bed when these resolutions were brought to his attention, and when asked what should be done with the communication his pathetic answer was "Publish it." To all who knew his extreme aversion to publicity in any form this reply indicates how keenly he felt the misrepresentation of the press.

Both in the case of Lilienthal and Langley their efforts have not been in vain. Others have continued their researches; and today the world is in possession of the first practical flying-machine — the creation of the brothers Orville and Wilbur Wright, of Dayton, Ohio. Indeed we have news from France that a second has just appeared constructed by the same Santos Dumont to whom the world already owes the first practical dirigible balloon.

The Wright brothers began by repeating the gliding experiments of Lilienthal with improved apparatus of the Hargrave type as modified by Chanute. (See Plate XII.) After having made many successful glides through the air without a motor, they followed in the footsteps of Langley and propelled their machine by means of twin screws operated by engine power. They were successful in launching their apparatus into the air, and it flew, carrying one of them with it. Their machine has flown not once simply, but many times, and in the presence of witnesses; so that there can be no doubt that the first successful flying-machine has at last appeared. Specially successful flights were made on the third and fourth of October 1905, which were referred to by the Wright brothers in a letter to the Editor of *L'Aerophile* published in that journal, January, 1906. They have also made a communication upon the subject to the Aero Club of America; and have received the formal congratulations of that organization upon their success.

Each of the Wright brothers, in turn, has made numerous flights over their testing field near Dayton, Ohio, sometimes at an elevation of about 80 feet, at other times skimming over the field at a height of about ten feet from the ground. They have been able to circle over the field of operation, and even to describe in the air the figure eight, thus demonstrating their perfect control over their apparatus both in the vertical and horizontal directions. They have succeeded in remaining continuously in the air for more than half an hour — thirty-eight minutes in fact — and only came down on account of the exhaustion of their fuel supply. They state that the velocity attained was one kilometer per minute, or about 37 miles an hour. The machine has not only sustained its own weight in the air during these trials, but has also carried a man, and a gasoline engine weighing 240 lbs., exerting a force of from 12 to 15 horse power, and in addition an extra load of 50 lbs. of pig-iron. The apparatus complete with motor weighed no less than 925 lbs. while the supporting surfaces consisted of two superposed aeroplanes each measuring six by 40 feet; so that the machine as a whole had a flying-weight of nearly two lbs. per square foot (1.9 lbs.).

Thanks to the efforts of the Wright brothers the practicability of aerial flight by man is no longer problematical. We can no longer consider as impossible that which has already been accomplished. America may well feel proud of the fact that the problem has been first solved by citizens of the United States.

A FEW NOTES OF PROGRESS IN THE CONSTRUCTION OF AN AERODROME.

For many years past, in fact from my boyhood, the subject of aerial flight has had a great fascination for me. Before the year 1896 I had made many thousands of still unpublished experiments having a bearing upon the subject; and I was therefore much interested in the researches of Professor Langley relating to aerodynamics. We were thrown closely together in Washington and although we rarely conversed upon aerodynamics we knew that we had a subject of mutual interest and showed the greatest personal confidence in one another. I did not hesitate to show him my experiments, he did not hesitate to show me his. At least as early as 1894, Professor Langley visited me in my Nova Scotia home and witnessed some of my experiments; and in May, 1896, he reciprocated by inviting me to accompany him to Quantico, Virginia, and witness a trial of his large sized model. The sight of Langley's steam aerodrome circling in the sky convinced me that the age of the flying machine was at hand. Encouraged and stimulated by this remarkable exhibition of success, I quietly continued my experiments in my Nova Scotia laboratory in the hope that I too might be able to contribute something of value to the world's knowledge of this important subject.

Warned by the experience of others, I have sought for a safe method of approach — a method that should risk human life as little as possible during the earlier stages of experiment. Experiments with aerodromes must necessarily be fraught with danger, until man, by practical experience of the conditions to be met with in the air, and of the means of overcoming them, shall have attained skill in the control of aerial apparatus. A man cannot even ride a bicycle without practice; and the birds themselves have to learn to fly. Man, not having any inherited instincts to help him in this matter, must first control his flight consciously, guided by knowledge gained through experiment. Skill can only be obtained by actual experience in the air; and this experience will involve accidents and disasters of various sorts before skill can be obtained. If these disasters should, as so often in the past, prove fatal to the experimenter, the knowledge obtained by the would-be aviator will be lost to the world, and others must begin all over again, instead of pursuing the subject where he left off, with the benefit of his knowledge and his experience. It is therefore of the utmost consequence to progress in the art of aviation, that the first attempts to gain experience in the air should be made under such conditions of safety as to reduce to a minimum the liability to fatal results.

The Wright brothers' successful flying machine travels at the rate of about thirty-seven miles an hour; and, judging from its great flying weight (nearly two pounds per square foot of supporting surface), it is unlikely that it could be maintained in the air if it had very much less velocity. But should an accident happen to a body propelled through the air with the velocity of a railroad train, how about the safety of the occupants? Accidents will happen, sooner or later, and the chances are largely in favor of the first accident being the last experiment. While therefore we may look forward with confidence to the ultimate possession of flying machines exceeding in speed the fastest railroad trains, it might be the part of wisdom to begin our first experiments at gaining experience in the air, with machines travelling at such moderate velocities as to reduce the chances of a fatal catastrophe to a minimum. This means that they should be light-flying machines; that is, the ratio of weight to supporting surface should be small.

While theory indicates that the greater the weight in proportion to supporting surface consistent with flight, the more independent of the wind will the machine be, yet it might be advisable to begin, if possible, with such a moderate flying-weight as to permit of the machine being flown as a kite. There would be little difficulty then in raising it into the air; and, should an accident happen to the propelling machinery, the apparatus would descend gently to the ground; or the aviator could cast anchor, and his machine would continue flying — as a kite — if the wind should prove sufficient for its support. If it could fly, as a kite, in a ten-mile breeze, then a velocity of only ten miles an hour would be sufficient for its support as a flying maching in calm air, while a less speed would suffice in heading into a moderate wind.

Such velocities would be consistent with safety in experiments, especially if the flights should be made over water instead of land, and at moderate elevations above the surface. Under such circumstances the inevitable accidents which are sure to happen during first experiments are hardly likely to be followed by more serious consequences than a ducking to the man, and the immersion of the machine. If the man is able to swim, and the machine to float upon water, little damage need be anticipated to either.

There are two critical points in every aerial flight — its beginning and its end. A flying machine adapted to float upon water not only seems to afford a safe means of landing, but also promises a solution of that most difficult of problems — a safe method of launching the apparatus into the air. If the supporting floats are so formed as to permit of the machine being propelled over the surface of the water like a motor boat, then, if sufficient headway can be gained under the action of her aerial propellers, the machine can be steered upwards into the air, rising from the water, after the manner of a water bird, in the face of the wind. This seems to be the safest method of gaining access to the air; but, of course, its practicability depends upon possibilities of lightness and speed yet to be demonstrated.

In any event, if the machine, man and all, is light enough to be flown as a kite, it can be towed out of the water into the air through the agency of a motor boat; and, upon land, it would not even be necessary for it to gain headway before rising, for, in a supporting wind, it would rise of itself into the air, if relieved of the weight of the man, and fly as a kite. It would then be a comparatively simple matter to lower the kite to a convenient height from the ground, and to hold it steadily in position by subsidiary lines, while the aviator ascends a rope ladder to his seat in the machine. In this way the man would not be exposed to danger during the critical operation of launching the apparatus into the air; and, by a converse process, a safe landing could be effected without bringing the machine to the ground. The chance of injury to the machine itself would also be much lessened by relieving it of the weight of the man during the initial process of launching, and the final process of bringing the machine down to the ground.

Such speculations as these of course are only justifiable upon the assumption that it is possible to construct an aerial vehicle large enough and strong enough to support a man and an engine in the air, and yet light enough to be flown as a kite in a moderate breeze with the man and engine and all on board. My experiments in Nova Scotia have demonstrated that this can be done; and I now therefore find myself seriously engaged in the attempt to reduce these ideas to practice by the actual construction of an aerodrome of the kite variety. The progress of experiment may be divided into three well marked stages — the kite stage, the motor boat stage, and the free flying-machine rising from the water.

THE KITE STAGE.

In April, 1899, I made my first communication on the subject of kites to the National Academy of Sciences in a paper entitled, "Kites with Radial Wings," which was reviewed, with illustrations, in the Monthly Weather Review for April, 1899 (Vol. XXVI, pp. 154–155, Plate XI). I made another communication to the National Academy on the 23rd of April, 1903, upon "The Tetrahedral Principle in Kite Structure," which was published, with 91 illustrations and an appendix, in the National Geographic Magazine for June, 1903 (Vol. XIV, pp. 220–251). The substance of the present address was presented, in part, to the National Academy of Sciences at their recent meeting in Boston, Mass., November 21, 1906. The experiments referred to, which were undertaken at first for my own pleasure and amusement, have gradually assumed a serious character from their bearing upon the flying-machine problem.

The word "kite" unfortunately is suggestive to most minds of a toy — just as the telephone at first was thought to be a toy — so that the word does not at all adequately express the nature of the enormous flying structures employed in some of my experiments. (See Plates XVI, XVII, XVIII.) These structures were really aerial vehicles rather than kites, for they were capable of lifting men and heavy weights into the air. They were flown after the manner of kites, but their flying cords were stout manilla ropes. They could not be held by hand in a heavy breeze; but had to be anchored to the ground by several turns of the ropes around stout cleats like those employed on steamships and men-of-war.

One of the great difficulties in making a large structure light enough to be flown as a kite, has been pointed out by Professor Simon Newcomb in an article in McClure's Magazine published in September, 1901, entitled "Is the Air-Ship Coming?"; and this difficulty had so much weight with him at that time as to lead him to the general conclusion that — "The construction of an aerial vehicle which could carry even a single man from place to place at pleasure, requires the discovery of some new metal, or some new force."

This conclusion the Wright brothers, and now Santos Dumont, have demonstrated to be incorrect; but Professor Newcomb's objections undoubtedly have great force, and reveal the cause of failures of attempts to construct large-sized flying-machines upon the basis of smaller models that actually flew. Professor Newcomb shows that where two aerial vehicles are made exactly alike, only differing in the scale of their dimensions, the ratio of weight to supporting surface is greater in the larger one than in the smaller; the weight increasing as the cube of the dimensions, whereas the supporting surfaces only increase as the squares. From this the conclusion is obvious that if we make our structure large enough it will be too heavy to fly even by itself — far less be the means of supporting an additional load like a man, and an engine for motive power. This conclusion is undoubtedly correct in the case of structures that are "exactly alike, excepting in their dimensions," but it is not true as a general proposition.

A small bird could not sustain a heavy load in the air; and while it is true that a similar bird of double the dimensions would be able to carry a less proportionate weight because it is itself heavier in proportion to its wing surface than the smaller bird — eight times as heavy in fact, with only four times the wing surface — still it is conceivable that a flock of small birds could sustain a heavy load divided equally among them, and it is obvious that in this case the ratio of weight to wing surface would be the same for the whole flock as for the individual bird. If then we build our large structure by combining together a number of small structures each light enough to fly, instead of simply copying the small structure upon a larger scale, we arrive at a compound or cellular structure in which the ratio of weight to supporting surface is the same as that of the individual units of which it is composed, thus overcoming entirely the really valid objections of Professor Newcomb to the construction of large flying-machines.

In my paper upon the tetrahedral principle in kite structure, I have shown that a framework having the form of a tetrahedron possesses in a remarkable degree the properties of strength and lightness. This is especially the case when we adopt as our unit structure the form of the regular tetrahedron, in which the skeleton frame is composed of six rods of equal length as this form seems to give the maximum of strength with the minimum of material. When these tetrahedral frames or cells are connected together by their corners they compose a structure of remarkable rigidity, even when made of light and fragile material — the whole structure possessing the same properties of strength and lightness inherent in the individual cells themselves.

The unit tetrahedral cell yields the skeleton form of a solid, and it is bounded by four equal triangular faces. By covering two adjoining faces with silk or other material suitable for use in kites, we arrive at the unit "winged cell" of the compound kite; the two triangular surfaces, in their flying position, resembling a pair of wings raised with their points upward, the surfaces forming a dihedral angle. (*A*, Plate XIII.) Four of these unit cells, connected together at their corners, form a four-celled structure, having itself the form of a tetrahedron containing in the middle an empty space of octahedral form, equal in volume to the four tetrahedral cells themselves. (*B*, Plate XIII.) In my paper I showed that four of these four-celled structures connected at their corners resulted in a sixteen-celled structure of tetrahedral form, containing, in addition to the octahedral spaces between the unit cells, a large central space equivalent in volume to four of the four-celled structures. (*C*, Plate XIII.) In a similar manner four of the sixteen-celled structures connected together at their corners form a sixty-four-celled structure. (*D*, Plate XIII.) Four of the sixty-four-celled structures form a two hundred and fifty-six-celled structure, etc., etc., and in each of these cases an empty space exists in the center, equivalent to half of the cubical contents of the whole structure, in addition to spaces between the individual cells, and minor groups of cells.

Kites so formed, exhibit remarkable stability in the air under varying conditions of wind, and I stated in my paper that the kites which had the largest central spaces seemed to be the most stable in the air. Of course these were the structures that were composed of the largest number of unit cells; and I now have reason to believe that the automatic stability of these kites depends more upon the number of unit cells than upon the presence of large empty space in the kites; for I have found, upon filling in these empty spaces with unit cells, that the flying qualities of a large kite have been greatly improved. The structure, so modified, seems to fly in as light a breeze as before but with greatly increased lifting power; while the gain in structural strength is enormous.

I had hitherto supposed that if cells were placed directly behind one another, without providing large spaces between them, comparable to the space between the two cells of a Hargrave box kite, the front cells would shield the others from the action of the wind, and thus cause them to lose their efficiency; but no very marked effect of this kind has been observed in practice. Whatever theoretical interferences there may be, the detrimental effect upon the flying qualities of a kite are not, practically, obvious; while the gain in structural strength and in lifting power outweigh any disadvantages that may exist. I presume, that there must be some limit to the number of cells that can be placed in close proximity to one another without detrimental effect; but so far my experiments have not revealed it.

To test the matter, I put together into one structure all the available winged cells I had in the laboratory — 1300 in number. These were closely attached together without any other empty spaces in the structure than those existing between the individual cells themselves when in contact at their corners. The resulting kite, known as "The Frost King," consisted of successive layers, or strata of cells, closely superposed upon one another. (See Plate XIV.) The lowest layer, or floor of the structure, consisted of 12 rows of 13 cells each. The cells forming each row were placed side by side attached to one another by their upper corners; and the 12 rows were placed one behind the other, the rear corners of one row being attached to the front corners of the row immediately behind. The next stratum above the floor had 11 rows of 14 cells; the next, 10 rows of 15 cells; etc., — each successive layer increasing in lateral dimensions and diminishing in the fore and aft direction; so that the top layer, or roof, consisted of a single row of 24 cells placed side by side. One would imagine that a closely packed mass of cells of this kind — 1300 in number — would have developed some difficulty in flying in a moderate breeze if the cells interfered with one another to any material extent: but this kite not only flew well in a breeze estimated at not more than about 10 miles an hour because it did not raise white-caps, but carried up a rope-ladder, several dangling ropes 10 and 12 meters long, and more than 200 meters of manilla rope used as flying lines, and in addition to all this, supported a man in the air. (See Plate XV.)

The whole kite, impedimenta and all, including the man, weighed about 131 kgs. (288 lbs.); and its greatest length from side to side was 6 meters at the top and three meters at the bottom. The sloping sides measured 3 meters and the length from fore to aft at the square bottom was 3 meters. It is obvious that this kite might be extended laterally at the top to twice its length without forming an immoderately large structure. It would then be 12 meters on the top (39 ft.) and 9 meters on the bottom from side to side, without changing the fore and aft dimensions, or the height. It would then contain more than double the number of cells and so should be able to sustain in the air more than double the load; so that such a structure would be quite capable of sustaintng both a man, and an engine of the weight of a man, and yet be able to fly as a kite in a breeze no stronger than that which supported the "Frost King."

An engine of the weight of a man could certainly impart to the structure a velocity of 10 miles an hour, the estimated velocity of the supporting wind, and thus convert the kite into a free flying-machine. The low speed at which I have been aiming — for safety's sake — is therefore practicable.

In the "Frost King" and other kites composed exclusively of tetrahedral winged cells, there are no horizontal surfaces (or rather surfaces substantially horizontal as in ordinary kites), but the framework is admirably adapted for the support of such surfaces. Horizontal aeroplanes have much greater lifting-power than similar surfaces obliquely arranged as in the tetrahedral construction, and I have made many experiments to combine horizontal surfaces with winged cells, with greatly improved results so far as lifting-power is concerned. But there is always an element of instability in a horizontal aeroplane, especially if it is of large size; whereas kites composed exclusively of winged cells are wonderfully steady in the air under varying conditions, though deficient in lifting-power; and the kites composed of the largest number of winged cells seem to be the most stable in the air.

In the case of an aeroplane of any kind the center of air-pressure rarely coincides with the geometrical center of surface, but is usually nearer the front edge than the middle. It is liable to shift its position, at the most unexpected times, on account of some change in the inclination of the surface or the direction of the wind. The change is usually small in steady winds; but in unsteady winds great and sudden changes often occur.

The extreme possible range of fluctuation is, of course, from the extreme front of the aeroplane to the rear, or *vice versa*, and the possible amount of change, therefore, depends upon the dimensions of the aeroplane — especially in the fore and aft direction. With a large aeroplane the center of pressure may suddenly change to such an extent as to endanger the equilibrium of the whole machine. Whereas, with smaller aeroplanes, especially those having slight extension in the fore and aft direction, the change, though proportionally as great, is small in absolute amount. Where we have a multitude of small surfaces well separated from one another, as in the tetrahedral construction, it is probable that the resultant center of pressure for the whole kite can shift to no greater extent than the centers of pressure of the individual surfaces themselves. It is, therefore extremely unlikely that the equilibrium of a large kite could be endangered by the shifting of the centers of pressure in small surfaces within the kite. This may be the cause of the automatic stability of large structures built of small tetrahedral cells. If so, one principle of stability would be: *Small surfaces — well separated — and many of them.* The converse proposition would then hold true if we desired to produce instability and a tendency to upset in a squall — namely: *Large surfaces — continuous — and few of them.*

Another source of danger with large continuous surfaces is the fact that a sudden squall may strike the kite on one side, lifting it up at that side and tending to upset it. But the compound tetrahedral structure is so porous, that a squall passes right through and lifts the other side as well as the side first struck; so that the kite has not time to be upset before the blow on one side is counterbalanced by a blow on the other. I have flown a Hargrave box kite simultaneously with a large kite of many tetrahedral cells in squally weather for the purpose of comparing them under similar conditions. The tetrahedral structure often seemed to shiver when struck by a sudden squall, whereas the box kite seemed to be liable to a swaying or tipping motion that would be exceedingly dangerous in a structure of large size forming part of a flying machine.

Another element of stability in the tetrahedral structure lies in the fact that the winged surfaces are elevated at a greater angle above the horizon than 45°.

Supposing the wings of a cell to be opened out until they are nearly flat — or at least until they each make a comparatively small angle with the horizon — say 20° — then if, from any cause, the cell should tip so as to elevate one wing (say to 25°) and depress the other (say to 15°) then the lifting-power of the wind will be increased upon the elevated wing and diminished on the depressed wing, so that there would be no tendency to a recovery of position, but the very reverse. The pressure of the wind would tend to increase the tipping action, and favor the production of oscillation and a tendency to upset. The lifting-power of the wind upon a surface inclined at 10° is less than at 20°; and greater at 25° than 20°. The more the wings are opened out, and the flatter they become, the more essentially unstable is the arrangement in the air.

Now suppose the wings to be raised until they are nearly closed, or at all events until they make a small angle with the vertical (say 70° from the horizontal), then if from any cause the cell should tip so as to elevate one wing (say to 75°) and depress the other (say to 65°), the lifting-power of the wind will be increased upon the depressed wing and diminished on the elevated wing; for the lifting-power of the wind is greater at 65° than at 70° and less at 75°. Thus the moment a tipping action begins the pressure of the wind resists it, and an active force is invoked tending to restore the structure to its normal position. The more the wings are raised, and the more they approach the perpendicular position the more stable essentially is the arrangement in the air.

The dividing line between these two opposite conditions seems to be drawn about the angle of 45°. As the tetrahedral wing-surfaces make a greater angle than this with the horizontal they constitute an essentially stable arrangement in the air; whereas a horizontal surface represents the extreme of the undesirable unstable condition.

These considerations have led me to prefer a structure composed of winged tetrahedral cells alone, without horizontal surfaces either large or small, although the lifting-power is less than when horizontal surfaces are employed, because the factor of safety is greater. One of the chief causes that have led to disasters in the past has been lack of stability in the air. Automatic stability under varying conditions is surely of the very first consequence to safety, for what would it profit a man were he to gain the whole world and lose his own equilibrium in the air? A kite composed exclusively of multitudinous winged-cells seems to possess this property of automatic stability in a very marked degree. If then its lifting-power is sufficient for our purpose there is no necessity for the introduction of a factor of danger by the addition of horizontal surfaces. Of course the addition of such surfaces would enable us to secure the desired lifting-power with a smaller and therefore lighter structure, and this would be of advantage if we could be sure of its stability in the air.

In employing tetrahedral winged-cells alone, upon the hollow plane of construction in which large empty spaces occurred within the kite, a practical difficulty was encountered arising from the enormous size of the structure required for the support of a man, combined with the increasing weakness of the structure as it increased in size. The discovery that the cells may be closely massed together without marked injurious effects has completely remedied this difficulty; for upon this plan, not only is the structural strength improved by an increase of size, but the lifting-power increases with the cube of the dimensions, so that a very slight increase in the dimensions of a large kite increases very greatly its lifting-power. We now have the possibility of building structures composed exclusively of tetrahedral winged-cells that will support a man and an engine in a breeze of moderate velocity, without the necessity of constructing a kite of immoderate size. The experiments with the "Frost King" made in December, 1905, satisfied me upon this point, and brought to a close my experiments with kites.

Conclusion.

Since December, 1905, my attention has been directed to other points necessary to be considered before an aerodrome of the kite variety can be made; and to the assembling of the materials for its manufacture.

I have had to improve and simplify the method of making the winged-cells themselves. Through the agency of Mr. Hector P. McNeil, Superintendent of the Volta Laboratory, Washington, D. C., who is now taking up the manufacture of tetrahedral cells as a new business, I am now able to obtain cells constructed largely by machinery, and with stamped-metal corners to hold the rods together. The process of tying the cells and parts of cells together had proved to be very laborious and expensive; and the process was not suited to unskilled persons. By the new process most of the work is done by machinery, and no skill is required to connect the cells together.

I have also had to go into the question of motor construction, a subject with which I am not familiar; and while waiting for the completion of the material required for the aerodrome I have been carrying on experiments to test the relative efficiency of various forms of aerial propellers. I have also been occupied with the details of construction of a supporting float adapted for propulsion over the water as a motor boat, and also adapted to form the body of the flying-machine when in the air.

Of course it would be premature for me to enter into any description of experiments that are still in progress, or to submit plans for an aerodrome which are still under discussion. I shall therefore simply say in conclusion that I have recently been making experiments in propelling, by means of aerial propellers, a life-raft supported, catamaran fashion, on two metallic cylinders. The whole arrangement, with a marine motor on board, is exceedingly heavy, weighing over 2,500 pounds; and it is sunk so low that the water level rises at least to the middle of the supporting cylinders, so that the raft is not at all adapted for propulsion, and cannot attain great speed. The great and unnecessary weight of this machine has led to an interesting and perhaps important discovery that might have escaped attention had the apparatus been lighter and better adapted for propulsion.

Under the action of her aerial propellers, this clumsy raft is unable to attain a higher speed than four miles an hour; and yet she is able to face a sixteen-mile white-cap breeze, and make headway against it, instead of drifting backwards with the wind. Under such circumstances her speed is materially reduced; but the point I would direct attention to is this, that she is not stopped by a current of air moving with very much greater velocity than her maximum possible speed in a calm. Of course there would be nothing remarkable about this if her propellers were acting in the water instead of the air, but they were not. They acted exclusively in the air, and the water was only an additional resistance to be overcome.

It is worthy of note in this connection that the rapid rotation of the propellers yield a theoretical efficiency of thirty or forty miles an hour, and that the mass of the machine and the resistance of the water drag this down to an actual performance of only four miles, so that at first sight it appears probable that the effect noted may be a result of the greater slip of the propellers acting in a calm. I am inclined to think however that this explanation is insufficient; and would suggest the following as more probable.

The enormous mass of the moving body enables it to acquire very considerable momentum with slight velocity; whereas, the opposing current of air has such slight mass, that it cannot acquire an equal momentum with a very much higher velocity.

If two bodies of unequal mass, moving with equal but opposite velocities, come into collision with one another, then the heavier body will not be completely stopped by the lighter. It will make headway against the resistance of the other even though the lighter should possess superior velocity, provided, of course, that it has a sufficient superiority of mass. We are here dealing with momentum (mv), not velocity (v) alone. The body having the greatest momentum will be the victor in the struggle whatever the actual velocities may be.

The suggestiveness of this result lies in its application to the flying machine problem. A balloon, on account of its slight specific gravity, must ever be at the mercy of the wind. In order to make any headway against a current of air it must itself acquire a velocity superior to the wind that opposes it. On the other hand it is probable that a flying machine of the heavier-than-air type, at whatever speed it moves, will be able to make headway against a wind of much greater velocity, provided its momentum is greater than the momentum of the air that opposes it.

DISCUSSION OF DR. BELL'S ADDRESS BY CHARLES M. MANLY.

It is a notable sign of the kind of attention aeronautical work is now attracting , that one who has to his credit the accomplishment of such big things as Dr. Bell has, should become so actively engaged in it. As Dr. Bell has already pointed out, the world owes much to Mr. Langley for taking hold of the subject when it was looked upon as the wild dream of cranks and enthusiasts and by putting it on a scientific basis made it seem worthy of serious attention. It is no less fortunate that we have to-day such men as Dr. Bell actively engaged in the construction of large man-carrying machines, for the influence of their example causes the work to be looked on by the public more and more seriously all the time.

Dr. Bell has pointed out that one of the advantages possessed by such a slow speed aerodrome as he will be able to construct by utilizing his important invention of tetrahedral cells, is the possibility of anchoring such a machine and having it maintained at a height through its ability to fly as a kite. This suggests the superiority which such a machine will possess not only as regards safety in case of a break-down of the machinery, but also as regards its use as a war machine. The ability to anchor and remain steadily over a given point will enable the operator or operators to thoroughly study and map out fortifications and the disposition of field forces, as there is very slight probability of so small an object as an anchor rope being discovered by the enemy, and even if it should be, the ability of the operator to cut the rope would render him comparatively free from capture.

As a war machine Dr. Bell's tetrahedral plan of cellular construction for the surfaces would also I think present another very great advantage. Such a machine might be badly riddled with shot and yet be able to maintain very good equilibrium, while a machine having large units of surface with large parts in the frame work of its surfaces, would be very seriously crippled should a chance shot disable one of the main supports on one side.

It may not be amiss to call attention also to the fact that the operator on any aerodrome or balloon when at a considerable height can plainly see submarine boats at any depth in the water. Such machines can therefore be used for determining the number of submarine craft in the enemy's force of harbor defenses, and by keeping the machine circling above a battleship or a fleet of ships, the possibility of attack by submarine boats would be very greatly lessened. In fact I should think that with Dr. Bell's multicellular machine there would be no great difficulty in maintaining the operator in the air for hours by simply flying the machine as a kite anchored to the ship.

I trust that Dr. Bell will pardon me for not agreeing with the explanation he suggested of the very interesting fact noted in regard to the propulsion of the "Catamaran Life Raft" by means of aerial propellers, namely that the raft advanced against a 16-mile breeze, although in a calm it was able to make only something like four miles an hour.

It seems to me that this ability of the raft to advance against a 16-mile wind is not due to the difference between the momentum of the raft and the momentum of the air, but to the fact that the raft presents very little resistance to the wind, while the propeller, being revolved at a high rate of speed by the engine, tends to advance in the air at a speed proportionate to its pitch multiplied by its number of revolutions in a given time; and I have no doubt that the raft would have advanced against any wind of a velocity less than that which would be created by the slip of the propeller revolving in still air at the same speed as when driving the raft. In other words, if the propeller had a pitch, let us suppose, of one foot (that is, tended to advance through the air one foot for each revolution, or forced the air backwards one foot for each revolution), such a propeller revolving at the rate of a thousand revolutions a minute would in a calm create a back wind of a thousand feet per minute, and of course a propeller of two feet pitch would create a back wind of two thousand feet per minute when revolving at the same speed. Such a propeller, then, of two feet pitch, revolving at this speed, when mounted on a raft should be able to prevent the raft being blown backwards in a wind of somewhere near two thousand feet per minute. I have no doubt that the back wind due to the propeller in Dr. Bell's experiment was of an even higher velocity than two thousand feet per minute.

Few of us can conceive of the affairs of the world being very different from what we are accustomed to. But there are certain definite effects which we can be fairly confident will follow definite changes. I am not a prophet nor the son of a prophet, but I feel safe in venturing a conservative prediction in regard to one of the effects of aerodromic work in the next few years. We may not be able to make it a general vehicle of transportation, as some enthusiasts predict; I myself, indeed, while unwilling to define the limits of the possible, certainly do not expect such results very soon. But I have no hesitation in asserting that the attainment of the ability to fly say three hundred miles, — a degree of success now practically certain to be attained within five years — will, at whatever risk of danger to the aeronaut, have as important an effect on warfare as the advent of wireless telegraphy, and a far greater one than the perfecting of the submarine boat or the Whitehead torpedo, both of which even now are causes of the greatest concern to the officers of even the last, and largest, and most expensive battleship.

It is interesting in this connection to learn, what I have just been told on good authority, that a prominent admiral of the navy who has just retired is planning to devote his time to a thorough study of aerodromics, foreseeing as he probably does the early advent of the flying war machine, which there seems ample ground for believing will prove to be the most important single step in the progress of the art of war.

I am pleased to hear Dr. Bell state publicly his confidence in the accuracy of the reports of the success of the Wright brothers, for I myself have had every confidence in them and have thoroughly appreciated the motives which have prompted them to withhold a public demonstration of their machine until business arrangements can be completed which will enable them to reap the financial profits which their success so richly deserves.

I trust that I shall be pardoned for emphasizing Dr. Bell's statement as to the importance of the fact that the Wright brothers have flown not only once but many times. The fact that a machine has flown successfully and carried a man not only a few hundred feet but something like twenty-five miles, will, when its significance is realized, have the greatest effect on the future progress of the work.

I have always wondered why it is that the more prominent polar explorers have been able to secure very large sums of money for use in their attempts to reach the north pole, yet no public benefactor has seemed ready to render substantial financial assistance in the solution of this problem of opening up for mankind the great aerial highway, which to me at any rate, seems of such vast importance to the world. The only reason I could assign for this has been, that while the existence of such a point as the pole is capable of mathematical demonstration, the possibility of a successful flying machine has seemed a subject not for science but for dreams.

It seems to me however, that the fact that success has already been achieved by the Wright brothers should put the whole problem on a very different footing and convince even the skeptical that the question of success is now merely a question of degree. As people of means who wish to perpetuate their name can do it in no better way than by assisting in a substantial manner in the progress of scientific investigation, they will surely now be ready to furnish the funds necessary to ensure more rapid progress in this work.

We must remember that in these days work of this kind progresses by leaps and bounds. It is barely seven years ago that the first annual automobile show was held in Madison Square Garden, New York. No attempt was made to utilize the galleries of the Garden and practically the entire area of the main floor was given over to a track which was used for demonstrating to the audience the fact that an automobile could be stopped in a very much shorter distance than a horse-drawn vehicle going at the same speed. The management in charge of this show, in order to fill up space, even provided seats which were arranged for the convenience of the visitors. Last winter, just six years after that date, instead of one show occupying only a small portion of the Garden, there were two shows of about equal size held simultaneously in New York, and the one which was held in the Garden not only filled it from cellar to roof, but the streets all around were filled with demonstrating machines, and instead of seats being provided, it was necessary to have policemen to see that the people followed the proper circuit of the building so that the crowd should be kept moving and all might have a chance to view the exhibition. As the outcome of industry which six years ago amounted to nothing, we have in the United States to-day something like ten million dollars invested in approximately 75 manufacturing establishments which, during the year which is just closing, have produced more than fifty thousand machines, and instead of the automobile being ridiculed by the cartoonist as a chimerical dream it has become the chariot of the millionaire and the freight truck of the industrial world, hauling goods and ore from the steamship piers and the mines.

Realizing that this enormous progress has been made in the short period of less than a decade, it is only a pessimist of the deepest dye who would dare predict that the next decade will not see not only enormous strides in the progress of aerodromics, but also the aerodrome itself an important factor in human affairs.

For thousands of years man was content to travel no faster than his ancestors, but the advent of the steam locomotive followed by that of the electric car has quickened the inventive genius of the world to its very core; and man, not content with being confined to travel at a high speed on a definite route marked by parallel steel rails, has quickly taken up the automobile which can follow not only the multitudinous roadways, but, if necessary, blaze out its own way through the fields and woods. Instead of having his ambition satisfied by this multiplication of his possible paths, he still thirsts for more freedom and will not be satisfied until he has opened up for himself access to the highways of the air, which are limitless in all directions and on which speed laws enforced through police traps, if not impossible, will at least be most difficult to maintain and enforce.

While for many years I have felt the deepest interest in aeronautical matters, it was only in 1898 that I first became actively engaged in the work. I had the pleasure and the honor of being associated for some seven years with the lamented Secretary Langley as his assistant in direct charge of the experiments which he conducted at the Smithsonian Institution. Dr. Bell has already referred to the fact that this later work which Mr. Langley conducted was carried on for the Board of Ordnance and Fortification of the War Department. As you are all no doubt aware, it is the custom of the War Department in conducting important tests to exclude not only the general public but also the representatives of the newspapers; and in undertaking this work for the War Department, Mr. Langley made a very definite agreement that the public should be excluded from witnessing the construction of the aerodrome and the tests of it, though in the interests of science he retained the privilege of later publishing whatever part of the work he might deem of importance to the scientific world. It could not be foreseen at that time that the carrying out in good faith of this agreement would bring upon him the bitter animosity of the whole corps of American newspaper writers who would vent their ill will in ridicule and in censure for failure to achieve complete success.

As those of you who followed the newspaper reports during the experiments in the summer and fall of 1903, will recall, the large houseboat, on which were stored both the large machine and a duplicate of it on a smaller scale, was carried down the Potomac River in July and anchored at a point about forty miles from Washington. The first experiments which were made were conducted with this model which was an exact duplicate of the larger machine but of exactly one quarter the linear dimensions. The object of the tests with this model was to determine whether the balancing of the large machine had been correctly calculated from the results of the many previous tests of the steam driven models of approximately the same size but embodying important differences in certain details. I will not burden you with an account of the long series of exasperating delays encountered, delays almost entirely brought about by the very unusual weather conditions which could not be foreseen and provided against; I will only say that the several newspaper representatives who went down the river early in July and remained stationed there for several months in a malarial district on the Virginia shore, and who had to row somewhat over a mile and a half in order to get within close range of the house-boat which was anchored in the middle of the river, were naturally not very favorably influenced either by the fogs and high winds or by their necessary exclusion from all real knowledge of the work going on within the house-boat.

I cannot emphasize too strongly that there was neither fault in design nor inherent weakness in any part of this large aerodrome. The whole machine had been subjected to the most severe tests and strains in the Institution shops in the endeavor to find any possible points of weakness and had shown itself able to withstand any strain it would meet in the air.

The experiments themselves convinced both Mr. Langley and myself that it would have been better to have conducted them over land rather than over water and we should thereby have avoided a great deal of expense and the major part of the delays and accidents which were encountered; yet it must be remembered that in work of this kind experiment is the only sure guide and that aftersight is always much clearer than foresight. It is my personal opinion that had the experiments been conducted over the land instead of over the water, not only would the funds which proved inadequate have been more than ample, but success would have been achieved as early as 1902 instead of what the public has judged to be failure in 1903.

Dr. Bell has told you that in the last experiment the aerodrome was broken to pieces through the ignorance and carelessness of the tugboat men in getting it out of the water. It was almost heart-breaking to look at the wreck that they made of it; but although Mr. Langley found himself without funds for making further experiments with the machine, yet at my earnest solicitation he allotted sufficient money to enable the frame to be repaired so that it is practically as good as new and stands to-day completely assembled with its engine and everything to enable it to fly except a new set of supporting surfaces.

It has been generally supposed that the work has been abandoned and this idea has been strengthened by Mr. Langley's death, but I think I can assure you that the work is not abandoned but merely temporarily suspended, for it is my purpose, at the earliest moment that I can possibly spare the time for it, to reëquip the aerodrome with proper supporting surfaces and using the same launching apparatus, to give the aerodrome a fair trial, this time over the land instead of over the water, when I feel very certain that it will fully demonstrate the correctness of its design and construction and crown Mr. Langley's researches with the success which they so richly deserve, and I trust that the day that this will be achieved is very near at hand. It was the launching apparatus, all will remember, which in both of the experiments caused the accidents that prevented any test of the aerodrome itself. These accidents were not due to defects in the design or fundamental construction of the launching apparatus, for the smaller apparatus of exactly the same design had been used more than thirty times for launching the smaller machines and without a single failure. Certain minute defects in the releasing mechanism were the sole cause of the trouble.

It has been very generally supposed that in his experiments Mr. Langley used exclusively what may be called "single tier" surfaces and that he did not recognize that the superposing of the lifting surfaces presented certain great advantages not only as regards ease of construction and strength, but also in reducing the size of the machine. This general impression is due to the fact that all of the photographs of the machines in flight which he published officially, and also those published by the newspapers, have shown the machine as equipped with "single tier" surfaces. I may say however that as early as 1890 and constantly from that time until the work was temporarily suspended in 1903, Mr. Langley experimented with superposed surfaces, the first experiments of course being with very small models having their motive power furnished by means of stretched or twisted rubber. The same large steam driven models which flew so successfully in 1896, the first flight of which Dr. Bell has just spoken of having witnessed, were in 1899 equipped with superposed surfaces and were tested in free flight during the months of July and August.

The quarter-size model of the large aerodrome driven by a gasolene engine which was first tested in 1901 and later in the summer of 1903, was also equipped with superposed surfaces, but in the test of August, 1903, which was witnessed by the newspaper representatives, the "single tier" surfaces were used. The prime reason that the large aerodrome was equipped with the "single tier" surfaces was that the best flights of the models were with such surfaces, and although in the beginning it was planned to build superposed surfaces for the large machine later, the early depletion of the funds provided by the Board of Ordnance and Fortification made it imperative to utilize what had already been constructed, as it was with the greatest reluctance that Mr. Langley continued the work with the funds of the Institution, and all expense which could be avoided was carefully guarded against. I have thought it well to mention this fact as I have had many inquiries as to why it was that Mr. Langley never realized that the superposed type of construction for the supporting surfaces presented important advantages.

It was my duty while connected with the Smithsonian Institution to prepare answers to the large number of letters on aeronautical subjects which were constantly received. While some of the writers sought advice, others offered it; and a large number of the letters indicated that the writers believed that the problem of constructing a successful machine required the discovery of some "secret." In view of this experience, I have thought that it might not be amiss to emphasize, that there is no "secret" which needs to be discovered in order to build a successful machine, but that success is to be achieved by laying out a good design based on a proper knowledge of the laws of aerodromics as at present known, next by giving the greatest care to constructing the parts as strong as possible for the permissible weight, and then trying the machine, not once only, but again and again under conditions presenting the least possible danger to the operator.

In this connection attention may be called to the fact that when a machine is planned and the weight of the different parts is allotted, so that the total weight shall not exceed a certain proportion relative to the supporting area, the experimenter need not be surprised to find, when he has completed his machine that it weighs forty or fifty per cent. more than he has calculated; for in carrying out the innumerable details of construction small increases in weight at almost every point finally increase the total weight surprisingly.

In all of the accounts which I have lately seen of the experiments of the Wright brothers, no mention has been made of the fact that the success of the Wrights has been built on the very valuable work of Mr. Chanute, who for many years carried on at his own expense work in the construction and testing of gliding machines, and who I understand, not only furnished the Wright brothers with the design for their first gliding machine, but also placed at their disposition his own machines with which they made their initial gliding experiments. There is perhaps no one who has made a closer study and has a more thorough understanding of the whole subject of aerodromics than Mr.

Chanute, and I should like very much to see him given due credit for the very important work which he has done.

DISCUSSION BY PROF. A. F. ZAHM, OF THE CATHOLIC UNIVERSITY OF AMERICA.

I fully concur with Dr. Bell in the opinion that aerial locomotion is practicable, and is likely soon to be of great moment in the affairs of the world. For the progress of this science, during the past decade or two, has been as positive, as continuous, as substantial as that of any branch of engineering or of architecture. Constantly and quietly, in various parts of the world, men have grappled with the difficulties of this apparently hopeless enterprise, and now, I believe, we are about to enjoy the fruitful and splendid issue of their labors.

The subject of aerial locomotion may be divided into four main branches: first, the science of captive and free balloons; second, the science of motor balloons; third, the science of gliding and soaring machines; fourth, the science of dynamic flying-machines. Each of these has had its ardent advocates, and each is, I believe, practically feasible.

The first branch, or that of captive and free balloons, is already a practical science, inasmuch as such balloons perform substantially the functions for which they are designed. The captive balloon can be sent aloft safely in all kinds of weather for taking observations, and making maps of the neighboring region, even in winds of upwards of forty miles an hour. The free balloon, likewise, is comparatively safe when made by an experienced manufacturer and managed by a properly trained pilot. Such balloons may be kept aloft for days, or even weeks, traversing, in that time, hundreds of miles, or possibly the width of a continent, if the wind be favorable. But, though we grant the practicability of balloons of this type, it must be said also that their functions are limited; their chief usefulness thus far being for the study of the atmosphere, for observations of the land beneath, for military operations, for public exhibitions, and now recently, for racing and sport.

The ideal of the motor balloon is more important and more difficult, though it also seems about to be realized. The function of such craft is to go forth in all kinds of ordinary weather, to run in all directions, with or against the wind, scores of miles at a stretch, and to remain under perfect control. Salverda has shown, by reference to the yearly wind records at Paris, that aerial navigation may be practically realized, for that locality, when a vessel can be driven twenty-eight miles an hour. Is such achievement possible? More than a decade ago theorists demonstrated mathematically that this speed, and even higher, was attainable by appliances then known. Now apparently the inventors, taking a lesson from Santos Dumont, have caught up with the computers, and are producing the high speed balloons. On the third of this month, an eye witness told me that he saw Count von Zeppelin's air-ship fly about Lake Constance at a speed of twenty-eight miles an hour, independently of the wind, and that she obeyed her rudder as perfectly as a boat on the water. It is reported that the inventor has deduced from these experiments that a larger vessel will operate still more effectively, that an air-ship of this type can be made to carry fifty passengers at a speed of more than thirty miles an hour. Count von Zeppelin writes that his present balloon, which is 410 feet long and 38 feet in diameter, has attained a speed of 33.5 miles an hour, and is able to go 1,860 miles through the air at a speed of 31 miles an hour, or 3,000 miles at a speed of 25 miles an hour, without stopping for supplies. To match this achievement in Germany, let me add that the French Government has just accepted the second Lebaudy motor-balloon, and has ordered one more like it, thus adding three modern air-ships to her aerial equipment. Such facts may give us at least a little faith in aerial locomotion of the second kind.

The goal of the gliding and soaring machines is to travel through the air on motionless wings, without the aid of gas or motive power, by the sole aid of wind and gravitation; not only to glide downward, but also to soar up to the clouds, and sweep over vast territories, as do the condor and the albatross. To some people this seems absurd; but there are the vultures and the gulls performing the impossible every day. Humboldt assures us that the condor can soar from the Pacific to the heights of Cotopaxi and Aconcagua without wing-beat. Here is a splendid field of research which thus far has remained practically unexplored.

Unfortunately, I can not quote an instance of real soaring by man; that is to say, gliding to an indefinite height and distance, without the use of motive power. Still, from the mechanical nature of the performance, I believe it is feasible. Dr. Langley was so convinced of the possibility of this kind of flight that he looked forward to the time when men would soar over vast distances, and possibly circumnavigate the globe without the expenditure of motive power, save in those regions of the atmosphere where there might be an extended calm or downward trend of the wind.

Two years ago the Wright brothers compared their power of aerial gliding with that of a vulture in North Carolina, among the Kill-Devil sand hills. On a day when there was little or no wind, they observed a buzzard tobogganning down the atmosphere parallel to the sloping sand and very near to it. Where the slope was steep enough the bird could glide indefinitely without wing-beat, but where the incline was too gentle, say seven degrees or less, the buzzard had to flap a little to maintain its flight. Having carefully noted a considerable stretch of sand where the bird could barely sail without flapping, they mounted their glider and skimmed over the same slope without motive power. From such experiments they concluded that they could glide fully as well as the buzzard, and possibly a trifle better. In other words, if they were placed on a perch with the bird in competition, in a large closed room, they would probably win the prize for long distance gliding.

In one other feat, also, they imitated the vulture. They hovered motionless above a sand slope for 59 seconds, neither rising nor falling, nor advancing nor receding. In this case, of course, the wind had a slightly upward trend, say of seven or more degrees, just as must be the case when any bird floats fixed and motionless in the air.

I put this question to them recently: "After beating the buzzard in the art of gliding, did you try to beat him in the art of soaring up to the clouds?" They replied that nothing would have given them more pleasure; but their power machine, on which they had worked so arduously, and so long, was ready for its first test, and Christmas was just at hand. So they went out in a bitter gale, launched their motor flying machine in the teeth of a tumultuous thirty-mile wind, and flew half a mile through the air, or three hundred and some feet over the ground. Thus ended their gliding and thus began their dynamic flight.

But they still envy that feathered professor of the atmosphere, and still have confidence that they may, to some extent, acquire his fascinating art. If they could dispose of their present power machine, doubtless they would return again to the sand-hills and plunge pell-mell into the soaring business.

As to the fourth type, or the motor flying-machine, I need add little to the excellent summary given by Dr. Bell. Without radical improvement, such machines may be driven through the air with the speed of the eagle, and made to carry several hundred pounds burden. The Wright brothers, in their recent communication to the Aero Club of America, conclude with these words: "It is evident that the limits of speed have not as yet been closely approached in the flyers already built, and that in the matter of distance the possibilities are even more encouraging. Even in the existing state of the art, it is easy to design a practical and durable flyer that will carry an operator and supplies of fuel for a flight of over 500 miles at a speed of 50 miles an hour."

In a great conflict like the recent oriental war, one such machine could do more reconnoitering than 50,000 armed men. For, in a few hours, it could completely survey and snap-shot the enemy's main field of operations, though covering hundreds of square miles. A fleet of such machines, armed with bombs and fire pellets, could devastate the whole of an enemy's border, both towns and villages, unless opposed by other flyers. Possibly, also, a fleet of this kind could protect a nation's seaboard against the attack of battleships, unless the latter were accompanied by an aerial squadron. Therefore, if one great nation keep flyers, all the world-powers must have them.

But this seems like hunting for trouble with a search light just before daybreak. Whatever be the mission of the flying-machine, I think we may say of it as the English do: "The thing is bound to come, whether we like it or not." "And damned be he who first cries hold!"

As to Dr. Bell's researches in this interesting and now popular field of inquiry, I would say, first, that every earnest friend of science should be very grateful to him for lending his illustrious name to a much ridiculed pursuit, at a time when it jeopardized one's peace and good name publicly to promote mechanical flight. I well remember with what apprehension Mr. Chanute consented to become chairman of the first international conference on aerial navigation in this country. And we all too well remember the attitude of many people toward Dr. Langley's painstaking and unobtrusive investigations. The Wright brothers, also, experienced hostile treatment in certain quarters before their success was known. Even after the news of their splendid flights of last year had been circulated privately among their friends, we heard many apparently intelligent dogmatists assert that it is not the design of Providence, or of Nature, that a human being should fly; and that, furthermore, the performance is manifestly impossible. This is another illustration of the value of public opinion in matters of technical import. But fortunately, the destinies of science are not dominated wholly by the vote of the majority, nor yet by grand officials, whether legislative or executive, else, I fear we never should have either a science or an art of aerial locomotion.

Another service for which we may thank Dr. Bell is his having met publicly, both by model and by argument, a profound objection of the mathematicians, based on that ancient Euclidean theorem connecting the surfaces and volumes of similar figures with certain powers of their homologous linear dimensions. Dr. Bell did not deny the law, as a chagrined or an angry person might; but, like a shrewd man of affairs, he admitted the law, and discovered a way to evade it.

Now that his reply is familiar to us, it may seem amusing that people urged the Euclidean objection so strongly; but the fact is that many persons, besides Professor Newcomb, advanced it as an argument against the practicability of mechanical flight. In the middle eighties an eminent geologist made it the basis of a magazine article, in which he proved, with fine eloquence, that it is impossible for a human being ever to fly. He further supported his contention by a vigorous biological argument, and possibly also by a theological or teleological one, I do not remember. He asserted that nature had tried for centuries to produce a flying creature as heavy as a man, but had failed; therefore, it is utterly impossible for man to achieve mechanical flight. By diligent experimentation she had tested and adopted the strongest possible materials, she had developed the most powerful motor for a given weight, she had employed the most favorable shapes and the most efficient mode of propulsion. But what was the outcome? Her largest flyer weighs hardly so much as a human dwarf. The ostrich is the limit. The ostrich is the living witness of nature's failure. And that picturesque old reptile, with the twenty-foot wings, that soared so grandly over the Cretacean seas, remains to-day the fossil proof of nature's utmost capacity, and therefore also of man's. Such argumentst such prettily woven sophistries, such quaint immemorial cobwebs, have Dr. Bell and his associates brushed reverently from the pages of science.

There are many features of Dr. Bell's remarkable kites, both structural and aerodynamic, that merit most careful attention; more particularly the relation of the forward resistance to the total upward lift, the effectiveness of the provision for automatic stability and equilibrium in all kinds of tumultuous winds, the distribution of stresses in the frame, and of the impulsive pressures over the sustaining surfaces. But these topics seem to me more suitable for experimentation than for abstrac, analysis.

One interesting phenomenon, however, I will notice in closing. Dr. Bell relates that his floating kites, which in calm weather, could advance but four miles an hour, still continued to make headway against a sixteen-mile wind. The momentum of the craft might maintain this forward motion for a few seconds, but not for a considerable period. For the total momentum in any direction is equal to the initial momentum plus the impulse of the resultant force in the line of progression. Or, in the language of algebra,

$$mv = m_0 v_0 + (F - F')t$$

in which mv is the momentum at the time t, $m_0 v_0$ the initial momentum, $F - F'$ the resultant of the average propulsive and opposing forces. If mv is positive for large values of t, the equation shows that F must at least equal F'. But Dr. Bell observed, that the kites continued always to advance, or that mv remained positive. Therefore the propulsive force continued, on the average, at least equal to the resistance. In other words, it was the propeller thrust, rather than the momentum, that maintained the indefinite forward progression.

But how, it may be asked, could the propeller thrust maintain headway against a sixteen-mile wind, if, in calm weather, it could support a speed of only four miles an hour? I would answer: first, that the water resistance was not greater in the sixteen-mile wind, but probably less; second, that the propeller thrust might be not very different in a calm and in a sixteen-mile wind, as Maxim found. This latter point Mr. Manly can elucidate readily from his extensive study of both the theory and actual working of screw-propellers.

It is well for the world when a man of Dr. Bell's fertility espouses some favorite science. He took up the kite as a toy, and now presents these wonderful structures; light and beautiful as butterflies, yet strong and stable enough for human life. If next he incline to magnificence, what lovely air-castles will follow! Serenely, one day, may he soar in a gossamer palace, when the blue waves blossom, and the wind sings over the sea!

Appendix A.

Details Concerning the Kite "Frost King."

Number of Cells in the "Frost King."

Layers of cells.	Number of rows.	Number of cells in each row.	Number of cells in each layer.
1st layer	1	24	24
2d layer	2	23	46
3d layer	3	22	66
4th layer	4	21	84
5th layer	5	20	100
6th layer	6	19	114
7th layer	7	18	126
8th layer	8	17	136
9th layer	9	16	144
10th layer	10	15	150
11th layer	11	14	154
12th layer	12	13	156

Total number of cells, 1,300

Dimensions. — Each cell had a side of 25 centimeters, so that the roof, or ridge pole, measured 6 meters extending laterally across the top of the structure. The oblique sides were 3 meters in length; and the bottom, or floor, formed a square having a side of 3 meters. The whole structure constituted a section of a tetrahedral kite — the upper half in fact, of a kite, having the form of a regular tetrahedron with a side of 6 meters.

Weight. —The winged cells composing this structure weighed on the average 13.84 gms. apiece, so that the whole cellular part of the structure which supported all the rest — consisting of 1,300 winged-cells — weighed 17,992 gms.

In addition to this, the kite carried as dead load stout sticks of wood which were run through the structure to distribute the strain of the pull upon the strong parts of the framework — that is, upon the junction points of the cells. The outside edge of the kite was also protected by a beading of wood. The whole strengthening material weighed 9,702 gms., and the kite, as a whole, weighed 27,694 gms. (61 lbs.).

Surface. — I estimate the surface of an equilateral triangle having a side of 25 centimeters, as about 270.75 square centimeters. In which case the silk surface of a single winged-cell, consisting of two triangles, amounts to 541.5 square centimeters; and the actual silk surface employed in 1,300 cells equals 70.3950 square meters (757.7 sq. ft.).

The surfaces are all oblique; and if we resolve the oblique surfaces into horizontal and vertical equivalents (supporting surfaces and steading surfaces) we find that the resolved horizontal equivalent (supporting surface) of a single winged cell forms a square of which the diagonal measures 25 centimeters, and this is equivalent to a rectangular parallelogram of 25 × 12.5 cm., having an area of 312.5 square centimeters.

Thus an actual silk surface of 541.5 square centimeters arranged as the two wings of a winged cell, yields a supporting surface of 312.5 square centimeters.

In kites, therefore, composed exclusively of tetrahedral winged cells, each having a side of 25 centimeters, the area of supporting surface bears the same proportion to the actual surface as the numbers 3,125 to 5,415; or 1 to 1.7328.

$$\frac{\text{Supporting surface}}{\text{Actual surface}} = \frac{1}{1.7328}.$$

A simple way of calculating the amount of supporting surface in such structures is to remember that there are 32 cells to the square meter of supporting surface. Therefore, the 1300 cells of the kite "Frost King" had a supporting surface of 40.6250 square meters (437.3 sq. ft.).

Ratio of Weight to Surface. — The actual silk surface employed in the "Frost King" was 70.3950 square meters (757.7 sq. ft.), the weight of the kite was 27,694 gms. (61 lbs.), so that on the basis of the actual surface, the flying weight was 393.4 gms. per square meter (0.08 lbs. per sq. ft.).

But for the purpose of comparing the flying weight of a tetrahedral kite with that of other kites in which it is usual to estimate only the aeroplane surfaces that are substantially in a horizontal plane, it would be well to consider the ratio of weight to horizontal or supporting surface in this kite.

The weight was 27,694 gms. (61 lbs.); the resolved horizontal or supporting surface was equivalent to 40.6250 square meters (437.3 sq. ft.), and the flying weight for comparison with other kites was 681.7 gms. per square meter of supporting surface (0.14 lbs. per sq. ft.).

The kite, in addition to its own weight, carried up a mass of dangling ropes and a rope-ladder, as well as two flying cords of manilla rope. The impedimenta of this kind weighed 28,148 gms. (62 lbs.). It also supported a man, Mr. Neil McDermid, who hung on to the main flying rope at such a distance from the cleat attached to the ground that when the rope straightened under the strain of the kite he was carried up into the air to a height of about 10 meters (over 30 ft.). The weight of this man was 74,910 gms. (about 165 lbs.). Thus, the total load carried by the kite, exclusive of its own weight, was 103,058 gms. (or 227 lbs.).

The whole kite, load and all, including the man, therefore, weighed 130,752 gms. (288 lbs.), and its flying weight was 1857.4 gms. per square meter of actual surface (0.38 lb. per sq. ft.); or 3218.5 gms. per square meter of supporting surface (0.66 lb. per sq. ft.).

APPENDIX B.

PARTIAL BIBLIOGRAPHY RELATING TO AERIAL LOCOMOTION, PREPARED, THROUGH THE COURTESY OF THE SMITHSONIAN INSTITUTION, BY DR. CYRUS ADLER, ASSISTANT SECRETARY, IN CHARGE OF LIBRARY AND EXCHANGES.

Dr. Adler says: "In accordance with your request, I am authorized to send you herewith a list of the writings of S. P. Langley, Octave Chanute, Otto Lilienthal, Lawrence Hargrave, and A. M. Herring, to be used in connection with your recent paper on aerial locomotion. I ought to explain that, excepting in the case of Mr. Langley's writings, I am not at all sure that the lists are complete, since the time afforded for bringing together the references was very short, and of course there may be publications in out-of-the-way journals which would only be revealed by a more extended inquiry. I have also appended a list of papers on the subject published by the Smithsonian Institution, as the Smithsonian publications are accessible in all libraries throughout the country, whereas many of the publications cited in the other lists are not readily to be found."

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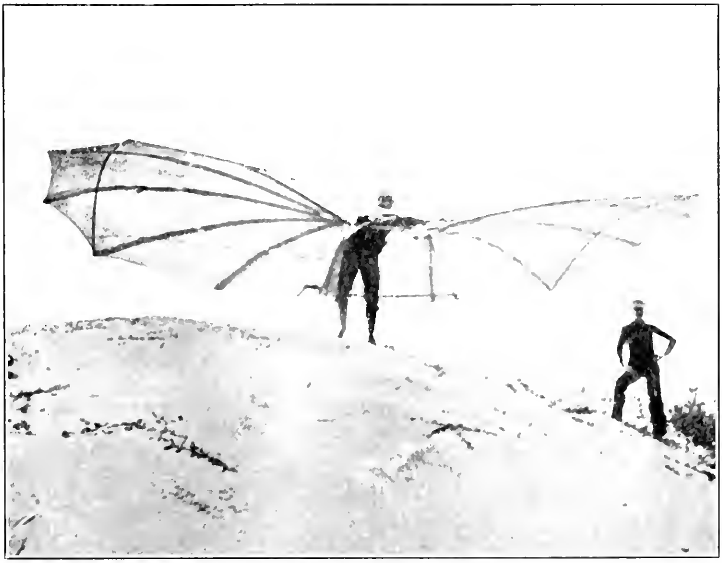
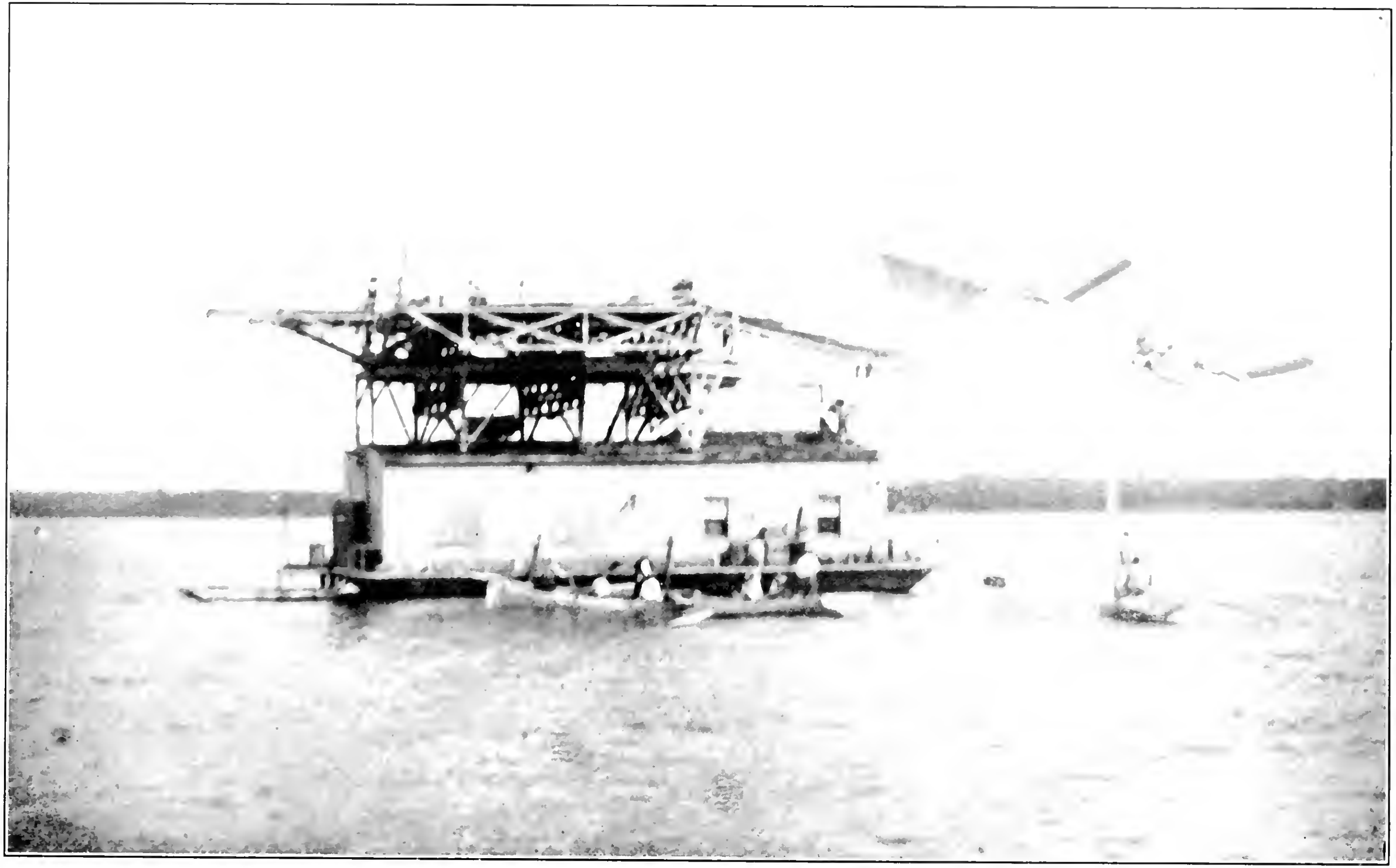


Lilienthal Gliding Machine as reproduced in America for Chanute by Herring.

Gliding through the air on Chanute's Multiple-winged Glider.

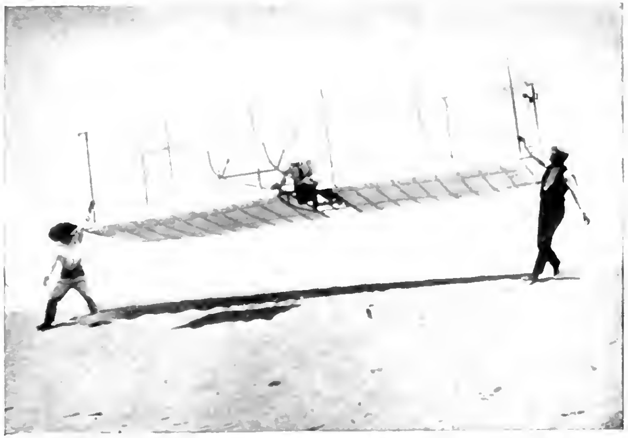
Langley's Aërodrome No. 5 in flight, May 6, 1896.

From instantaneous photograph by Alexander Graham Bell.

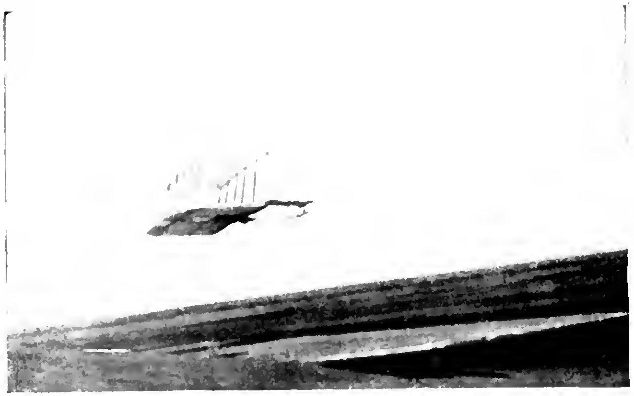


The accident to Langley's Aërodrome.

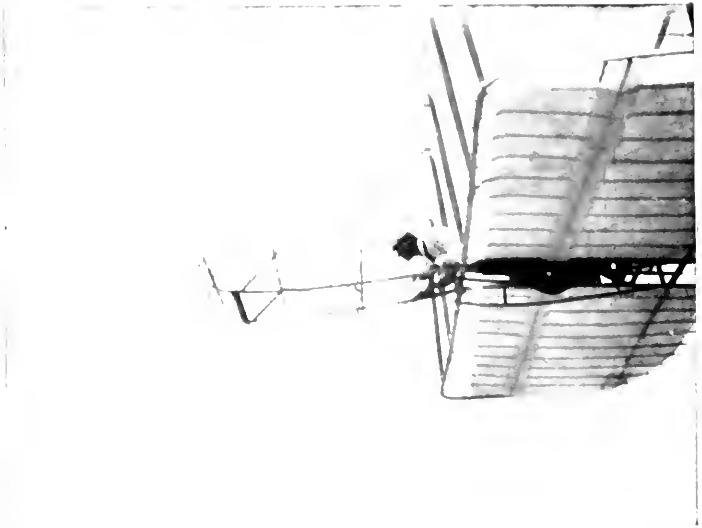
From an instantaneous photograph loaned by the Smithsonian Institution The machine caught in the launching ways and was injured, being precipitated into the water without having a chance to show what it could do in the air.



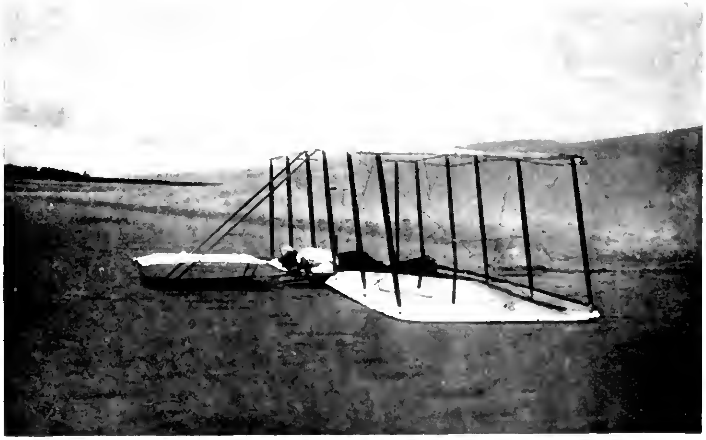
1. Starting a flight.



2. A high glide.

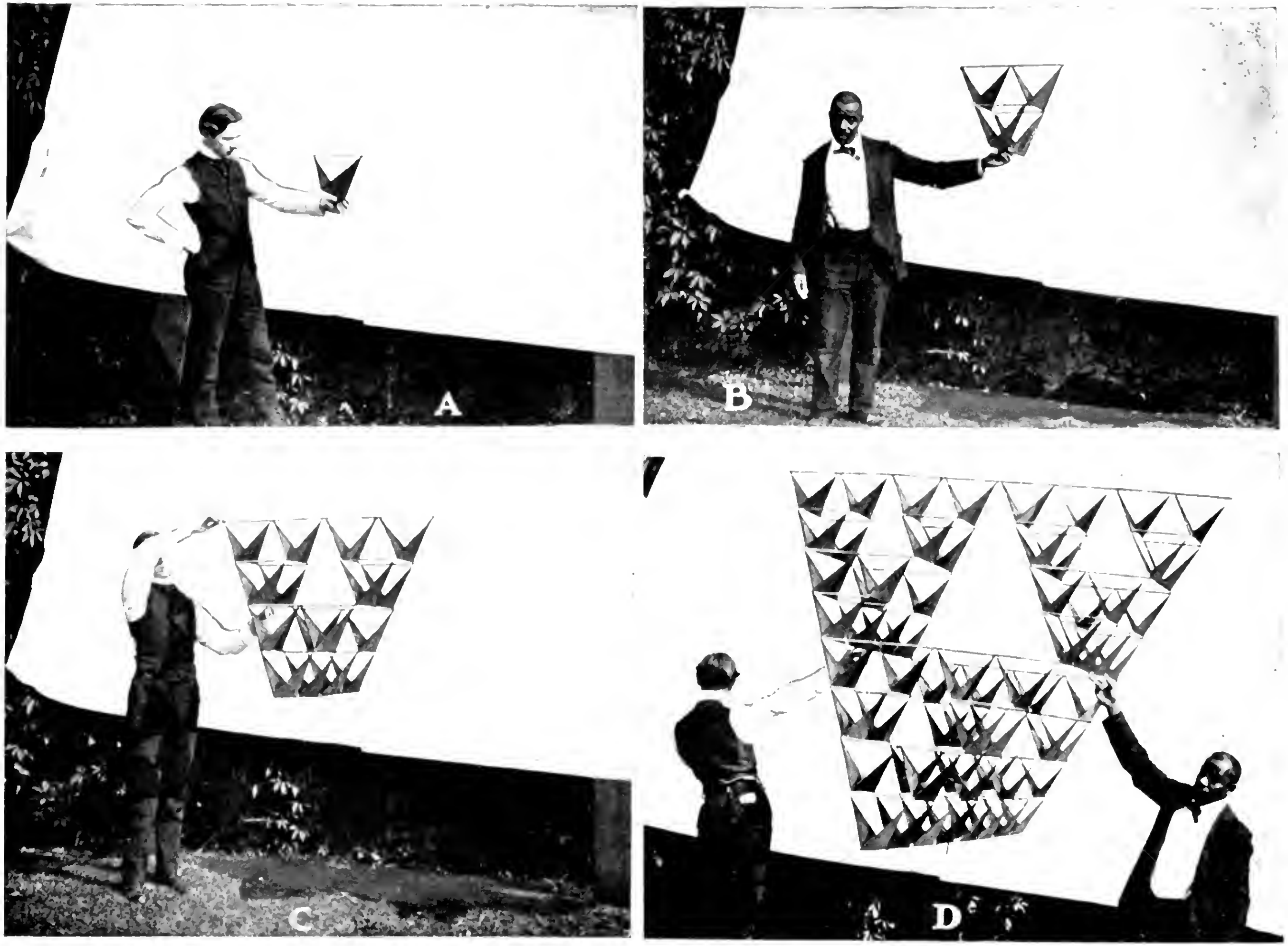


3. Soaring.



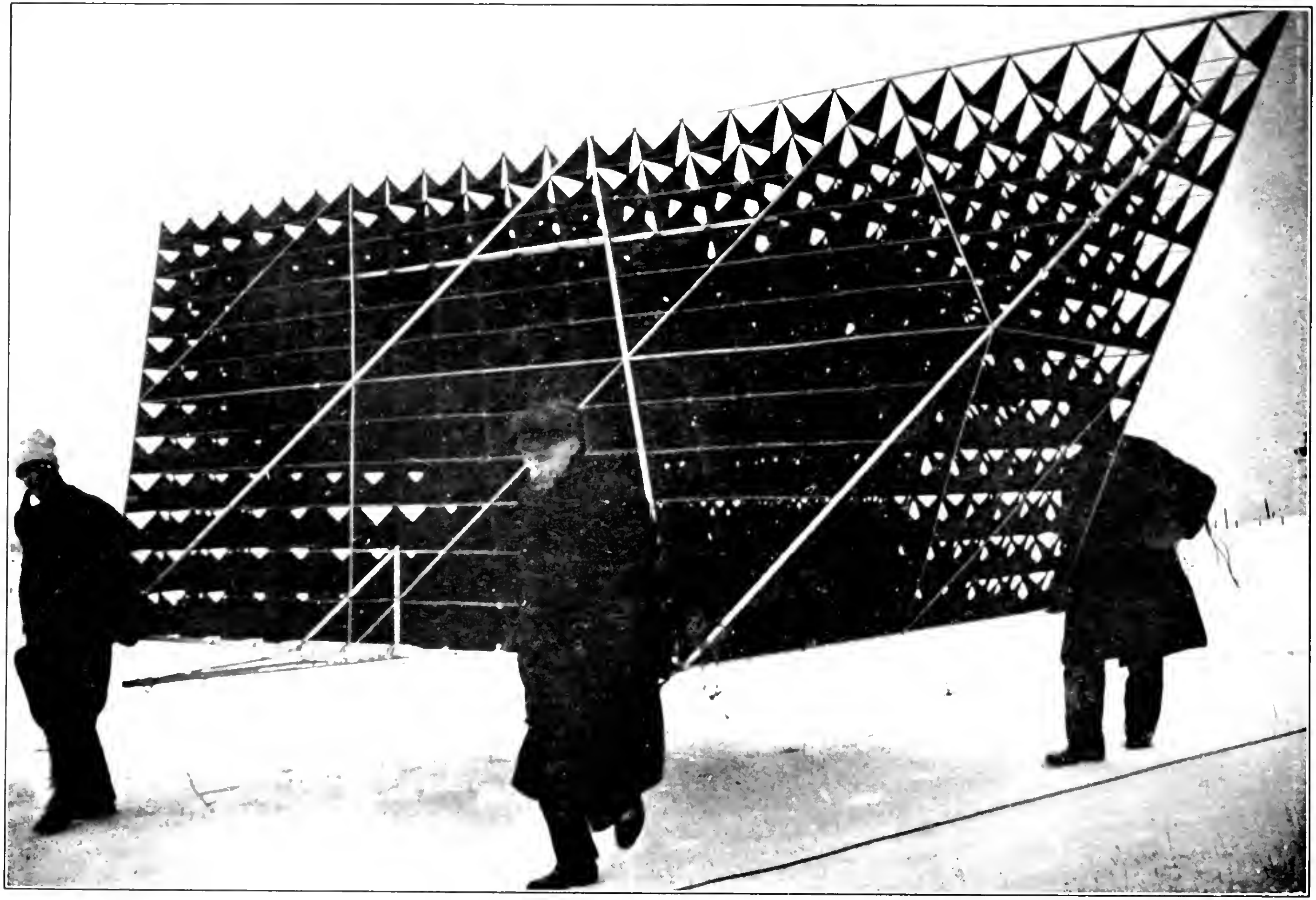
4. Landing.

The Wright Brothers' Gliding Machine.



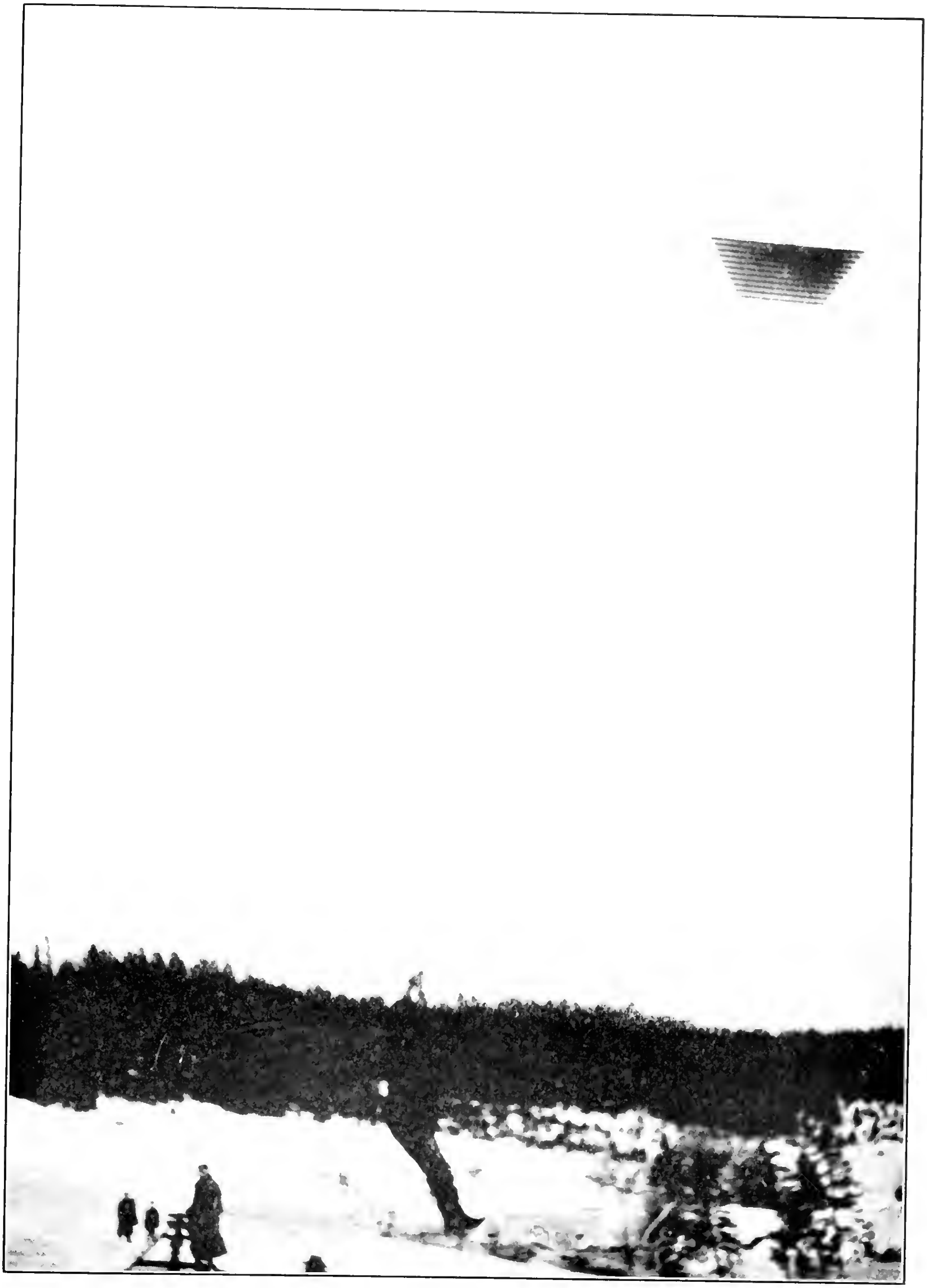
A. Single-winged cell. B. Four-celled kite. C. Sixteen-celled kite. D. Sixty-four-celled kite.

On this, the hollow plan of construction, an empty space appears in the middle of each kite, B, C, or D, equivalent in volume to one-half of the cubical contents of the whole structure. Illustration from the National Geographic Society.



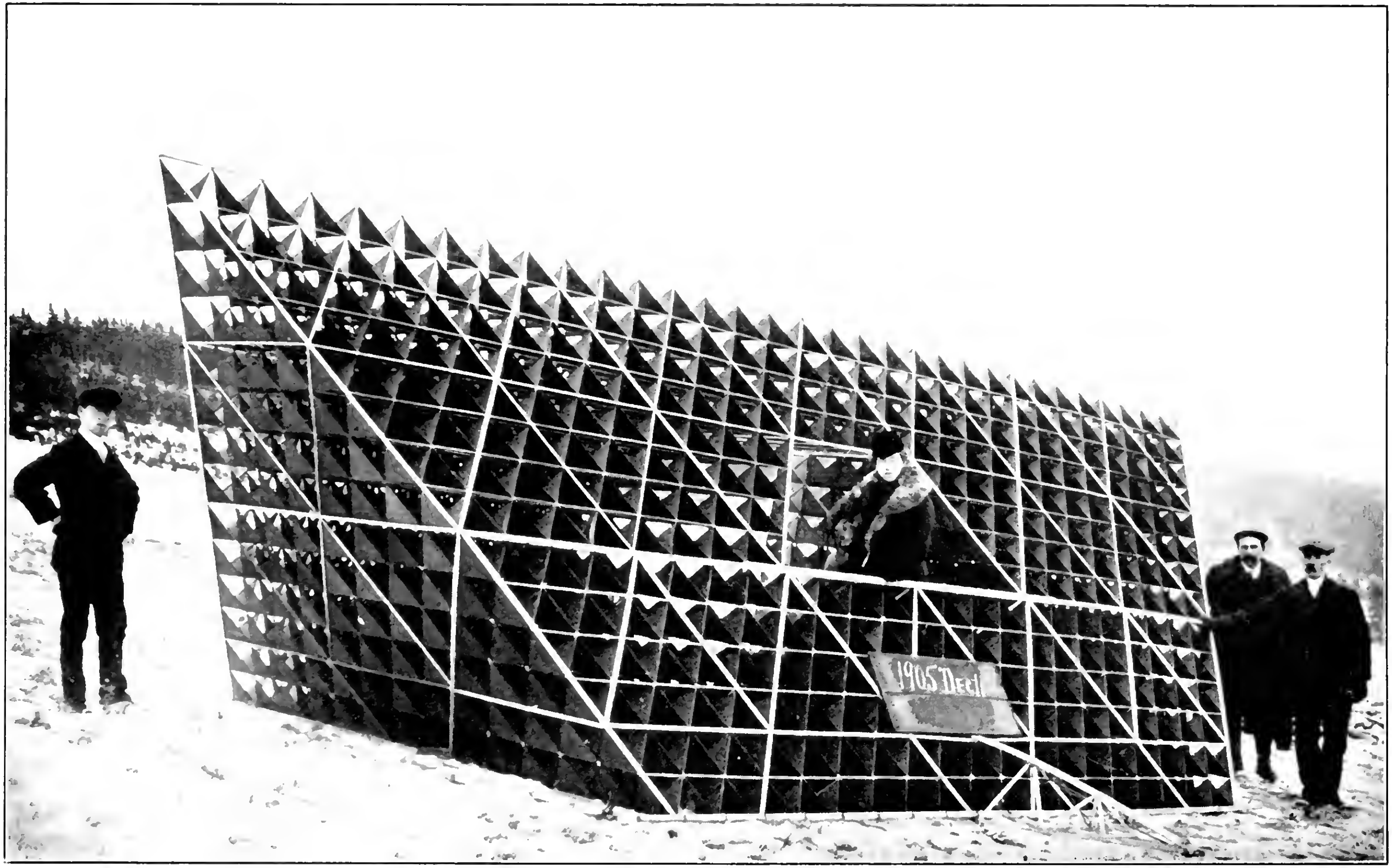
Carrying the Frost King on to the testing ground.

This kite was composed of 1,300 light-winged cells closely massed together. Photograph by E. H. Cunningham. Illustration from the National Geographic Society.



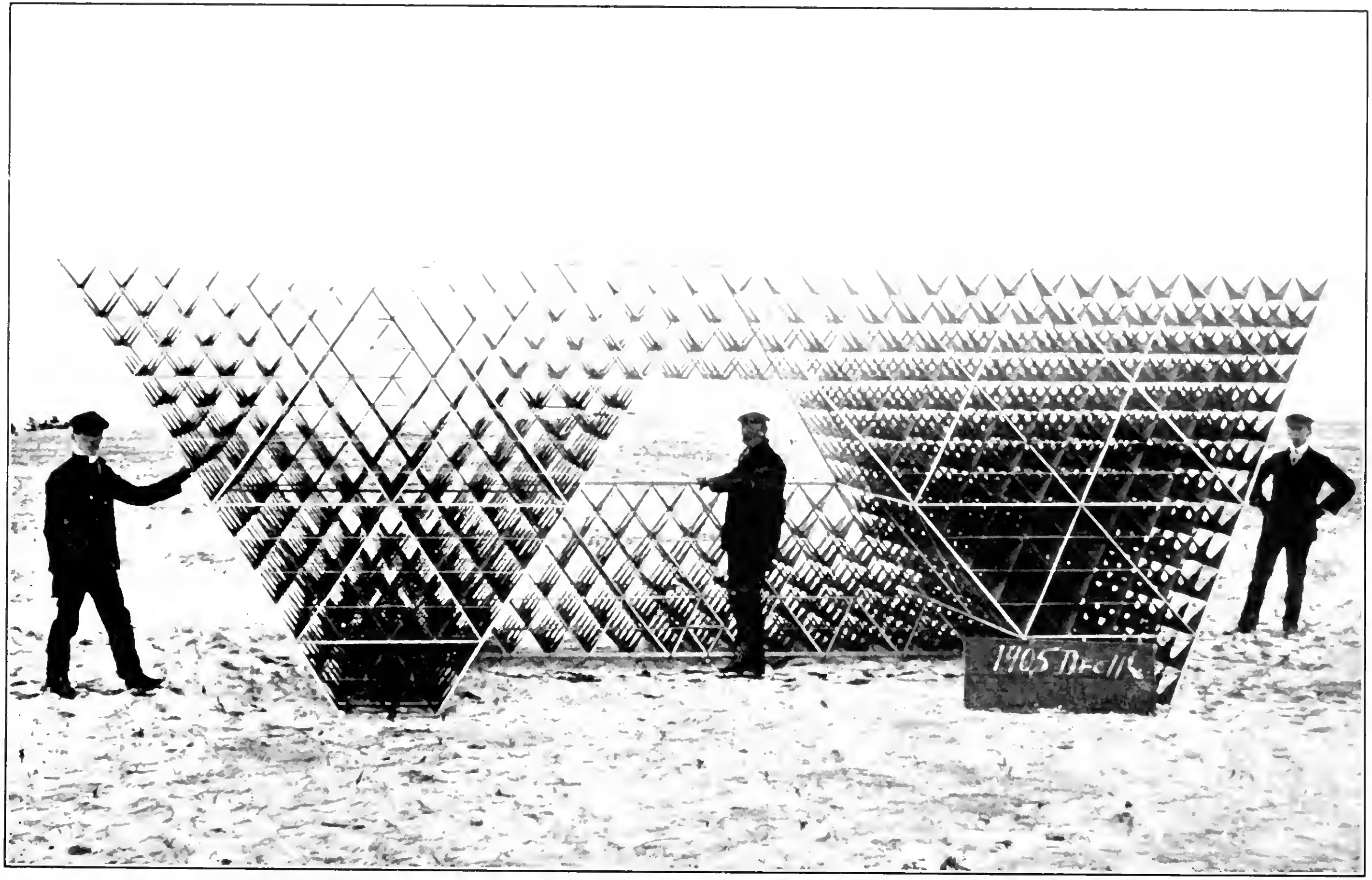
The Frost King in the air, flying in a ten-mile breeze, and supporting a man on the flying rope.

During the experiment the rope straightened under the pull of the kite, and the man was raised to a height of 30 or 40 feet. He was in great peril, but fortunately was brought down safely. Photograph by Alexander Graham Bell. Illustration from the National Geographic Society.



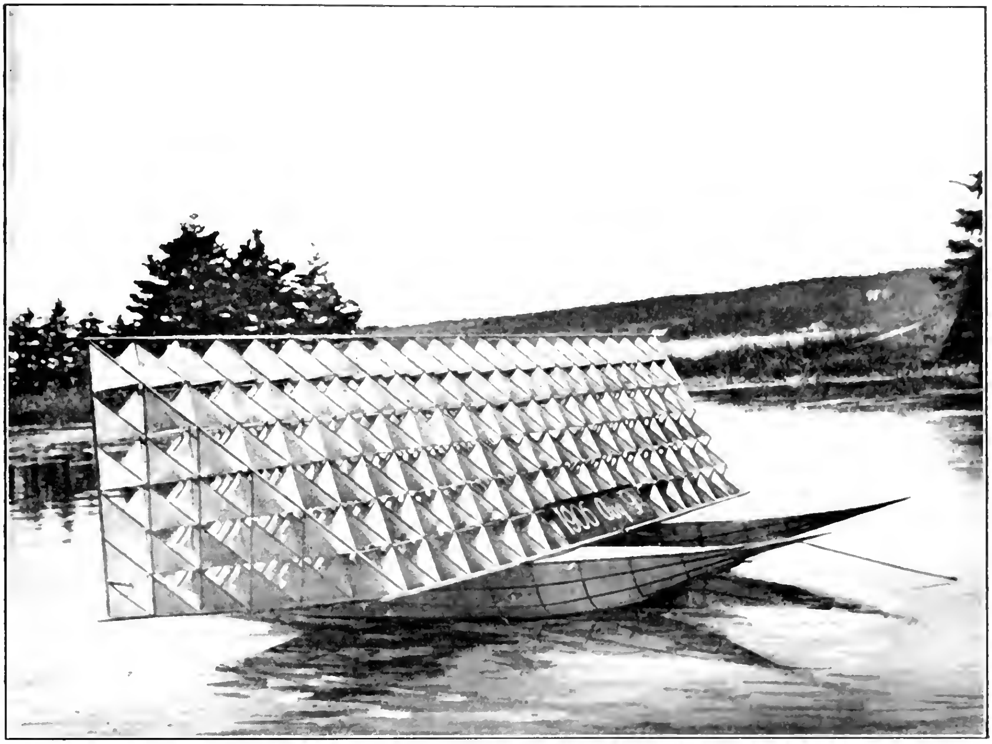
Kite "Siamese Twins" seen from the front.

This kite was supported in the air by a strong wind exceeding, probably, 25 miles an hour. It was too heavy to be blown in a moderate breeze. Photograph by E. H. Cunningham. Illustration from the National Geographic Society.



Kite "Siamese Twins," seen from the rear, looking inside kite.

Composed of two distinct kites connected by a bridge, or truss, of strong cells, well beaded, for support of man. Photograph by E. H. Cunningham. Illustration from the National Geographic Society.

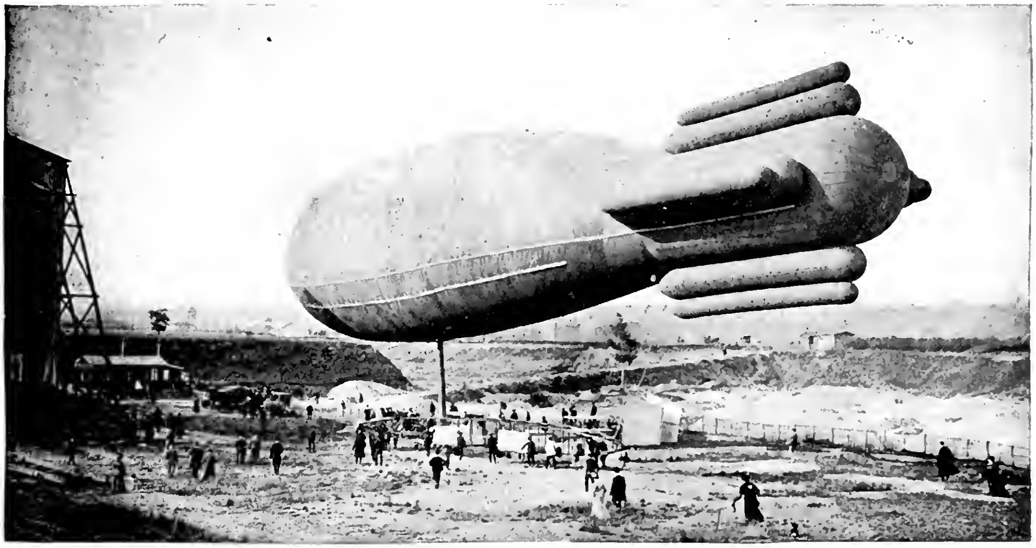


A Floating Kite, adapted to be towed out of the water.

Kite consists of a bridge, or truss, of tetrahedral cells with wings of Japanese waterproof paper upon two floats of light framework covered with oilcloth. A stout towing pole extends laterally across the lower part of the wing-piece at the front. Photograph by Douglas McCurdy. Illustration from the National Geographic Society.

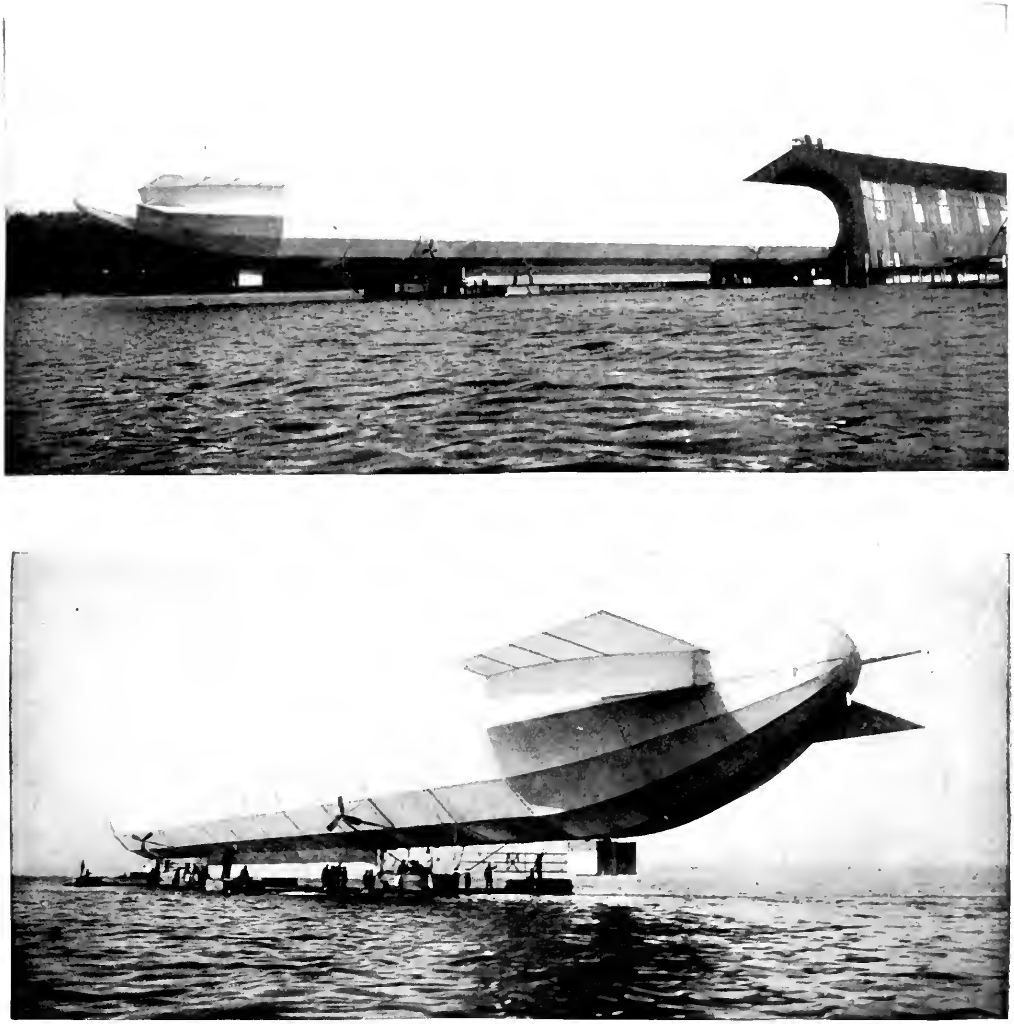
The French Military Dirigible, "Patrie," in flight.

The latest French airship, "La Patrie," is 33¾ feet in diameter by 196 feet long, and has a capacity of 111,195 cubic feet. Driven by a 70-horsepower motor and two propellers, this dirigible has recently made about 30 miles an hour. Its lifting capacity is 2,777 pounds. Illustration from the *Scientific American*.



The New Deutsch Airship, "Ville de Paris," the latest dirigible balloon.

The peculiar arrangement of twin, hydrogen-filled cylinders forms a sort of balancing tail. This airship has a length of 60 meters (196.85 feet) and a diameter of 10.8 meters (35.43 feet) while its capacity is 3,000 cubic meters (105,943 cubic feet). Its propellers are placed on either side of the body framework, or "nacelle," and at about the center of the latter, which is boat-shaped. The weight which can be carried, outside of the equipment and the fuel sufficient for a ten hours' run, is about 1,100 pounds. A 70-horsepower Panhard motor is used. Illustration from the *Scientific American*.



Count Von Zeppelin's Airship—the largest and fastest thus far constructed—coming out of its shed and performing various evolutions above Lake Constance.

This airship, which is 38 feet in diameter by 410 feet in length and which has a capacity of 307,120 cubic feet, held itself stationary against a 33½-mile-an-hour wind in January last, by means of two 35-horsepower gasoline motors driving four propellers. The airship can lift three tons additional to its own weight, which gives it a radius of 3,000 miles at 31 miles an hour. On October 11, 1906, Count Zeppelin maneuvered this dirigible balloon above Lake Geneva, ascending to a height of 2,500 feet and steering the huge cigar-shaped aerostat very nicely. The airship is mounted on floats, so that it works equally well on the water. During one flight it remained in the air an hour and twenty minutes, although the steering-gear was caught in the skeleton framework and became partly unmanageable. The attempts proved also that the airship was dirigible in spite of its great size, as several complete circles were made while in the air. Illustrations from the *Scientific American*.

PROCEEDINGS

OF THE

WASHINGTON ACADEMY OF SCIENCES

VOL. VIII, PP. 449–458. PLATES XXI–XXIII MARCH 4, 1907.

ON A COLLECTION OF FISHES FROM BUENOS AIRES.[1]

BY CARL H. EIGENMANN.

THE present paper is a report on a collection of fishes obtained near Buenos Aires, Argentina, by Prof. W. B. Scott, of Princeton University. The collection adds several species to the La Plata fauna. These are marked *. Four of these species are new. The types are in the Museum of Princeton University, and a series of cotypes and duplicates is in the Museum of Indiana University.

The fresh-water fish fauna of Buenos Aires is essentially Amazonian and in striking contrast to the fresh-water fauna of North America of corresponding latitude and equally remote from the mouth of the Amazon which lies on the equator. None of the Amazon genera has passed much beyond the borders of the United States. Most of them do not reach beyond Panama. The Paraguay, whose sources are in contact with those of the Tapajos and Madeira, southern tributaries of the Amazon, has provided an easy and open road for the Amazon fauna to the Lower Parana and La Plata. But few Amazon types extend south of Buenos Aires.

SILURIDÆ.

Luciopimelodus pati Valenciennes.

One specimen.

Pseudaplatystoma coruscans Agassiz.

One specimen.

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* Contributions from the Zoölogical Laboratory of Indiana University, No. 80.

Rhamdia quelen Quoy & Gaimard.

One specimen.

Pimelodus clarias macrospila Günther.

Two specimens, each with 3 series of large spots.

Pimelodus albicans Valenciennes.

One specimen.

Pimelodus valenciennis Kröyer.

Four specimens.

Iheringichthys labrosus (Kröyer).

Several specimens.

Doras granulosus Valenciennes.

A single specimen, 470 mm. long.

Lateral line 22, the hooks of the lateral plates beginning under the end of the dorsal.

LORICARIIDÆ

Plecostomus commersoni Cuvier & Valenciennes.

Four specimens.

* **Plecostomus laplatæ** Eigenmann, new species. (Plate XXI.)

Depth 5 in length; head 3.4 (3.28 in cotype); D. 1, 7 (not counting the fulcrum); A. 1, 4; scutes 31 + 1 caudal scute; depth of head 1.75 (1.66); width of head 1.2 in its length (1 +); length of snout equaling depth of head (1.5 in head); interorbital 2.8 in head (2.66); length of mandibular ramus 3 in interorbital (2 +); barbel more than half length of eye; snout spatulate, rounded; supraorbital margin not raised; supraoccipital ridge very feeble, temporal plates not carinate; scutes of sides little keeled, spinulose, 7 between dorsal and adipose, 14 to 16 between anal and caudal; supraoccipital bordered by a median and two or three lateral scutes. Lower surface of head and belly entirely granulose in the type, partly naked between the base of pectoral and ventral. First dorsal ray about equal to length of head, last ray .66 (.5) length of head; base of dorsal equal to its distance from end of second scute beyond tip of adipose spine; pectoral extending to second sixth of the ventrals; caudal distinctly emarginate; caudal peduncle a little more than 3 times as long as deep.

Color of type: Sides, ventral surface and head profusely spotted, the spots largest on the belly, minute on the head; lightish streaks along the lateral keels; dorsal dusky with one or two rows of spots between every two rays; caudal unspotted, the lower part dusky; anal dark, unspotted; ventrals and pectorals dusky, the former with large spots, the basal two thirds of the latter with very numerous minute spots similar to those of head.

Color of cotype: Ventral surface plain; sides with obscure large spots, the light streaks along the keels much more evident; head profusely covered with spots much larger than those in the type; dorsal with a series of large spots on the posterior half of each interradial membrane; caudal sooty, anal obscurely spotted; entire upper surfaces of ventrals and pectorals spotted, the spots of the pectoral more numerous and smaller, but not as small as those of the head.

Apparently related to *Plecostomus carinatus vaillanti* and *tietensis*.

Type in Mus. Princeton Univ., a specimen 410 mm. long, from Buenos Aires; coll. Prof. W. B. Scott. Cotype, no. 11351, Mus. Ind. Univ., a specimen 214 mm. long, from same place.

Loricaria vetula Cuvier & Valenciennes. (Plate XXII.)

One specimen.

Loricaria anus Cuvier & Valenciennes.

Six specimens.

These specimens have the lateral keels separate to the last 3 or 4 scutes; the dorsal without spots but with the second half of the membrane dark.

CHARACIDÆ.

Curimatus platanus Günther.

One specimen.

Curimatus gilberti Quoy & Gaimard.

Two specimens.

Prochilodus lineatus (Valenciennes).

Six specimens, the largest 430 mm.

Leporinus obtusidens (Valenciennes).

One specimen. Depth 3.5; head 4.33; interorbital equals snout; snout conical; teeth short, truncate; lateral spots obscure, vertical, the caudal spot most prominent; anal concave, the second and third ray reaching much beyond the tip of the last, nearly to caudal.

Astyanax rutilus (Jenyns).

Five specimens.

D. 11; A. 28 in one, 30 in the others; scales 6 or 7–37 to 39–5 to 7.

* **Acestrorhamphus brachycephalus** (Cope).

One specimen. D. 10; A. 26; head 3.75; depth 3.33; eye 4 in head; scales 11–55–9.

Acestrorhamphus hepsetus (Cuvier).

One specimen.

* **Acestrorhamphus ferox** (Günther).

One specimen.

Salminus maxillosus (Cuvier & Valenciennes).

Three specimens.

In the older ones the dark lateral lines are much more conspicuous than in the younger.

Serrasalmo marginatus Valenciennes.

Two specimens.

Hoplias malabaricus (Bloch).

Two specimens.

CLUPEIDÆ.

Pomolobus ? melanostomus Eigenmann, new species. (Plate XXIII, Fig. 6.)

I am not sure of the identification of this species. It differs from the other American relatives of *Clupea* in having the dorsal inserted *behind* the ventrals.

D. 13 to 16; A. 17 to 20; head 4.5 to 5; depth 3.33 to 3.66; ventral serræ strong, beginning near posterior margin of preopercle, 26–29. Eye a little longer than snout, 3 to 3.5 in head; mouth oblique, the lower jaw included; maxillary extending a little beyond front of eye; gillrakers about two thirds as long as eye; no teeth on vomer; alimentary canal short, peritoneum white; dorsal short, its origin over some part of the last third of the ventrals, a little nearer caudal than tip of snout. Scales caducous, crenulate.

A dark band along the entire back, median predorsal line free from pigment; a faint dusky streak along the upper part of the side to the middle of caudal; no humeral spot; upper lip black, tip of snout and lower jaw dusky; sides of head and body without pigment cells.

The reproductive organs indicate that the larger specimens are mature.

Type in Mus. Princeton Univ., a specimen 85 mm. long, from Buenos Aires; coll. Prof. W. B. Scott. Cotypes in the collections of Princeton and Indiana Universities (No. 11364, Mus. Ind. Univ.), 14 specimens 58 to 85 mm. long, from same place.

STOLEPHORIDÆ.

Ilisha flavipinnis (Valenciennes).

Two specimens.

Stolephorus olidus Günther.

Seven specimens.

Upper margin of silvery band well defined, the lower margin not, the silvery area in the adult covering the entire sides. Anal about 26; depth about 5.5 (4.5 in the types).

MUGILIDÆ.

Mugil platanus Günther.

Five specimens. These agree with Günther's description, except that in the three better preserved specimens and the smallest the upper half of the base of the pectoral is black, the rest of the fin uniform.

ATHERINIDÆ.

Atherinichthys bonariensis Cuvier & Valenciennes.

Four specimens.

Atherinichthys argentinensis Cuvier & Valenciennes.

Origin of spinous dorsal behind anus. A. 1, 15; scales 50, 8 between dorsal and anal; depth 6.5 to base of caudal; head 4.33; scales rounded behind; pectorals equal head less mouth; lateral band one sixth depth of body.

SCIÆNIDÆ.

Pachyurus bonariensis Steindachner.

Many specimens.

CICHLIDÆ.

Heros autochthon Günther.

Two specimens.

Geophagus australe Eigenmann, new species. (Plate XXIII, Fig. 7.)

Closely related to *G. duodecimspinosum* = *balzanii*, from the Paraguay. It differs from that species in the more pointed snout, less steep profile, more rapidly descending dorsal slope, longer, more slender caudal peduncle, narrower interorbital, etc. It differs from its next nearest relative, *G. gymdogenys*, in the scales of the cheek and in the color.

Head 3 to 3.16; depth 2 to 2.4; D. XII to XIV, 10 or 11; A. III, 8; lateral line 28 to 30 (16 to 18 + 10 to 12); 25 to 27 scales along the middle of the side.

Subrhomboidal; dorsal outline unequally arched, the highest point at the origin of the dorsal. In *G. balzanii* the dorsal profile is much more regularly arched from the tip of snout to end of dorsal; anterior profile convex in front of dorsal, nearly straight on head; caudal peduncle rather long and slender, its depth 1 to 1.33 in its length; interorbital very convex, the bony portion 3.5 in the head (2.5 in *balzanii*); cheeks with 3 series of scales on their upper part, the lower portion naked (about 7 series in *balzanii*); 7 or 8 tubercular gillrakers on lower half of arch; a single complete series of scales on the subopercle with a few scales forming an imperfect second series below them. Eye 4 to 4.5 in head; nares half way between tip of snout and eye (distance of nares from tip of snout 1.6 in their distance from eye in *balzanii*).

Ventrals reaching the anal papilla or slightly beyond origin of anal; pectoral reaching to first anal spine or first anal ray; soft dorsal and anal high, reaching considerably beyond base of caudal; caudal lunate or but slightly emarginate, its base much less densely scaled than in *G. balzanii*; bases of dorsal and anal with few scales; fold of the lower lip not continuous.

A dark area across back in front of the dorsal; bases of some of the scales of the back frequently very dark brown; side with about 6 cross-bands, each of those on middle of side composed of double dark lines with a band of light of equal width between them; no dark spot on side; pectoral light; ventrals blue-black; dorsal dusky, with ascending light stripes which are largely replaced by light spots on the soft dorsal; caudal dusky, with round hyaline spots on the rays similar to those on soft dorsal; anal with similar but smaller and less distinct spots; no spot or ocellus on the caudal.

Type in Mus. Princeton Univ., a specimen 155 mm. long, from Buenos Aires; coll. Prof. W. B. Scott. Cotypes in Princeton and Indiana Universities (no. 11352, Mus. Ind. Univ.), 6 specimens 100 to 150 mm. long, from same locality.

Batrachops scottii Eigenmann, new species. (Plate XXIII, Fig. 8).

? *Crenicichla semifasciata* Pellegrin (not Heckel) Cichlides, 339, 1904 (Buenos Aires; Montevideo).

This species is closely related to *semifasciata* of Heckel, from which it differs conspicuously in color. *B. semifasciatus* was described from specimens collected in the Paraguay River at Caiçara in Matto Grosso. No other specimens have been found unless those recorded by Pellegrin belong to *semifasciatus*. The two species may be distinguished as follows:

a. D. XXII, 10; A. III, 7; lateral line 25 + 12; scales 56 or 57; greatest thickness 1.25 in greatest height which is 5 in the total length; depth of caudal peduncle equals five eights of the greatest depth; eye 1.5 diameters behind tip of lower jaw, 5.5 in head; suborbital one third the diameter of eye; peropercular margin turned forward; a dark band from eye to opercle, 7 or 8 dark lines from base of dorsal to middle of side, darkest below lateral line and fading out below; a dark ocellus on base of caudal; each scale of the side yellow, with a dark brown margin; fins without spots, ... *semifasciatus*.

aa. D. XXI or XXII, 13; A. III, 8 or 9; lateral line 25 + 14; scales 57; head 3.4 to 3.5; depth 4 to 4.5; greatest thickness 1.5 in greatest depth; depth of caudal peduncle 2 in greatest depth; eye 2.5 diameters behind tip of lower jaw, 5.5 to 7 in the head; preorbital 1 (in adult) to 2 (in youngest) in the eye; peropercular margin slanting obliquely backward;

tips of dorsal and anal reaching caudal; a dusky shade from eye to edge of opercle continued faintly in the young to the caudal; very conspicuous markings extending from eye down and back; they consist first of a black blotch followed by two or four parallel black lines, these followed after an interval by one to 5 similar ones and these again in some specimens by other similar ones; back to the lateral line in the young with very obscure cross shades; side, and in the adult the back also, with light stripes along the middle of the scales and prominent zigzag dark stripes between each two rows of scales; entire dorsal and base of anal spotted; caudal obscurely spotted; pectorals and ventrals plain.

The black markings below the eye are so unique and conspicuous that they attract the attention at once and give the impression of India ink pen strokes.

I take great pleasure in dedicating this species to the collector, Prof. W. B. Scott, of Princeton University.

Type in Mus. Princeton Univ., a specimen 280 mm. long, from Buenos Aires; coll. Prof. W. B. Scott. Cotypes in Princeton and Indiana Universities (No. 11420, Mus. Ind. Univ.), 145 to 165 mm. long, from same place.

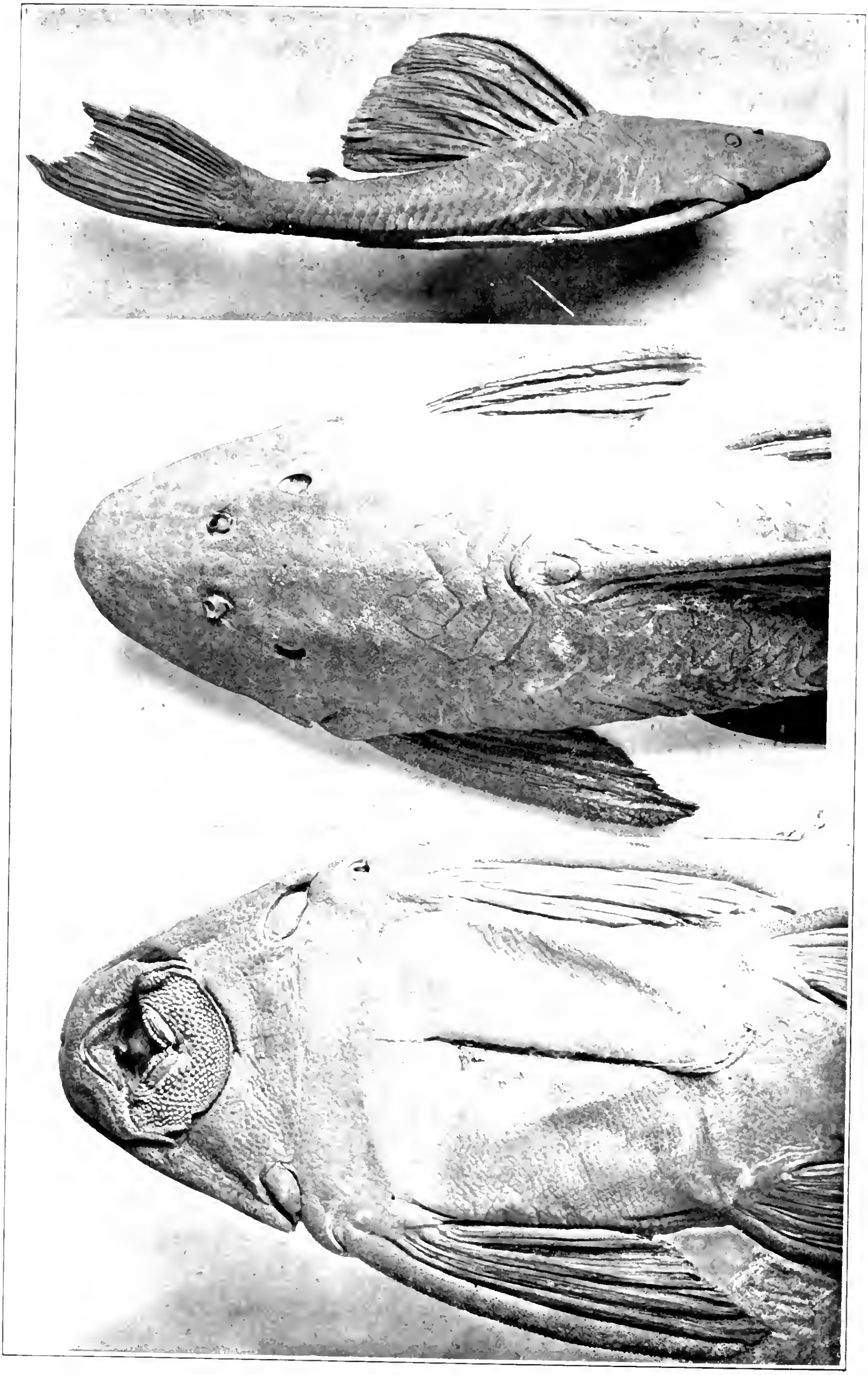
PLEURONECTIDÆ.

Achirus lineatus (Linnæus).

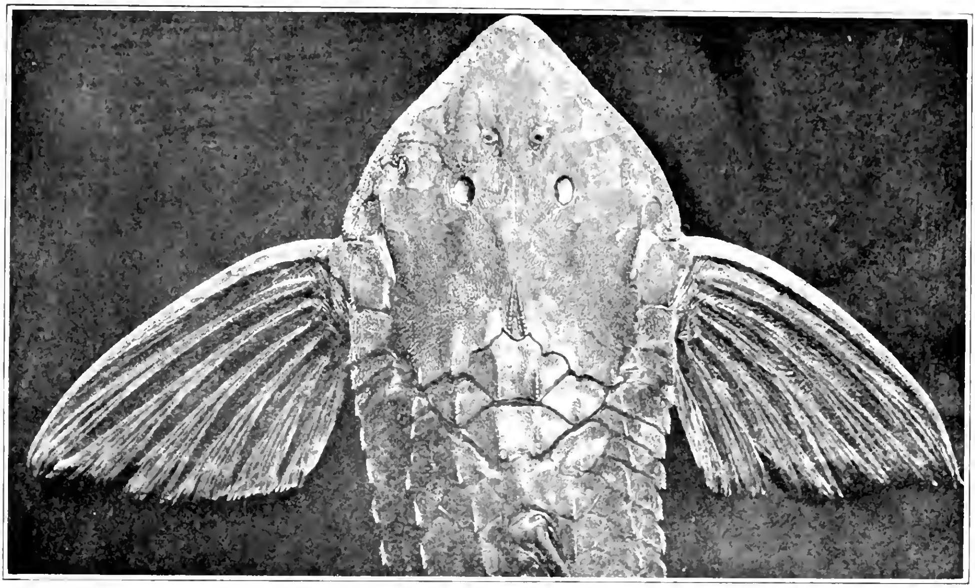
Two specimens.

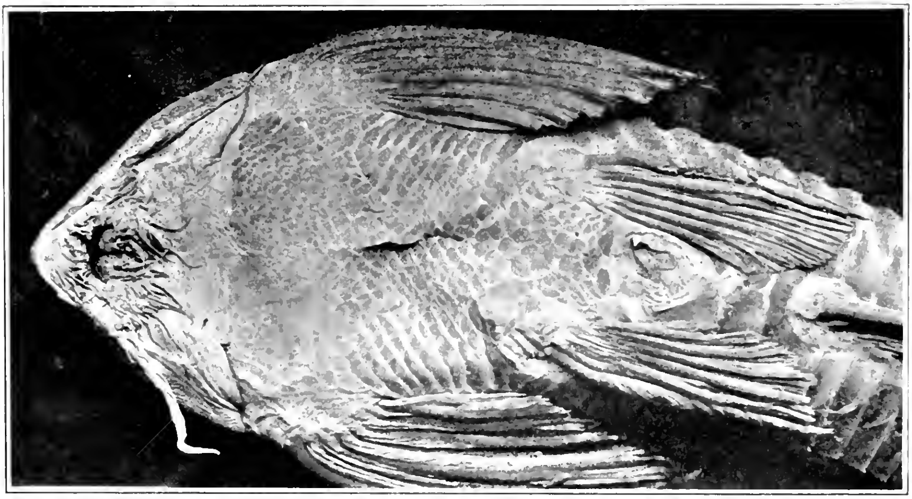
EXPLANATION OF FIGURES.

1-3. *Plecostomus laplatæ* Eigenmann, type.
4-5. *Loricaria vetula* Cuvier & Valenciennes.
6. *Pomolobus melanostomus* Eigenmann, type.
7. *Geophagus australe* Eigenmann, type.
8. *Batrachops scotti* Eigenmann, type.



FIGS. 1-3. PLACOSTOMUS LAPLATÆ EIGENMANN, NEW SPECIES.





FIGS. 4 & 5. LORICARIA VETULA CUVIER & VALENCIENNES.

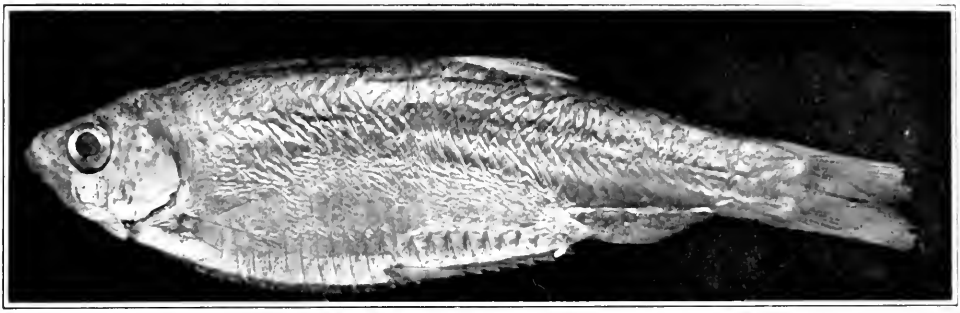


FIG. 6. POMOLOBUS MELANOSTOMUS EIGENMANN, NEW SPECIES

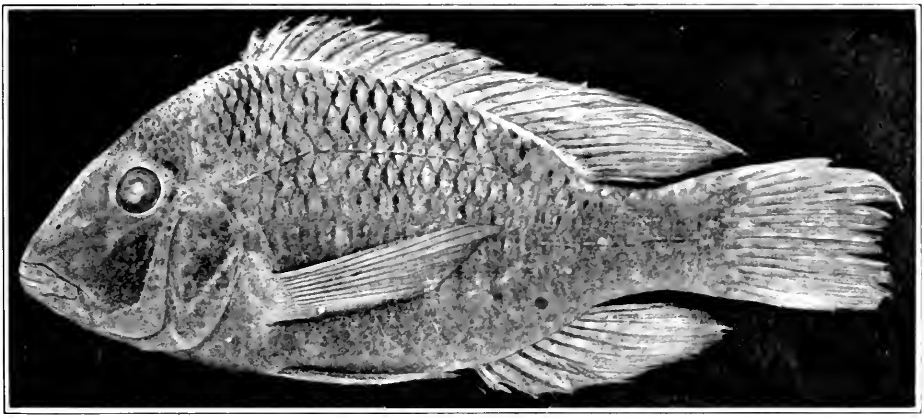


FIG. 7. GEOPHAGUS AUSTRALE EIGENMANN, NEW SPECIES.

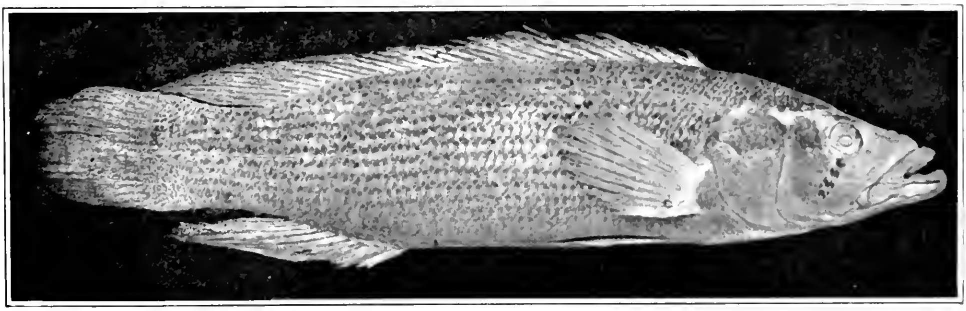


FIG. 8. BATRACHOPS SCOTTII EIGENMANN, NEW SPECIES.

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HISTOLOGY AND DEVELOPMENT OF THE DIVIDED EYES OF CERTAIN INSECTS.

BY GEORGE DANIEL SHAFER.

EXNER, 1891, Zimmer, 1897, and Kellogg, 1898, 1900, and 1903, have discussed the divided-eye condition of certain crustaceans and insects. It is the purpose of the following paper:

1. To describe the histological structure of the divided compound eyes of *Sympetrum corrupta*, *Anax junius*, *Bibio hirtus*, two species of Blepharoceridæ and two species of *Callibætis*.
2. To describe the development of the large-facetted area of the eye in *Callibætis* and *Sympetrum corrupta*.
3. To refer briefly to the significance of the divided-eye condition in these eyes.

This investigation was made in the Entomological Laboratory of Stanford University, under the direction of Prof. V. L. Kellogg. I wish here to thank Professor Kellogg, Mr. Doan and Miss McCracken for help in the laboratory; also Professor Aldrich, Dr. Needham and Mr. Grinnell for identifying some of the material used.

SYMPETRUM CORRUPTA Hagen.

The compound eyes of *Sympetrum corrupta*, as shown in Fig. 1, Plate XXIV, are divided by a curved line into almost equal upper and lower parts. The lower half of the eye is dark and a good hand lens shows it to be made up of very small facets. The upper half is lighter in color and made up of larger facets. Longitudinal sections of the ommatidia of both these parts of the eye may be obtained by making vertical cross-sections, or by making longitudinal sagittal sections of the head. Fig. 2 shows a vertical section passing through both the upper and the lower portions of the eye. Most of the eye elements are cut longitudinally. A few in the region *a*, of the upper part of the eye are represented in diagonal cross-section. A glance at the figure makes clear the deeply pigmented condition of the narrow eye elements of the lower half as contrasted with the less pigmented larger elements of the upper half of the eye. There is no gradual transition in the pigmentation or in the size of the eye elements. The line of division is as sharp within the eye as it appears in the outside facet view. No septum marks the division; but with the first larger ommatidial element, passing toward the upper part of the eye, the deep black iris pigment stops and a brownish less dense iris pigment begins. This is true also of the deeper seated pigments, but these are a little darker in color in the large element half of the eye than in the iris pigment in the same part. Figs. 3 and 4 show some of the details of structure of the upper and lower parts of the same eye. The corneal region is made up of hexagonal lens-like segments each of which may be called a corneal lens. In vertical section each lens is seen to consist of a thin cuticular portion and a thicker stratified layer just beneath. The cuticular portion takes and retains nuclear stains well. The under portion takes stains readily enough but gives them up easily. No hypodermal cells or nuclei have been observed in the eye, but the bases of the pseudocones lie close to the under portion of the lens. The cells which compose these pseudocones have lost their identity entirely in the lower portions, and nearly so in the upper, outer, larger portion of the cones. However, in the extreme upper ends, the cone cells have each secreted a denser curved plate-like body within itself, and this stains deeply. Four of these may be found in each pseudocone. Two are shown in the longitudinal sections at *cn*. Each plate appears to surround a cell nucleus. In the case of the pseudocones of the small ommatidial elements, cross-sections made just below the little plates mentioned show four cells as represented in

Fig. 3, *B*. Two of these cells are always larger than the other two. Two of the plates of the pseudocones are always larger when four are seen — sometimes only 2 can be found. The pseudocones of the large ommatidia are wider, longer and farther apart than those of the small ommatidia. Both have relatively the same shape. The inner portion of each pseudocone tapers nearly but not quite to a point. Each inner end is really truncate and appears to have a funnel-like opening. Extending along the line of the longitudinal axis of the pseudocone and beginning immediately beneath the truncate cone tip is the retinula. This has a darker rhabdome portion along the axis from the tip of the pseudocone to the basement membrane. The axis itself, however, is occupied by a very narrow light band. Often, if the sections are jammed a little in the cutting, the rhabdome portion takes a wavy form as shown in the fragment at *w* (Fig. 4, *A*). The retinulæ of the large ommatidia are wider, but no longer than those of the small ommatidia.

Immediately beneath the basement membrane, in all parts of the eye is a network of tracheal vessels, 2 of which are shown in cross-section at *tr* (Figs. 3, *A*, and 4, *A*). Under the tracheal network is a narrow layer of retinular-like bodies *rb* (Figs. 3 and 4, *A*). These bodies have their long axes parallel with each other, but not always exactly parallel to the retinular axes above them. Some sections show a definite fibrous or continuous cell connection between the ends of the retinula at the basement membrane *bm*, and the upper outer ends of these retinular-like bodies. These connecting strands are always narrower than either the retinula or the retinular-like bodies, and they curve around the tracheæ, often, in order to make the connection. It seemed impossible to demonstrate the presence of retinular nuclei satisfactorily in old adult eyes used, but they were easily shown at *rn* (Fig. 4, *A*), in the eye of a young insect dissected from an old nymph case when the adult was just ready to issue.

Here and there along the upper part of some cells of the retinular-like bodies large nuclei have been found (*n*, Figs. 3 and 4, *A*). These nuclei appear larger than the ordinary pigment cell nuclei. Whether they have any special significance has not been determined. Cross-sections of the retinular-like bodies under the large ommatidia are shown in Fig. 4, *B*. Regularly, they appear as shown, with 4 cells — one large, 2 smaller and 1 very small cell. Cross-sections of the corresponding retinula above show that the separate cells there have almost lost their identity in the adult eyes; but in the very young teneral adult 4 nucleated cells may be seen (Fig. 4, *C*) in cross-section. From the lower part of the retinular-like bodies extend branching tree-like nerve fibers which break up into brushes of fibrils at their inner ends.

The pigment of the region of the small ommatidia may be described under 4 heads:

1. That grouped in dense black masses around the pseudocones and already named the iris pigment. It is contained in 2 kinds of cells called by Grenacher, 1879, primary and secondary pigment cells. The secondary cells are long, narrow and closely packed around and among the pseudocones — their axes lying parallel with the cone axes. Around cross-sections of the upper parts of the cones 20 to 22 of these pigment cells may be counted in a circle touching the outer boundary of the cone (Fig. 3, *B*, *sip*). In the sections near the inner tapering tip of the cone as few as 14 pigment cells have been counted touching the cone. Below that the separate cells could not be counted, but they are packed all the way between the different pseudocones, being densest on the middle plane of the cone. There are 2 chief pigment cells for each eye element. They are short and thin and the 2 encircle the cone tip (Figs. 3 and 4, *A*).

2. Pigment occupies the retinula and the cells between the retinula from the apex of the cones to the basement membrane. Beginning near the distal ends of the retinula this pigment becomes denser and denser toward the basement membrane until a plane (*ec*, Fig. 3, *A*), is reached a little below the middle of the retinula. From this plane to the basement membrane the pigment is again less dense.

3. A band of dense black pigment lines the basement membrane and on the inner side of this membrane, extends down to the distal ends of the retinular-like bodies. It is densest immediately beneath the basement membrane, around the trachea and

in a thin band, *i*, which marks its lower boundary along the distal ends of the retinular-like bodies.

4. A black pigment similar to that along the retinula surrounds the retinular-like bodies, and ends at the proximal ends of these bodies in a narrow densely black band of pigment, *gp* (Figs. 3 and 4, *A*). This in *Sicyonia sculpa*, has been named the pigment or tapetum sheath of the optic ganglion by Exner, 1891.

The same description of pigment holds for the large ommatidial part of the eye except that the iris pigment and retinular pigment in this case are brownish yellow and everywhere in this part of the eye the pigment is very much less dense than in the small ommatidial region.

ANAX JUNIUS Drury.

The facets of the compound eyes of the male of *Anax junius* are not all of the same size. Facets may be found that differ as much in size as those of the different areas on the eye of *Sympetrum*, but no line divides the eye of *Anax* into 2 regions. In this case the larger facets are found on the upper and inner surfaces of the eyes, and the smaller facets on the outer lower margins. The 2 sizes grade into each other. It was not until sections were made of the eye that this condition was noticed. Fig. 12 was made from a cross-section of the head of a male *Anax*, cut in a plane passing through the ocellus and perpendicular to the facet area of the compound eye. The figure shows clearly this gradation of the large facets on the upper inner part of the eye into the smaller ones at the outer margin. As is shown also, along with this gradation in the size of facets, the elements of the ommatidia pass through a like gradation in size and length. Moreover, a similar but reverse condition holds for the pigmentation in this eye. Around the smaller shorter elements at the outer margin of the eye the pigment is densest and occupies the whole length of the retinulæ. Passing toward the inner part of the eye, the pigment becomes less and less dense around the proximal ends of the retinulæ until in the region of the largest ommatidia almost no pigment is present except the iris pigment. Other than this difference in size and pigmentation, the large and small ommatidia are very similar as may be seen in Figs.

13, *A*, and 14, *A*. Beneath the corneal lenses and lying above the distal ends of the pseudocones is a distinct hypodermal layer. In longitudinal section, two apparent nuclei are present above each pseudocone, *sn* (Figs. 13 and 14, *A*). The pseudocone itself has a structure similar to that of *Sympetrium*, its upper part showing still the boundaries of 4 cells which may be seen in cross-section (Fig. 13, *C*).

Each retinula is made up of 4 retinular cells which enclose a single rod-like rhabdome, *rb* (Figs. 13, *A* and *B*, and Figs. 14, *A* and *B*). The retinular cells of the ommatidia from the 2 extreme parts of the eye described vary, somewhat in shape (as seen in Figs. 13, *B*, and 14, *B*) but there are always the 4 cells present, each with its nucleus (Fig. 13, *B*). Extending up between the different retinulæ and lying parallel with them are many open spaces or lumina (Fig. 13, *A*, *l*). The smaller ends of these extend even between the distal parts of the pseudocones and their surrounding pigment cells (Fig. 13, *C*, *l*). The iris pigment of this eye occupies cells of 2 types called by Grenacher and others the primary or chief pigment cells and the secondary pigment cells. Two primary pigment cells surround the small proximal end of each pseudocone (Figs. 13 and 14, *A*, *cip*). These cells are shown as they appear in cross-section in Fig. 13, *D*, *cp*. The nuclei of these cells have not been satisfactorily seen although the nuclei of the retinular cells and secondary pigment cells in the same sections were deeply stained and easily seen. Eight to 10 pigment cells have been counted around each pseudocone. They are longer and more slender than the primary cells around which they lie, and they extend down a little between the distal ends of the retinulæ (Figs. 13 and 14 *A*, *nsp*). As has already been said, the pigmentation of the smaller outer elements of the eye occupies the whole length of the retinulæ. This pigment lies in the retinular cells themselves, and it is densest always in the distal half of the cells.

BIBIO HIRTUS Goef.

The compound eyes of the male *Bibio* are much larger than those of the female. They nearly touch along the narrow front and occupy almost the entire head. The whole facet area is thickly covered with slender hairs[1] and the remarkable double character of the eyes may be easily overlooked.

Indeed, it is only upon careful observation that the densely black, small, facetted area is seen at all. If the head of the fly is tilted back by lifting up the proboscis, a hand lens will show the narrow black small facetted area on the extreme ventral surface of the compound eye. This area is scarcely one sixth that of the entire eye and is separated from the large facetted upper surface by a narrow groove or offset. Fig. 11 shows the position of the small facetted part of the eye. Fig. 8, perhaps, shows better the relative extent of the 2 kinds of elements as seen in longitudinal sagittal section. As shown in this Fig. 8, the elements beneath the small facetted region are little more than half the length of those under the large facets. Moreover, the part occupied with small elements is densely pigmented. The rest of the eye has but little pigment.

The elements of a large ommatidia consist of a thin cuticular hexagonal facet, a pseudocone, a retinula, and iris pigment cells surrounding the pseudocone. The cells of a pseudocone cannot be distinguished from each other in the outer large part of the cone. The lower truncate or slightly rounded apex of the cone is a little denser than its upper part and this denser portion stains more readily. Here the 4 cells making up the cone can be distinguished, each having its nucleus (Figs. 9 and 10, *cn*, and Fig. 9, *B*). Cross-sections of the distal ends of 3 neighboring retinulæ are shown in Fig. 9, *C*. Each retinula is made up of 6 cells arranged in a circle around a seventh cell in the center. The inner borders of each of the 6 cells has a rounded deeply stained rhabdomere (as this part of the eye was named by Grenacher, 1879). The rhabdomere of the seventh cell occupies the axis of the retinula. At their distal ends the 6 retinular cells overlap entirely the rounded denser apex of the pseudocone, *d* (Figs. 9, *A*, and 10). The seventh cell, together with its rhabdomere and those of the other 6 cells, stop snugly against the inner end of the pseudocone. Near the middle part

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[1] Whether these apparent tactile hairs, which cover the eye of *Bibio* so densely and are found on the eye of *Blepharocera* less abundantly, are really supplied with tactile sense organs has not been determined by me.

of the retinula this seventh cell, which is entirely surrounded at its distal end, is found squeezed out between the other 6 retinular cells and is not here completely surrounded by them (Fig. 9, *E*). This condition holds for the retinula for its entire proximal half. It is true also that this seventh cell crops out in every case on the same side of the retinula, namely, on that side of the retinula turned toward the inner ventral angle of the eye. Fig. 9, *D*, shows 3 adjacent retinulæ in cross-section in the region of the nuclei. These nuclei are long-elliptical in shape (Fig. 9, *A*, *rn*), and in cross-section they are not all the same size, since some are cut near the middle and some near their ends. In the cross-section of every retinula, however, the nucleus of the narrow seventh cell may be found near its outer margin (Fig. 9, *D*, 7*n*). The rhabdomeres are all smaller at the proximal end of the retinula, but they are always 7 in number, the odd one occupying the axial position at the inner part of the narrow seventh cell. These facts, taken with that of the constant presence of the seventh nucleus, make it certain that this peculiar seventh structure is truly a retinular cell whose distal end is entirely surrounded by the corresponding ends of its 6 companions. The proximal ends of the retinulæ are bounded by a very thin basement membrane, *bm* (Figs. 9, *A*, and 10). A little beneath this membrane spreads a somewhat thicker granular tapetum, *tp* (Figs. 9 and 10), and immediately under this is a network of tracheæ, *tr*. Leading from the inner proximal end of each retinula through the basement membrane, the tapetum, and between the tracheæ is a narrow bundle of nerve fibers, which are soon lost in a fine granular layer, *gr* (Figs. 9, *A*, and 10), just within the trachial network.

The iris pigment of the large element part of the eye is comparatively slight. It is contained in narrow pigment cells, *nsp* (Figs. 9 and 10), which surround the pseudocones and extend a little way down between the retinulæ. Fig. 9, *C*, *sip* shows the arrangement of these cells between the retinulæ. The proximal three fourths of the retinulæ have no pigment cells around them at all and the retinulæ themselves touch each other (Fig. 9, *D*).

The conditions described above also hold for the small eye elements with the following exceptions. The cuticular facets of this portion of the eye are much denser than those above the large elements. The iris pigment is black and extremely dense. A heavy black pigment occupies the retinular cells throughout their entire length. Drawing 10 was made from a section that had been depigmented with conc. nitric acid and absolute alcohol, equal parts. The tapetum and the basement membrane in this part of the eye are always a little farther apart than in the large element region. Under the trachea and between the nerve strands that lead down from the retinulæ of both the large and the small elements are numerous large round or oval nuclei which stain deeply (*gn*, Figs. 9 and 10, *A*). No pigment is present around these nuclei. It might be added here that cross-sections of the retinulæ of the small ommatidia did not show the number of retinular cells present so clearly as those cut across the large ommatidia. Judging from the number of retinular nuclei however, the number of retinular cells is the same in the retinulæ of both regions of the eye.

[1]BLEPHAROCERA CAPITATA Loew.

Kellogg, 1903, has called attention to the fact that both males and females of the Blepharoceridæ have divided compound eyes. In all the genera described by Kellogg the large facetted area of the eye is dorsal, and the small facetted deeply pigmented area of the eye is lateral. Moreover, the dorsal area of the female eye is greater than that of the male. Males and females of species representing 2 genera (*Blepharocera capitata* and *Bibiocephala elegantulus*) were studied by me. The histological structure of the eye elements in the 2 genera and in both sexes is practically the same. The description and drawings given here are taken from *Blepharocera capitata*. Fig. 30 is a microphotograph showing the optic ganglion, as well as the dorsal and the lateral eyes of the right side of the head of this species. It will be convenient hereafter to speak of the two areas as the dorsal and the lateral eyes since they are separated from each other by a narrow but distinct groove and the outer lobes of the

[1] I am glad to make reference to a recent preliminary note on the "Morphology and Development of the Divided Eyes of *Blepharocerca tenuipes*" by Dr. Wm. A. Riley, in *Science*, Sept. 7. 1906.

optic ganglion beneath each area are distinct. The corneal lenses over the greater part of the dorsal eye have been torn from this section. The remaining 2 entire elements, however, show the ommatidia in this dorsal eye to be about two and a half times the length of those in the lateral eye. The lens and the pseudocone of a dorsal ommatidia are continuous. That is, the inner surface of the corneal lens is not noticeably separated from its adjoining cone beneath. This is easily seen in microphotograph 29 and Fig. 15. The rounded apex of each of the pseudocones is denser than the rest of the cone and stains readily. Cross-sections through this denser apex show the cone to be made of 4 cells and the nucleus of each cell is found in this denser part (Fig. 15, *A*). In the outer larger part of the cone the cell walls cannot be distinguished. Surrounding the tip of each one are 2 very thin primary iris pigment cells (Fig. 15, *A*, *cip*). Outside of these, sheathing the distal part of each cone and extending down between the retinulæ are 22 to 24 slender secondary pigment cells (Fig. *A*, *sip*, and Fig. 29, *sip*). A retinula in this eye is composed of 7 cells — 6 entirely surrounding the seventh for its entire length. The rhabdomere of each cell is distinct (Fig. 15, *C*, *rb*). The distal ends of the retinular cells abut closely against the rounded cone tip and in their extreme proximal ends just above the basement membrane, lie the 7 large retinular nuclei (Fig. 15, *A*, *rn*). A definite bundle of nerve fibers leads from the base of each retinula through the basement membrane (Figs. 15, *A* and 29, *nj*).

The number and position of the cells in the ommatidia of the lateral eye of this fly is the same as that just described for the dorsal eye. The corneal lenses of the lateral eye are more distinctly formed and the retinular cells as well as the iris pigment cells (primary and secondary) are densely packed with pigment. In the dorsal eye the pigmentation in the iris is very slight and it is absent in the retinular cells of this eye.

CALLIBÆTIS HAGENI Etn.

Several references have already been made by different investigators to the condition of the compound eyes of certain mayflies (Pictet, 1845; Ciaccio, 1880; Carriere, 1893; and

Zimmer, 1897). The large facetted dorsal eyes have been called turban eyes and the smaller deeply pigmented eyes, the lateral eyes. The females have only the small lateral pigmented eyes. Zimmer, 1897, has given the histological structure of the eyes of 7 genera of mayflies according to Pictet's classification and he discussed also the physiological significance of the turban eyes of these insects.

The structure of the eyes of *Callibætis hageni* differs in only a few points from that given by Zimmer for *Cloe fuscata* Pict. It will be well, however, to describe briefly the structure of the eye in the adult male of *Callibætis hageni* before taking up the development of the turban eye in that species. Microphotograph 24 (a cross-section through the head) shows the relative size, position, pigmentation and the general structure of the right turban and lateral eyes. The large and small eye elements are entirely separated here by a deep, rather wide, groove. A single partly divided optic ganglion lies beneath the right turban and lateral eyes and a similar ganglion beneath the left eye *opg* in Figs. 23, 25 and 26. Drawings in Fig. 16 show more clearly the structure of 2 entire elements of the turban eye. The light-gathering or dioptric apparatus consists of a corneal lens, 16 *Ac*, a cone, *Aco*, and a hypodermal space between the lens and the cone, 16 *Ahs*. The cornea is made up of rather distinct convex lenses, *Ac*, which are continuous with each other. The outer third of each of these lenses appears to be denser than the inner two thirds. The cone is composed of 4 crystaline bodies so closely associated along their inner faces that they appear in all except cross-sections as one solid cone body with its slightly convex base facing the cornea. This is the *eucone* type of Grenacher, 1879. The outer faces of each crystaline body are surrounded by the less dense protoplasm of the mother cone cell and in this protoplasm just distal to the base of the cone are the cone cell nuclei (Fig. 16, *A*, *cn*). The cross-section made just distal to the cone base *B*, shows the 4 cone cells and their nuclei. The hypodermal space contains no nuclei, and it is filled by transparent fluid only. Zimmer demonstrated 2 nuclei in this space for *Cloe*. He did not figure the nuclei in this space for the eye of *Bætis cerca* Pict., or for that of *Chiro-*

tonetes ignotus Walk., but speaks of the space nevertheless as being formed by 2 hypodermal cells.

Closely surrounding the entire length of the cone cells and the hypodermal space are 20 to 22 secondary pigment cells (Figs. 16, *A*, *nsp* and *B*, *sip*). No primary pigment cells are present. The distal ends of the secondary pigment cells touch the cornea and their proximal ends are in contact with the outer or distal retinula (Fig. 16, *A*, *drn*). It is proper to speak of a distal retinula in this eye because there is also an inner or proximal retinula *prn* in each ommatidia — the 2 retinular parts being connected by a very delicate strand (*rs*, Fig. 16, *A*). Both proximal and distal retinulæ are composed of 7 retinular cells. Fig. 16, *C*, shows the 7 short distal retinular cells and their nuclei. These cells surround the tip of the cone rosette fashion. The proximal retinula is of about the same length as the connecting strand. Fig. 16, *D*, shows the 7 nucleated cells of this part in cross-section, and Fig. 16, *E*, is a similar section near the middle part of a proximal retinula. The rhabdome in its cross-section here is seen to be a 7-pointed star within a circle which bears on its circumference 7-knobbed projections, *w*, radiating along the same lines as the points of the star and lying between the boundaries of the retinular cells. The knobbed parts, *w*, are the *secondary rods* of Zimmer, 1897. This large surfaced rhabdome terminates a little short of the outer end of the proximal retinula in a single blunt rod tip as shown in Fig. 16, *D*. The outer end of the retinula therefore appears filled with transparent liquid. Zimmer has described these transparent ends in *Cloe* as "bladder trachea," and he figures no nuclei in them. My sections of the turban eye of *Callibætis* show the 7 nuclear structures present always, as represented in Fig. 16, *D*. The inner faces of the distal retinular cells bear an extremely thin rhabdome plate next to the tip of the cone (Fig. 16, *C*, *drb*). Near the distal ends of the proximal retinula the connecting strand, *rs*, breaks up, Fig. 16, *A*, into smaller strands which seem to be continuous with the 7 secondary rods, *w* of Fig. 16, *E*. The connecting rods may be seen in the photograph no. 27. The space around the rods, between the distal and proximal retinulæ, appears to be filled with an almost transparent liquid —

tiny pigment granules being present in some sections. But these may have been carried there by the razor. Upon the basement membrane are short pigment cells which are sometimes above the membrane between the proximal ends of the retinulæ; sometimes beneath the membrane between the nerve fibers, *nf*; and sometimes partly above, partly beneath the membrane. A second delicate membrane *k* marks the lower limit of migration of this pigment.

Fig. 17, *A* and *B*, show the structure of two ommatidiæ in the lateral pigmented eye of *Callabætis*. One of the elements is represented in its normal pigmented condition, the other depigmented so that the position of nuclei may be seen. The corneal lenses in this eye are thin as compared with the turban eye and their inner faces fit snugly upon the distal bases of the cones. These cones are not as dense as those of the large elements just described. They are 4 in number, however, and appear to have the same density throughout. The cone cell nuclei *cn*, are found in the extreme distal base of the cone. In depigmented sections the nucleated distal ends of the retinular cells may be seen touching the tip of the cone. There are 7 of these retinular cells surrounding the rod-like rhabdome as represented in Fig. 17, *B*. No primary iris pigment cells are present, and there are but half the number of secondary pigment cells found in the turban eye. The 11 cells (Fig. 17, *B*), which are present, however, are densely pigmented, and they overlap the cones and the upper retinulæ. The retinular cells are deeply pigmented through their entire length. Just beneath the basement membrane is a narrow almost transparent granular tapetum and under that an irregular broader band of pigment. So far, this pigment has not been observed above the basement membrane in the lateral eye. Nerve fibers *nf* (Fig. 17, *A*) lead from the inner ends of the retinula through the tapetum and the underlying pigment.

Another species of *Callibætis* (probably *californica*) was studied in connection with *hageni*. The latter is the larger of the 2 species but the eye structure of the male of this smaller form differs from that just described for *hageni* in but two particulars that are worth attention:

1. The cornea of the turban eye of the smaller species is thinner and its lenses less convex than those in *C. hageni*.

2. The retinular connecting strands in the eye of the smaller species are about one and one third times longer than the proximal retinulæ. That is, the strands in this species are relatively a third longer than they are in the eye of *C. hageni*.

DEVELOPMENT OF THE LARGE FACETTED EYE AREA (TURBAN EYE) IN CALLIBÆTIS Etn., AND IN SYMPETRUM CORRUPTA Hagen.

As is well known, the young of dragonflies and mayflies pass through incomplete metamorphoses in their post-embryonic development, and the young of both live in fresh water. Young nymphs of both species of *Callibætis* and of *S. corrupta* were collected from still or slowly running water near Stanford University in March and reared to the adult stage in the laboratory. In this way material was obtained representing different stages in the development of the large facetted-eye areas. Carriere, 1886, first briefly called attention to the origin of the elements of the turban eye of mayflies from elongated epithelial cells near the dorsal edge of the lateral eye. His observations in the main agree with the following account.

All nymphs of *Callibætis* under 4 mm. in length have only lateral pigmented eyes. When the nymphs are 4 to 5 mm. long however, the lateral eyes have about completed their development. Then a narrow yellowish or light brown band appears above the dorsal edge of each lateral eye of the male nymphs. This marks the first noticeable beginning of the large facetted eye, and cross-sections made of the head of such a nymph show the hypodermis, just beneath the light brown band, to be made up of modified long slender hypodermal cells with a second layer of much shorter cells lying against their inner bases. Already 2 membranes very close together are forming here. One of these membranes (Fig. 21, *A*, *k*), marks the inner boundary of the second layer of cells *A*, *2hn*. The other membrane *A*, *bm*, marks the inner boundary of the outer layer of modified long hypodermal cells. The nuclei of some of the cells of the second layer are above the membrane *A*, *bm*, and some are below it. These 2 membranes were found also beneath the developing unpigmented ommatidia in the upper eye of young *S. corrupta* (Fig. 7, *A*, *bm* and *k*, and Fig. 6). The upper membrane is found throughout the further development of the eye and corresponds to the basement membrane of the adult. The lower membrane, *k*, seems to be identical with the limiting membrane, *k*, of the lower pigment cells in the adult eye (Fig. 16, *A*). This second layer of cells (Fig. 21, *A*, *2hn*), then, appears to be that from which developed the lower pigment cells of the adult eye. If that is true, it is clear how it is possible for those pigment cells to migrate up and down through the basement membrane in the adult eye since that membrane is formed, in the beginning, at the inner ends of the outer hypodermal layer of cells (Fig. 21, *A*, *1hn*), around these developing pigment cells *A*, *2hn*, not as an entire or closed membrane above them.

In cross-sections of the head made at a little later stage of development, cells of this upper modified hypodermal layer just described are found to be differentiating into an outer and an inner layer so that 2 rows of nuclei may be seen above those which lie along the basement membrane (Fig. 21, *B*, *1fa*). Long undivided hypodermal cells may still be seen, however, at the edges of this developing turban eye, Fig. 21, *B*, *x*, next to the normal hypodermis, and at *y*, next to the dorsal edge of the lateral pigmented eye. In a still later stage of development (Fig. 22) the cone cells and the secondary iris pigment cells are found occupying the position of the outer row of nucleated cells described in Fig. 21, *B*, opposite *x*. The retinulæ, each already definitely formed of its 7 cells occupies the position of the second row of nucleated cells in Fig. 21, *B*, opposite *o*. Here again the elements in the middle of the developing eye (Fig. 22, *1fa*) are easily recognized as the older elements. Younger elements at the edges, *x* and *y*, are seen much below the cornea. At each molt of the growing nymph these newer elements at the margin of the eye rise to their normal position under the cornea and thus increase the size of the eye. Fig. 22 represents the stage of development of the turban eye when the nymph is 8 to 9 mm. long. The pigmented eye has practically the same size as that in the 5 mm. nymph.

None of the sections offers definite proof as to how the group of 7 retinular cells or, of the 4 cone cells, in a single element arise — whether by multiplication of a single mother cell to form each retinula for example, or by association of the original mother cells into groups of cells. The secondary pigment cells however, seem to be homologous or identical with some of the original long hypodermal cells of the first upper hypodermal layer (Fig. 21, *A*, *1hn*). The evidence for this is very strong at least, in the young nymph eye of *S. corrupta*. Fig. 7, *A*, shows a single developing ommatidia from the unpigmented area of the eye of a young nymph. In this eye, some of the cells of the first hypodermal layer separate into upper and lower parts, the latter giving rise to the retinular layer as in *C. hageni*. The upper part then becomes two-layered again and cells of the lower of these layers (Fig. 7, *A*, *npc*) become chief pigment cells; the upper, gives rise to the cone cell layer *A*, *cn*. Other cells of the first hypodermal layer appear simply to elongate. They grow very little and are seen surrounding the cone, chief pigment cells and retinular elements at *A*, *nsp*. These elongated dormant cells lie in the position of the secondary pigment cells in the adult eye. Fig. 7, *B*, shows 2 elongated hypodermal cells from the developing margin of the eye (Fig. 6, *x*). They are almost identical in size and shape with what are evidently secondary pigment cells in Fig. 7, *A*, *nsp*. As development goes on, the young short retinulæ lengthen rapidly.

In the 9 mm. stage of development of the *Callibætis* nymph, the rhabdomes are found as round rod-like bodies in all the older middle retinulæ. By the time the sub-imago is ready to issue, the cones have all practically finished development. A few very small undeveloped cones are found around the outer margin, but most of these remain still undeveloped in the adult.

Photographs 23 and 25 are made from cross-sections of the heads of sub-imagoes. The turban and lateral eyes are so definitely formed here that one might suppose development complete. Fig. 18, *A*, shows the structure of 2 ommatidia in a turban eye of a sub-imago of *C. hageni*. The corneal lens is definite but thin. The retinulæ are slightly constricted just beneath the tips of the cones. In the cross-section (Fig. 18, *B*) the rhabdome is seen to be star-shaped with the "secondary rods" beginning to develop between the boundaries of the retinular cells. Fig. 19 shows the structure of the turban eye elements of an old sub-imago of *C. californica* — *i. e.*, just before time for the adult to issue. The cornea is still thin, but the secondary pigment cells have pushed it up a little and the distal ends of these cells may be seen overlapping the bases of the cones between *c* and *cn* (Fig. 19). The retinula is now more nearly pinched into two. I was unable however, to demonstrate the presence of any nuclei in this retinula of the sub-imago below the constriction (*d*, Fig. 19) as might perhaps be expected. Otherwise the preparation for the separation of the distal and proximal retinulæ and for the formation of the hypodermal space seems complete in this stage of the development.

It is wonderful to see the rapid enlargement of the turban eyes as the adult issues from its sub-imago stage. Sub-imagoes issue from the nymphs in less than 3 seconds. The process for the adults is longer — 40 to 60 seconds — but the head enlarges immediately upon breaking through the chitin, and the turban eyes expand almost to bursting with a liquid. When photographs 24 and 26 of the adult eye are compared with 23 and 25 of the sub-imago or drawing 16, *A*, with drawing 19, it is clear what happened to permit the enlargement. The secondary pigment cells which overlapped the bases of the cones have straightened up. The cornea has been lifted to permit this and thus the hypodermal space is formed — being bounded by the cornea, the cone and the surrounding secondary pigment cells. The liquid contents of this space and the secondary pigment cells together, undoubtedly secrete the thicker corneal lens of the adult eye. That is to say, the hypodermal space is analogous to a cell in this eye, but it is in no sense homologous to a cell as is shown by its origin. Furthermore, the space between the distal and proximal retinulæ is to be directly associated with the rapid expansion of the eye of the issuing adult. The narrow connecting portion of the retinula of the old sub-imago (Fig. 19) has been stretched to form the connecting strands of the adult. It must be observed here also that the proximal retinulæ outnumber the distal in the old sub-imago and in the adult. The extra retinulæ are found in a ring around the outer margin of the eye. This has been noted by Pictet, and figured by Zimmer, 1897, and named by them the "abkonical ring" in the adult eye.

Fig. 20 shows the structure of 2 ommatidia from the turban eye of an unidentified mayfly. It has primary pigment cells. No adults of this species were reared, but the development of the eye up to the sub-imago stage is, in general, identical with the development of the eyes just described.

TABLE OF MEASUREMENTS OF DIVIDED–EYE ELEMENTS.

	Small pigmented Ommatidia.			Large Ommatidia.		
	Length. mm.	Greatest Diameter. mm.	Greatest Thickness. mm.	Length. mm.	Greatest Diameter. mm.	Greatest Thickness. mm.
1. *Sympetrum corrupta* Hagen.						
Corneal lens			0.546			0.728
Pseudocone	0.728	0.273		1.82	0.546	
Retinula	4	0.395		4	.5	
2. *Anax junius* Drury.						
Corneal lens			0.32			0.36
Pseudocone	1.09	0.205		1.5	0.45	
Retinula	4.5			6		
3. *Bibio hirtus* Goef.						
Lens and pseudocone	0.348	0.19		0.507	0.327	
Retinula	0.65	.18		1.54	0.3	
4. *Blepharocera capitata* Loew.						
Lens and pseudocones	0.3	0.2		0.7	0.42	
Retinula	.507	.18		1.33	.39	
5. *Callibætis hageni* Etn.						
Corneal lens			0.07			0.158
Hypodermal space	measured along the cone axis.					0.19
Cone	0.348	0.095		0.44	0.125	
Entire retinula	1.268	.07		2.73		
Proximal retinula				1.18	0.12	
6. *Callibætis californica* Banks.						
Cornea			0.07			0.09
Hypodermal space	measured along the cone axis.					.126
Cone	0.35	0.9		0.368	0.124	
Entire retinula	1.23	.05		3.8		
Proximal retinula				1.26	.11	

In an eye like that of *Anax* where the large elements in one part of the eye pass gradually over into smaller elements in another part of the eye, both kinds of elements seem to develop from the same center — the smaller elements being the last formed.

As has been shown in the 2 divided eyes studied (*Callibætis* and *Sympetrum*) the large ommatidial elements begin development after the pigmented lateral eye is complete. In this case the optic ganglion which has already been formed for the pigmented eye appears to bud or enlarge to receive the nerve fibers of the new eye elements. To support statements already made and for further reference the accompanying table of measurements of the eye elements of the different eyes studied is given.

SIGNIFICANCE OF THE DIVIDED EYE CONDITION.

Exner, 1891, has shown that an eye with a structure like that of the turban eye of *Callibætis* (adult) is capable of forming an image of superposition upon the proximal retinulæ as well as an image of apposition upon the distal retinulæ. By means of this repeated formation of images upon the retina, the eye with the superposition image is enabled to see, even if somewhat indistinctly, in dim light where the small facetted deeply pigmented eye could not see at all. Zimmer has shown that this is of advantage to the mayflies in mating, since the males seek the females on the wing in the twilight.

In the case of all the other large facetted eyes discussed in this paper, an image of superposition would be impossible, since the retinulæ in every case lie rather close together and are not divided into proximal and distal parts. In every eye however, the increase in the size of the dioptric apparatus accompanies the decrease in pigmentation. Both of these conditions favor the admission of more light. This would admit of a better apposition image being formed in dim light. The small dioptric apparatus and dense pigmentation accompany each other and both favor the formation of a distinct apposition image in extremely bright light. Whatever the *special* adaptation then, the divided condition of the eyes may be regarded as an adaptation of different parts of the eye to suit different intensities of light.

Moreover, it would be of as much advantage to increase the sensitive receiving surface (rhabdome surface) in the eye used in dim light as to increase the dioptric or light gathering surface. The complicated rhabdome surface of the turban eye of *Callibætis* shows this increased sensitive surface and furthermore, the retinulæ of the "abkonical ring" each have well developed rhabdomes. The rhabdomes of the larger ommatidia of all the divided eyes are larger than those of the small ommatidia.

Stanford University,
April 28, 1906.

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EXPLANATION OF FIGURES.

The sections from which the following drawings and microphotographs were made were cut 3 to 6 microns in thickness. They were stained either with Haedenheim's iron hæmatoxylin or by a modified Weigert's hæmatoxylin method. Some sections were cross-stained with good results by safranin in analin. Depigmentation was done with absolute alcohol and C. P. nitric acid, equal parts, mixed. Killing of live material was done with best results in hot Gilson's fluid. The drawings were outlined with a camera lucida.

Abbreviations not found in the following list are explained in the text itself.

c. Corneal lens (cornea).
cn. Cone-cell nucleus.
tr. Trachea.
Bm. Basement membrane.
rn. Retinular nucleus.
nsp. Nuclei of secondary iris pigment cells.
sip. Secondary iris pigment cell.
lfa. Large facetted area (dorsal eye).
sfa. Small facetted area.
tp. Tapetum.
opg. Optic ganglion.
cip. Chief iris pigment cell.
up. Dorsal part of the head.
rb. Rhabdome (rhabdomere).
sn. Semper's nuclei in hypodermis.
co. Cone or pseudocode.
nf. Nerve fibers leading from retinula.
hs. Hypodermal space.
drn. Distal retinula nuclei.
prn. Proximal retinula nuclei.
rs. Connecting retinular strand.
h. Tactile hair.
œ. Œsophagus.
tb. Turban or dorsal large facetted eye.
la. Lateral pigmented eye.
tls. Transparent liquid space around the connecting strands.
drb. Rhabdome of the distal retinula.

PLATE XXIV.

FIGS. 1 to 7. Male of *Sympetrum corruptum* Hagen.

FIG. 1. Head of adult showing relative size and shape of the large and small facetted areas, × 8.

FIG. 2. Cross-section of the right eye of adult, × 34.

FIG. 3. *A.* A few elements from the small facetted deeply pigmented part of the eye (adult), × 141.

B. Cross-section of a cone and its surrounding secondary pigment cells from *A*, × 500.

FIG. 4. *A.* Ommatidia from the large facetted part of the eye of *S. corrupta*, × 141.

B. Cross-section of three of the rhabdome-like bodies, *rb* of 4, *A*, × 500.

C. Cross-section of the retinula in the region of the nuclei from Fig. 4, *A*, × 385.

FIG. 5. Head of a male nymph *S. corrupta*, showing the triangular large facetted area forming.

FIG. 6. Cross-section of one eye of Fig. 5.

FIG. 7. *A.* A single ommatidial element from the developing large facetted area of a nymph of *S. corrupta*, × 385.

B. Two of the upper modified hypodermal cells from the margin *x* of Fig. 6, × 385.

FIGS. 8 to 11. Eye of male *Bibio hirtus* Goef.

FIG. 8. Longitudinal sagittal section of right eye, × 41.

FIG. 9. *A.* Three ommatidia from the large facetted area, × 205.

B. Cross-section of cone tip through cone nuclei and surrounding secondary pigment cells.

C. Cross-section of three retinulæ near their distal ends.

E. Cross-section of a retinula near its middle.

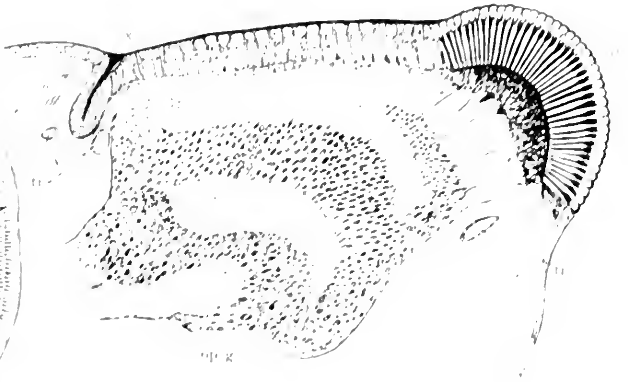
D. Cross-section of three retinulæ in region of retinular nuclei.

1

2


tr
sfa

6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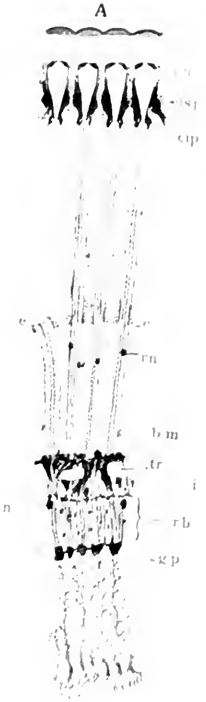
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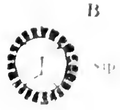
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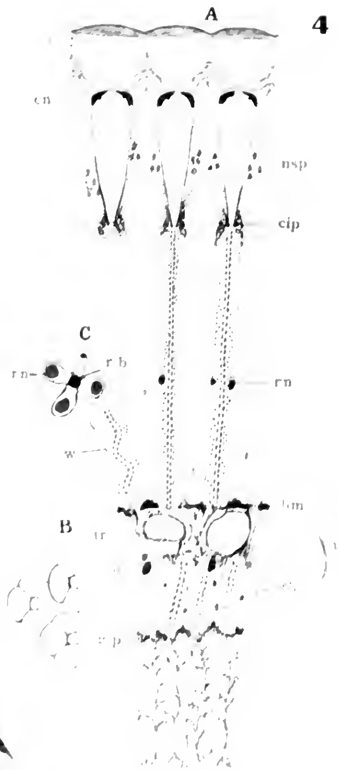
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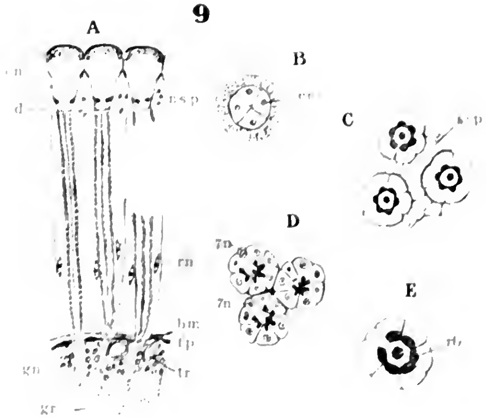
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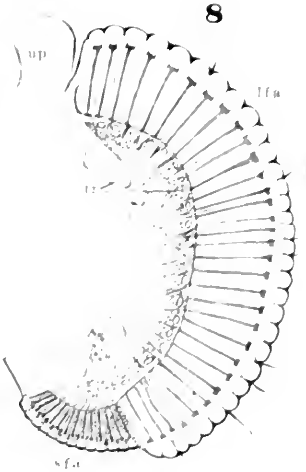
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PLATE XXV.

FIG. 10. Ommatidia from the small facetted pigmented area of male *Bibio* eye, × 900.

FIG. 11. Head of male *Bibio hirtus*.

FIGS. 12 to 14. Eye of *Anax junius*, Drury.

FIG. 12. Cross section of a single eye of adult, × 41.

FIG. 13. *A*. Two ommatidia from the upper largest facetted part of the eye, × 102.

B. Cross-section of the retinula through the nuclei.

C. Cross-section of cone and surrounding secondary pigment cells and lumina.

D. Cross-section of cone tip showing surrounding primary or chief pigment cells and secondary pigment cells.

E. Cross-section of three retinulæ and enclosed lumina.

FIG. 14. Two ommatidia from the smallest facetted part of the eye, × 102.

FIG. 15. Eye of *Blepharocera capitata* Loew.

A. Two ommatidia from the large facetted division of the eye (dorsal), × 205.

B. Cross-section through tip of cone showing four cone cells with their nuclei and the surrounding secondary pigment cells.

C. Cross-section of a retinula showing the rhabdomeres.

FIG. 16. Adult eye of a male *Callibœtis hageni* Etn.

A. Two entire ommatidial elements from the turban or dorsal eye and parts of two proximal retinulæ whose corresponding cone elements are not shown, × 385.

B, *C*, *D*, and *E*. Cross-sections of corresponding parts of Fig. *A* as indicated by the lines.

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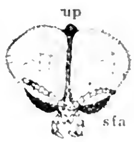

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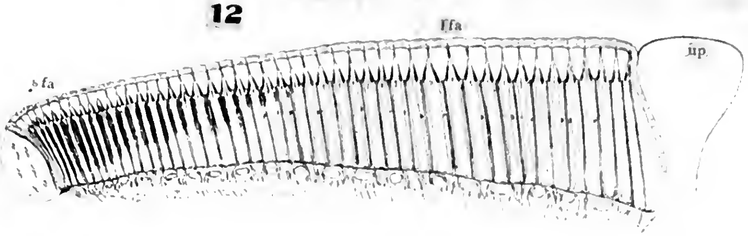

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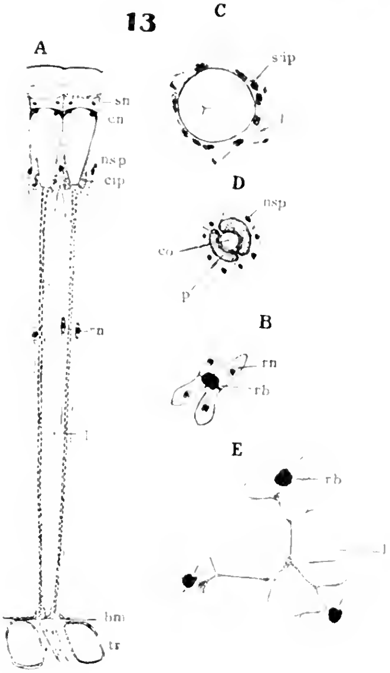

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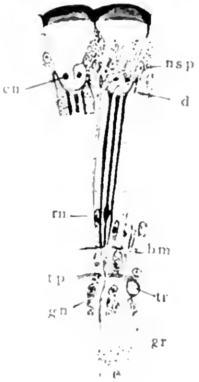

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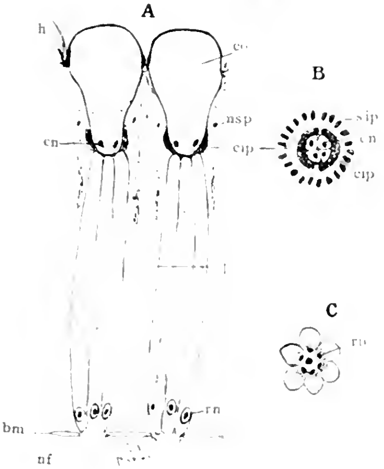

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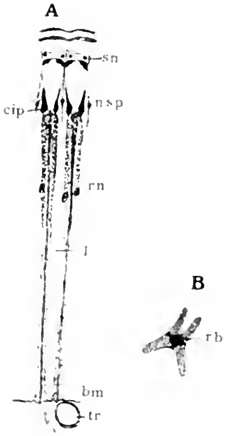

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PLATE XXVI.

FIG. 17. *A*. Two ommatidia from the lateral pigmented eye of adult male *C. hageni* Etn. One element is represented as depigmented, × 385.

B. Cross-section of retinula of *A*.

FIG. 18. *A*. Two ommatidia of a turban eye of a male subimago of *C. hageni* Etn.

B. Cross-section of retinula of *A*.

Fig. 19. Two ommatidia from the turban eye of a male subimago of *C. californica* Banks. An old subimago just before adult was ready to issue, × 385.

FIG. 20. Two ommatidia from the turban eye of male subimago of a mayfly of unknown species showing chief pigment cells. Adult of this species was not reared.

FIGS. 21 to 22. Eye of nymph of *C. hageni* Etn.

FIG. 21. *A*. A small part of the earliest developmental stage of the turban eye of *C. hageni* observed.

B. Entire eye of a young male nymph at a little later stage of development than *A*, *i. e.*, nymph 5 mm. long, × 120.

FIG. 22. Entire eye (turban and lateral) of a male *C. hageni* nymph 8 to 9 mm. long, × 120.

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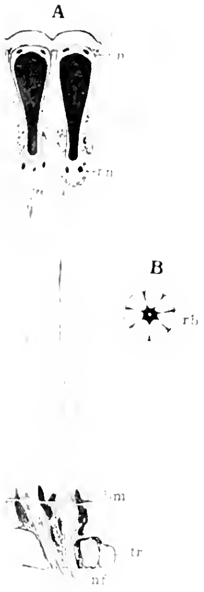

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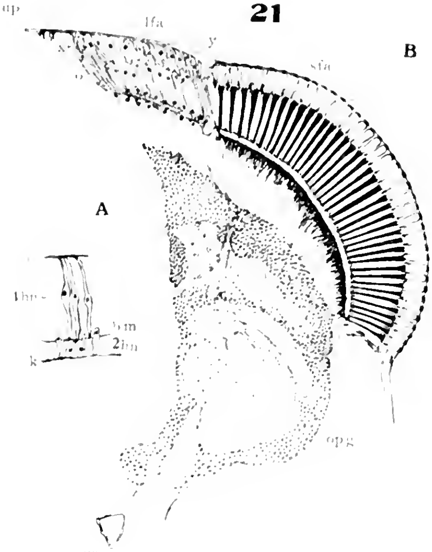

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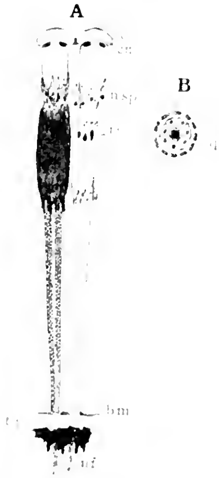

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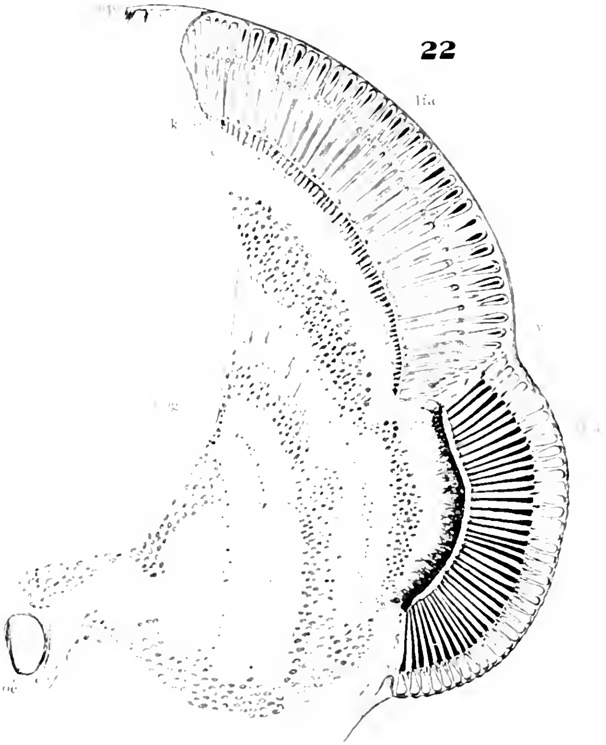

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PLATE XXVII. MICROPHOTOGRAPHS.

FIG. 23. Cross-section of head of subimago of male *C. hageni.*

FIG. 24. Cross-section of a head of adult male *C. hageni.*

FIG. 25. Cross-section of head of subimago of male *C. californica.*

FIG. 26. Cross-section of male adult of *C. californica.*

FIG. 27. Cross-section of part of large turban eye of an adult male *C. hageni*, showing the connecting strands between the proximal and distal retinulæ.

FIG. 28. Microphotograph of cross-section of head of an old nymph of *S. corrupta*, the adult of which was about to issue. The section passes through the edge, only, of the pigmented part of the eye which in its largest part was about equal to the upper large facetted area as is shown by the size of the optic ganglion.

FIG. 29. A few ommatidia from the dorsal eye of a female *B. capitata.*

FIG. 30. Left dorsal and lateral eyes of a female *B. capitata* showing optic ganglion also. Most of the cornea of the dorsal eye is torn away. See Fig. 29.

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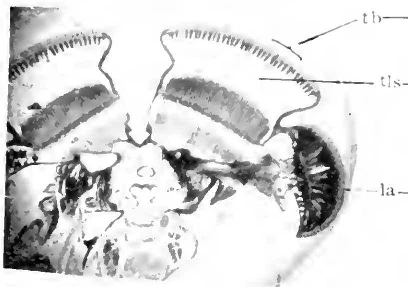

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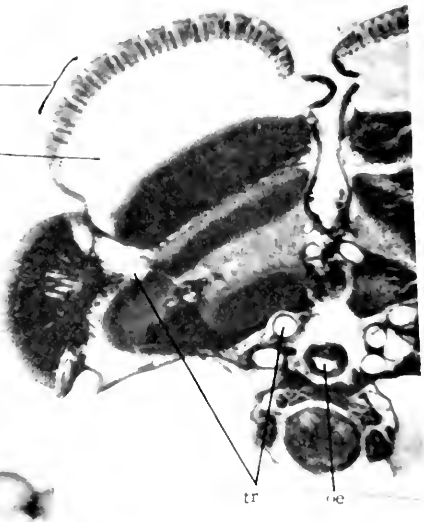

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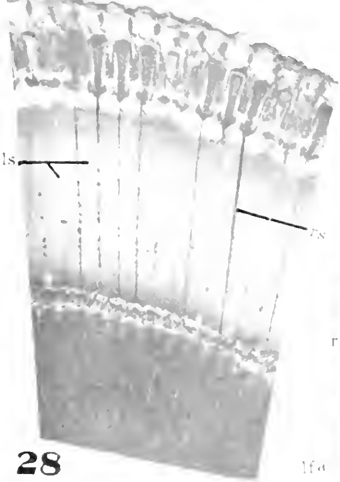

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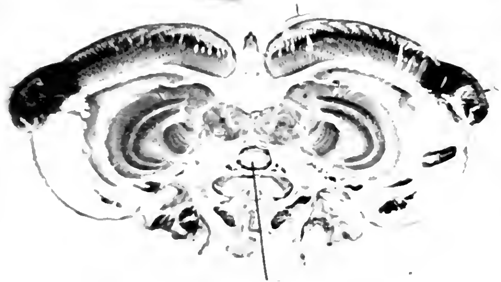

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INDEX.

NOTE. — New names in **black-face type**, synonyms in *Italics*.

For index to paper on "Aspects of Kinetic Evolution" by O. F. Cook, see pp. 400-403.