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ARTICLE VIII.—A STATISTICAL STUDY OF THE PARASITES OF THE UNIONIDÆ.

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ERRATA.

Page 136, line 2, and page 182, line 17 from bottom, for '*95a* read '*95*.

Page 226, line 2, page 263, line 17 from bottom, and page 267, lines 2 and 15, for '*98*, read '*96*.

Page 233, line 15 from bottom, for '*82* read '*82a*.

Page 355, line 2 from bottom, for C. *F.* Hudson read C. *T.* Hudson.

Page 389, foot-note, for Vol. *V.* read Vol. *IV.*

Page 457, line 5, for *Genera* read *Genus*.

ARTICLE VIII.—*A Statistical Study of the Parasites of the Unionidæ.* By H. M. KELLY.

The studies on the quantitative occurrence of parasites in different species of the *Unionidæ* which form the basis of the present paper were made at the Illinois Biological Station, at Havana, early in the summers of 1896 and 1897 and continued both seasons at Mt. Vernon, Ia., and at Lewisburg and Phœnixville, Pa., the material used being secured in the above mentioned localities and examined while fresh. It was the purpose of the investigation to determine, if possible, under what conditions infestation would be found to vary in a series of closely related species of a given locality or of several localities, and to what extent this variation could be regarded as a specific characteristic.

The Illinois, Iowa, and Pennsylvania waters from which collections were made are indicated in Table I., and for the purposes of this paper may be briefly characterized as follows: (1) The Illinois River at Havana is a large sluggish stream with alluvial banks and largely muddy bottom, full of organic matter of various origin. (2) Spoon River, a tributary of the Illinois, is at Bernadotte and Duncan's Mills, where collections were made, small, with rapid current and rocky bottom. It drains a purely agricultural region, and is subject to frequent and sudden floods. (3) Quiver Creek, near Havana, is a smaller tributary to the Illinois, draining a sandy plain. (4) Thompson's Lake is a shallow body of water about six miles long and one mile wide, lying in the low alluvial flood plain of the Illinois River, with very muddy bottom and little change of water except as affected by change of level in the river, with which it is connected. (5) The Cedar River, near Mt. Vernon, Ia., is a rapid shallow stream with shifting sandy bottom for the most part, draining

a rolling prairie region. (6) Abbey Creek is a small, sluggish, and muddy tributary of the Cedar, flowing through a wooded region of rich black soil. (7) The Schuylkill River at Phœnixville, Pa., is rapid and shallow, with a rocky bed. Its waters are largely contaminated with the sewage of the populous region through which it flows, with manufacturers' wastes, and with the acid pumpings of anthracite coal mines. (8) Pickering Creek, a tributary of the Schuylkill, is an uncontaminated, swift-flowing stream, constant in volume, and draining a restricted rocky area. (9) French Creek, a near-by branch of the Schuylkill, is of similar size, but traverses a country of clay soils, and is subject to frequent inundations. (10) The West Branch of the Susquehanna River is, upon most of its course, a large but shallow mountain stream with rapid current. It is quiet for some miles at Lewisburg, Pa., where it crosses one of the fertile valleys of the Appalachian system.

Fifteen hundred and thirty-seven individual unios from the above localities, belonging to forty-four species, were personally examined by me with reference to their parasites; and with the data thus obtained I have incorporated the results of an examination of seventy-seven individuals, belonging to eighteen species, made by Dr. C. A. Kofoid in 1895 and 1896, which were placed at my disposal. It is unfortunate that my material did not furnish equal representation for each host species, and that the examination extended over such a long period of time. For control on both these points an effort was made to examine, if possible, about twenty individuals of each species which were all taken at the same time from the same locality and under the same conditions.

Whenever it was practicable individuals of or above the adult average in size and age were chosen for examination. Only ninety-seven of the sixteen hundred and fourteen individuals examined could be regarded as immature, and these were well distributed among the several species. The inclusion of records for these younger and smaller individuals would presumably reduce somewhat both the probability of and capacity for infestation. However, in the case of

TABLE I. GEOGRAPHICAL DISTRIBUTION OF UNIONIDÆ EXAMINED.

NAMES OF SPECIES.	No. of Individuals.	ILLINOIS.				IOWA.		PENNSYLVANIA.				Total No. of localities.
		Illinois River.	Spoon River.	Quiver Creek.	Thompson's Lake.	Cedar River.	Abbey Creek.	Schuylkill River.	Pickering Creek.	French Creek.	Susquehanna River.	
Quadrula multiplicata Lea.	28	26	2	...	...	...	...	...	...	...	...	2
tuberculata Bar.	41	18	21	...	...	2	...	...	...	...	...	3
metanevra Raf.	36	2	...	...	...	34	...	...	...	...	...	2
lachrymosa Lea.	29	...	29	...	...	...	...	...	...	...	...	1
asperrima Lea.	21	21	...	...	...	...	...	...	...	...	...	1
pustulata Lea.	20	20	...	...	...	...	...	...	...	...	...	1
granifera Lea.	1	1	...	...	...	...	...	...	...	...	...	1
pustulosa Lea.	87	29	28	...	...	30	...	...	...	...	...	3
plicata Say.	89	45	8	...	...	36	...	...	...	...	...	3
trigona Lea.	27	22	5	...	...	...	...	...	...	...	...	2
rubiginosa Lea.	40	1	1	...	...	38	...	...	...	...	...	3
ebena Lea.	23	23	...	...	...	...	...	...	...	...	...	1
Unio gibbosus Bar.	35	25	10	...	...	...	...	...	...	...	...	2
complanatus Sol.	137	...	...	...	...	...	...	62	14	20	41	4
heterodon Lea.	4	...	...	...	...	...	...	1	1	2	...	3
Alasmodonta confragosa Say	35	34	1	...	...	...	...	...	...	...	...	2
complanata Bar	64	11	8	...	...	37	8	...	...	...	...	4
rugosa Bar.	18	...	1	...	...	17	...	...	...	...	...	2
marginata Say	51	...	...	...	...	1	...	...	30	20	...	3
undulata Say	3	...	...	...	...	...	...	...	...	3	...	1
tappaniana Lea	1	...	...	...	...	...	...	1	...	...	...	1
Strophitus edentulus Lea.	36	12	2	...	...	18	2	1	...	1	...	6
Anodonta imbecilis Say.	49	47	...	...	...	2	...	...	...	...	...	2
suborbiculata Say	20	...	...	...	20	...	...	...	...	...	...	1
grandis Lea.	8	...	3	...	...	5	...	...	...	...	...	2
corpulenta Coop.	45	35	...	...	10	...	...	...	...	...	...	2
Obliquaria reflexa Raf.	32	26	1	...	...	5	...	...	...	...	...	3
Plagiola securis Lea.	5	5	...	...	...	...	...	...	...	...	...	1
elegans Lea.	48	25	3	...	...	20	...	...	...	...	...	3
donaciformis Lea.	37	21	3	...	...	13	...	...	...	...	...	3
Lampsilis parvus Bar.	31	25	...	...	...	...	6	...	...	...	...	2
ellipsis Lea.	14	3	...	...	...	11	...	...	...	...	...	2
higginsii Lea.	1	1	...	...	...	...	...	...	...	...	...	1
ligamentinus Lam	91	24	2	...	...	65	...	...	...	...	...	3
luteolus Lam.	25	11	2	10	...	2	...	...	...	...	...	4
nasutus Say.	4	...	...	...	...	...	...	3	...	1	...	2
anodontoides Lea	62	49	4	...	...	9	...	...	...	...	...	3
rectus Lam.	49	10	2	...	...	37	...	...	...	...	...	3
ochraceus Say.	1	...	...	...	...	...	...	...	...	...	1	1
ventricosus Bar.	108	10	2	40	...	56	...	...	...	...	...	4
alatus Say.	60	38	3	...	...	19	...	...	...	...	...	3
lævissimus Lea.	4	1	3	...	...	...	...	...	...	...	...	2
gracilis Bar.	89	40	16	...	...	33	...	...	...	...	...	3
tenuissimus Lea	5	...	...	...	...	5	...	...	...	...	...	1
Totals { Individuals.	1614	661	160	50	30	495	16	68	45	47	42	...
Totals { Species.	44	32	24	2	2	23	3	5	3	6	2	...

Quadrula pustulosa,* where the highest proportion of undersized individuals is included in the tabulation,—twenty out of eighty-seven,—it appears that the infestation of these younger hosts did not differ materially in kind or degree from that of the larger individuals.

The sex of fourteen hundred and eighty-three individuals of the sixteen hundred and fourteen examined was determined by microscopical examination, seven hundred and eighty-two being males and seven hundred and one females. In one hundred cases the determination of sex was not attempted. In the thirty-one remaining, it was indeterminable by microscopic examination, all but five being infested by *Bucephalus* or other cercaria forms to the utter destruction of the proper reproductive tissue. From the shape of the shells eight of these thirty-one individuals were pronounced males and two females. Others, also belonging to species in which the shells of the two sexes are normally characteristic, had shells of such shape as to render the sex problematical and to suggest that infestation by *Bucephalus* or other cercaria, when early acquired and long continued, may so alter the form of the shell of the female as to cause it to resemble that of the male or, if acquired later, may produce an intermediate form. Moreover, females infested with *Bucephalus* or other cercaria rarely (in but three observed cases) carried glochidia, though examined when the marsupia of other females of their species were normally inflated with young. This is especially noteworthy in *Lampsilis gracilis*, in which determination of the sex of the clam by the form of the shell is usually certain. Of the eighty-nine individuals of this species examined, thirteen were infested with *Bucephalus* or other cercaria. Of these, seven appeared to be males, one was a female with glochidia in the gill, three were doubtfully regarded as females although no germinal tissue was discernible, while the sex of two was problematical.

In thirty-eight of the forty-four species examined the num-

* For the convenience of those who have not followed the recent changes in unionid nomenclature a list of the names mentioned in this article is given in the first column below, each name being followed in the second column by the one

ber of infested males and females for each species did not differ materially. The exceptions are as follows:

Unio heterodon,	4 males,	0 females.
Anodonta suborbiculata,	18 males,	2 females.
Plagiola securis,	5 males,	0 females.
Lampsilis parvus,	0 males,	31 females.
Lampsilis lævissimus,	4 males,	0 females.
Lampsilis tenuissimus,	5 males,	0 females.

The disparity of the sexes in these few species has no significance, however, in this connection, for in no case where both sexes were liberally represented in the host species could a different capacity for infestation be established for the two sexes. The only seeming exception, in the case of

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previously in common use. The specific names remain the same, except that *cornutus* becomes *reflexa*, and *plana* is now considered a form of *grandis*.

Quadrula multiplicata	Unio multiplicatus
tuberculata	tuberculatus
metanevra	metanever
lachrymosa	lachrymosus
asperrima	asperrimus
pustulata	pustulatus
granifera	graniferus
pustulosa	pustulosus
plicata	plicatus
trigona	trigonus
rubiginosa	rubiginosus
ebena	ebenus
Unio gibbosus	gibbosus
complanatus	complanatus
heterodon	heterodon
Alasmodonta confragosa	Margaritana confragosa
complanata	complanata
rugosa	rugosa
marginata	marginata
undulata	undulata
tappaniana	Unio tappanianus
Strophitus edentulus	Anodonta edentula
Anodonta imbecilis	imbecilis
suborbiculata	suborbiculata
grandis	plana
corpulenta	corpulenta
Obliquaria reflexa	Unio cornutus
Plagiola securis	securis
elegans	elegans
donaciformis	donaciformis
Lampsilis parvus	parvus
ellipsis	ellipsis
higginsii	higginsii
ligamentinus	ligamentinus
luteolus	luteolus
nasutus	nasutus
anodontoides	anodontoides
rectus	rectus
ochraceus	ochraceus
ventricosus	ventricosus
alatus	alatus
lævissimus	lævissimus
gracilis	gracilis
tenuissimus	tenuissimus

infestation by *Bucephalus*, has already been explained as the result of the unsexing of the host.

Though this study was instituted primarily with the trematodes alone in mind, record was made of all parasites whose presence did not appear to be accidental. I have presented in Table II. a concise record of these parasites and of the species and number of their hosts, while the relations of the one to the other are set forth in the discussion which follows.

Aspidogaster conchicola von Baer, the most common parasite of the *Unionidæ*, is confined for the most part to the pericardial and nephridial cavities of the host. In four hundred and thirty-five cases it was found in the pericardium only, in seventy in the kidneys only, and in one hundred and thirty-four cases both cavities contained the parasite. In only one host species showing any considerable degree of infestation, *Lampsilis parvus*,—where twenty out of thirty-one individuals examined were parasitized,—were the flukes restricted wholly to one cavity (the pericardium), and here the small size of the host may perhaps account for such restriction. As a rule, though there are many exceptions, flukes appear in both chambers only when the parasites are very numerous; and as the number in the pericardium is usually much larger than that in the kidneys, and as the pericardial infection is the more frequent, it would seem that only in excessive parasitism is the nephridial cavity invaded. A single *Aspidogaster* was found encysted in the lateral wall of the visceral mass of the host. In four cases only, in all of which the pericardium was ruptured in opening the shell, were individuals of this species detected in other than the usual localities, and then their positions were always such as to suggest escape from the broken pericardium. This parasite was most frequently found in the adult stage, but eggs and embryos in abundance and young of varying sizes were found when the parasitism was considerable. The presence of the mature trematode in the pericardium and of eggs within the nephridia is not infrequent.

Cotylaspis insignis Leidy is found adherent to the surface

of the host in the angle between the inner gill and the visceral mass. Its range is usually restricted to this axilla, and the number infesting one host is small. In one case, however,—that of *Anodonta corpulenta*, recorded by Dr. Kofoid,—where the number reached the unparalleled extreme of ninety-two, the flukes extended well out upon the inner surface of the gill; and in another, under my own observation, some of them were crowded down upon the abdominal surface. In *A. suborbiculata*, in which *Cotylaspis* attains its maximum average, thirty-eight to each host, not only are the axillæ and the adjacent surfaces of both inner gill and visceral mass invaded, but some are usually found within the tubes of the inner gill, and occasionally even in those of the outer gill. Such migration from the usual seat of infestation to immediately adjacent regions is perhaps to be expected in cases of overcrowding such as are instanced. In a single *Lampsilis ellipsis*, one *Cotylaspis* unmistakably occurred in the pericardium along with twenty-three specimens of *Aspidogaster*. Since *Cotylaspis* normally frequents the region of the nephridial openings, an invasion of the pericardium by way of the nephridia might not be impossible. All the *Cotylaspis* found were adults varying little in size. Eggs were not infrequently observed in the surface slime collected in the vicinity of the parasites.

Four forms of *Distomidæ* have been found, probably of as many different species, all immature, and none sufficiently developed for specific determination. One of these forms—referred to in the table as "Free Distomata"—is found in loose salmon-colored masses either upon or slightly within the tissue of the mantle, along or near the dorsal fold. In *Quadrula*, *Unio*, *Plagiola*, and *Lampsilis* this parasite is most frequently located immediately between the cardinal teeth, less commonly between the lateral teeth, or, again, upon the sides, extending over the external surface of the mantle on a line parallel to its attachment to the viscera. In the genera *Strophitus* and *Anodonta* the distribution of this parasite is lateral, as just described, often extending over the mantle surface like a large widely-open inverted V, with its

apex just below the umbo and its arms reaching even beyond and below the anterior and posterior adductor muscles.* This trematode has not in my experience been found singly, the number associated having varied from four to many hundreds. They are habitually loosely adherent by their suckers to the mantle surface and to each other, but may be slightly insinuated within the loose tissue of the mantle, especially when found between the hinge teeth. The position of this parasite is usually marked by rusty stains in and upon the nacre, by malformation of the shell or of the hinge teeth, and not infrequently by a number of dark, poorly formed pearls. Though these conditions of the superimposed shell do not always accompany infestation by this trematode, and though similar abnormalities are found without its presence being discerned, yet these malformations are very constant where the mass of the parasites is considerable, and the size and location of the ferruginous stain or injury correspond to those of the infesting colony. When but few are present and there is no injury to the nacre, the irritation is no doubt too slight or too recent for much interference with the normal secretion of the mantle. A malformation characteristic of the presence of this parasite but unaccompanied by it, would seem to imply desertion for another host. Such implication is strengthened by the fact that in the case of some of the host species, individuals are frequently found in which none of these salmon-colored masses of trematodes are present, but which nevertheless present malformations of considerable size in which the rusty, altered, and diseased nacre is covered with a normal layer of later deposit. The parasite is, moreover, uniformly immature, no matter at what season it is observed.

The other three species of *Distomum* were found encysted in the following situations respectively: (1) in the pericardium of a single individual in each of the species *Quadrula rubiginosa*, *Plagiola elegans*, and *Lampsilis anodontoides*; (2) in the ventral muscular margin of the mantle in four

* H. L. Osborn ('98, Zoöl. Bull., Vol. I., No. 6) describes in like manner this parasite and its mode of infestation in *Anodonta plana* (= *grandis*) and *Strophitus edentulus* from Chautauqua Lake, N. Y.

individuals of *Lampsilis ligamentinus*; and (3) within the ovary of a single specimen of *Lampsilis ventricosus*. These are evidently all immature forms, the clam serving them only as an intermediate host.

Bucephalus polymorphus von Baer and two other cercaria forms were found within the viscera of the host. These usually occurred in such abundance as to obliterate totally the normal tissue of the sexual glands, rendering the whole abdomen as granular as fish roe, or fibrous with the sporocysts of the *Bucephalus*. Extensive infestation with the latter parasite also involves the nephridia, which may be much swollen, their ducts being nearly obliterated by the tangled fibers of sporocysts. This unsexing of the host, and the accompanying changes in the form of the shell have already been referred to.

Various species of *Atax* are common ectoparasites of the *Unionidæ*. Their favorite situations are upon the body surfaces, between the gills or between the gills and abdomen, between the labial palps, or among the papillæ fringing the mantle edges at the inhalent siphon. Their eggs are laid either in the body wall, the gills, or the mantle.

Dr. Robert H. Wolcott, to whom a part of the *Atax* material collected in the course of this study was sent, kindly furnished the determinations of the species of this genus included in the following table, which indicates the host species from which these different parasites were derived, and also the total number of individuals of each species of *Atax* found in a given host species.

Conchophthirus hirtus Ehrbg. and *C. anodontæ* Ehrbg., ciliated *Infusoria*, inhabit the slime investing the body surfaces. In the accompanying tables no attempt is made to separate the two species.

Chætogaster limnæi von Baer, an oligochæte, is also found in the slime of the various surfaces and in the kidneys.

The frequent presence of leeches and planarians upon the shell and on the mantle edges, at times indeed within the branchial chamber, was regarded as accidental, and they are consequently not included in the accompanying tabulations.

HOST SPECIES.	Atax abnormipes Wolcott	Atax arcuata Wolcott.	Atax fossulatus Koenike.	Atax indistinctus Wolcott.	Atax serratus Wolcott.	Atax stricta Wolcott.	Atax ypsilophorus Bonz.
Quadrula tuberculata	.....	.....	.....	.....	.....	363	.....
lachrymosa	.....	.....	.....	.....	.....	12	.....
asperrima	.....	.....	.....	.....	.....	5	.....
pustulosa	.....	.....	.....	.....	.....	115	.....
plicata	.....	.....	.....	.....	.....	43	.....
Alasmodonta rugosa	.....	.....	.....	.....	.....	.....	4
marginata	.....	18	.....	.....	.....	.....	.....
Anodonta imbecilis	11	.....	.....	8	.....	5	3
suborbiculata	.....	.....	.....	.....	.....	.....	37
corpulenta	.....	.....	.....	.....	.....	.....	16
Obliquaria reflexa	.....	.....	.....	.....	.....	10	.....
Lampsilis anodontoides	26	.....	.....	.....	.....	.....	.....
rectus	.....	.....	.....	.....	.....	8	.....
ventricosus	14	.....	6	.....	.....	1	.....
alatus	.....	.....	6	78	.....	636	.....
lævissimus	.....	.....	6	.....	.....	.....	.....
gracilis	3	30	.....	82	.....	1	.....
Sp. ?	.....	.....	.....	.....	8	.....	.....

Table II. is an exhibit of the results of all the examinations, the body of the table giving the number of individuals of the various host species examined, and the number of such hosts infested by each of the nine parasites named in the headings. The footings of the columns and the subjoined percentages give the number and per cent. of species and individuals infested. On the right, one column gives the number of kinds of parasites found in each host species, and another the total number of individuals in the species examined which were infested to any degree. A comparison of the data in these two columns, note being taken of the number of individuals examined in the several species, as given in the first column, shows a marked variation among the different host species in the number of kinds of parasites harbored and in the number of individuals of each species infested. It is seen that *Aspidogaster* is by far the most widely distributed and abundant parasite; that *Cotylaspis*, *Atax*, and *Conchophthirus* must be classed as very frequent; that the free distomid and *Bucephalus* are less common; and that the remaining three parasites occur but occasionally. It is remarkable that at least two sufficiently examined

TABLE II. SPECIFIC DISTRIBUTION OF PARASITES.

HOST SPECIES.		No. of Hosts Infested with										
NAMES.	No. of individuals examined	Aspidogaster.	Cotylaspis.	Free Distomata.	Encysted Distomata.	Cercaria.	Bucephalus.	Atax.	Conchophthirus.	Chætogaster.	Kinds of parasites.	No. of individuals infested.
Quadrula multiplicata	28	3	...	...	...	...	...	3	8	...	3	11
tuberculata	41	33	12	2	...	...	...	23	5	...	5	38
metanevra	36	12	1	20	...	...	...	12	...	...	4	28
lachrymosa	29	21	...	...	...	...	...	7	...	...	2	22
asperrima	21	21	...	1	...	...	...	9	13	...	4	21
pustulata	20	5	11	...	...	...	...	16	...	...	3	18
granifera	1	1	...	...	...	...	...	1	1	...	3	1
pustulosa	87	28	9	6	...	...	1	50	6	...	6	59
plicata	89	62	...	...	...	1	...	36	5	...	4	70
trigona	27	3	4	...	...	...	...	...	4	...	3	10
rubiginosa	40	10	...	...	1	...	...	3	2	...	4	15
ebena	23	7	...	...	...	...	...	..	...	...	1	7
Unio gibbosus	35	9	...	1	...	1	...	1	17	...	5	21
complanatus	137	37	...	...	...	...	1	1	113	...	4	120
heterodon	4	1	...	...	...	...	...	...	1	...	2	1
Alasmodonta confragosa	35	9	3	...	...	...	1	1	2	...	5	12
complanata	64	10	2	...	...	1	3	21	6	...	6	36
rugosa	18	...	...	...	...	1	1	9	8	3	5	13
marginata	51	9	...	...	...	4	...	39	33	...	4	47
undulata	3	...	...	...	...	...	...	...	...	...	...	...
tappaniana	1	...	...	...	...	...	...	...	...	...	...	...
Strophitus edentulus	36	6	5	3	...	...	6	3	10	...	6	26
Anodonta imbecilis	49	25	17	...	...	...	...	1	28	33	5	46
suborbiculata	20	20	18	...	...	...	...	15	19	...	4	20
grandis	8	8	5	5	...	...	...	1	5	...	5	8
corpulenta	45	37	40	21	...	...	1	32	21	...	6	43
Obliquaria reflexa	32	3	...	...	...	..	..	13	6	1	4	19
Plagiola securis	5	...	...	...	...	...	...	...	2	...	1	2
elegans	48	3	...	...	1	...	3	4	1	...	5	10
donaciformis	37	21	...	1	...	...	1	1	...	1	5	22
Lampsilis parvus	31	20	2	...	...	...	...	...	...	2	3	21
ellipsis	14	12	11	10	...	...	...	1	..	...	4	14
higginsii	1	...	1	...	...	...	...	...	...	...	1	1
ligamentinus	91	...	13	...	4	5	12	20	9	...	6	51
luteolus	25	3	4	3	...	...	2	12	1	...	6	17
nasutus	4	1	1	...	...	...	...	...	2	...	3	3
anodontoides	62	47	18	...	1	...	2	38	15	..	6	54
rectus	49	7	21	11	...	3	3	32	18	...	7	44
ochraceus	1	...	...	...	...	...	...	1	..	...	1	1
ventricosus	108	30	24	58	1	...	10	72	...	...	5	94
alatus	60	49	27	4	...	...	...	48	26	...	5	57
lævissimus	4	3	...	...	...	...	...	2	...	...	2	3
gracilis	89	77	46	...	...	1	13	57	11	...	6	86
tenuissimus	5	5	3	...	...	...	...	1	...	...	3	5
No. of individuals infested	...	644	297	146	8	17	60	586	398	40	...	1197
No. of species infested	...	37	24	14	5	8	15	35	30	5	...	42
Percentage of individ. infested	...	40	18	9	0.4	1	4	36	25	2	...	74
Percentage of species infested	...	84	55	32	11	18	34	80	68	11	...	95

species, *Alasmodonta rugosa* and *Lampsilis ligamentinus*, show no infestation with the generally prevalent *Aspidogaster*, and this is especially noteworthy in the case of the latter, whose infestation with other parasites is both frequent and severe.

Table III. brings into comparison the number of kinds of parasites found infesting individuals of each host species and

TABLE III. DEGREE OF INFESTATION OF INDIVIDUAL HOSTS.

HOST SPECIES.			PERCENTAGE OF INDIVIDUALS INFESTED.					
NAMES.	No. of individuals examined.	Kinds of parasites infesting host species.	To any degree.	With 1 kind.	With 2 kinds.	With 3 kinds.	With 4 kinds.	With 5 kinds.
Quadrula multiplicata	28	3	39	29	11	....	....	....
tuberculata	41	5	93	20	59	15	....	...
metanevra	36	4	78	33	42	3	...	....
lachrymosa	29	2	76	55	21	....	....	....
asperrima	21	4	100	33	24	43	....	....
pustulata	20	3	90	25	55	10	....	....
pustulosa	87	6	68	32	26	8	1	....
plicata	89	4	79	43	34	2	..	....
trigona	27	3	37	33	4	. ..	....	....
rubiginosa	40	4	38	35	3	....	....	...
ebena	23	1	30	30	....	....	....	....
Unio gibbosus	35	5	60	40	17	3	....	....
complanatus	137	4	88	64	24	....	....	..
Alasmodonta confragosa	35	5	34	26	6	3	....	....
complanata	64	6	56	44	13	....	....	....
rugosa	18	5	72	28	39	6	. ..	....
marginata	51	4	92	31	47	14	....	....
Strophitus edentulus	36	6	72	58	6	8	....	....
Anodonta imbecilis	49	5	94	18	39	27	10	....
suborbiculata	20	4	100	....	5	30	65	...
corpulenta	45	6	96	9	11	20	36	20
Obliquaria reflexa	32	4	59	50	6	3	....	....
Plagiola elegans	48	5	21	17	4	....	...	....
donaciformis	37	5	59	48	11	....	....	....
Lampsilis parvus	31	3	68	58	10	...	....	..
ellipsis	14	4	100	....	57	43	....	....
ligamentinus	91	6	56	43	11	2	....	....
luteolus	25	6	68	52	4	8	4	....
anodontoides	62	6	87	18	40	19	10	....
rectus	49	7	89	24	31	20	12	2
ventricosus	108	5	87	25	37	19	6	....
alatus	60	5	95	13	22	33	27	....
gracilis	89	6	97	16	45	23	13	....
Totals	1577	....	74	32	25	10	5	0.6

the number harbored by each species considered as a unit. In this table and in the succeeding one the data regarding host species in which less than fourteen individuals were examined are not included. While the comparisons between the species included are thus rendered the more reliable, it will be seen that the general conclusions deduced from Tables III. and IV. only confirm the findings of the more general statistics of Table II. While nine kinds of parasites are here listed for the *Unionidæ*, no species of the family was found to harbor more than seven, and the average was but four or five. Moreover, in but four species—*Quadrula lachrymosa*, *Q. ebena*, *Q. pustulata*, and *Anodonta suborbiculata*—were individuals found with the maximum variety of parasites listed for its species, and in these the maximum variety is four or less. It is perhaps futile to imagine what variety of parasites an individual host might successfully sustain, but it is noticeable that in this table the mean individual infestation lies closer to the species minimum than to its maximum. A close inspection of the data of all examinations further confirms the inference that the individual host is unable to realize the maximum capacity of its species for infestation, since in no case is the presence of an unusual number of one parasite accompanied either by like severe infestation by another or by a considerable variety of parasites. It is true that one individual of *Lampsilis gracilis* with sixteen specimens of *Aspidogaster* in the pericardium and six in the nephridia, harbored also two of *Cotylaspis* and one each of *Atax* and *Bucephalus*, and that one *Lampsilis ventricosus* infested with thirty-one specimens of *Aspidogaster* contained large numbers of *Bucephalus*; but these are exceptional cases, and even in these individuals, when we consider the size of the host and the established maximum capacity of their species, the extreme limit can hardly be said to be reached. The ectoparasites probably require but little from their hosts, but they rarely occur in numbers upon clams exhausted by *Bucephalus*.

Table IV. gives the percentage of the hosts which were infested with *Aspidogaster*, *Cotylaspis*, and *Atax*, the most

abundant parasites, and also the maximum, minimum, and average number of these parasites found in the hosts. The frequency of occurrence of any one of these parasites in relation to the total infestation of a species is to be learned by a comparison of Tables III. and IV. Thus in a total of fifteen hundred and seventy-seven examinations,—in which seventy-four per cent. were in some measure infested (Table

TABLE IV. COMPARISON OF INFESTATION BY DIFFERENT PARASITES.

HOST SPECIES.		Percentage of hosts infested with			Number of parasites in one host.			Average No. of parasites in one host.		
NAMES.	Individuals examined.	Aspidogaster.	Cotylaspis.	Atax.	Aspidogaster.	Cotylaspis.	Atax.	Aspidogaster.	Cotylaspis.	Atax.
Quadrula multiplicata...	28	11	....	11	1–5	....	1–2	2	....	1
tuberculata....	41	80	29	56	1–19	1–8	1–78	6	3	23
metanevra.....	36	33	3	33	1–6	1	1–2	2	1	2
lachrymosa....	29	72	....	24	1–41	....	1–6	12	....	2
asperrima.....	21	100	....	44	2–13	....	1–3	6	....	2
pustulata.....	20	25	55	80	1–5	1–7	1–4	2	3	2
pustulosa.....	87	32	11	57	1–5	1–2	1–18	2	1	3
plicata.....	89	70	....	40	1–20	....	1–20	4	....	6
trigona	27	11	15	....	1–6	1–2	....	3	2	....
rubiginosa	40	25	...	8	1–6	....	4	4	....	4
ebena	23	30	..	....	1–24	..	....	6	....	....
Unio gibbosus.....	35	26	....	3	1–7	....	1	2	....	1
complanatus.....	137	27	....	1	1–28	....	1	3	....	1
Alasmodonta confragosa.	35	26	9	3	1–75	1–4	Eggs	27	3	Eggs
complanata	64	16	3	33	1–85	1	1–6	11	1	1
rugosa.....	18	....	....	50	....	....	1–3	....	....	2
marginata.	51	18	....	76	1–12	..	1–7	3	....	3
Strophitus edentulus....	36	17	14	8	1–10	1–2	1–22	3	1	8
Anodonta imbecilis	49	51	35	20	1–9	1–7	Eggs	3	2	Eggs
suborbiculata.	20	100	90	75	1–37	1–86	1–8	13	38	3
corpulenta....	45	82	88	71	1–50	1–92	1–75	8	12	8
Obliquaria reflexa.....	32	9	....	41	1	....	1–3	1	....	2
Plagiola elegans.....	48	63	....	83	1–6	....	1–6	4	....	2
donaciformis....	37	57	....	3	1–7	....	1	2	....	1
Lampsilis parvus.....	31	65	7	....	1–26	1	....	5	1	....
ellipsis	14	86	79	7	1–63	1–5	4	14	2	4
ligamentinus..	91	....	14	22	....	1–8	1–4	....	3	2
luteolus.....	25	12	16	48	1	1–5	1–8	1	2	3
anodontoides .	62	76	29	61	1–33	1–6	1–12	6	2	4
rectus	49	14	43	65	1–5	1–9	1–20	2	4	3
ventricosus ...	108	28	22	67	1–13	1–15	1–9	18	3	3
alatus.....	60	82	45	80	1–63	1–10	1–108	16	2	50
gracilis	89	87	52	64	1–77	1–12	1–31	15	3	5
Totals.....	1577	41	18	37	....	....	...	....	....	...

III.),—forty-one per cent. were parasitized by *Aspidogaster*, eighteen per cent. by *Cotylaspis*, and thirty-seven per cent. by *Atax*—as shown in Table IV. It may be seen from the tables under discussion, as well as from Table II., that there is a marked difference between the several host species in capacity for infestation in both kind and degree.

The range in number of parasites infesting one host, and their average number, may depend to some extent upon the size of the host,—*Anodonta suborbiculata* and *A. corpulenta* showing high numbers and *Strophitus edentula* and *Anodonta imbecilis* low,—and this applies with force in case of occupation of the pericardial and nephridial cavities by *Aspidogaster*, where the volumes of the organs closely limit the possible number of invading parasites. But size is not the sole determining factor, else *Lampsilis luteolus* and *L. anodontoides*, *L. ligamentinus* and *L. alatus*, *Quadrula multiplicata* and *Lampsilis ventricosus*, and *Quadrula plicata* and *Lampsilis gracilis* should harbor similar, rather than so widely different, numbers of parasites, and little *Lampsilis parvus* should not show such large infestation and such a wide range in the number of parasites harbored.

The tables seem to indicate in the different species a general correspondence between the frequency of infestation, the variety of parasites, and the average number of individual parasites harbored by a given host. Thus *Quadrula tuberculata*, *Anodonta suborbiculata*, *A. corpulenta*, *Lampsilis ellipsis*, *L. ventricosus*, *L. alatus*, and *L. gracilis*, all figuring largely in the tables, are frequently parasitized, carry a large variety of parasites, and, in proportion to their size, a high average number individually; while the statistics concerning *Quadrula multiplicata*, *Q. trigona*, *Q. ebena*, *Unio gibbosus*, *Obliquaria reflexa*, and *Plagiola elegans* show a like uniformity in infrequent infestation, little variety in kinds of parasites, and a low average number harbored by the individual host.

In the light of the latest views upon the natural classification of the *Unionidæ* it may be said that closely related species exhibit somewhat similar capacities for infestation. In general the species of *Anodonta* and also those of *Lamp-*

silis are of large parasite capacity; those of *Unio* (restricted) and of *Plagiola* are of low capacity; while within the genera *Quadrula* and *Alasmodonta* we find wide extremes of infestation. Within the limits of the above genera this correspondence is more or less evident between members of groups of closely related species, especially when taken in considerable numbers in similar situations. For example, we may note the correspondence between *Lampsilis ligamentinus* and *L. luteolus; Quadrula ebena, Q. trigona,* and *Q. rubiginosa; Lampsilis alatus* and *L. gracilis;* and *Quadrula lachrymosa* and *Q. asperrima.*

Seasonal changes have been found to modify the distribution of the parasites in the case of *Atax* and *Conchophthirus* only. As the water grew colder in late October and November, the examinations of *Unionidæ* from the Cedar River gave relatively fewer adult *Atax* and more abundant eggs. The presence of these eggs was regarded as potential infestation, and therefore these data may properly be included in the tabulation. The reliability of the tabulations may be somewhat vitiated by the fact that *Conchophthirus* is much more plentiful in the warmer months, during which the greater part of my collections were made.

TABLE V. GEOGRAPHICAL DISTRIBUTION OF PARASITES.

		LOCALITIES.									
		ILLINOIS.				IOWA.		PENNSYLVANIA.			
		Illinois River.	Spoon River.	Quiver Creek.	Thompson's Lake.	Cedar River.	Abbey Creek.	Schuylkill River.	Pickering Creek.	French Creek.	Susquehanna River.
Hosts.	Individuals examined	661	160	50	30	495	16	68	45	47	42
	Species	32	24	2	2	23	3	5	3	6	2
Parasites.	Aspidogaster	×	×	×	×	×	....	×	×	×	×
	Cotylaspis	×	×	×	×	×	...	×	....	....	....
	Free Distomata	×	....	×	×	×	....	....	....	....	....
	Encysted Distomata	×	....	....	....	×	....	....	....	....	....
	Cercaria	×	×	....	....	×	....	....	×	×	....
	Bucephalus	×	×	×	....	×	....	....	....	×	....
	Atax	×	×	×	×	×	×	....	×	×	×
	Conchophthirus	×	×	....	×	×	....	×	×	×	×
	Chætogaster	×	....	....	....	×	....	....	....	....	....
	Kinds of parasites	9	6	5	5	9	1	3	4	5	3

Table V. indicates the range of the different parasites in the several localities supplying the material. In all probability the blanks opposite the more usual parasites are due to the absence of the proper host species or to the examination of an insufficient number of these species rather than to peculiarities in the localities themselves, for the variety of parasites listed for any situation varies with the number of individuals and the variety of species examined from each locality. Thus the absence of *Atax* from the Schuylkill and its occurrence in the tributary French and Pickering creeks may be accounted for by the fact that with the exception of a single occurrence, this parasite was never found by me, in any locality, in the particular species examined from the Schuylkill. Again, an examination of twenty individuals of *Anodonta corpulenta* from Abbey Creek, Ia., made since these tabulations were completed, has increased the list of unionid parasites from that stream to six, adding *Aspidogaster*, *Cotylaspis*, free *Distomata*, *Bucephalus*, and *Conchophthirus*, the smaller number of parasites reported in the table being due in a large degree to the particular species of *Unionidæ* previously examined from the stream. An examination of Table VI. shows, however, that there is quite a great variation in the infestation of the same species in different localities. This variation is the greatest, as would be expected, in the host species least frequently parasitized, and especially in the case of those parasites that are infrequent or unusual in a given host. Again in the case of the larger streams as compared with the smaller ones, whenever a given host is especially plentiful and *Unionidæ* in general are abundant the infestation is relatively larger and a greater variety of parasites occur. For example, in the Illinois and Cedar rivers, both large streams, a large proportion of the *Unionidæ* are excessively parasitized, but in the Spoon River, a smaller stream, only such species are extremely infested as are abundant or dominant, as, for example, *Quadrula tuberculata*, *Unio gibbosus*, and *Lampsilis gracilis*. The fact that *Unio complanatus* from the Schuylkill River is but slightly parasitized in comparison with individuals from its tributaries,

TABLE VI. COMPARISON OF LOCAL INFESTATION.

HOST SPECIES.	Locality.	Number examined.	PERCENTAGE INFESTED WITH							
			Aspidogaster.	Cotylaspis	Cotylaspis Free Distomata	Encysted Distomata	Cercaria.	Bucephalus.	Atax.	Conchophthirus.
Quadrula tuberculata.	Illinois Riv.	17	76	71	12	...	...	...	29	29
	Spoon Riv.	21	81		..	...	...	..	86	...
Quadrula pustulosa.	Illinois Riv.	29	45	31	7	..	...	...	90	21
	Spoon Riv.	28	29	...	...	..	...	...	64	...
	Cedar Riv.	30	23	...	13	..	..	3	20	...
Quadrula plicata.	Illinois Riv.	45	76	...	...	...	...	...	67	11
	Spoon Riv.	8	63	...	...	...	...	...	20	...
	Cedar Riv.	36	61	...	...	...	...	...	3	...
Unio gibbosus.	Illinois Riv.	25	20	...	4	...	...	...	4	56
	Spoon Riv.	10	40	...	...	...	10	...	...	30
Unio complanatus.	Susquehanna Riv.	17	59	...	...	...	...	...	...	94
	Schuylkill Riv.	20	15	...	...	...	...	...	...	70
	Pickering Cr.	14	43	...	...	...	...	...	...	86
	French Cr.	20	30	...	...	...	...	5	5	80
Alasmodonta complanata.	Illinois Riv.	11	27	18	...	...	...	...	18	55
	Spoon Riv.	8	...	...	...	...	...	...	38	...
	Cedar Riv.	37	19	...	...	...	3	5	27	3
	Abbey Cr.	8	...	...	...	...	...	...	67	...
Alasmodonta marginata.	Pickering Cr.	30	27	...	...	...	10	...	80	70
	French Cr.	20	5	...	...	...	5	..	75	60
Strophitus edentulus.	Illinois Riv	12	25	33	25	...	..	8	8	17
	Cedar Riv.	14	21	7	...	..	..	29	7	29
Anodonta grandis.	Spoon Riv.	3	100	...	...	...	...	...	33	33
	Cedar Riv.	5	100	100	100	...	...	...	...	80
Anodonta corpulenta.	Illinois Riv.	20	90	95	75	...	...	5	85	65
	Thompson's L.	10	90	100	40	...	...	...	90	60
Plagiola elegans.	Illinois Riv.	25	12	...	...	4	...	8	4	4
	Cedar Riv.	20	...	...	...	...	..	5	15	...
Plagiola donaciformis.	Illinois Riv.	21	67	5	5	...	...	5	5	...
	Cedar Riv.	13	54	...	...	...	...	...	..	...
Lampsilis ellipsis.	Illinois Riv.	3	100	100	67	...	...	...	...	...
	Cedar Riv.	11	82	73	73	...	...	...	9	...
Lampsilis ligamentinus.	Illinois Riv.	24	...	50	...	...	...	...	37	4
	Cedar Riv.	65	...	2	...	6	8	18	17	11
Lampsilis luteolus.	Illinois Riv.	10	30	20	10	...	...	...	90	...
	Quiver Cr.	10	...	...	10	...	...	10	30	...
Lampsilis anodontoides.	Illinois Riv.	20	100	55	...	...	...	5	75	60
	Spoon Riv.	4	...	...	...	...	...	...	...	50
	Cedar Riv.	9	22	11	...	11	...	...	...	...
Lampsilis rectus.	Illinois Riv.	10	20	60	...	...	...	...	60	30
	Cedar Riv.	37	14	57	30	...	8	3	70	38
Lampsilis ventricosus.	Illinois Riv.	10	60	60	30	...	...	...	60	...
	Quiver Cr.	40	18	5	48	...	...	23	43	...
	Cedar Riv.	56	29	29	63	...	...	2	82	...
Lampsilis alatus.	Illinois Riv.	20	95	80	...	...	...	...	95	95
	Cedar Riv.	18	94	11	22	...	...	...	77	39
Lampsilis gracilis.	Illinois Riv.	40	83	83	...	...	...	13	78	25
	Spoon Riv.	16	94	...	...	...	...	25	75	...
	Cedar Riv.	33	85	36	...	...	3	24	60	3

French and Pickering creeks, and from the Susquehanna River, may be due to the very peculiar conditions, referred to on page 400, which exist in the Schuylkill. Again, in *Alasmodonta marginata* the extensive amount of parasitism in the material from Pickering Creek as compared with that from French Creek, is explained by the fact that this is an abundant and dominant species in Pickering Creek, while it is relatively infrequent in French Creek.

Some attempt was made to discover whether purely local conditions in the habitat, such as the character of the bottom and association with other species of *Unionidæ*, bear any relation to the character and degree of infestation. The examination of representatives of nine species taken at one time from a restricted locality below a bar in the Illinois River, where *Unionidæ* were unusually abundant and at least twenty-nine species represented, gave results which did not differ materially or in any one direction—save in the slightly larger infestation to be expected because of the hosts' unrivaled opportunities for infestation—from those obtained from the same species collected in other localities.

A purely qualitative examination of the food of the various species of *Unionidæ* showed no differences that could be correlated with their capacities for infestation. The nature of the food would hardly determine to any appreciable degree the parasites of other organs than those closely connected with the alimentary canal, and least of all those whose lodgment would be effected by mere entrance to the branchial chamber.

In conlusion, the results arrived at by the foregoing studies may be summed up as follows: The host species seem to exhibit unlike capacities for infestation, both as to the number of individuals and the kinds of parasites present. It appears that the differences shown are attributable only in a minor degree to the age and size of the host, the size of the stream, and the density of the unionid population. They are not sufficiently accounted for by the seasonal variation, —which is shown to exist to some degree at least in the case of certain parasites,—nor by the very slight difference in

general structure between the various host species. The evidence therefore seems to indicate that the capacity for infestation in each host species is to a large extent a specific characteristic.

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Just before going to press the nomenclature and systematic arrangement of the host species have been revised by Mr. Hart to bring them into accord with the more natural classification which is now being elaborated for this group.

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