Zoo 219 Dec. 13, 1960 Keith Nelson

HAIR-SPLITTING AMONG THE MBUNA OF LAKE NYASA

Fryer, G. 1959 The trophic interrelationships and ecology of some littoral communities of Lake Nyasa with especial reference to the fishes, and a discussion of the evolution of a group of rock-frequenting Cichlidae. *Proc. zool. Soc. London* 132(2): 153-282.

Lake Nyasa - about 600 km. long, 50 km. wide, and very deep - lacks a pronounced hydrological cycle; this produces abyssal regions barren of all save anaerobes, and even the pelagial zone is remarkably poor in plankton. The bulk of the lake's productivity is confined to the very rich, very narrow littoral shelf, which consists of monotonously alternating rocky and sandy stretches.

While covering rather thoroughly the ecology of a rocky shore, a sandy beach and two minor habitats, Fryer was primarily concerned with a rock-dwelling species-flock, the Mbuna. Of 28 Mbuna in the lake, at Nkata Bay 18 were found to be restricted to rocky shore, and an additional two were restricted to an intermediate zone, that is to an ecotone, between the latter and the sandy beach habitat.

The rocky shore has but one kind of primary producer: many species of algae forming a thick mat on the upper surfaces of the rocks, which Fryer designates *Aufwuchs*, and subdivides into two components, a flocculent, largely diatomaceous *Loose Aufwuchs*, and filamentous blue-greens, *Calothrix*, which are firmly attached.

The invertebrates are of few species, but they abound: 7 chironomids, 2 copepods, and 20 ostracods in a cm^2 of *Aufwuchs*. Total organic matter (dry wt. minus ash) varied erratically between 563 mg/dm^2 at 23 cm. and 87mg/dm^2 at 91 cm. below the surface. The fishes are equally abundant: 7-11 $fish/m^2$.

Of ca. 34 species of fishes on the rocky shelf, only 5 were of non-*Haplochromis* derivation. Two groups are of special interest: 17 *Aufwuchs*-eaters of which 12 were common, and 15 were of *Haplochromis* stock, and 9 invertebrate-eaters, of which 8 were common and but 2 were non-cichlids. For the record, the other "niches" were occupied as follows: 5 cichlid predators on fish, none Mbuna; a cyprinid surface-feeder; an "emancipated" plankton-feeding Mbuna; and - Lordy * a fish-scale-feeding Mbuna.

3 of the invertebrate-eaters took crabs in their diet; the other 6 are listed in the table. The first 2 and the last are Mbuna, the middle three are less-specialized *Haplochromis*. Observe that the Mbuha overlap less with each other than with their more distant relatives. Are they sufficiently distinct? Obviously, but.....

Note that three spp. take both kinds of Aufwuchs, while 10, including the two restricted to the ecotone, take no *Calothrix*. Of the latter, the non-cichlid feeds only upon horizontal surfaces, the two inshore-skulkers are quite different in size, one of the ecotone spp. scrapes the Vallisneria as well as the rocks, and the midshelf Mbuna appear to use quite different methods to accomplish the same end. Fryer feels, however, that these differences are insufficient to prevent certain of the spp. from coming into competition, and that in these cases "superabundance of food" prevents this from occuring. He feels predation is the limiting factor, but realizes the difficulties attendant upon his position. He believes that if one prey species became too abundant, the predator would naturally tend to focus its attentions on it, and so restore the balance.

These fish hunt largely by sight. The Mbuna contain some cryptically colored spp., notably the skulkers, which live inshore out of reach of the predators, and some very brightly colored forms, several of which exhibit remarkable color polymorphism. Perhaps these latter taste bad, but the natives eat them. Further, he postulates that it is competition which is keeping the ecotone species out of the rocky shore, and vice versa. Finally, he found but one 10-cm. Mbuna in 27 stomachs, and that in that of the largest *Haplochromis* predator examined. This suggests that predation is almost restricted to juveniles.

These Mbuna and *Haplochromis*, incidently, appear to all be mouth-brooders, and those for whom data was available appear to have no breeding season.

Ponder the evolutionary and ecologic "laws" which appear to be violated by this one little group of fish; it may be that we will be forced to revise not only our concepts of evolutionary rate and mechanism, not only our ideas of what constitutes effective ecological distance and what it is that we call a "niche", but even our approach to the ecotone and the problems of lake productivity.

Ecology of the Aufwuchs-eaters of the rocky shore.

both tables modified from Fryer, 1959.

Labeo and Varicorhinus are Cyprinids, all others cichlids

species	size range of sample IN CM.	numbers	loose Aufwuchs	Calothrix	"demeanor"	(above) position of mouth (below) dentition	feeding method	marginal foods	shoreline	distribution	edge of shelf
Labeotropheus spp. (2)	3-11	48	++	+	parallel to substrate	ventral scraper	series of "nibbles" ①	none		——————— – –	
Pseudotropheus tropheops	5-13	202	++	+	"hovers" over rocks	sub-term. fine comb	nip-scrape nibble ④	none		——————— – –	
P. zebra	5-11	114	++	-	slow conspicuous	terminal open comb	Combing w/ sucking ②	none		——————— – –	
P. auratus	5-9	12	++	-	bold conspicuous	as in fuscus	as in fuscus ③	none		——————— – –	
P. fuscus	6-11	35	++	-	"skulking"	terminal blunt	nibbling, wrenching ②	none	———		
P. elongatus	?	few	++	-	similar to fuscus ? ②			none	?		
P. minutus	5-65	18	++	-	not easy to see	similar to fuscus, médian teeth larger ③		none	———	– ? –	
Petrotilapia tridentiger	4-19	48	++	* RARE	slow conspicuous	terminal spoons	Combing w/ sucking ②	none		—————————	
Haplochromis fenestratus	5-13	74	++	-		terminal unspecial.	unselect. scraper	chir. ostra. cope.		——————— – –	
Haplochromis guentheri*	6-13	13	+	-		terminal weak	fil. algae not Caloth.	chir. ostra. cope.		– – ? – –	
Labeo cylindricus	12-34	65	++	* RARE	conspicuous	ventral horny pad	scraping horiz. surf.	none (here)		—————————	
Varicorhinus nyasensis	17-29	43	-	++	Shoals migratory	similar to Labeo		omnia	not restricted to one area		
Cyathochromis obliquidens	8-12	64	++	-	similar in all respects to zebra, except for oblique teeth, scrapes Vallisneria as well as rocks ②			gelatinous algae, Vall., sand;		intermediate zone	
Pseudotropheus lucerna	?	28	++	-	similar to zebra, but straight anterior border of lower jaw; skims material from sand and rock ②			grit other algae		intermediate zone	

Relative importance of different foods for 6 invertebrate-eating rocky-shore fish

		zoo-plankton	cope.	ostra.	chiro. larvae	hydrops. larvae	mayfly nymphs	Eubrianax larvae	Corethra larvae	other larvae	terrest. insects	algae	misc.
26	L. vellicans		*	***	*****	****	*	*		**		*	*mites
FEW	L. caeruleus			*	***	*****	****	**	*	*			*mites
[illegible]	H. kiwinge	*****			**	*	****				***	*	
FEW	H. euchilus		*	***	****	**	*****	*		*	*		*FISH PRAWN SNAIL
6	H. ornatus		**	****	*****	**	***	*		*		*	*MITES
6	Ps. fuscoides				*. **	*	*****			*	*	*	*SNAIL

* FEE[illegible]S NEARLY EXCLUSIVELY IN SOME CASES ON FILAMENTOUS [illegible]NS AND BLUE-GREENS SCRAPED FROM ROCKS

Nov. 29, 1960

Zoology 219 Richard B. Root

On the Nature of the Avian Niche

MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology 39: 599-619.

It is generally agreed that interspecific competition is the critical process which determines the horizontal organization of a community. Mac Arthur's study of five species of the genus Dendroica stands as an important advance in our understanding of this process. By restating Gause's Hypothesis in a way which better agrees with the meaning implicit in the original mathematical models, MacArthur both clarifies and extends the meansing of this concept. Instead of the sterile "no two species can occupy the same niche," he interprets Gause to mean that "to coexist, each species must inhibit its own further increase more than it inhibits the others'." This definition emphasizes searching for the ways in which coexisting species limit their growth and acknowledges interspecific competition has acted as an important selective force in determining the niches of sympatric species. The data resulting from such an approach has bearing on problems in community organization because the methods used also demonstrate how the total resource available to a class of similar niches is partitioned. The basic nature of the approach which MacArthur has developed can be more fully realized when studies are extended to include all species within a community whose feeding niches overlap to a significant degree (guilds).

The data are presented in the attached pages. It was found that while there was overlap in morphology, stratification, and feeding behavior, there were also clearcut modalities which significantly separated the Cape May, Black-throated Green, and Bay-breasted warblers. In light of Hairston's recent evaluation of mathematical models for community organization, the fact that the Myrtle warbler had the widest feeding adaptation coupled with the lowest density is interesting. MacArthur shows that the density of all the warblers is directly related to the volume of foliage on an area. When the distribution of the birds within the foliage is compared with similar data presented by Morris for the spruce budworm, it appears that the warblers are attracted to prey concentrations ie. all areas of the tree are not equally attractive as seems to be assumed in some of MacArthur's comparisons. Thus the observed differences in microhabitat could be the result of differential response to a concentration of a single prey species and not of a single instinctive reaction to the vegetation structure.

The author concludes that these warblers are able to coexist because differences in behavior cause them to partition the community in such a way that the population of each is limited by a different factor. This conclusion can be contended because of the presence of a generalized species such as the Myrtle warbler, because no critical data on food are presented, and because it appears that all species respond to the spruce budworm, although to differing degrees. Perhaps MacArthur's strongest support for the action of Gause's Hypothesis, is that each species limits itself by territorial behavior more than it influences the populations of other species. Unfortunately, MacArthur did not study territoriality directly, although the data of others seems to substantiate this conclusion. By extending MacArthur's explanation, it seems that we can conclude that intraspecific territoriality might be an important factor in allowing birds to avoid intense interspecific competitions without becoming highly specialized in their feeding niche. The resulting lability is clearly of adaptive advantage in regions where food supplies fluctuate. By assuming this view, we can explain why there is so much overlap in the stratification and behavior of these five warblers and why competition has not resulted in greater divergence in bill size.

It seems, then, that the factors which limit the size of the avian niche are, the degree to which territoriality imposes regulation, interspecific competition, and the constitutional limitations of the parental stock (see Svardson for a similar statement). It is admited that there are several complications to this hypothesis which involve interspecific territoriality and the degree to which competitors influence the size of the intraspecific territory. It seems that these complications can be easily incorporated into the general scheme presented.

Morris, R. F. 1955. The development of sampling techniques for forest insect defoliators. Canadian J. Zool. 33: 225-294.

Svardson, G. 1949. Competition and habitat selection in birds. Oikos 1: 157-174.

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Zoology 219

6 December 1960
Robert J. Behnke

Niche Delimitation in Congeneric Species

Kohn, Allan J. 1959 The ecology of Conus in Hawaii. Ecol. Mono., 29:47-90.

The gastropod genus Conus contains many closely related sympatric species. Are these sympatric species also ecologically closely related? Do their niches overlap? In other words, is there interspecific competition? If so, how much and what are the effects on the species involved? These were the questions Kohn sought to answer.

Kohn examined 18 species of Conus in two basically different habitats: 1. Marine benches and 2. subtidal coral reefs. The species of Conus are readily divisable into three strictly ecologically isolated groups: 1. mollusc eaters, 2. fish eaters, and 3. worm eaters, which comprised the bulk (12 species) of the snails in Kohn's study.

Although his data were scanty on the molluscan and fish-eating Conus, Kohn believed there was little or no interspecific competition between any of these species. With the worm eaters, however, Kohn was forced to carefully dissect the niches before he arrived at his conclusions.

Kohn accepted Odum's definition of niche: "The position or status of an organism within its community and ecosystem resulting from the organisms structural adaptations, physiological responses, and specific behavior." The ecological niche is multi-dimensional. The multi-dimensional niche concept was fruitfully applied to this study and resulted in demonstrating the ecological separation of the sympatric worm-eating species of Conus. After thoroughly examining the many dimensions of the niches found in the worm-eating Conus, Kohn concluded that even between the most similar species, ecological isolation is pronounced. That . . . "overlap of niches in one or more dimensions does not prove occurrence of competition . . . ." "Ecologically similar species are just that--and not ecologically identical."

Kohn, however, was not able to delineate the factors which regulate the density of Conus. Perhaps the adult density is regulated by conditions during the development of the larval and early young stages.

Keith Nelson Zoology 219 November 8, 1960

'NATURAL COEXISTENCE', GAUSE'S 'LAW' AND THE NICHE CONCEPT

Savage, J. M. 1958 The concept of ecologic niche, with reference to the theory of natural coexistence. Evolution 12: 111-112

Ross, H. H. 1958 Further comments on niches and natural coexistence. Evolution 12: 112-113

A. Savage's response to Ross (1957) first states that the principle aimof Ross was to demonstrate that 'Gause's Law' (sic) was not a universally valid generalization.

B. Savage takes 'Gause's Law' to mean that "no two species have the same ecologic niche at the same time and place, or...no two species have identical ecologies".

C. Although Many zoologists and almost all botanists have used it (niche) as synonymous with habitat,

D. modern ecologists - Elton (1927,p.63), Lack (1947), Odum (1953,p.15), Andrewartha and Birch (1954,p.3) and Clarke (1954,p.468) - are coming to use it in the functional sense:

E. "the sum total of the activities of the organism". He argues that in this functional concept, the organism's energy relations are important, but not all-important, citing burrowing activities of fossorial animals as examples. He states that

F. Gause's Law applies to this concept of niche.

G. He then argues that as Ross' attempted refutation was based upon niche "as a synonym of habitat" it fails completely,

H. and that Ross has no basis for his thesis until he shows that his leafhoppers have "wholly identical ecologies". He concludes by praising his own niche concept.

I. Ross in his reply examines the niche concepts of the gentlemen cited by Savage, and concludes that Clarke's is a food niche, Andrewartha and Birch mention niche only in passing, both Elton and Odum, while associating it with at least three or four different concepts, almost invariably link it to the food-chain, and Lack does also.

J. He argues for a unitary functional niche concept: food-niche, hibernation-niche, etc. - as being the most useful for comparative community studies, and suggests that

K. "bionomics" be used for Savage's concept.

L. He would eliminate a species' predator-relations from consideration of its niches, citing Elton as considering these as part of the niche-relations of the next higher trophic level;

M. he feels that Savage's concern over Erythroneura's predator-relations is "therefore not relevant"

N. He interprets Gause's use of niche as compatible with his own, and considers Savage's rephrasing as "inadmissible". He reiterates the main conclusions of his study, and adds that the pattern of leaf-puncture and from all indications the predators are the same for all six species.

O. Finally , the definition of niche was only incidental to his main point, which was that these species occupy the same food niches at the same time and place.

In the following critique let it be understood that I am in no way attempting to deny the all-important role that competition plays in evolution and community ecology; I am emphasizing that this and the competitive *exclusion* principle are not inseparable, and that evidence pertaining to the former does *not automatically* pertain to the latter.

I will also be suggesting that when a *term* (not concept) is "loaded" with connotation *a priori*; when it is in current use in a scientific discipline to denote three connected *but quite* different ideas, often by the same author in the same publication; and when there is evident confusion over which concept an author refers to when he uses the term, it is time to consider whether or not that discipline would be better off by discarding the term altogether.

A. is answered indirectly by C. Let's say it was *a* principle aim.

B. Gause's "law" is considered By Crombie (1945), by MacArthur (1958), and implicitly by Hutchinson (1957), to be a verbal restatement of the Lotka- Volterra equations. They all add conditional phrases to Savage's bare core, as they interpret those equations to require. Let us examine these:

1.the growth curves of the separate populations must follow logistig equations of the type $dN/dt = bN(K-N)/K$. The nature of the competition must be such that m, the number of places occupied by species B which could otherwise be occupied by species A, may be expressed *linearly* as $m = \alpha N$", where α is a coefficient of influence of B on the replacement *rate of A*, that is, a *constant*.

2. The environmental conditions, other *than that* exerted by the species upon each other, must be constant, or if not, must vary only within narrow limits with a period small compared to the postulated peplacement time so that mean values may be taken, and must show no trend.

3.All of the factors likely to be limiting must be density-dependent and of the type $(K-N))/K$.

4. It is helpful if the environment is homogeneous.

B,above, is thus apparently not a very accurate statement of "Gause's Law", unless natural populations conform to all these requirements, which they manifestly don't.

Is it a "law"? It is an empirical generalization, not a law. It won't be one until it has been shown, empirically, to have an operational probability close to one. Has, or can, this be shown - that is, how meaningful a *principle* is it? Hutchinson,a proponent, dismisses the experimental evidence as *follows*: "It would of course be most disturbing if confirmatory models could not be made from actual populations when considerable troubleis taken to conform to the postulates of the deductive theory."

What about the observational evidence? Unfortunately, most workers seem to regard Gause's principle as a law, and utilize it only to prove a point, instead of the other way around. Thus, Lack (1947,1949) uses it to add weight to his conclusions with regard to the differences in *Geospiza* beak size. Hutchinson, on the other hand, feels that this case offers *remarkable indirect* evidence for Gause's principle. Neither seem to realize that while Lack's work may indeed show the role of competition in evolution, it says nothing whatever about competitive exclusion. There's a subtle distinction here. To say that there is a selective advantage in avoiding competition is *not* to say that competition must inevitably lead to niche or geographical displacement or to extinction. Other selective pressures may predominate.

Perhaps the most damning objection of all has come all unwittingly from the pen of one of the leading Gausistas, A. C. Crombie(1947);"The same conclusion applies to organisms with *similar* rather than identical ecologies, but the necessary degree of similarity can *only be* discovered empirically. That is to say, species have too similar ecologies to coexist if they have too similar ecologies to coexist. What, by the way, is meant by "no two species can have identical ecologies?" Nothing, for it is a tautology: the probability that two species could have absolutely identical habits, biomass per individual, RQs,etc., without being in reality just one species, that is, and still be genetically distinct, is infinitely small.

Hutchinson describes a method developed by MacArthur which involves plotting species-numbers against number of species for species of roughly equivalent adaptive norms, and comparing the resultant curve with the expected curves for random niche overlap and non-overlap. It is probably too coarse a method to be expected to show more than that niche overlap is not the rule (nobody claims it is) and in any event it can only be applied when: 1. the habitat or large subdivision is "homogeneous in its heterogeneity", 2. the ratio total individuals/total species is constant, and3. there are enough species in the particular adaptive type selected to make comparison meaningful, thus practically eliminating from consideration those habitats where density-independent factors are most likely to be limiting.

We must conclude that for the present at any rate, Gause's principle fails the big test of an empirical generalization, namely, that it be capable of proof.

C. If many zoologists do, why don't we all, and adapt (K) bionomics, say, for the functional niche concept?

D. There is some doubt in my mind about who has what niche concept. A careful reading of the authors cited partially bears out Ross' contention (I),to the extent that each either uses niche in the food-chain sense alone, or first pays lip-service to the total-function concept, and then proceeds to use it in the food-chain sense.

F. Gause also pays lip-service to Elton's concept, as far as Elton went, but his usage and all his experiments employ or imply the unitary sense of Ross (J,N).

G. It is patent that Ross used niche in a food-niche sense, not in the habitat sense; the assumption is that this distinction escaped Savage.

L. I can go along neither with this statement nor with the next (M). I feel that the delineation of a species' niche, niches or bionomics is terribly incomplete without description of the species'status *qua* prey.

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Appendix II *

The Lotka-Volterra equations:

$$(1)\quad \frac{dN'}{dt} = b'N' \, \frac{K'-N'-\alpha N''}{K'} \,, \qquad \frac{dN''}{dt} = b''N'' \, \frac{K''-N''-\beta N'}{K''} \,.$$

N', b' and K' represent the numbers at time t, ideal growth rate and limit for species A. α and β are the coefficients of competition- the influence of a member of species B on one of species A, in a sense, and vice versa.

Equilibrium is obtained only when the rate of change of size of both populations is zero, that is, when $dN'/dt = dN''/dt = 0$. There are four such possibilities:

(2) when $\frac{1}{K''} > \frac{\alpha}{K'}$, and $\frac{1}{K'} > \frac{\beta}{K''}$, when each limits its own potential increase more than that of the other,

$\lim_{t\to\infty} N' = \frac{K'-\alpha K''}{1-\alpha\beta}$, $\lim_{t\to\infty} N'' = \frac{K''-\beta K'}{1-\alpha\beta}$, which give the limiting number that each species may obtain in the presence of the other. MacArthur, Gause and Crombie all conclude that conditions such that each limits itself more than it limits the other can only be met, stabilized, when there is a different limiting factor for each. They thought this was self-evident; it isn't, as Hutchinson has shown. The extreme case would be, for example, where each of two bird species were limited by the size of territory a member could defend against conspecifics, and where there was no interspecific influence on territory size. Then α and β and hence α/K' and β/K'' all approach zero.

(3) and (4) when $\frac{1}{K''} > \frac{\alpha}{K'}$, $\frac{\beta}{K''} > \frac{1}{K'}$ or $\frac{\alpha}{K'} > \frac{1}{K''}$, $\frac{1}{K'} > \frac{\beta}{K''}$

$\lim_{t\to\infty} N' = K'$, $\lim_{t\to\infty} N'' = 0$ $\qquad$ $\lim_{t\to\infty} N' = 0$, $\lim_{t\to\infty} N'' = K''$

where the first inhibits the potential increase of the second more than the first inhibits its own, while the second inhibits its own more than it does that of the first; or vice versa; one drives out the other.

(5) $\frac{\alpha}{K'} > \frac{1}{K''}$, $\frac{\beta}{K''} > \frac{1}{K'}$ Each inhibits the other more than it does itself; one drives out the other depending on the values of α, β, K' and K'', and on the size of the initial populations.

* after Gause (1934) and Crombie (1945), modified.

Conus snail

Dec. 6

VERTEBRATE REVIEW
(Zoology 243)

M. Konishi May 3, 1960

Much has been done and discussed on the 'vertical organization' of ecologic communities, whereas the 'horizontal organization' has received much less attention by vertebrate ecologists (Elton, 1946) The question as to what extent the patterns of the horizontal organization exert influence upon the intrinsic rates of natural increase of the populations concerned is yet to be determined.

It is now well established that morphological and physiological specializations accompany niche occupancy (Lack, 1947; Gibbs, 1954; Snow, 1954; and others). However it has also been shown that there are many examples of ecologic overlap (Hartley, 1948, for fish; Gibbs, 1954, for birds, are examples). Interspecific competition has been defined in many ways, but in my opinion any definition is meaningful only when it has ecologic significance. I consider that "seeking for the same resources" by more than one species (of the same trophic level) is the most logical definition.

Hartley(1948) investigated the food habits of 11 fish species in a British river and concluded that "with the exception of the fish-eating pike, there is a great degree of general competition between all the fish of the community" although he gave no account of the territorial or dominance relationships among these species. Gibbs (1954) has reported the best data on birds for this subject. He studied the feeding habits of 5 sympatric species of Parus and found that there was a varying degree of diversity in feeding and that there was also a considerable amount of combat between the species. He reported the order of dominance to be Great = Blue > Marsh > Coal. Pitelka (1951) after studying the territorial and dominance relationships between Anna and Allen hummingbirds reported that the aggressive behavior of the Anna affected the habitat selection of the Allen. There was some mutual effect on their populations, with more negative effect upon the latter population. Dixon (1954) reported that in competition between the chestnut-backed chickadee and the Plain titmouse in an area recently invaded by the former that the titmouse tended to dominate. Petrides (1959) reported that there is much competition between African vultures when feeding at carcasses. Udvardy (1951) cites some anecdotal examples of competition for European birds and mammals as does Simmons (1951) who suggests that interspecific territoriality is a competition-preventing device. I have found competition in the mixed feeding flocks of two species of Corvus in Japan.

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sheets for term paper

Atherinidae - silversides
- 2 dorsal fins
✓ Grunion - no teeth in mouth - protractile mouth

✓ jack smelt - small unforked teeth in bands

✓ top smelt - forked teeth in single series
- non protratile pre max.

✓ Mugilidae - mullets.
- mugil cephalus

✓ Sphyraenidae - Baracuda
Calif. barracuda
Carangidae - jacks.
Calif. yellowtail
Seriola dorsalis
✓ jack mackeral
Calif. bonito
skipjack
Thunnidae -
bluefin tuna
. albacore
yellowfin tuna
Scombridae - mackerels
✓ — Pacific mackerel
Sciaenidae · croakers
✓ - kingfish or tomcod croaker
- small barbels.
- White seabass
-Embiotocidae -
striped perch
Taeniotoca lateralis
Rubber-lip
Rhacochilus toxotes
Pacif. white perch
Phanerodon furcatus

✓ Barred perch
Amphistichus argenteus
✓ - Hysterocarpus traski

Scorpaenidae - rockfishes
Bocaccio -
Sebastodes
✓ Ling cod
Ophiodon elongatus

Cottidae -
staghorn -
✓ Cabezon
Cottus beldingi

✓ Cottus asper
Cottus aleuticus

✓ Gasterosteidae
-3 spine

- not in this test -

- know - -

are fish
native or introduced
families & order names
- minnows - herrings - trout
sunfish
genera & species only
of Salmonidae

nomenclature of anatomy
fin rays, teeth
(every year most people
don't recognize
basibranchial teeth)

- scale types -
- Lake Temescal field trip
-

Ictaluridae

- white cat - native?
- brown bullhead - bottom feeders
  - surface feeder
  -
- sand dab - L. hand
- Calif. Halibut - R. hand + L. hand - name parts - pelvic fin
  - anal
  - dorsal - ventral
- starry flounder. R. hand.
  - which is largest?
  - most impt. commercially? - range -

Gadiformes
- burbot. - .

Serranidae -
striped bass - pseudobranch
- native range
- ,

Esocidae - pikes

Catostomidae - suckers

C. <u>occidentalis</u>

Cyprinidae

- Carp
- greaser blackfish
- golden shiner
- squawfish
- Tui. chub :- Diamond L - Pyramid.
- hardhead
- hitch

- Importance of introductions - more than birds & mams (esp. in Calif.) - original fauna
- trash - game fish - 2 pts. view.

- qualities of good
- forage fish - grow to fit availability

name orders, fam. — species (common name)

Temescal fishes

30 pts.

138 30 21 85 70
50 180
120 50

12. Fill in the information called for in the following table. (~~30 pts.~~)

Species	Family	Habitat Found in fresh brackish or salt water or all salinities of water?	~~feeding type.~~ Main ~~Food if~~ diet Habitat: cold or warm water?	If present in ~~Introduced~~ or ~~native~~ size I for int N for native ~~Spring or fall spawner?~~	Spawns in lakes or streams or both?
Sacramento squawfish Ptychocheilus grandis					
sockeye or ~~Kokanee salmon~~ Oncorhynchus nerka kennerlyi Threadfin shad Dorosoma cere					
Mountain Whitefish Prosopium williamsonii					
White catfish Ictalurus ~~furcatus~~ catus					
Sacramento perch Archoplites interruptus					
smallmouth bass ~~Threespine stickleback~~ Gasterosteus aculeatus					

Zoology 116
Part II - Fisheries Management
Laboratory Exercise No. 14

Subject: Introduction to fish scale reading and the use of fish scales in age and growth studies. Review reading in ~~Lagler, pp. 52 - 63.~~ Bennett 85-89

Materials: (1) Slides of dry-mounted, yellow perch scales, each slide containing the following: standard length of the specimen at time of capture, weight, and other data; compound microscopes; graph paper.

(2) Standard lengths of 57 yellow perch listed herewith.

Work Program:

(1) (a) After the slide demonstration on the use of annuli in reading the age of fish from scales, study the scale slide provided and familiarize yourself with the appearance and location of annuli, checking the age indicated on your slide.

(b) Roughly sketch the scale indicating the annuli.

(2) Using the following list of standard lengths, arrange the lengths into a table in 10 millimeter groups starting at 60 millimeters. Then plot a curve giving the length-frequency distribution. The ordinate will be numbers of fish and the abcissa, standard length in millimeters.

(3) (a) From the modes of the length-frequency distribution, indicate the apparent age-groups present without reference to their actual age as listed in the following table. Indicate age by using "O, I, II, III" etc., to represent years of life. The zero ("O") age group for instance contains fish less than one year of age; I's are fish past their first birthday and in their second year; II's are fish in their third year, etc.

(4) From age data supplied in the following table make a graph of frequency distribution based on ages as determined from the scale readings. Plot age as (O, I, II, III, IV, etc.) on the abcissa and numbers of fish as the ordinate. Compare the results of age groups determined from size distribution with the age groups as determined from scale readings. Explain the deviations.

(5) Calculate the length of one perch at the time the first annulus was formed. Use the following formula:

$$\frac{\text{Length of scale at annulus x}}{\text{Total length of anterior field of scale}} = \frac{\text{Length of fish at end of year x}}{\text{Length of fish at time of capture}}$$

?

Standard length in millimeters of *Perca flavescens*
From Lake of the Woods, Oregon; April, May, June, July, 1947
by C. E. Bond

	Age May 1		Age May 1		Age May 1
61	0	145	IV	165	V
67	0	145	IV	165	V
70	I	145	V	165	IV
73	I	147	III	167	V
73	I	147	IV	177	IV
73	I	149	III	178	IV
75	I	149	III	180	IV
75	I	152	IV	180	IV
85	I	153	III	187	V
100	II	154	IV	188	V
105	II	155	V	189	V
128	III	155	V	190	V
131	II	155	V	194	V
136	III	155	IV	197	IV
137	III	155	V	207	V
140	IV	156	IV	209	V
141	IV	157	IV	220	V
142	III	162	IV	227	V
145	IV	161	IV	308	VII

chapt. 4, 5, 7 – graph paper

Zoology 116
Part II - Fisheries Management
Laboratory Exercise

Subject: Study of growth curves, condition factors and length-weight relationships.

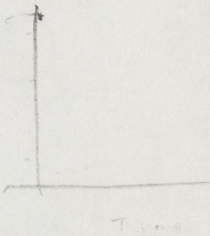
Reading Assignment: Bennett ~~85-89~~ 181-183 ~~Rounsefell and Everhart, pp. 297-309.~~

Work Program: Presented below are the results of planting 168 rainbow trout in 1941 in an experimental stream (Convict Creek) 310 feet long averaging 7.5 feet in width. The rainbow were hatchery-reared, from fall spawning stocks, approximately 7 months of age and averaged 3.7 inches in length at planting time in early April. The brown trout totaled 27 in number and were wild fish produced by natural propagation in the stream. Screens held the fish in the experimental stream area. Water temperatures over the experimental period in 1941 averaged 58.6°F. and the experiment was operated for a total time of 179 days over the summer and fall.

1. **Growth.** Using the data in Table I, plot the growth curves for each lot of trout on the same graph. Use ordinate for length and abcissa for time.

Table I. Changes in average total length in millimeters of planted rainbow and wild brown trout measured and released on a series of consecutive dates between May and Oct. 1941.

Date	Planted rainbow trout	wild brown trout
May 3	93 mm	112 mm
June 1	98	125
July 1	104	130
July 31	109	139
Aug. 29	112	147
Sept 30	114	152
Oct. 29	117	154



1. Over the period covered, what are the comparative, total growth increments in millimeters for each lot of fish?

2. Why should wild brown trout grow so much faster than planted rainbow under the same conditions?

2. **Condition Index:** This is a sensitive measure of "plumpness" or condition of fish in relation to body form. As a general rule, fat, well-formed fish will have high condition factors while thin, emaciated fish will show low condition factors. The index will vary with season, size, age, sexual maturity, and sex. In some populations there appears to be a gradual increase in condition with age; in others a gradual decrease, while others may remain the same.

The coefficient of condition K, may be determined from the following formula:

$$K = \frac{W\,10^5}{L^3}$$

– many dif. form.

where W = weight in grams
L = standard length in millimeters
and 10 is a factor to bring the value of K near unity.

In Table 2, calculated from the above formula, will be found the K values for the fish listed in Table 1. Using another sheet of graph paper, plot the K values for each group. Use ordinate for coefficient of condition (K) and abcissa for time.

Table 2. Average K values in 1941 for the same two groups of trout listed in Table 1.

Date	"K" Values for planted rainbow trout	"K" Values for wild brown trout
May 3	1.18	1.291
June 1	1.154	1.223
July 1	1.189	1.141
July 31	1.150	1.160
Aug. 29	1.097	1.122
Sept. 30	1.113	1.100
Oct. 29	1.161	1.128

1. What reason would you assign to the fact that the K values in both lots of fish declined steadily for most of the summer and then rose again in the fall?

3. Length-Weight Relationship: Since it is frequently necessary to estimate the weights or lengths of fish when only one of these items may be known, data have been compiled on the length-weight relationships of many species of fishes (Carlander 1950). Such curves enable fishery workers to compute weights of fish when only lengths are known or to estimate lengths when only weights might be known.

Weight may be considered as a function of length and since form and specific gravity of fishes are not constant throughout life, the formula:

W = el is used where
W = weight
L = length
? c and n = constants determined from data based on a large series of specimens.

This formula should not be confused with the cube law or K formula given above because description of condition and expression of length-weight relationships are two separate and distinct things.

Using the data for brown trout in Table 3, plot a length-weight curve. Use weight on the ordinate and length on the abcissa.

Table 3. Weight in grams and total lengths in mm. of brown trout at selected intervals.

Length	Weight	Length	Weight	Length	Weight	Length	Weight	Length	Weight
60	2.4	110	14.6	160	45.0	210	102.0	260	193.3
70	3.7	120	19.0	170	54.0	220	117.1	270	216.5
80	5.6	130	24.1	180	64.1	230	133.8	280	241.5
90	8.0	140	30.2	190	75.5	240	152.1	290	268.3
100	11.0	150	37.1	200	88.0	250	172.0	300	297.0

1. If you caught a brown trout that weighed half a pound (227 grams) how long should it be in total length according to your curve? ________

2. Determine from your curve how much a brown trout should weigh that was 155 mm. in total length. ________

COMPUTATION OF FISH POPULATIONS
FROM PLANTS OF MARKED FISH

(Example: Convict Lake, rainbow trout average total length 5.67" planted July 20, 1935)

Formula $\frac{a}{b} = \frac{x}{c}$ where

a = number of marked fish planted

b = number of marked fish reported caught

c = number of unmarked fish reported caught

x = number of unmarked fish present at time plant of marked fish was made (July 20)

$a + x = y$ (total fish population July 20)

Summary

	Population July 20	Reported Caught	Remaining at end of Season
Planted (Marked) Population	2014 (a)	349 (b)	1665
Calculated (unmarked) Population	1639 (x)	284 (c)	1355
Total Population	3653 (y)	633	3020

$$y = (b + c)\left(\frac{a}{b}\right)$$

The calculations shown in the above table can only be considered as extremely rough approximations by reason of the following sources of error:

—Calif striped bass gold carp

(1) Incomplete returns. For this reason the computed number of fish remaining at the end of the season is certainly too high because of fish caught but not reported. Since marked fish predominated in the shore catches and since unmarked fish were taken more largely by the boat fishermen, complete returns would have raised the number of marked rainbow caught with reference to the number of marked fish planted, and therefore given a higher value for the number of unmarked fish present July 20.

(2) Marked fish may be more easily caught than unmarked fish. This is an assumption based on the general experience that young hatchery-raised trout freshly planted are more easily caught than wild trout of the same age. The marked rainbow averaged 5.67 inches in length when planted and fish of this size usually take bait or flies readily. This factor would make for imperfect sampling of the unmarked population, and for this reason also the number of unmarked rainbows in the lake was probably higher than computed, both on July 20 and at the end of the fishing season.

(3) Losses of fish due to predators, disease, and cannibalism. There was undoubtedly loss of fish due to these causes. These factors would tend to lower the population remaining at the end of the season below the computed number.

(4) Lack of proof that in-shore and off-shore populations were representatively sampled by anglers. Since marked trout were taken chiefly near shore and no doubt were more numerous there, any disproportionate sampling of this population would distort the calculated values. These sources of error are quite unmeasurable, and today no ready means is apparent for estimating either their magnitude or their direction. Since the error may be great, these computations must be regarded as only very rough approximations.

ZOOLOGY 116
Part II Fisheries Management
Data for Term Paper

Presented below is basic data on Lake Temescal for the use of students in developing a fish stocking and management policy for this lake. The paper should not exceed eight double-spaced typewritten pages. Maps or charts will not be included as part of the eight page limitation.

The stocking and management policies presented must be backed by adequate reasons with proper documentation in a bibliography. A list of literature pertinent to this term paper is attached and has been placed on reserve in the Biology Library. Your recommendations should cover all factors relative to the proper stocking and management of the lake. Assume that the fish or other material required will be supplied by the California Division of Fish and Game.

History of the Lake

Lake Temescal was built some 88 years ago as one of the first water supply reservoirs for the City of Oakland but is now used principally for recreation. Heavy silting has occurred over the years so that now its surface area is only 12.5 acres at maximum surface level. The sole source of water is the stream feeding the lake which drains a watershed area of approximately 1,665 acres.

On January 4, 1951, the lake was chemically treated with rotenone to destroy an enormous stunted population of black crappie (*Pomoxis nigro-maculatus*). A list of the weights and numbers of fish removed during this operation follows herewith.

Weights and Numbers of Fishes Removed from Lake Temescal
following Chemical Treatment on January 4, 1951

Species		Fish Taken Weight in Pounds	Number
Black crappie	*Pomoxis nigro-maculatus* (LeSueur)	1,775	27,300
Bluegill sunfish	*Lepomis macrochirus* Rafinesque	6	100
Green sunfish	*L. cyanellus* Rafinesque	3	50
Warmouth bass	*Chaenobryttus coronarius* (Bartram)	6	100
Carp	*Cyprinus carpio*(Linné)	280	51
Goldfish	*Carassius auratus* (Linné)	1 3/4	1
Hitch	*Lavinia exilicauda* (Baird and Girard)	1/2	2
White catfish	*Ictalurus catus* (Linné)	7	7
Mosquito fish	*Gambusia affinis* (Baird and Girard)	None (taken by dipnet, April, 1950)	
	Total	2,079	27,611
	Per acre	165	2,191

Between January 4 and May 15, 1951, the lake was left without fish in order to allow a sufficient period of time for the rotenone to be oxidized by natural processes and become safe for fish life. On May 16, 1951, it was restocked with the following fishes by the California Department of Fish and Game:

Species	Number	Size
Largemouth blackbass (Micropterus salmoides)	3,000	1" fry
Common bluegill (Lepomis macrochirus)	300	6" - 7" adults

Following planting these fish evidently thrived very well for collections made by seining on December 11, 1951, approximately seven months later, produced bass from six to almost ten inches. Young bluegills around an inch in length were also taken in abundance, which indicated successful spawning by the planted adults.

In 1952, both excellent bass and bluegill fishing was had but since then bass have become extremely scarce and the main fishery is almost solely for bluegills. Two small boys reported taking 107 of these fish in three hours' time in the spring of 1953. Studies of growth rates from scale studies has shown their growth to be rapid and comparable or better than that of bluegills in some Michigan lakes. Successful spawning has occurred each year. Early in 1953, however, some evidence of stunting of bluegills was obtained.

It should be noted that the hitch (Lavinia exilicauda) appeared in the lake again in 1953. How they got back into the lake is not known but they could have been introduced by live bait fishermen fishing for bass or they could be the progeny of hitch that were in the inlet stream above the lake and escaped the chemical treatment of January 4, 1951.

In summary, Lake Temescal may be said to be a eutropic lake without thermal stratification in winter or summer, with organic materials, larger aquatic plants, and plankton fairly abundant. Water temperatures seldom exceed 75°F.

A field trip will be made to Lake Temescal and collections taken of both fish and food organisms to determine in further detail the trends taking place there and to familiarize students with the general nature of the lake in preparation for writing the second term paper.

Just before fishing season ~~in May~~

rainbow trout

7. The lake is in May seined and 1000 ~~fish~~ of catchable

all naturally reproduced.

to the lake. complete

size are fin clipped and returned. A creel

~~at the close of the season~~ rainbows

census shows that ~~by Sept~~, 2500 ~~fish~~ were

during the season

caught, ~~during~~ 250 being marked fish.

a. How many rainbows ~~were~~ catchable size were there in the lake at the beginning of the season?

b. How many at the end?

c. What per cent of the catchable size rainbows were harvested by the fishermen during the season?

d. What factors are we ignoring which may make our conclusions erroneous?

e. How much does ~~this~~ our figures tell us about the total population and biomass of rainbows in the lake?

- Mullet are catadromous.
- catadromous

Temescal

lacsemet

Centrarchidae - sunfish fam.

Largemouth bass - mouth - dorsal fin - scales — where family native (only N. Am.) where introduced; - world

smallmouth bass - — Sac. Perch

warmouth - 3 - teeth on tongue — nest building + guarding

green sunfish - 3 - short round pectoral fin - mouth

pumkinseed - 3 - long pointed pectoral - opercle membrane stiff - gill rakers short

bluegill - 3 - " " " " " flexible - rakers long

rockbass - 6 - 11-12 dorsal

Sacramento perch - 6-7 - 2 patches tongue teeth - Pyramid Lake

white crappie - 6 - dorsal spine 5-6-7 * - nests

black crappie - 6 - dorsal spine 7-8

fecundity -

Cypriniformes

Ictaluridae - adipose fin

✓ - White cat. I. catus. - most impt. Calif.

✓ - Channel cat. - I. lacustris

✓ - Yellow bullhead

✓ - black bullhead

✓ - brown bullhead

- Gadiformes - codfishes

Gadidae

✓ Tomcod LoYz 1.Yz

- Pleuronectiformes - flatfishes

- Bothidae - left. handed -

✓ Pac. sanddab - Citharichthys sordidus

✓ Calif. halibut - Paralichthys californicus

Pacif. halibut - Hippoglossus stenolepis — Pleuronectidae R. handed flounders

✓ Starry flounder. Platichthys stellatus

Perciformes

Serranidae -

✓ Striped bass - anadromous - introduced

✓ white bass

kelp bass

- Percidae ranges -

✓ - yellow perch - ecology

- walleye -

Dr. Ralph Smith
Sci. Ed. 116
Syllabus No. 2, 4th wk. (4/15/53)

Misc

> Forsan et haec olim
> meminisse javabit--
> Virgil, circa 25 B.C.
> "Perhaps these things in the future
> to remember it will please you"

> 'Tis twice happy the man with a hobby
> His is two worlds to pursue and explore--
> (Anon)

FISHES

INTRODUCTION

Historically, (600-50 B.C.) any wholly aquatic animal was considered to be a fish. Soon thereafter with the interest and pursuits of Aristotle, (384-322 B.C.) Petrus Artedi (1705-1735) Linnaeus (1707-1778), Louis Agassiz (1807-1873), and other intellectual "fathers" of that age this loose generalization was reduced to a more seemly grouping. The Greeks knew the fishes as "ichthyes", the Romans, "pisces". Accordingly students of fishes are called *ichthyologists* (Gr. ichthys, fish; logos, discourse or study of); the subject which deals with the study of fishes is called *ichthyology*, and a "lover of fishes" might be called a "*pisciophile*" if one chooses to coin a word from the Latin (piscis, fish) and the Greek (phil, love). While Petrus Artedi lived but 30 years (1705-1735), his contributions of the early 18 C were sufficiently noteworthy to establish him as the "father of ichthyology". It is interesting to note that two of our most eminent American ichthyologists are associated with instutions in California, one Dr. George Sprague Myers (Stanford), the other Dr. Carl L. Hubbs (Scripps Institute of Oceanography, La Jolla; U.C.L.A.). Other primary and famous repositories in our area are the world renowned library and collections of David Starr Jordan (Stanford Mus., Nat. Hist.), Calif. Acad. Sci., S. F., and Steinhart Aquarium, S. F. which compares favorably with the great Shedd Aquarium, Chicago. California residents and teachers should avail themselves of the materials and facilities offered by these institutions and projects.

GROUPS OF FISHES AND FISH-LIKE FORMS

No single system of classification is universally acceptable. The following groups will serve for the work here anticipated:

I. Phylum, CHORDATA ($65,000^+$ species).

This major grouping includes the relatively obscure "lower chordates", sea squirts, lancelets, acorn worms, etc. as well as the "higher chordates" which are more obvious and better known, e.g., fishes, amphibians, reptiles, birds, and mammals. Modern scientists accept the following categories:

Class, Cyclostomata The round mouths
Two common forms frequent our coastal waters.

1. Pacific Lamprey (*Entosphenus tridentatus*)
   By some called "lamprey eels"; enter our local drainage, e.g., Coyote Creek, to spawn, So. Calif. to Alaska
2. Pacific Hagfish (*Polistotrema stouti*)
   By some called "slime eels"; all marine, Lower Calif. to Alaska

Class, Chondrichthyes. The cartilaginous fishes.
Here we include sharks, rays, and ratfishes, all being represented in Monterey Bay.

Class, Osteichthyes (Pisces of some authors) The bony fishes. Includes most of our commonly observed fishes. Estimated in excess of 30,000 species, world-wise; in salt, brackish, and fresh waters.

NATIVE AND INTRODUCED SPECIES

During the quarter you will have an opportunity to observe and learn the names of our common local fishes. These will be available both alive and preserved. Each student is asked to observe these specimens each week. See hallway project. Strive to become readily familiar with their common names, importance, care, habits, and possible use in a classroom or home aquarium. Ask your instructor for references to further knowledge. A list of our commonest local species follows:

Family Petromyzontidae (Lampreys)
Pacific Lamprey (Entosphenus tridentatus)
Both young larval forms ("ammocoetes") and adults are seen commonly in our local streams. Adults anchor themselves to rocks and fishermen often refer to them as "eels". There are no true eels west of the Rockies. Thus the common entry on eastern menus, "eels and onions"--here to delight the palate of the gourmet. Am. Eels migrate to sea in the autumn, there to spawn in deep water dnd die. You are urged to read Rachel L. Carson's dramatic account of Am. Eel. The Odyssey of the Eel, p. 478 (Wm. Beebe's The Book of Naturalists (library). This especially if you are a gormet, natural history--adventure-minded, or just one who appreciates sterling writing ability. R. Carson is the author of The Sea Around Us, a current best-seller. You will find The Sea Around Us a notable and profitable evening-reading adventure. (Both of these volumes are available in our library.

Family, Cyprinidae (carps and minnows; about 1500 spp.)
Common Carp (Cyprinus carpio)
See in hall; note barbels ("whiskers") and large scales. Native to China but early introduced into Europe for food, thence from Germany to U. S. in 1877 where it is now common and whidely distributed. Formerly considered a "coarse" or "trash" fish here but now esteemed as a sport fish and considered a tasty treat when properly prepared. During World War II widely propagated on farms as a protein substitute. Now recognized as a possible solution to possible problems of over-population and food shortage. For a good recent account of the carp see Emmett Gowens' I'll Take The Lowly Carp, TRUE MAGAZINE (April), p. 44. World record 83 lbs. in So. Africa.

Goldfish (Carassius auratus)
Long under domestication in its native China; many varieties (fan tail, comet, etc.); relatively common in ponds and sluggish waters, Old River area, et. al. Often reverts to wild color with loss of "pet-shop gold". See our specimens from Old River. Note absence of barbels and color.

Western Golden Shiner; Breem (Notemigonus crysoleucas)
Locally under propagation for bait-minnow trade.

Greaser Blackfish (Orthodon microlepidotus)
Not especially common in our drainage.

Western Roach; Breem (Hesperoleucus symmetricus)
Probably our commonest local minnow. See our hall specimens.

Speckled Dace (Rhinichthys osculus)
A dark-colored, mottled fish commonly found in this area.

Family Ameiuridae (catfishes)
Six species in California (Ameriurus spp.; several frequent our waters.

Family, Cyprinodontidae (egg-laying tooth-carps; Killifish; Killies)
Many small aquarium fishes are members of this family.

Desert Pupfish (Cyprinodon macularius); sev. spp.
Common in warm-water springs of our desert country. See our specimens from the Palm Springs area; males have the dorsal and anal fins edged with black. Males become bluish in breeding season, whence the Indian name, "bluefish". Does well in aquarium but not recommended for community tanks since it is known to be a fin-nipper which may kill other specimens in the tank. A close relative of this fish, Cyprinodon diabolis, is said to have the distinction of the "smallest range of any vertebrate species. It occupies Devil's Hole, a pool about 40 feet long and 15 feet wide, a remnant of the prehistoric chain of lakes which in the moist late-glacial (Pleistocene epoch (1,000,000 yrs. ago) formed the Death Valley Lake System. The pool is located about 45 miles east of Furnace Creek Ranch in S.W. Nevada. Pressure by Dr. Carl L. Hubbs of U.C.L.A. has resulted in a recent (H. Truman) proclamation to set the area aside as a detached unit of the Death Valley National Monument. A side trip to this pool should prove interesting to members of this group. For further details see Home of Unique Desert Fish, Aquarium Journal (Mar., 1952), p. 50 (library).

Family, Poecillidae (live-bearing tooth-carp; top-minnows)
Male representatives of this family may be distinguished by the presence of a finger-like intromittent organ (the modified anal fin) which lies close against the "belly" region and functions as a structure to aid in the passage of "zoa" into the female.* A blackish triangular spot (gravid spot) on either side of the body at the juncture of the body and tail portion of the fish will serve as it enlarges and darkens to warn of the approaching birth of live fry. Members of this group may drop from a few to 60 or more young every 3-6 weeks. The parents should be removed to avoid possible cannabalism. *The male organ is called a gonopodium. Many popular aquarium fishes are members of this group.

Western Mosquito Fish (Gambusia affinis)
Common in our area. Famous for its help in rendering the Panama Canal Zone inhabitable for man. Mosquito larvae (wrigglers) are eaten in huge quantities by this diminutive fish. Widely planted (at least 70 countries) and used by all the mosquito abatement districts in California.

Until the market was saturated, advertised as "the eighth wonder of the world" and at $2.00 per pair. A hardy fish but unpopular in community tanks because of fin-nipping activities. See parasitized specimens in hall.

Family, Centrachidae (Sunfish Family)
These are warm water fishes (60-70°F). They afford much sport to after-work fishermen who frequent the several dams and reservoirs in our area.

Small-mouth Bass (Micropterus dolomieu)
Feed poorly at temperatures above 70°F. hence probably destined for expiration in our area and being replaced by Large-mouthed Bass.

Large-mouthed Bass (Micropterus salmoides)
Common to 2-3 lbs in Anderson Dam, et. al.

Common Bluegill (Lepomis macrochiris)
Common in this area.

Family, Cottidae (Sculpin family)
Five spp. in Calif.; at least two scalpins frequent our drainage. See our specimens from Alum Rock Park, Pemitentia Creek.

Family, Gasterosteidae (Sticklebacks)
Three-spined Stickleback (Gasterosteus aculeatus)
Very common in local drainage where it frequents fresh and brackish water. Males have a vermillion throat. For excellent account of habits see N. Tinbergen's account in Sci. American (Dec., 1952), pp. 22-26.

Family, Salmonidae (salmon and trout)
Properly placed this relatively unspecialized group should have appeared first in this list.

King Salmon (Oncorhyncus tshawytscha); many vernaculars.
Our most important Pacific salmon both fisheries and sport-wise. The commonly caught species in Monterey Bay brings .28/pound wholesale off the commercial crafts of the Santa Cruz area. The commercial catch in Monterey Bay has totalled millions of pounds annually, although spawning does not occur normally south of Golden Gate Bay.

Silver Salmon (Oncorhyncus Kitsutch)
Not uncommon in Monterey Bay. Together with the King Salmon our most important Monterey area salmons. Five species of salmons and two species of sea-run (anadromous) trouts are known to frequent California waters.

Steelhead Rainbow Trout (Salmo gairdnerii)
Our common coastal streams trout. Optimum temperature, low 50's. Enters practically all suitable California coastal streams to spawn. Unlike the Pacific salmons this trout does not die after spawning. Sea-going trowls are known in the West under the local name , "steelhead", a local term not used on the East coast. This name is associated with the steel-gray of the back which develops during the 2-3 years at sea. Certain people insist that steelhead represent a distinct species because of this color change. However this stand is untenable. Thus a steelhead in central California is merely a sea-going rainbow trout. In northern streams (Humboldt and Del Norte counties), the sea-going Cutthroat Trout (Salmo clarkii) is also called a "steelhead". It is known that some rainbows and other sea-going trouts may become land locked, or for reasons

not yet explained, take up residency in coastal waters without the usual sea run. It is presently the concensus (marking experiments, etc.) that steelhead return to the stream of their origin to spawn after the sea run, certainly a most interesting detail when one considers the number of coastal waters along the Pacific seaboard. The comparative table below will, *if properly applied*, separate salmons from trouts.

	TROUTS		SALMONS
1.	Lining of mouth whitish	1.	Lining of mouth blackish
2.	Caudal fin (tail) essentially square (except lake trout)	2.	Caudal fin notched or curved inward.
3.	Caudal peduncle relatively deep (thick)[1]	3.	Caudal peduncle relatively slender
4.	Dorsal fin with definite blackish spots	4.	Dorsal fin of adults plain or with dark blotches; definite blackish spots absent.

DEFINITIONS AND THUMB-NAIL FISH FACTS

1. Parr marks--the conspicuous vertical dark markings characteristic of young trouts and salmons. Disappear with age.
2. Charrs--Originally British and now also American designation for any trout in the genus *Salvelinus*; thus an eastern brook trout may properly be called a "charr".
3. Anadromous--Those fishes which spend a portion of their lives in the ocean, later returning to fresh water to spawn, e.g., rainbows, cutthroats, and some eastern brook trout, etc.
4. Catadromous--Fishes which leave fresh water to spawn in the ocean, e.g., American and European Eels.
5. Smallest fish, world-wise and length-wise. *Pandaka pygmaea* (Phillapine Croby, about 10 mm. long. "The smallest vertebrate question mark in the world" since essentially nothing is known about its life history pattern.
6. Smallest fish, world-wise and volume-wise. *Mistichthy luzoneusis* (Luzon Goby); about 1/2 inch long.
7. Smallest live bearer *Heterandria formosa* (So. Mosquito Fish); adult female about 1¼ inch; adult male about 3/4 inch, indeed somewhat shorter than its technical name!

---

[1] It is relatively difficult to hold a trout by the caudal peduncle, readily possible to hold a salmon due to this anatomical detail.

8. Most fishes are oviparous (egg-layers) although many individual species and all members of some groups are live-bearers.

9. Historical reports of "red fish-rains" are thought to refer to torrential storms which swept millions of sticklebacks into the air, later depositing them on land at points considerably distant from water ways. The red color of the males is thought to explain "red fish rains" which go back to Biblical days.

10. Largest fish. **Marine: Whale sharks (Rhineodon typicus) freshwater: Sturgeons (Acipeuser)**

11. Isinglass. Best grades originally from "sounds" (air bladder) of ssturgeons found in the rivers of Western Russia; now largely secured from the sounds of cod, catfishes, carp, ling, etc.

12. Mermaids--Sources for such stories doubtlessly variable but many seem to evolve from observations of manatecs and habor seals which assume strange postures and antics at sea. Some individuals translate these observations as mermaids, others "sea monsters", "old men of the sea", etc.

13. Sea serpents. Probable that these stories evolve from observations of follow-the-leader activities as porpoises and perhaps whales and sharks "roll through the surface, breaking water as they dispost themselves". Such activity could conceivably impress a witness with the length and vertical undulations of the rich mythical serpent lore.

SELECTED REFERENCES

Curtis, Brian 1949. The life story of a fish, his morals and manners. New York, D. Appleton-Century Co., Inc.
A most interesting account of fishes by an able student of fishes and former long-time member of the Calif. Dept. Fish and Game.

Norman, J. R. 1931. A history of fishes. London, Ernest Benn, Ltd.
Probably our best modern general account of fishes presently available. Intended to be non-technical but a classical treatment of the subject.

______ and F. C. Fraser 1949. Giant fishes. New York, Putnam and Sons. Field book series.
Excellent non-technical account of giant fishes, whales, and dolphins.

Many special papers by state and federal agencies, some available gratis and others for a small fee. Write for lists to U. S. Fish and Wildlife Service, U. S. Dept. Interior, Wash., D. C. and Calif. Dept. Fish and Game, Ferry Bldg., San Francisco. A letter to Mr. Phil M. Roedel, Editor, Terminal Island Fisheries Laboratory, San Pedro, Calif. will place your name on the mailing list for Calif. Fish and Game Bulletin, a most valuable quarterly.

Shapovalov, Leo and W. A. Dill 1950. A check list of the fresh-water and anadromous fishes of California. Calif. Fish and Game Bull., Vol. 36, No. 4. Our most authentic guide to the official common and technical names for our Calif. fresh water fishes. Available by writing Mr. Leo Shapovalov, Bureau of Fish Conservation, Calif. Dept. Fish and Game, Ferry Bldg., San Francisco, Calif.

Other pertinent literature and materials will be placed on the laboratory tables for inspection. During the laboratory period you are asked to make a bibliography card for each title (as previously outlined) and to submit these in a file box at the termination of the quarter. Following instructions cited in Syll. #1 make a 5 x 8 card for the animals and plants that are out on the table forinspection and study.

ANNOUNCEMENT

An event of noon, April 9 lends credulance to the possibility that our beautiful pair of Mexican Imperial Boa Constrictors (Constrictor constrictor imperator) may present the college with progeny. Vital statistics: Range, Central America to No. Mexico; live bearers (20-24 inches at birth); gestation period unknown but probably 3-6 months.

Since Pythons are often confused with boas a few notes on gross differences may lend succor. Appearance very similar and both are members of the same family, Boidae. Technically reported on basis of skull characters. Pythons except for a rare Mexican species are all Old World forms; also they are in general egg layers (oviparous). Boas are New World forms; most of them bear their young alive (probably ovoviviparous in light of present knowledge).

Dr. R. A. Smith

C53-66

COMMON PARASITIC DISEASES OF FISHES IN FRESHWATER AQUARIA

A. Diseases Caused by Animal Parasites.

1. Flatworm infection.

*a. Gyrodactylus. Affects all tropicals, especially cyprinodonts.	Symptoms: Fish dash wildly about tank when disturbed, may "shimmy", rub body on plants or sand. Body and gills may darken.	Cure: Treat in tank with $KMnO_4$, 1 grain to 3 gals. Change water after 24 hours. OR 3 second dip in 1.5% H_2O_2 soln.

2. Protozoan infection

*a. Ichthyophthirius multifilis (Ich). Affects all tropicals.	Symptoms: Gritty white pustules covering skin and gills.	Cure: Treat in tank with 4 drops of 2% mercurochrome per gal. OR 2 drops of 5% methylene blue per gal. Keep tank warm (85°F).
*b. Oodinium limneticum (Velvet). Affects danios, barbs, rasboras, labyrinth fishes.	Symptoms: Yellowish brown patchy film near dorsal. Later pustules resembling tiny grains of sand.	Cure: Place copper sponge in tank for 24 hours. Water should be slightly saline. Change water after treatment. Keep fish in dark for 24 hours.
c. Chilodon cyprini, and Cyclochaeta. Affects all tropicals.	Symptoms: Fish lose appetite. Often lie on one side on bottom of aquarium. Disease obvious only in late stages.	Cure: Treat in sea salt soln. (5 tsp. per quart) until fish turn over. Place quickly in new aged water.

B. Diseases Caused by Plant Parasites.

1. Bacterial infection.

*a. Mouth fungus. (Infection by motile slime bacteria.) Affects all tropicals.	Symptoms: White cotton-like growth on mouth parts. Quickly fatal if untreated.	Cure: Positive cure by four hour bath in soln. of aureomycin (30 mg. per gallon). 500 mg. per 15 gal.
*b. Fin and Tail Rot i) Affects all tropicals. ii) Affects male guppies.	Symptoms: i) Disintegration of outer fin margins. Greyish white discoloration of torn edges. ii) As above with dark red granules at torn edges.	Cure: i) Treat as velvet. OR 1 to 2 minutes dip in $CuSO_4$ soln. (1 gm. $CuSO_4 \cdot 5H_2O$ in one qt. of water). Dip in salt soln. and place in new aged water. ii) Always fatal.

2. Mold-parasitic infection. (Mycoses)

a. Saprolegnia ferax and Achlya. A secondary invader of all tropicals.	Symptoms: Cotton-like fungus on any part of body.	Cure: Treat in tank with 1 to ~~2~~ 20 000 tsps. ~~of~~ malachite green sea salt per gal. Change water after recovery. (Invited by low pH water).

*Highly contagious

COMMON DISEASES OF FISHES IN FRESHWATER AQUARIA

C. Diseases of Unknown Origin

a. Consumption. Affects cyprinodonts.	Symptoms: Abdomen becomes sunken. Body and gills darken. Fish will not breed, but may live for years in this condition.	Cure: Not known. Prevention: Avoid overfeeding dry food. Avoid low pH. Keep tanks clean.
b. Dropsy. Affects all tropicals.	Symptoms: Abdomen becomes enormously swollen. Scales may stand out from body.	Cure: Not known.
c. Exopthalmus. Affects most tropicals.	Symptoms: "Pop-eyes". Cornea(s) becomes largely distended due to hemorrhage in eye socket capillaries.	Cure: (Not always effective). Treat as for Chilodon. Swab eyes with 5% argyrol before returning to aquarium.
*d. Itch. (Probably a flatworm infection). Affects cyprinodonts.	Symptoms: Fish "scratches" on sand or plants in tank. Fish does not dash about as in Saprolegnia. Rarely fatal.	Cure: Treat in tank with 1/8 grain of KMno$_4$ per gallon. Change water in tank after 2 hours.

*Contagious

NOTE: Before placing a newly acquired fish in an aquarium, treat fish as follows:

1. Place for NO MORE THAN 30 MINUTES in a bath containing 12 drops of 40% formaldehyde per gallon.
2. After formaldehyde treatment, place for 4 hours in a bath containing 50 mg. of terramycin or aureomycin per gallon.

TENTATIVE LABORATORY SCHEDULE
Part II, Zoology 116
Fisheries Management
November 8, 1962

Thurs.	Nov.	8	- Measurements and external anatomy of fishes.
Tues.	"	13	- Identification: Pacific lamprey through the American grayling; Lab Manual.
Thurs.	"	15	- Identification: trout and salmon.
Tues.	"	20	- " " mud pickerel through hitch.
Thurs.	"	22	- THANKSGIVING HOLIDAY
Tues.	"	27	- Field trip to nearby lake or stream. Transportation will be provided.
Thurs.	"	29	- Work up field materials collected.
Sat. Sun.	Dec. "	1) 2)	- Optional field trip to the Sagehen Creek Wildlife and Fisheries Station near Truckee, California. Transportation will be provided. Leave 8:00 AM Saturday., return to Berkeley by 6:00 PM Sunday.
Tues.	"	4	- Identification: white catfish through walleye perch.
Thurs.	"	6	- " " sunfish family Centrarchidae, including black bass, crappie, sunfishes, and allied forms.
Tues.	"	11	- Identification: grunion through sculpins and sticklebacks.
Thurs.	"	13	- LABORATORY AND LECTURE MIDTERMS (Review laboratory, Wed. Evening, Dec. 12, 7-9 PM, Room 3090 LSB)
Tues. through Tues.	" Jan.	18 1	- CHRISTMAS RECESS through - NEW YEARS HOLIDAY
Thurs.	"	3	- Population calculations, growth curves and condition factors.
Tues.	"	8	- Age analyses of fishes from scale readings.
Thurs.	"	10	- FINAL LABORATORY EXAMINATION. The fisheries term paper and laboratory notes on Part II are due on this date. (Review Laboratory, Wed. Jan. 9, 7-9 PM, Room 3090 LSB)

Questions

lab. 3 Salmonidae
know Genera

Salmo

rainbow
cutthroat
(a) clarki > basibranchial teeth
(b) lewisi
brown

Salvelinus

- lake, brook, arctic

Oncorhynchus

king, silver, kokanee

- Factors limiting

IV

check
½(-) ½ ½
- Pikes - mud all pickerel, pike, muskellunge
- scales (cheek, opercle)
order family - introductions - teeth - predatory -

Catostomus occidentalis

+ pharyngeal teeth
Cyprinidae
- Carp - ~~native range~~ - introduced - why harmful?
up to
- greaser blackfish - how many eggs laid (350,000)
length of intestine.

frenum - hardhead - largest Calif. minnow
golden shiner
hitch } - ridge
squawfish - predator -

- cleared - stained
- teeth.

Salmonidae

Salmo

- Rainbow - salar?
- golden -

Cutthroat
- Coastal
- Lahontan
or lewisi

Brown trout

Salvelinus

E.B.
Lake
malma
alpinus

Oncorhynchus

King or Chinook
Silver or Coho
Red or Sockeye - kokanee
Dog or Chum
Pink or Humpback

For Jr. your lab notebook

draw soft rayed (ex. trout)
& spiny rayed (ex. crappie)
fish - ~~tint~~ indicate the
structures & characters mentioned on pgs.
69-71 - ~~mea~~ note position
of pelvic fins.

class Agnatha
order Petromyzoniformes - Know what scale formula is.
Pacific lamprey fam. Petromyzonidae
<u>Entosphenus</u> <u>tridentatus</u>
adult & ammocoetes

1. anadromous
2. What eats
- larval form -

class Osteichthyes.
order Acipenseriformes super order
fam. Acipenseridae
White sturgeon - bottom feeder
- barbels
- caviar

fam Polyodontidae
- paddle fish

order. Amiiformes | super order
fam. Amiidae
Bowfin
- range

order Lepisostiformes eiformes
fam. Lepisosteidae
gars - - largest freshwater fish
✱- ganoid scale (not in lab. manual)

super order Teleostei (rest of course)
order Clupeiformes
fam ~~Clupeidae~~ · Elopidae
Ten-pounder
– – Clupeidae
shad
* introduced (not small streams)
– anadromous *

Pacific
– ~~Sardine~~ * once most impt.

Pacific herring -
Threadfin shad * - introduced
– forage fish for res.
– limited by temp.
– requirements of good forage fish

Engraulidae
Anchovie

Osmeridae = smelt
surf smelt
eulachon

Coregonidae - whitefish -
Prosopium Rocky Mtn. whitefish * show [illegible]
C. clupeaformis

Thymallidae
grayling

* anadromy * homing

Trout

identify clarki clarki - C. lewisi parr marks

which ~~native~~ approximate native range

rainbow - A. B. C.

basibranchial teeth

brown - introduced
native range

← brown
- parr marks
- homing

- why don't trout live in Florida?

Char

lake - predaceous

arctic -

brook - identify
ranges - native
introduced

IV
field trips
- gear - Ekman dredge - name - what used for
(benthos)
plankton net - "
Surber sampler - streams -
- bottom type - of Temescal
- organism typical
- lab - bluegill - hitch
scale demonstration -
orders & families of Temescal fishes.

Test Questions

Lab I.

cycloid - ctenoid scale - spiney s/f rayed fishes

Vomer - pharyngeal - palatine teeth - basibranchial

- Ray formula
- gill rakers (herring) - food gathering

II

- lamprey - anadromy - parasitic
    ammocoets = larvae
- sturgeon - barbels - bottom feeder - caviar - family in Europe - Asia -
- bowfin - name - range - predator
- gars - ganoid scale - largest freshwater fish -
- Clupeidae - herring fam.
    - recognize - shad - Threadfin - Pac. herring
        - feeding - range - introductions
- Engraulidae - anchovie
    Osmeridae - smelt - pterygoid teeth
    Coregonidae - Prosopium - cisco - feeding types > - widespread in California?
    Thymallidae

III Salmonidae

- factors limiting - temp., O_2, purity, competition predation
- king salmon - most important in Calif. - largest
- kokanee - freshwater life cycle - introduced
- silver - smaller creeks - local.
    - die after spawning -
    - How many species in N. am. in genus.
    - genus of Atlantic salmon.

Problems

A. A sample of rainbow trout was taken from a Sierra stream and found to have an average weight of ~~190~~ grams and an average length of ~~120~~ mm.

a) What is the condition factor K for this group of fish?

~~1728) 1900 (1.1~~
~~1728~~
~~172~~

K = ~~1.100~~

b) A sample of Sacramento squawfish was found to have a condition factor of 1.092. What does comparison of this figure with the K found in (a) tell you about the relative value of the habitats in which these two groups of fish live? Explain very briefly.

B. 1500 marked rainbow trout were planted in a lake known to be well adapted to rainbows. Catch data for the subsequent fishing season showed the following catch:

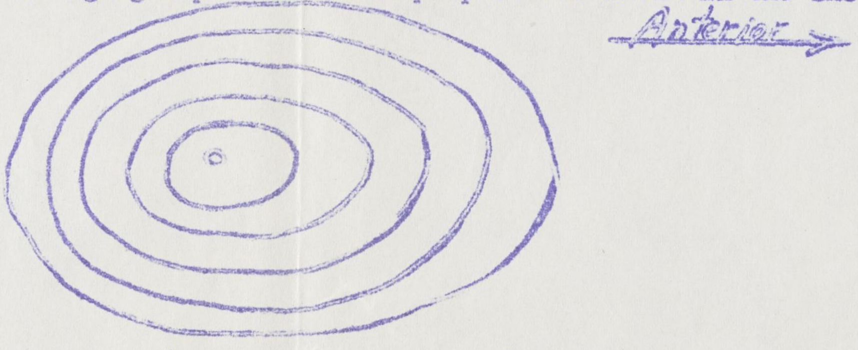
Marked trout - 450.
Unmarked trout - 380.

a) How many trout were present in the lake before planting? 1267

b) How many trout remained in the lake after the season ended? 887 + 1050 = 1937

c) Give two reasons why the above computations may be in error.

C. A scale from a fish in age group IV. had the proportions shown in the sketch below:



(Circuli are not shown).

If the fish was 280 mm. long when caught, what was its length when the first annulus was formed? (Assume a length of 40 mm. when the scale was formed).

100 mm.

1. A. Boccacio
B. Striped bass.

a. What is the family of A?
b. ~~which~~ Does A or B represent the largest volume of the Calif. sport fishery?
c. Identify the specimen native to Calif. waters.
d. Which (if either) is considered inedible?

2. A. Great Basin Sculpin.
B. Staghorn Sculpin.

a. Give the genus of A.
b. Identify B.
c. To what family do they belong?
d. Which is ~~confined to fresh water?~~ usually found in marine habitats?

3. Striped Perch

a. Identify (2)
b. Is the maximum length nearest to 8, 11, 14, or 17 inches?
c. Give a common food.

4. A. Lingcod
B. Largemouth Bass

a. Identify A.
b. What reproductive behavior do these two have in common?
c. Name 2 of the 3 important biochemicals which A provides (2).

5. A. Freshwater Viviparous Perch.
B. Sacramento Perch

a. Identify A.
b. How does this species differ from others in the same family?
c. Are A and B the same family?
d. Give a reason for your answer to c.

6. Cabezon a. Identify
b. What is its habitat?
c. Is it entirely edible?
d. What member of this family is larger than this?

7. Stickleback a. Identify.
b. Give the family.
c. What are the extreme limits of habitat of the family.
~~d. Name the family.~~
d. What foods do they eat?

8. A. Slim sculpin
B. Prickly sculpin
C. Great Basin Sculpin
a. Identify any one.
b. Give a morphological character typical of this family.
c. What is their ecological importance?
d. What value have they for anglers?

9. In the diagram representing the scale of Perca flavescens, name a, b, c, d.

10. a. What is the length in mm. of a brown trout weighing 145 gms.?
b. What is the weight in gms. of a brown trout 260 mm. long?

11. A. Rubberlip Perch.
B. Hardhead.
a. Identify A.
b. Give the family of B.
c. Which is the more important food fish?
d. Which (if either) is viviparous?

12. A. Pacific White Perch
B. Barred Perch.

a. Identify A and B. (2)
b. Name the family of A and B.
c. Which is the most important commercially?

13. A. White seabass.
B. Squawfish

a. What is the habitat of A?
b. ~~Does~~ Do A and B ever occur together?
c. Identify the one which grows larger.
d. ~~Identify~~ Which (if either) is of major commercial importance?

14. In the formula
$W = cL^n$

a) What do W and L represent?
b) ~~How are c and n found~~?
What are the values of c and n based on?

15. Explain briefly how age groups are found from a curve of length-frequency distribution.

16. Give one character by which you can distinguish:
a. Oncorhynchus from Salmo
b. Steelhead from King salmon.
c. Rainbow from cutthroat.
d. Serranidae from Centrarchidae.

LAB. EXAM - ANSWERS.

1. a. Scorpaenidae.
   b. A.
   c. Boccacio
   d. Neither.

2. a. Cottus
   b. Staghorn Sculpin
   c. Cottidae
   d. B - Staghorn

3. a. Striped Perch (2)
   b. 14 inches.
   c. Crustaceans.

4. a. Lingcod.
   b. Males guard eggs.
   c. Insulin, Vit. A + D.

5. a. FW Viviparous Perch
   b. Fresh water
   c. No.
   d. Scales on dorsal, etc.

6. a. Cabezon
   b. Bottom - Kelp beds.
   c. Poisonous roe.
   d. None

7. a. 3-spined Stickleback
   b. Gasterosteidae
   c. Cosmopolitan.
   d. Crustacea, insects.

8. a. Slim sculpin, Prickly, or
   Great Basin.
   b. Suborbital stay
   c. Food for trout, etc.
   d. Bait.

9. a. Circulus.
   b. Annulus.
   c. Focus
   d. Ctenii

10. a. 236 mm.
    b. 195 gms.

11. a. Rubberlip Perch
    b. Cyprinidae.
    c. A - Rubberlip
    d. A - "

12. a. A - Pac. White Perch
    B - Barred Perch.
    b. Embiotocidae
    c. A - White Perch

13. a. Kelp beds - near shore.
    b. No.
    c. White Seabass
    d. Neither.

14. a. Weight - Length
    b. Empirical data

15. Modes in curve

16. a. Anal fin rays.
    b. do
    c. Basibranchial teeth
    Cutthroat marks
    d. Pseudobranchiae

95	II
94	I
93	I
92	
91	
90	I
89	IIII
88	I
87	I
86	
85	
84	
83	
82	
81	I
80	
79	
69	I

Median 89

Mean 88

Vincent

Zoology 245 Fall 1960

SYSTEMATICS AND EVOLUTIONARY MECHANISMS

Instructor: R. M. Bailey
Room 1039 Museums

Room 2009 Museums Bldg.
Tues. and Thurs. at 8 a.m.

Course description: An examination of the principles and practices of classification viewed in relation to modern evolutionary theory.

Principal references (available on reserve shelf, Museums Library):

MLU - Mayr, Linsley and Usinger: Methods and Principles of Systematic Zoology. McGraw-Hill, 1953.

M - Mayr: Systematics and the Origin of Species. Columbia Univ. Press, 1942.

D - Dobzhansky: Genetics and the Origin of Species. Columbia Univ. Press, 3rd ed. rev., 1951.

SM -- Schenk and McMasters: Procedure in Taxonomy, new ed. Stanford Univ. Press, 1948.

Course requirements: Most of the class periods will be devoted to lectures by the instructor (or other staff members), but certain periods may include discussion of materials covered in lectures or assigned readings. There will be a midterm examination on November 17, an assigned term paper, and a final examination.

PRINCIPLES OF SYSTEMATICS

The basis of taxonomy (systematics) may be expressed in the form of three principles: diversity, phylogeny, and classification. The first two are biological; the third is operational.

I. Diversity. The organic world presents an obvious diversity of phenotypes which express the fundamental and underlying genetic diversity among organisms.

1. The phenotype of the individual organism includes the entire spectrum of qualitative and quantitative aspects of its structure and function (e.g., morphology, mode of reproduction, chromosomal behavior, habitat-specificity, parasite-host relationships, developmental processes, behavior, etc.). Thus phenotype is understood to be the full embodiment of interaction of genotype with environment.

2. Diversity among organisms is a matter of degree. It is most evident in the gross variations visible when the whole world of living things is examined; at the other end of the scale it exists, though less obviously, among the individuals of a given species. Diversity thus extends all the way from that produced by the environment between genetically identical individuals (members of clones and identical twins) to the extremes exemplified among plants by a unicellular alga contrasted with a complex seed plant and among animals by a protozoan contrasted with an insect or a mammal.

3. Similarity among organisms permits grouping. The similarities among the organisms existing at any one time level make them appear to form aggregations separated by gaps of varying magnitude.

II. Phylogeny. The patterns resulting from diversity among organisms are the product of evolution, and hence call for a phylogenetic interpretation.

1. Evolution, or descent with change, is the sum of processes that result from interaction between genetically diversified organisms and the multiplicity of available environments.
2. All living individuals and groups have had their origin in pre-existing individuals and groups, to which they are tied by direct descent.
3. All evolutionary lineages (except some of those at or below the species level) have as one of their characteristics the fact that they have been diverging continuously through time. This is not invalidated by the so-called "parallelisms" and "convergences" in adaptive modifications.
4. Phylogeny involves the study of ancestry and divergence, and hence is the history of genetic relationship.
5. Phenotypic similarity, in the absence of known genealogies, is the best guide to relationship.

III. Classification, based on the present patterns of similarities and differences supplemented by the fossil record, can be done in such a way that the arrangement reflects evolutionary sequence.

1. A classification should, ideally, synthesize and systematize for general use all pertinent biological data of a comparative nature.
2. Comparative procedures make it possible to determine degrees of relationship that permit delimitation of natural groups of organisms.
3. Any classification is tentative, and, like any other hypothesis in science, is subject to continuous reevaluation in the light of new evidence. Thus, any grouping shown to contain discordant elements demands revision.
4. Groupings are based on similarities; separation of groups is made possible by the differences between them, i.e., by discontinuities in the total applicable pattern of variation.
5. Genetic discontinuity may be inferred or measured by the study of genetical or cytological behavior, mating behavior, and geographical distribution, as well as by other modes of comparison.
6. A hierarchical system of categories has been developed for the formal expression of the observed patterns of similarity and diversity among organisms. This system, differing slightly for plants and animals, is internationally accepted. Its categories of a given rank should be regarded as arbitrary units of expression, not necessarily equivalent as applied to different groups of organisms. Once the biological aggregations have been assigned to categories the resulting taxa may be arranged to express phylogeny on the basis of evolutionary specializations or modifications.
7. Uniform codes of zoological and botanical nomenclature are necessary for precision and ease of intercommunication.

DIVERSITY AMONG ORGANISMS

1. THE VARIETY AND MULTIPLICITY OF LIVING THINGS.

One of the most striking phenomena of life is the tremendous number of different kinds of organisms existing today. We can only roughly estimate how many kinds have been described and named, and guess at the number remaining to be discovered. In 1951 Epling estimated the number of described plants at 265,000, of which the angiosperms made up more than one-half (150,000); he estimated 70,000 fungi, 15,000 mosses, 14,000 algae, 10,000 pteridophytes, 6,000 liverworts, and 500 gymnosperms. The most recent estimate for the animal kingdom is that by Mayr in our text (p.4), totalling 1,120,310 species, of which 923,000 are arthropods, including 850,000 insects. According to his figures there are about 37,800 vertebrates (3,200 mammals, 8,600 birds, 6,000 reptiles and amphibians, and 20,000 fishes). Other large groups are the mollusks with 80,000 species, the protozoans with 30,000, the nematodes with 10,000, the coelenterates with 9,000, the annelids with 7,000, and the flatworms with 6,000. The greatest uncertainties in estimate relate to the insects; the number of described species is placed by various recent authors at from 625,000 to 1,500,000, and 700,000 can be taken as a reasonable and conservative figure. With this correction, Mayr's 1953 estimate for the total number of described animal species drops to about 1,000,000.

Within this vast array we encounter the widest variations in size, form, degree of complexity of organization, methods of self-maintenance and reproduction, and relation to environment and to other organisms.

A. Diversity. Organisms differ from one another. Probably no two individual organisms in the world are exactly alike, even in the uncommon instances in which they share a common genotype (clones, identical twins). Depending upon what organisms we compare, we may find that they differ in most of their observable characteristics, or in only a few. Surveying the whole living world, the amount or degree of difference between organisms forms a spectrum extending from almost complete resemblance at one end of the scale to a difference in all but a few fundamental characteristics at the other. Differences enable us to separate organisms.

B. Resemblance. The obverse of the coin of diversity is difference; the reverse is resemblance. Organisms are grouped in classification on the basis of their resemblances.

C. Characters. The features in which organisms resemble or differ from one another, and which are available for use in classification, are called characters (characteristics). A character may be defined as any phenotypic manifestation of the genotype which can be used, alone or in combination, as an aid in classifying an individual and the groups to which the individual is assigned. The significance of characters for classification has to be evaluated in the light of the principles to be discussed under that topic, in terms of variability, relation to other characters, relation to environmental influences, etc. Although the most commonly used characters are morphological, they may be of any sort.
Read: Mayr, Linsley & Usinger, Ch. 6.

D. Discontinuities. At any given time level the spectrum of diversity among organisms is discontinuous; not all the possible combinations of characters are present. Regardless of the reasons for it, this fact permits the separation of groups of coexistent organisms from one another.

Examples of major discontinuities: in any natural assemblage in a region or habitat

Examples of minor discontinuities: in the species of a genus

E. *Keys and Artificial Classifications.* Construction of keys; their uses; some of their pitfalls; marks of an artificial classification.

F. *Groupings based on Resemblance.* Text, pp. 40-41.

(1) *Possession of common characters.* Examples. Number of shared characters a rough measure of closeness of "relationship" and degree of compactness of grouping.

(2) *Forming a step in an orderly sequence of differences.* Examples of such "evolutionary trends" and their use in grouping; relation to (1) above.

(3) *Choice among possible alternatives.*

2. VARIATION AND ITS TAXONOMIC TREATMENT.

A. *The Individual.* Although some morphological characters may be repeated in the structure of an individual and show variability within this individual, in taxonomy we deal with the individual as our lowest unit; *variation is a phenomenon studied in assemblages of similar individuals, or populations.* Our term *specimen*, used for an individual preserved in some fashion for study, for many persons still bears the connotation of *example*, as though all the individuals of a taxonomic unit were identical. It may also be noted that although it is quite correct to say of a specimen of *Pieris rapae* L. "this is a cabbage butterfly", it is never correct to say "this specimen is *Pieris rapae* L." or the equivalent.

B. *The Population.* As used by students of systematics and evolution, the term "population" generally refers to a "local population," made up of all the conspecific individuals of a particular locality that together comprise a single potential interbreeding unit (Mayr 1942:24). In a larger sense, it may comprise the sum of all such local units and thus be coextensive withthe species. In systematics the study of variation is the study of the nature and extent of the variability of the individuals making up the population (*individual variation*), and of the variation between populations (*group variation*).

The population and not the individual is the lowest systematic unit in modern taxonomy. In practice, however, no one can study a population, as it exists in nature. In fact, no one has probably ever seen a natural population or a species.

C. *The Sample and the Hypodigm.* Analysis of samples is our only means of predicting the properties of "natural" populations, which are themselves forever inaccessible to study. Such samples are the *series* of the naturalist. By the study of samples we attempt:

(1) To determine the degree of constancy (variability) of a given taxonomic character in a given population;

(2) To determine pattern-configurations of characters and variability within a given population;

(3) To determine qualitative and quantitative degrees of difference between sampled populations with respect to one or many characters.

Read: Mayr, Linsley & Usinger, Ch. 7.

Simpson (1945:30) has introduced the useful term *hypodigm* (Gr. *hypo*, under + *digma*, sample; hi´-po-dĭm) to include the entire series of specimens which forms the basis of a group concept in zoology, i.e., a sample including all the specimens that are, by any one student at any one time, believed to belong in the postulated group. For this purpose every specimen in the series has equal value. The hypodigm of any taxonomic group is a series of concrete specimens, the whole sample used as a basis of inference. As such it may include many samples of individual populations. The contents of any given hypodigm naturally vary from time to time and from person to person, depending on the discovery and availability of specimen and on the criteria, skill, and taste of the procedure of inference.

Some Terminology

Biologists, like other scientists, have a tendency to pre-empt perfectly good English words of broad significance and to give them special, narrow meanings for the sake of precision. Thus, a certain type of taxonomist, fortunately now less typical of his kind than formerly, typifies the attitude of many of the workers of the past century who held the morphotypic concept of species, by insisting that the type of a species be a typical specimen instead of merely the name-bearer. In the last sentence, only the underlined word represents the special use of type to which the word is restricted in the realm of nomenclature. Similarly, biologists commonly give the terms used to describe variation somewhat narrower meanings than they carry in general speech.

Variation is generally used in biology to connote differences between the offspring of a single mating, or between the individuals or groups of individuals placed in a single species, subspecies, or race (Robson and Richards, 1936). As used by Mayr, individual variation refers to the differences that occur among the individuals of a single interbreeding population; group variation is variation between different populations within the species. Sometimes the differences that exist between members of the higher categories are also included under variation, but this is a less common usage.

Variability means, strictly, the ability to vary; in biology it is generally used in reference to the amplitude of variation with respect to one or many characters within a population, or to the frequency with which variations in these characters occur.

Variance is a statistical measure of the extent of the variability of a character in a given sample of a population. After the specimens have been measured or counted with respect to this character, and the mean value of the character found, the individual measurements are compared with this mean, and the amount of the difference, plus or minus, is squared. The sum of these squares divided by the number of specimens in the sample is the variance about the mean, fundamentally the most important statistical constant measuring dispersion. In practice it is more convenient to use the square root of the variance, a quantity known as the standard deviation (S.D. or σ). Variance has other meanings; only the more modern dictionaries would list this one.

Variant, as an adjective, means different or variable; as a noun it refers to something that deviates from the typical condition of its class or from that of another example.

D. The Classification of Variation. Studies of and speculations about variation began long before the time of Darwin; but with the establishment of the fact of evolution variation became one of the most important phenomena in all biology. Many attempts were made to classify variations; one of the landmarks of the science is Bateson's massive work called "Materials for the Study of Variation" (1894). With the growth of the science of genetics it became firmly established that all variation in organisms can be classified, on the basis of cause, into two classes:

(1) Modifications. Variations produced by the interplay between a given genotypic constitution and various different environmental factors, external or internal. Variations of this sort are not inherited, and are "reversible"; they are often listed as being "environmentally produced," which is, of course, only

a half-truth. Although modifications themselves are not inherited, the genotypes which have the capacity to produce these modifications are inherited, and modifications may thus, under some circumstances, be of evolutionary importance.

(2) Mutations (in the wide sense). Variations produced by a change in a gene or a group of genes or in gene arrangements and combinations, and which are consequently inherited. This type of variation provides the basic material for variation, evolutionary change, and splitting of stocks.

Mayr, Lindsey & Usinger (1953, pp. 81-98) classify Individual Variation according to the following scheme, with discussion and examples:

I. Extrinsic (non-inherited [modifications])
    A. Progressive
        1. Age
        2. Seasonal
    B. Social (social polymorphism)
    C. Ecological
        1. Habitat (ecophenotypic)
        2. Host-determined
        3. Density-dependent
        4. Climatically induced
            (Clyclomorphic)
        5. Heterogonic
            (Differential growth) - see Huxley, Problems of Relative Growth, 1932
        6. Neurogenic color variation
    D. Traumatic (caused by injury or faulty development)
        1. Parasite-induced
        2. Accidental and teratological

II. Intrinsic (inherited [mutations and recombinations])
    A. Sex-associated
        1. Primary sex differences
        2. Secondary sex differences
        3. Alternating generations
        4. Gynandromorphs
        5. Intersexes
    B. Non-sex-associated
        1. Continuous
        2. Discontinuous (genetic polymorphism)
        3. Sex-limited

This classification is useful in ordering our thoughts about kinds of individual variation, but the practicing systematist finds it very hard to apply. Only experiment can distinguish between characters that are inherited and those that are not, although in the light of our present knowledge of genetics and ecology we can often make an informed guess that is very probably correct. Furthermore, the categories of this classification are hardly more than a catalogue; they are not logically related nor even entirely exclusive, and they are very unequal in content. This last will be self-evident when it is realized that all inherited differences which are not sex-associated or sex-limited (and this includes the overwhelming majority) fall in categories II-B-1 and 2, "continuous" and "discontinuous" variation. Although this distinction was formerly considered of much importance, as distinguishing between slight individual differences and the clearly marked and uncommon variations sometimes called "sports," thought to differ in origin and mode of inheritance or at least in evolutionary significance, modern genetics has tended to minimize the importance of this distinction. There is no essential difference between them, except that "continuous" variation has a continuous and commonly "normal" distribution in the population, while "discontinuous" variation shows two or more peaks in the distribution curve, or gaps in the distribution.

Group variation may be the result of similar responses by the individuals of a population to the same environmental factor(s), or be a genetic phenomenon caused by differences in the genotypic composition of two populations. An example of the first would be the grasshopper Chortophaga viridifasciata, which in drier regions or seasons has brown males and largely brown females, in moister regions and seasons green females and largely green males; these differences have been experimentally shown to be produced in individuals reared respectively on dry and succulent vegetation. Most differences between populations, however, appear to be largely genetic in origin.

E. The Analysis of Variation. Differences between populations as well as the characteristics of single populations may be studied in either or both of two different ways: (1) by the statistical analysis of the variation shown by single characters or small groups of characters, and (2) by the study of pattern data.

1. Conventional Statistics. In this approach the variation of one or more characters in a sample of a population is recorded in terms of measurements or counts. The resultant data are grouped and tabulated in the form of a frequency distribution, which may be graphed to show the distribution pattern as a frequency polygon or histogram. This pattern approaches a curve, which may be any of several types, but very often is of the familiar bell-shaped symmetrical form, high in the middle and low at the sides, known as the normal curve. In distributions of this and related types the variates are more frequent near some one value and become less and less frequent in departing from this value in either direction; there are several ways of determining the point around which the observations tend to cluster and the extent to which they are concentrated around it. Among the measures of central tendency commonly used are the arithmetic mean, the median, the mode; any of these is an average, though unless otherwise specified average usually is taken to signify arithmetic mean, or else a group that includes all but the extreme deviates. Simpson and Roe (1939, pp. 104-5) have an excellent discussion of the meanings variously attributed to "average," "typical," and "normal." The degree of crowding toward or spreading away from the central tendency is measured in various ways: by the observed range, by the mean deviation from the arithmetic mean, by the variance about the mean (see p. 5), or by the more commonly used derivative of the variance, the standard deviation. From the last, divided by the mean and multiplied by 100, is obtained the coefficient of variation, or of variability, which is a pure number that does not stand for any unit of measurement. All statistical procedures up to this point have to do with determining the nature and extent of variation in a single character in a sample of population. Further steps in the analysis have to do with methods of estimating the probability that the values determined from the sample will be approximately the same as those of the population, with the size of sample required for making a reliable estimate of the condition of a population, with comparisons of samples to determine whether they were probably drawn from the same or from different populations, with studying the relationship between variates whose changes are related to one another (correlation), and with ways of expressing these and other statistical distributions and relations by mathemetical expressions and graphic analysis.

Conventional statistics is an essential tool in taxonomy. It is, however, laborious, and limited in the number of characters it can deal with simultaneously under the conditions governing most taxonomic work (no electronic computers). The analysis of masses of data by statistical methods can yield no answers to questions that have not previously been formulated; and often the best use of statistics by the biologist is to test a conclusion already reached by other methods. In general, it is probably good advice to say: "Never use statistics until you are forced to do so, but never fail to do so when you reach the stage where statistics is needed."

Two of the most useful references for the systematist who wishes to use statistics in his work are: (a) the elementary "Introduction to Quantitative Statistics" by Cazier and Bacon, Bull. Amer. Mus. Nat. Hist., 93 (5), New York, 1949;

and the much more complete and advanced "Quantitative Zoology" by Simpson and Roe, McGraw-Hill, 1939.

2. Pattern Data. The botanist Edgar Anderson has been vigorously advocating the increased use (and training of students in the use) of what he calls "pattern data" for the rapid organization and evaluation of multiple-character variation. Reference should be made to his book on "Introgressive Hybridization" for a description of some of the techniques, and also to the following recent articles: "Efficient and Inefficient Methods of Measuring Specific Differences," in "Statistics and Mathematics in Biology" Ed. O. Kempthorne, et al, Iowa State College Press, Ames Iowa, 1954; "Natural History Studies and Applied Mathematics," American Journal of Botany, 43 (10): 882-889, 6 figs., Dec. 1956. In the last Anderson says: "One of the outstanding points about Natural History is the large extent to which it deals with pattern data, rather than with pointer readings, lengths, widths, densities, weights, etc." Faced with a large and complex problem, the scientist trained in Natural History "looks around for significant repeatable patterns in the data, and reasons back and forth from observation to hypothesis until he has found his way into the problem. The finicky pointer reading data, single sense impressions, lengths, widths, weights, so useful for precise analysis, are best deferred until we know what kind of a problem we are up against. Pattern data have a broader observational basis than pointer-reading data, as Minot pointed out (1911. The method of science. Science, 33: 128) half a century ago in his pioneer attempt to fit growth curves. Therefore they are invaluable in the early stages of any complex problem. Before we have some notion of what we are about, pointer readings by themselves are little help. Lengths, densities, weights, though accurately determined, merely allow us to phrase our ignorance more elegantly. Precision has little advantage until we have enough understanding to use precise analysis." Anderson also takes issue with some of the central concepts and assumptions of conventional statistics, so far as their application to biological problems is concerned: probability, randomness, and chance. He quotes a statistician: "Statistics is not interested in the individual;" (but the biologist often is, and sometimes the individual may be the decisive evidence in a critical experiment or observation); "in many cases individuals behave at random" (most certainly not, says Anderson—we do not live in that kind of a world. The better we understand any particular problem, the less do we have to assign random behavior to any of the factors in it); "certainties barely exist for the statistician" (but with efficient use of pattern data the scientist may be as certain as it is possible to be, and any scientist given the same data would reach the same conclusion. How certain can you get?). In dealing with pattern data, conventional statistics is inefficient and sometimes positively misleading. According to Anderson, "The brilliant successes of statistical methods with number data have blinded all but a few scholars to: (1) their inefficiency in dealing with patterns; (2) the various dangers of using concepts based on randomness in what is obviously a very non-random universe; (3) the peculiar advantages of Natural History in dealing with pattern data; and (4) the need for the development of logical basic procedures in fields where Natural History, Statistics, and Applied Mathematics come together."

In Ch. 6 of his book, "Introgressive Hybridization" (John Wiley, 1949), and in the first of the two papers cited above Anderson deals with various means of recording simultaneously several characters; he discusses scatter diagrams, pictorial scatter diagrams, ideographs, radiate indicators, hybrid indices, standardized photographs, and extrapolated correlates. Of these the pictorialized scatter diagrams are the most generally useful, and are here summarily described.

(a) Pictorialized Scatter Diagrams. The ordinary scatter diagram is a simple alignment of dots in a two-dimensional field. It is most useful in showing various relationships between the variations in two characters; but it is restricted to only two characters considered at a time. The number of characters that can be dealt with simultaneously can be increased by letting the shape of the dot represent a third character, its color or intensity a fourth, and still other features such as projecting radii of various lengths additional characters. The maximum number of characters which it is useful to treat in this way is limited only by the ability of the eye to discriminate between and see the similarities of the various resulting symbols. Each symbol records the characteristics of an individual specimen; the number of individuals which it is necessary to graph is only that sufficient to make the pattern of the data begin to appear clearly.

The most common uses of such scatter diagrams are (1) to compare two populations to determine the nature and extent of the differences and similarities between them as a basis for judging their taxonomic status, and (2) for analyzing a single population to determine whether it is homogeneous or a mixture of two or more different populations. [Remember it is the samples that are studied, not the populations. Our conclusions about the populations are deductions from our analysis of the samples.]

The following example of the use of this method is from the first of Anderson's papers cited on p. 7. For simplicity, two species of the lily genus <u>Uvularia</u> (bellwort) were chosen—<u>U. grandiflora</u> and <u>U. perfoliata</u>—which all botanists agree are perfectly good, distinct species without taxonomic complications. They are quite similar in appearance, but differ in many characters such as the presence or absence of hairs on the lower surface of the leaf and of curious glandular outgrowths on the inner face of the perianth, and by many minor and more or less correlated differences in size, proportion, texture, number, and arrangement of the various internodes, leaves, and scales of which the body is made up. It is these last differences which are treated here, since they are more characteristic of species differences in general, and the pubescence differences serve as a check on conclusions but make it too easy if included in the test.

The characters chosen for analysis should be changed as little as possible and yet thrown into something like mathematical form. In this instance, 10 specimens of each species were chosen at random from the herbarium collection; for each an ideograph was made, diagrammatically recording from measurements the length of every leaf, of every internode (joint of the stem), and the position of every flower and of every scale leaf. On the diagrams the widths of leaves, size of flowers, angles at which leaves are held, and angle of branching were all conventionalized and without significance.

As a test, these 20 ideograms were shown to many persons, some trained botanists and others without biological training. Certain botanists could sort them correctly to species and recognize that there were two and only two species involved. The untrained persons could not do this, but it was found by experiment that most groups of people (including many non-biologists) can, operating as groups, classify the diagrams correctly. They find it hard to say just how they do this, however; they are comparing total sense impressions. Upon analysis it turns out that the more important differences are: (1) <u>U. g.</u> is in general larger than <u>U. p.</u>; (2) max. internode length is greater in <u>U. g.</u>; (3) position of max. internode in <u>U. g.</u> is usually immediately below the first branch or at most one node lower, while in <u>U. p.</u> it may be several internodes below the first branch; (4) number of leaves below first branch is usually higher in <u>U. p.</u> than in <u>U. g.</u> (biologically correlated with (3); (5) length of sterile (flowerless) branches is usually greater in <u>U. g.</u> than in <u>U. p.</u>; (6) the total number of leaves on sterile branches is higher in <u>U. g.</u>; (5) and (6) are correlated but can vary independently. The internode pattern differs in the two species; successive internodes decrease regularly in <u>U. g.</u>, while there is no such harmonic regularity in <u>U. p.</u>; (7) on the whole <u>U. g.</u> tends to have more flowers than does <u>U. p.</u>

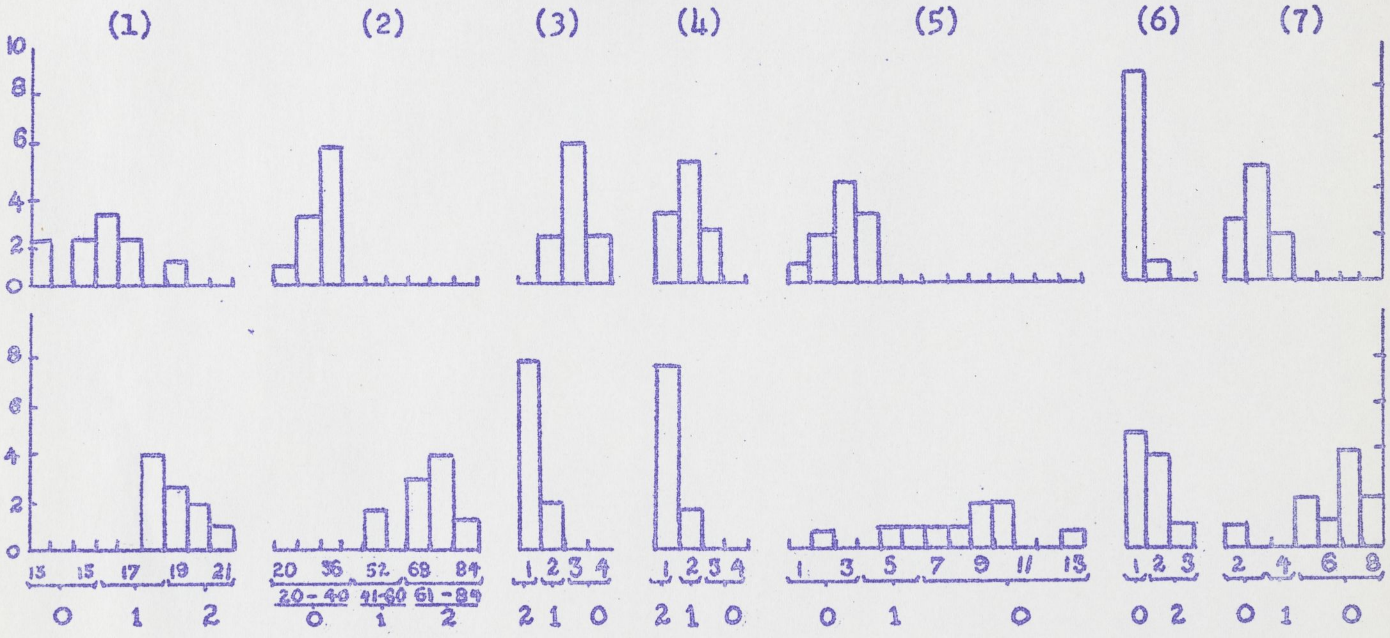
For purposes of exact measurement these 7 attributes were defined as follows: (1) length in mm. of leaf subtending lowermost branch; (2) length in mm. of longest internode; (3) no. of nodes from lowest branch to maximum internode (including the node at the branch); (4) number of true leaves below lowest branch; (5) length in mm. of longest sterile branch; (6) total no. of flowers; (7) no. of leaves on lowest sterile branch.

Frequency distributions are shown as histograms for each of these 7 characters in the figure below. Although the average values of the characters differ for the two species, all but one of the distributions are overlapping between the two spp. even in these small samples. The only one which does not overlap (maximum internode length) proves to overlap in larger samples.

Thus, although no one element in the pattern is effective in discriminating between the two species, obviously the design as a whole must be, or else how could so many people classify the ideographs correctly?

A simple combination of these seven elements into one index demonstrates this point objectively. By dividing each frequency distribution into approximate thirds one can give each individual a score of 0, 1, or 2, according to whether its measurement on that character is in the lower, the middle, or the upper third. This gives a scale running from 0 + 0 + 0 + 0 + 0 + 0 + 0 = 0 for "good" U. perfoliata to 2 + 2 + 2 + 2 + 2 + 2 + 2 = 14 for good U. grandiflora. Figure 2 shows the scoring.

Fig. 1. Frequency distributions of 7 characters, each of which more or less differentiates Uvalaria grandiflora (lower) from U. perfoliata (upper).



Note: The lower row of figures (0 to 2) are the assigned index values.

Fig. 2. The distribution of index values from the same twenty plants used in making the preceding graph of frequency distribution of characters, showing the separation of the samples.

Number of Individuals	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14
	X											X			
	X											X			
	X	X		X								X			X
	X	X	X	X			X			X	X	X	X	X	X

Index Value

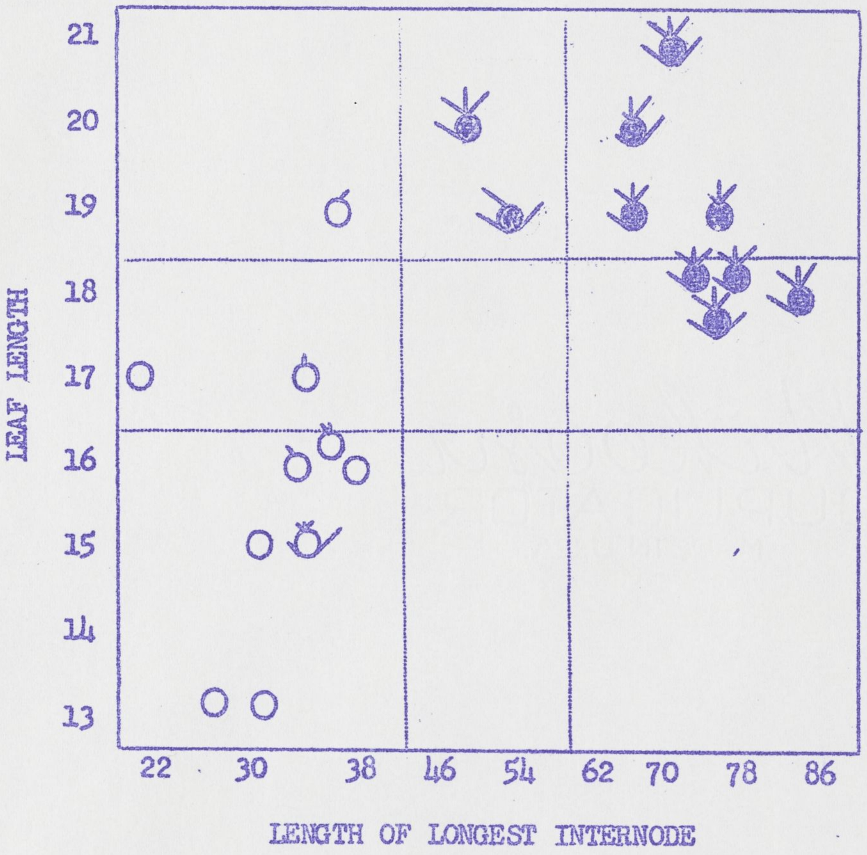
The data individually graphed in Fig. 1 may be combined into a single pictorial scatter diagram by the following procedure. Two of the variables are chosen to be measured along the *x* and *y* axes. For this purpose variables are preferred in which the error of measurement has been low, which can be determined for a large number of intermediate values, and which are good discriminators between the two populations (or rather, samples). In this problem these are leaf length and length of longest internode. The other five variables are measured by the lengths of five rays, each variable being diagrammed on a ray of easily distinguished position. (Other devices may be used, but it has been found by experiment that by having the rays originate from the upper half of the dot, and by having them all extend more or less in the same direction, they do not cut across one's field of vision, and the entire diagram is easier to grasp and interpret). For each of the variables diagrammed on the rays, there is *no ray* if the value is in what is roughly the lower third of the range of variation, a *short ray* if it is in the middle third, and a *long ray* if it is in the upper third. With only five rays, positioned as shown in the diagram, the eye can distinguish almost instinctively between the five variables and help the mind to see the whole complex of interrelationship.

For the particular type of problem here treated, one can further aid the mind by setting up the index scales in such a way that the long rays of the symbols are always associated with one complex (in this instance *Uvularia grandiflora*) and the short rays or absence of rays with the other (typical *U. perfoliata*). If the information about leaf pubescence is now added to the diagram, by using solid dots to denote pubescence, open circles lack of pubescence, the diagram will appear as is shown below, and from it one can study the relationship between the two samples, which in this instance are known in advance to represent samples of two species.

O = Index value 0
O̍ = Index value 1
O̎ = Index value 2

(1) Leaf length. Measured along *Y*-axis.
(2) Length of longest internode. Measured along *X*-axis.
(3) Position of longest internode. Symbol -O
(4) Number of leaves below first branch. Symbol ⟍O
(5) Length of longest sterile branch. Symbol O̍
(6) Total number of flowers. Symbol O/
(7) Number of leaves on longest sterile branch. Symbol Ó
(8) Leaf pubescence: absence, open circle; presence, solid dot.

Fig. 3. Pictorialized scatter diagram showing how the ten plants of Uvularia perfoliata differ from the ten plants of U. grandiflora for seven different variable characters (in addition to the 8th invariable character, presence or absence of leaf pubescence, as shown by dot color).



From this diagram the following facts are apparent:

(1) The two sets of specimens are readily distinguished, considering all seven variables at once.

(2) The two sets, as distinguished by the seven variables, are identical with the two sets distinguished by pubescence differences.

(3) Uvularia grandiflora is represented by a coherent group of individuals. The only conspicuous departures from the average are immature specimens.

(4) Uvularia perfoliata is not so coherent. Typical specimens depart from the average in the direction of U. grandiflora, suggesting the possibility that introgression of genes from that species may be responsible for these variants.

It should be noted that all these tentative conclusions, based on the analysis of 10 herbarium specimens of each species, were subsequently confirmed and extended by Dietz in 1952, on the basis of field studies, transplant experiments, and numerous mass collections of natural populations of both species.

Commenting on these results, Anderson says: "For this problem the method of pictorialized scatter diagrams has done everything we asked of it and more. It has separated the two species as effectively as one could by "biological intuition."

The somewhat intermediate specimens of U. perfoliata were given intermediate rankings. The method goes farther than our eyes in suggesting something previously unsuspected—that the entire sample of U. perfoliata tends to vary in the direction of U. grandiflora. The method, in other words, can be used for analysis as well as for a mere record.

"Unlike most statistical methods, the method ... has done a good job with samples of only 10 individuals. In conventional statistics we have a few observations on each of a large number of individuals. In both instances the total number of observations is large enough to yield significant results. In employing the method on this problem, each of the 10 individuals was analyzed as seven interrelated facts. If we consider only the 7 variables, then we have 7 facts for each of 20 specimens, a total of 140 facts. However, the method does more than this; it demonstrates to the eye many of the various relations between these facts. If, for instance, we consider only a, the length of the longest internode; b, the length of the leaf; c, the number of sterile leaves; and d, the number of leaves below the first branch; then, within and between these two samples of 10 each, it shows graphically: the relation between a and b, between b and c, between a and d, between b and c, between b and d, and between c and d; it demonstrates as well the complex interrelationships of these variables taken 3 at a time, and finally, their overall relationship considered all 4 at once. All these facts were in the raw data, and the method is efficient in preserving them. When four such facts are presented graphically so that the trained eye can perceive not only the magnitude of each variable but also the eleven interrelationships.... then the presentation has the force of many separate facts, except as there are correlations between the four variables. Obviously, if two of the variables were completely correlated, we could get little more out of the two measurements than out of either one. Where as many as 7 variables per individual are diagrammed in this way so that the various interrelationships are taken in by the eye, then the number of individual reports per plant rises exponentially. Our little samples of 10 plants each, in terms of raw data presented in frequency distributions for such single pointer readings as weight, length, and the like, are the equivalent of many separate readings per species. If we make a generous allowance for the lowering of this figure owing to correlations, our population of 20 Uvularias [sample] still has at least the significance of one pointer reading per plant for several hundred plants of each species.

"There are, therefore, reasons why such a graphical method turns out reliable results with what at first sight seems like very small samples. Just as Fisher, in setting up his analysis of variance methods, was able to pool all his sampling errors and hence get reliable results from small samples, so in a somewhat similar fashion these graphical methods if properly set up can pool so many basic observations that reliable estimates can be obtained from small numbers of individuals.

"The method of pictorialized scatter diagrams was originally worked out for comparing samples of maize from different fields and from different regions. It was found by trial and error that it produced reliable results when the interrelationships of 4 characters were analyzed, with samples of 25 plants. ... It gave consistent results, discriminating between radically different varieties grown in the same environment yet classifying as essentially similar the same variety grown on manured and unmanured plots. Its usefulness in that problem suggested its extension to such problems as the comparison of F_2 and backcross generations in hybrids between species, the detection of introgression in natural populations, etc. It has been widely enough used... with various genera of plants and animals to show its general adaptability to such problems. However, it should be considered a stopgap, or an exploring device, to be laid aside when mathematically more elegant methods of equal efficiency are eventually available."

Anderson comments on the need for simpler and more direct methods of studying trends in form and proportion with changes in size (the results of heterogony) than are furnished by traditional regression methods. He also generalizes his conclusionsas follows:

(1) In problems (such as those concerned with yield of corn) where the basic facts are a single numerical datum for each individual, analysis of variance methods has been highly successful.

(2) In problems of growth and development, where for each individual we have a limited number of more or less interrelated numerical facts (litter size, weight at birth, age of mother, etc.), then methods of path analysis have been almost equally effective. As the problem becomes more and more complicated, however, it becomes more and more difficult to set up the path analysis model for dealing with the problem. [Sewell Wright's method of path coefficients is a semigraphical method for exploring factor interaction; it is in part a device for making pattern data out of pointer-readings. Anderson 1956: 887].

(3) In problems involving multiple sense impressions, such as differences between species or varieties, where from each individual a seemingly infinite number of numerical facts could be derived (weights, lengths, positions, ratios, colors, densities, etc.), the customary methods of biometry are still inappropriate and ineffective. Their success in problems involving yield has led to numerous attempts to use them in these fields. While the best of these investigations have produced works of theoretical interest, they have not yet advanced to the stage of practical use. To the plant breeder or the student of evolution, fascinating though multiple regression methods may be, graphical and semigraphical methods will for the present yield more useful and biologically reliable results.

To the criticism that this method is using subjective criteria, Anderson replies: (1) the method meets the practical test of experience:
(2) we can make objective tests of subjective judgments, by submitting the same data to a number of persons, and subjecting their results to appropriate statistical analyses. The method of pictorialized scatter diagrams, he states, has repeatedly passed both of these tests.

A word of caution. Edgar Anderson is an enthusiast. He is so firmly convinced of the power of this analytic method that he sometimes pulls a boner when he tries to demonstrate its use to a zoologist, for example, using materials with which he is not wholly familiar. Thus, a year or so ago, he demonstrated its use with some snails while visiting here, and showed quite incontestibly that the sample contained two distinct lots, which he suggested were taxonomically different. In all probability what he had separated were two age classes. Thus, the method will group individuals, reveal correlations, and do nearly everything that Andersons says it will; but what it will not do is to interpret its results. That is the function of the systematist and the test of his knowledge, judgment, and skill.

2. Quality Control Statistics. The following brief and inadequate description of this method of treating pattern data has been abstracted from the Training Manual for Statistical Quality Control, produced by the American Society for Quality Control for use at its 6th Annual Convention, May 22-24, 1952, at Syracuse, New York, and written by Arthur Bender, Jr., and George W. McDermott of the Delco-Remy Division of General Motors Corp. and Edward J. Oakley of General Motors Institute. It is copyrighted by Delco-Remy Division, Anderson, Indiana. The discussion is original.

This procedure is designed to determine by sequential sampling whether the variation in a single characteristic in a population falls in a pattern which is consistent with the individual measurements all being part of a single "family" of variants or not, and with the determination of the average, the spread, and the "control limits" of this family. From these values a "control chart" is constructed and successive samples are plotted on this chart. In dealing with the production of parts by a machine, for example, four parts might be measured each half-hour and the average of these four measurements entered on the "control chart." So long as the successive spots fall within the "control limits" it may be assumed that the variation remains within the same "family" (statistical universe) and that none of the three variables affecting the process (operator, material, machine) have changed.

The effectiveness of this procedure rests upon the assumption that the variation in the sampled population is of normal or near normal type (the bell-shaped curve), which is the case in the majority of instances, both for machines and biological variation. Variation not of this sort will show up in quality control charts as "out of control" measurements, which may result from the shift of a normal distribution away from the "control path" defined by the mean and "control limits", by pronounced skewness, or by the existence of two or more families of variants in the samples being measured. It is, then, the consistency with which individual measurements or group means fall within the "control limits" that gives this method its usefulness; it is usually not necessary to take more than a small number of successive samples to determine whether or not they fall into this pattern. In the factory any departure from this pattern means that something has changed—man, material or machine. In biological usage, the significance of such a departure would depend upon what was being sampled, and how. If the sequential samples were from populations occupying successive areas along a geographical transect, transgression of the "control limits" would be expected to occur where the constants of the "family" of variation of the character concerned changed; both a gradual drift and an abrupt change could thus be detected and distinguished.

In the Manual referred to above, the following steps are outlined for making a standard "X and R Control Chart."

1. Select a sample size. This should remain constant throughout the operation.
2. Take samples and record measurements. [For example, 4 individuals each half hour—a group sample; or 1 individual each 15 minutes, etc. For use in biology various analogous methods of sequential sampling may be worked out with some thought.]
3. Calculate the average for each group or sample.
4. Calculate the range for each group or sample—the difference between the lowest and highest value in each group or sample.
5. Total the averages.
6. Divide step (5) by the number of groups or samples, to obtain the Grand Average (symbol X double bar = $\bar{\bar{X}}$).
7. Total the differences or Ranges (4).
8. Divide step (7) by the number of groups, to obtain the Average Range ($\bar{R}$).
9. Select proper scales for the Control Chart.
10. Plot the Average points (step 3) on the Control Chart for Averages.
11. Draw the Grand Average (step 6) on the Control Chart for Averages.
12. Plot the Range points (step 4) on the Control Chart for Ranges.
13. Draw the Average Range (step 8) on the Control Chart for Ranges.
14. A. From Table I (reproduced below) find the value of D_4 which corresponds to the sample size selected in step (1).
    B. Multiply step (14A) by step (8), to obtain the Upper Control Limit for Range.
15. A. From Table I find the value of D_3 which corresponds to the sample size selected in step (1).
    B. Multiply step (15A) by step (8), to obtain the Lower Control Limit for Range.
16. A. From Table I, find the value of A_2 which corresponds to the sample size selected in step (1).
    B. Multiply step (16A) by step (8).

C. Add the value found in step (16B) to the Grand Average, step (6). This is the Upper Control Limit for Averages.

D. Subtract the value found in step (16B) from the Grand Average, step (6). This is the Lower Control Limit for Averages.

17. A. Draw the Upper Control Limit for Averages, step (16C) on the Control Chart for Averages.

B. Draw the Lower Control Limit for Averages, step (16D) on the Control Chart for Averages.

18. Draw the Upper Control Limit for Range, step (14B) on the Control Chart for Ranges.

19. Draw the Lower Control Limit for Range, step (15B) on the Control Chart for Ranges.

20. If the process is "In Control" (all plotted points falling within the Control Limits), make the following calculations:

A. From Table I, find the value of E_2 which corresponds to the sample size selected in step (1).

B. Multiply step (8) by step (20A). If the process is "In Control", this is equal to 3 Standard Deviations (3σ), or the width of three zones in the Normal Distribution Curve.

C. Add the value found in step (20B) to the Grand Average, step (6). If the process is "In Control", this is the Expected Upper Limit for Individual Measurements.

D. Subtract the value found in step (20B) from the Grand Average, step (6). If the process is "In Control", this is the Expected Lower Limit for Individual Measurements.

21. If the process is "In Control", plot the Expected Limits for Individual Measurements, steps (20C) and (20D). Plot these as end points of a Distribution Curve to the right of the chart.

22. Compare step (21) to the drawing or specification limits.

23. If samples have been collected over a sufficient period of time to insure a cross section of the process, and if the process is "In Control" at the proper level, the Control Limits and centerlines can be projected forward on the Chart, for maintaining future Process Control.

The projected Control Limits are the highway on which future process Average and Range points must travel. If these points do not follow the projected highway, then something has changed. This change can be due to either Man, Material, or Machine. To get the process back on the highway requires work, careful investigation, and sound reasoning.

<u>Comment</u>: The above outline was prepared for use by men untrained in statistics in relation to a specific problem—the sampling and evaluation of the product of their machines. The table I referred to and sample Control Charts are shown on the succeeding pages.

<u>Note</u>: In dealing with measurements such as a series ranging from .847 to .873, the data are usually coded. In this instance .860 might be taken as 0, and each .001 above and below be counted as one unit. .863 = +3, and .856 + -4.

TABLE I

FACTORS AND FORMULAS FOR COMPUTING CONTROL CHART LIMITS — SMALL SAMPLES

NUMBER OF OBSERVATIONS IN SAMPLE	CHART FOR AVERAGES	CHART FOR RANGES		CHART FOR INDIVIDUALS		NUMBER OF OBSERVATIONS IN SAMPLE
	FACTORS FOR CONTROL LIMITS	FACTORS FOR CONTROL LIMITS		FACTORS FOR INDIVIDUALS		
		Lower	Upper			
n	A_2	D_3	D_4	d_2	E_2	n
2	1.880	0	3.268	1.128	2.659	2
3	1.023	0	2.574	1.693	1.772	3
4	0.729	0	2.282	2.059	1.457	4
5	0.577	0	2.114	2.326	1.289	5
6	0.483	0	2.004	2.534	1.183	6
7	0.419	0.076	1.924	2.704	1.109	7
8	0.373	0.136	1.864	2.847	1.053	8
9	0.337	0.184	1.816	2.970	1.010	9
10	0.308	0.223	1.777	3.078	0.974	10
11	0.285	0.256	1.744	3.173	0.945	11
12	0.266	0.284	1.717	3.258	0.920	12
13	0.249	0.308	1.692	3.336	0.899	13
14	0.235	0.329	1.671	3.407	0.880	14
15	0.223	0.348	1.652	3.472	0.864	15

SYMBOLS AND FORMULAS

X = An Individual Measurement

$\bar{X}$ = Average (mean) of each group

$\bar{\bar{X}}$ = Grand Average of all groups

$\bar{\bar{X}} \pm A_2(\bar{R})$ = Control Limits for Averages

R = Range in each group

$\bar{R}$ = Average Range

$D_3(\bar{R})$ and $D_4(\bar{R})$ = Control Limits for Ranges

Spread of Individual Measurements:

(To be used only if the process is "In Control" and is known to be Normal or near Normal)

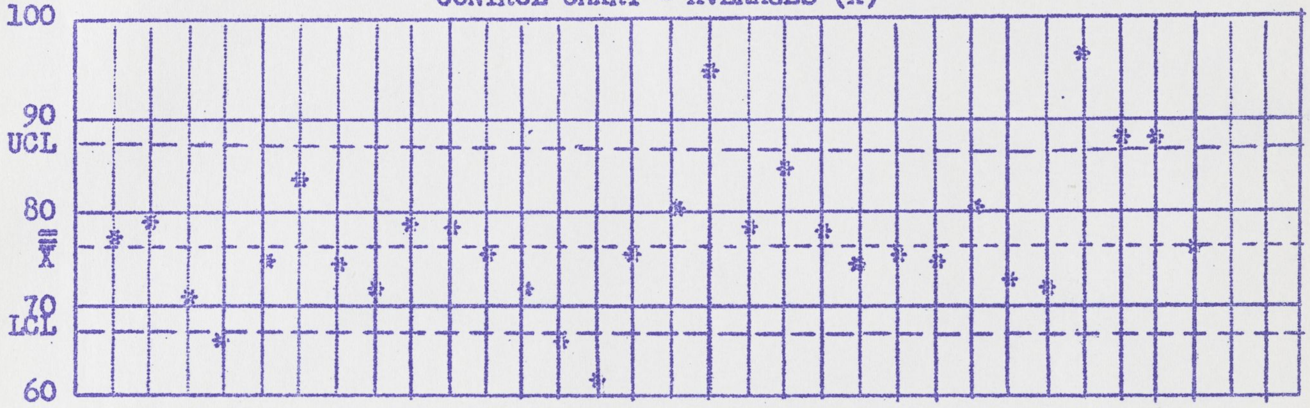
$$\bar{\bar{X}} \pm \frac{3\bar{R}}{d_2} \quad \text{or} \quad \bar{\bar{X}} \pm E_2\bar{R}$$

Two examples are given on the following pages, to illustrate the use of Control Charts in sequential sampling procedures and their interpretation.

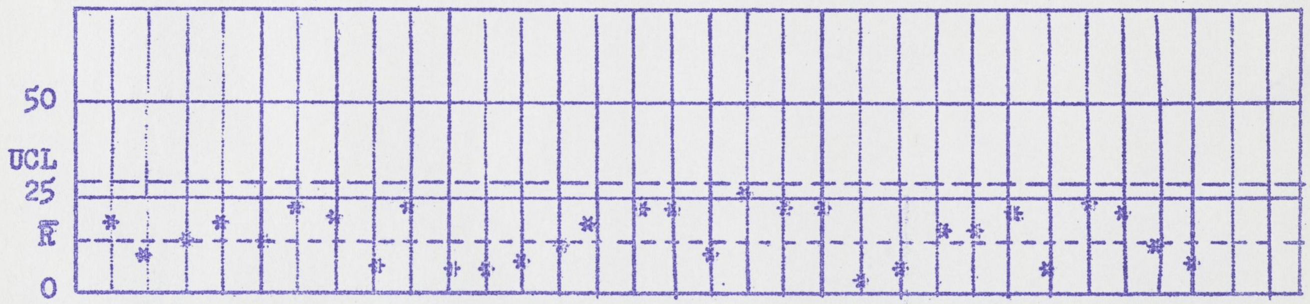
Example I. B-36 switch. Test: Pounds required to operate. Specification: 45 to 100. Tally shows approximately normal distribution. Samples of 4 individual switches tests each half hour; each such sample = one group. Data furnished on 30 groups.

Grand Average ($\bar{\bar{X}}$) of 30 groups = 77
Average Range ($\bar{R}$) of 30 groups = 13
Plus or minus spread of Control Limits for Averages = 0.729 x $\bar{R}$ = ±9
Upper Control Limit for Averages = $\bar{\bar{X}}$ + 0.729$\bar{R}$ = 77 + 9 = 86
Lower Control Limit for Averages = " - " = 77 - 9 = 68

CONTROL CHART - AVERAGES ($\bar{\bar{X}}$)



CONTROL CHART - RANGES (R)



Comment: This chart shows the process to be "Out of Control", and, therefore, not predictable. This gives more information than the approximately normal distribution shown in the tally. The range of variation in the samples does not fall outside the control limit, but the sample averages do.

Note that in sampling, in the $\bar{X}$ chart the fourth sample taken fell outside the Lower Control Limit, establishing a probability that the process was not "in Control"; samples 5-12 fell within, but 13 and 14 were outside. In this method one deals not with a fixed sample of a certain size, but continues adding to it until a conclusion is reached or a change is apparent.

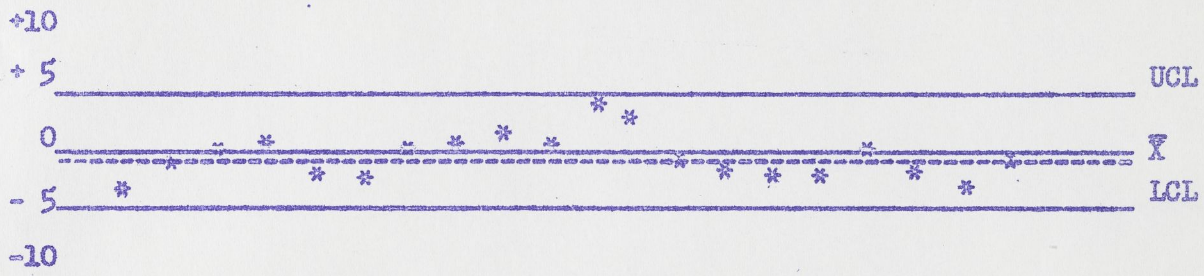
Example II. U-235 Spring. Dimension: Length. Specification: .860 ± .015. Data coded; .860 = 0 , + and - departures in units = .001.

Samples of 5 individuals = group size 5. Measurements on 20 grps
Grand Average = +1.1; Average Range 7.3
Plus and Minus Spread of Control Limits of Averages =
.577 X 7.3 = ± 4.2
Upper Control Limit of Averages = -1.1 + 4.2 = 3.1
Lower Control Limit of Averages = -1.1 - 4.2 = -5.2
Upper Control Limit for Range = 2.114 x 7.3 = 15

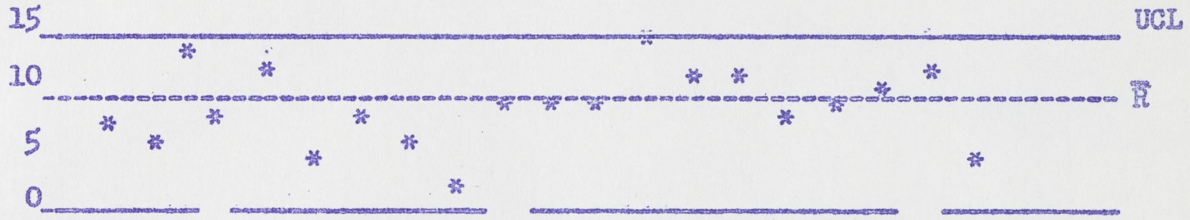
Plus and minus spread of individuals = 1.289 x $\bar{R}$ = ± 9.5
Upper expected limit for individuals = +8.4
Lower expected limit for individuals = -10.6

Without drawing the whole grid, the distribution in relation to means and limits proves to look like this:

Control Chart - Averages ($\bar{X}$)



Control Chart - Ranges (R)



Comments: This process is "In Control" and therefore predictable. The prediction shows that it meets the Specification and is therefore satisfactory. The Control Limits, representative of experience gained through this period of sampling, can be projected. In the future, points falling within these projected Control Limits are a good indication that the process has probably not changed. If points fall outside these projected Control Limits they are a good indication that the process has changed.

3. Multiple Correlation Statistics, and Graphs based upon them. Anderson, in the papers referred to above, has commented on the method of discriminant analysis developed by Fisher (1936) and others, as being too laborious for general use in systematics. Klauber (1940) proposed, as a measure of the divergence existing between two populations with respect to some single character, that the difference between the means of the two populations be divided by the average of the means, giving an index of divergence that is independent of the units in which the character is recorded. Clark (1952) has presented the necessary formulas to permit the extension of the coefficient of divergence for use with multiple characters. His method sums up the differences in several characters into a single coefficient the value of which lies between 0 (no resemblance) and 1 (complete identity in all the characters compared). This method has the advantage of being much less laborious than Fisher's, but it yields only a single measure of degree of relationship in which the contributions of the various elements are not distinguished.

Klauber (1943) discussed a graphic method of showing relationships based on consideration of several or many characters which are combined into a single value by means of plotting the coefficients of divergence as coordinates to obtain a graph showing the relationships of a specimen to two known groups, or of a group to two other known groups.

The publications mentioned above are: Fisher, 1936. The Use of Multiple Measurements in Taxonomic Problems. Ann. Eugenics, 7 (2): 179-188. Klauber, 1940, Trans. San Diego Soc. Nat. Hist., Vol. 9, 195-214; 1943, A Graphic Method of Showing Relationships. Bull. Zool. Soc., 18: 61-76. Clark, 1952, Copeia, No. 2: 61-64.

CLASSIFICATION

1. SOME FUNDAMENTAL ASSUMPTIONS

A. Objectives.

(1) The primary purpose of classification is to provide a convenient, practical means by which biologists may know what they are talking about and others may find out (Simpson). It is designed to furnish the names and categories needed for the expression and exchange of information about animals and plants.

(2) Secondarily, classification serves as a guide to relationships. It is not only helpful for the primary purpose but an essential aim that it should be consistent with the most important thing that evolutionary taxonomists have to talk about—that is, with affinities and phylogeny.

(3) Since utility is a prime function of classification, stability in nomenclature and in the rank of groups should be preserved wherever possible, so long as it does not conflict with phylogenetic interpretation of taxonomic data or with the rules of nomenclature.

(4) A good classification should not only meet the above requirements, but should also synthesize and systematize for general use all pertinent biological datsof a comparative nature bearing on relationships, so far as this can be done.

B. Biological Assumptions

(1) Resemblances between organisms can be classified under two main categories:

(a) Homologous, caused by descent from common ancestors and presumably produced by a common set of inherited genes, and hence direct evidence of genetic relationship; and

(b) Analogous, caused by evolutionary modification in two "unrelated" or distantly related stocks resulting in adaptively and functionally similar morphological or other characterists, which are not direct evidence of close relationship.

(2) Homologous and analogous resemblances may be combined in various ways and degrees, and are frequently hard to distinguish in practice.

(3) This is particularly true in groups of fairly closely related organisms (for example, at the generic and family levels), in which parallel or convergent trends of modification may exist in different phyletic lines of common origin. In such instances the concepts of homology and analogy lose their sharpness and most of their usefulness in thinking.

(4) Morphological and other discontinuities permit delimitation of groups of organisms and their assignment to categories in a systematic hierarchy. It is assumed that such groups, to be natural, are monophyletic at least in the sense of having come from a group of closely related ancestors.

(5) It is possible by comparative procedures to determine degrees of affinity between natural groups. In the absence of genetic evidence, phenotypic resemblance is the best guide to relationship.

(6) Genetic discontinuity may be inferred or measured not only by the study of genetic or cytogenetic behavior, but also by analysis of phenotypic variability and geographic distribution of populations.

(7) All classification is based upon biological data and is tentative; It is continuously subject to re-evaluation in the light of new evidence.

2. CLASSIFICATION AND PHYLOGENY

A. Classification and Phylogeny contrasted.

Modern classification is based on phylogeny, but the two are not to be confused.

Phylogeny is the actual evolutionary history of animals and plants. There was one phylogeny and only one. It was the produce of natural selection, conditioned by changing environmental factors and causing change in genetic constitution, and of isolation, causing splitting of the descendants of one stock into separate stocks. It was natural, continuous, and dynamic.

Classification is the produce of man's effort to group and arrange organisms in a scheme comformable with his interpretation or reconstruction of phylogeny. It utilizes the discontinuities that exist among organisms at any one time level, and seeks for accidental gaps in the fossil record or sets up arbitrary limits in unbroken time sequences; in this sense it is unnatural. It is also unnatural in that it perforce ignores the vast majority of the available phylogenetic groupings, and selects a few for recognition and naming in the hierarchy. Some might add that since it is subject to change it is also active, but scarcely dynamic. Above all, classification is arbitrary, in the sense that even were phylogeny completely known, many classifications could be constructed from the same phylogeny, all equally valid.

B. Phylogeny.

The morphology of recent and fossil organisms provides the bulk of data for the solution of problems of phylogeny. However, other disciplines such as ecology, physiology, genetics, geography, and embryology, all add significantly to the data available for such studies.

Phylogenetic classifications are different in their basis from the older *archetypal* ones such as those adopted by Linnaeus and other early naturalists; but they are often similar to them because the grouping of animals or plants by resemblances and differences leads to similar classifications, regardless of the reasons which are given to explain the existence of such resemblances and differences. Nevertheless, an archetypal classification, such as a modern key, needs no other justification than convenience, while a phylogenetic classification must conform with the evidence of phyletic affinities, even though it cannot express such relationships.

Largely by means of cross combinations involving comparisons of three or more animals or plants (or groups of organisms) the sequence of discontinuities among existing forms of life is determined, and the phylogenetic pattern is revealed. Homology is the basis for such studies; parallelism affords valid but less certain evidence of a more general nature; convergency is not acceptable as evidence of affinity. Any group determined by renewed study to be polyphyletic should be broken into monophyletic elements. However, in this connection the following remarks of Simpson are pertinent:

> "Animals may resemble one another because they have inherited like characters (homology) or because they have independently acquired like characters (convergency). On the average, two animals with more homologous characters in common are more nearly related—their ancestral continuity is relatively more recent—than two animals with fewer. There is no theoretical reason why this should *always* be true, and there certainly are many cases in which it is not true, particularly among abundant, small units, like species, and between other groups whose discontinuities arose within a relatively short span of time. Such groups are, however, related in approximately the same degree, and any errors in inferring the exact sequence among them are rather unimportant and do not essentially falsify the general picture of phylogeny.

It is not possible and not particularly desirable from a practical point of view that phylogeny should be so exact a science that it could establish any difference in degrees of affinity, however slight. The rule that degree of homology is directly proportional to degree of affinity is true within limits narrow enough for most purposes and is a valid working principle. For larger groups, particularly, greater discrimination of degrees of affinity can frequently be obtained from paleontological data, and such determinations are, of course, preferable when they are obtainable" [and unambiguous - THH].

(1) Parallelisms and phylogeny. The term parallelism is descriptive of the fact that distinct groups of common origin frequently evolve in much the same direction after the discontinuity between them has arisen, so that at a later stage the two stocks may have characters in common that were not visible in the common ancestry, but that tend, nevertheless, to be more or less in proportion to the nearness of that ancestry. This proportional tendency distinguishes parallelism from convergence, but the distinction is far from absolute. The two phenomena intergrade continuously and are often indistinguishable in practice.

(a) In the most restricted sense virtually all evolution involves parallelism. Homologous genes tend to mutate in the same way. The chances of survival of a single mutation are extremely small, and a mutation must usually occur in parallel (in different animals or plants) many times before it becomes permanently established and sufficiently widespread to be characteristic of a population. This process is not immediately affected by development of a discontinuity in the breeding structure of the population. The separate and now discontinuous groups still carry homologous genes, and these genes will still continue to give rise to the same mutations. Thus such separated populations and the groups of which they are the pregenitors may, and in all probability frequently do, develop homologous characters that are not typical of their common ancestry or directly inherited, but which are nevertheless caused by inheritance; the inheritance of genes prone to mutate in the same way. This may be called mutational parallelism; it is based upon common inheritance.

(b) A second type of parallelism based upon common inheritance may be called heterogonous parallelism, since it results from the operation of genetically controlled differential growth rates. Body proportions and the size and form of various structures such as horns and other weapons, ornaments, or recognition characters of sexual significance are not inherited as such, but instead factors are inherited that determine what the proportions will be at any particular gross size that the animal may happen to attain. Then if two distinct but related lines of descent carrying similar differential growth factors both evolve in the direction of increased size (and in vertebrates this is so common as to be an accepted rule, with the usual exceptions) they may develop characters of proportion that are the same in both and quite different from those of the common ancestry, but that were nevertheless inherited from that ancestry. Such instances are in practice difficult (and often impossible) to distinguish from the mutational parallelisms discussed under (a); but many of the long-term trends seen among the fossil mammals (titanotheres, proboscideans, perissodactyls, artiodactyls, etc.) and other vertebrates are probably wholle or in part parallelisms of this sort.

(c) A third type of parallelism does not arise primarily from common inheritance like (a) and (b), but from adaptive convergence (through selection) in groups of common origin which retain or develop similar habits and environmental preferences. Convergence that is strictly such and not of types (a) or (b) is likely to occur under these circumstances, and if it does it acts in the same direction as the conservative element of homology. The coincidence of convergence and homology produces particularly close morphological parallelism. Simpson cites as an example the resemblance between the fossil borhyaenid and dasyurid carnivores among the mammals. Like the others, this category of parallelisms is easier to distinguish in theory than in practice. It may be called convergent parallelism.

(2) Similarities versus dissimilarities as evidence in phylogeny.

Homology is always valid evidence of affinity.

Parallelism is less direct and reliable, but it is also valid evidence within somewhat broader limits. It may lead to overestimates of degree of affinity, but is not likely to induce belief in wholly false affinity.

Convergence may be wholly misleading as evidence of relationship, and a principal problem in making a morphological classification on a phylogenetic basis is the selection of characters that are homologous or parallel and not convergent. The greater part of the difference between archetypal and phylogenetic classification has arisen from the difficult and still incomplete task of distinguishing convergent resemblances from others. In this connection, however, it should be noted that the more difficult it is to distinguish between convergence and parallelism, the more likely it is that the resemblances fall into category (c) of the preceding section, and that they do indicate some degree of relationship. In other words, the maximum possible effects of convergence also tend, although much less closely, to be in proportion to nearness of affinity.

Dissimilarities, like similarities, must be divided into those that do and those that do not indicate the proximity of ancestral continuity. Thus, considering the kangaroo, the thylacine or marsupial wolf, and the true wolf, a placental, the differences between the first two are perhaps as numerous but affect less fundamental characteristics compared with those between the thylacine and the wolf. The kangaroo-thylacine differences are interpreted as having developed in different stocks (suborders) of Marsupialia, descended from a common ancestral stock at the ordinal level; the more fundamental differences between the superficially more similar thylacine and wolf are interpreted as having developed subsequent to a more remote dichotomy in the mammalian stock, and the two are treated at the subordinal level as of different origins. As Simpson puts it, the thylacine-wolf differences arose by divergence among the ancestors of these forms at a very remote time, but their persistence today in spite of convergence illustrates the descriptive principle of conservation.

(3) The principle of irreversibility (an extension and special case of the principle of conservation) is widely used in phylogenetic studies, but is very often misapplied or misunderstood. Broadly stated, it is that morphological structure in phylogeny does not wholly return to a marked different ancestral condition.

This has been interpreted to mean that a specialized character never returns to a more primitive condition, and that a lost character is never regained. In this form it is not literally true, and has led to serious errors of interpretation. There is good paleontological evidence that the direction of evolution has changed markedly within phyla, and that single characters under such circumstances do sometimes return to an ancestral condition and that lost characters are sometimes regained.

The principle of conservation, of which Dollo's "irreversibility" is a special case, is that the morphology of an organism has evolved through all the distinguishably different morphological stages in the phyletic ancestry of this organism, and that the given structure would be different had any of those steps been different. This principle is not theoretically demonstrable. Complete reversion and complete convergence are theoretically possible but highly improbable in the light of modern genetic and evolutionary theory. Empirically the principle seems to have no exceptions if only higher structural grades or hierarchic categories are taken into account. Whether exceptions may occur on the generic or specific level is a matter of opinion; but none seems ever to have been clearly demonstrated.

In application, this principle means that *no degree of convergence has produced identity of structure, and that a homogenous morphological group does not arise from two or more different groups.* In the closest and most striking instances of convergence known, the groups are still readily distinguishable, and animals do not become so modified that no perceptible evidence of their broader affinities remains. Simpson disposes of the criticism that this is arguing in a circle by the claim that while this may be true of the principle and its abstract application, the interpretation here given is based on many proved examples and no contradictory case has been similarly proved. In other words, it seems reasonable and it works, even if we can't prove it.

The conservation of ancestral characters, or of less immediate effects of ancestral structural stages, sets limits to:

(1) the degree of divergence of lines of common origin, and
(2) the degree of convergence of lines of different origin.

(4) *The role of paleontology in phylogeny.*

The interpretation of similarities and differences in terms of homology, parallelism, and convergence, and the principle of conservation, are the most important means whereby we construct phylogenetic groupings on the basis of morphological characters. These methods are fundamental and can never be discarded, but in some groups (especially the vertebrates) they are increasingly supplemented and their results often modified or amplified by paleontological sequences that give more direct and certain evidence of phylogeny. If the morphological variations in successive "fossil populations" overlap and form a trend, it is assumed that they represent the expression of a changing population genotype and hence of a true phylogeny. Though this may not be true in the most strict, exact sense, Simpson holds that it must in all such cases be so nearly true that it is mere quibbling to refuse to accept it.

Where minor gaps occur in paleontological sequences they may be filled by inference if the trends continue across them. For larger gaps, especially those in the earliest stages of branching between major stocks which are so usual, application of the fairly obvious and simple criteria for homology, divergence, convergence, and conservation will often give the answers.

(a) Characters shared by early members of two groups are likely to be *homologues*.

(b) Characters shared by early and late members of one group are *conservative*.

(c) If the early members of two groups are more alike than the later, their later dissimilarities are *divergent*.

(d) If the early members of two groups are less alike, their later similarities are *convergent*.

(e) If the early members of two groups are much alike, and the later members have further likenesses, these are *parallel*.

The fossil record is thus helpful only in certain groups of animals; for most animals and for most plants it is too fragmentary, too difficult to interpret, or both for it to play much part in the construction of a phylogenetic scheme of classification.

C. Phylogenetic Classification

(1) Classification cannot "express" phylogeny, because:

(a) no method of classification has ever been devised capable of expressing sufficiently or consistently the multiplicity, complexity and diversity of the phylogenetic pattern, and

(b) the system that is actually used for the classification of animals and plants was not devised to express phylogeny and is notably incapable of doing so.

(2) Phylogeny is nevertheless the basis of modern classification. This means that:

(a) The groups to be recognized should be as nearly as possible valid phylogenetic entities. Any subdivision of a general phylogeny that includes only series of populations that are genetically continuous in space and/or time and through any included intermediaries is a valid and consistent phylogenetic group.

(b) The criteria of definition of groups are to have phylogenetic implications.

(3) Numerous equally valid classifications could be based on any single completely known phylogeny. There is such an enormous number of possible phylogenetic groups that could be recognized and made the units of classification that the number of possible classifications for any given phylogeny would certainly run into the millions, all different and all valid and natural in the sense of being consistent with phylogeny.

(4) Choice of the particular classification to be used therefore depends on other factors in addition to consistency with phylogeny.

(a) Historical continuity: to be useful a classification must serve as a means of communication, which requires a consensus on the meaning of its terms and categories. Good classification is conservative.

(b) Selection among equally available alternatives, on the basis of taste, experience, and authority (the latter being the product of the taste and experience of others). Simplicity and utility are among the criteria to be considered.

(c) Readjustment and innovation, including regrouping and subdivision, to bring classification into line with new knowledge of phylogeny or to take into account increase in the number of known groups and the amount of knowledge available about each.

(5) What is it that is classified in classification?

A category of classification is theoretically defined (at least by implication) in phylogenetic and genetic terms. The thing thus defined is a group or population in which the objective units are individuals, but it is not the individuals as such that are defined. This group is real, natural, and absolute, since it consists of a finite number of real individuals with definite characteristics and related in a stated way. But the thing actually available and studied by the classifier is not this group, but only a series of specimens (the hypodigm), constituting, by hypothesis, a sample drawn from such a group. And the group boundaries and differences as drawn in practice are not established on genetic data but on morphological data (supplemented occasionally with other information).

The theory is that there exists in nature a morphologically definable unit that tends to correspond with the practically indefinable genetic unit.

Thus the actual procedure in classifiation, in almost all cases, is this:

From a series of concrete specimens in hand an inference is made as to the nature of a morphological group from which the sample came, and an endeavor is made to frame the morphological concept in such a way that the inferred morphological group will approximate a genetic group.

The thing that is actually classified is an inference, a purely subjective concept, which approximates a real but unobservable morphological unit, which in turn approximates an equally real but even less observable genetic unit.

3. THE SYSTEMATIC HIERARCHY. See Mayr, Linsley & Usinger.

For reference the complete hierarchy in most common use is given here, with the obligatory categories in capital letters, the optional ones in capitals and lower case:

KINGDOM
PHYLUM
Subphylum
Superclass
CLASS
Subclass
Infraclass
Cohort
Superorder
ORDER
Suborder
Infraorder
Superfamily
FAMILY
Subfamily
Tribe
Subtribe
GENUS
Subgenus
SPECIES
Subspecies

The hierarchy most commonly used in botanical classification uses somewhat fewer categories and names some of them differently.

In Zoology:
Family names end in idae
Subfamily " " " inae
Tribe names " " ini
Generic names are capitalized
Specific names are never capitalized

(1) The Indefinability of the Hierarchical Categories. It is an extraordinary peculiarity of classification as a science that not one of the ranks in this hierarchy can be satisfactorily defined in absolute terms. The basic unit in theory and the most nearly definable rank in practice is the species (in zoology at least); but very little acquaintance with taxonomic literature is needed to show that its definition is one of the most discussed of all problems in taxonomy, and that the species of different authors, even those working in the same group, are not of equal rank. The various definitions of species will be considered later. Above the species level there are no objective criteria for any category, and there appear to be no differences in kind or in importance between the so-called obligatory and optional categories.

(2) Criteria for Super-specific Categories. All categories above the species have in common that they may include groups discontinuous, genetically and morphologically, between themselves. A genus with only a single known species (called a monotypic genus) does not, in fact, include such a discontinuity, and there are many such genera. Here the criterion used in practice is not that provided in theory, but is related in the latter. The practical classifier grants to a genus a certain "size," by which is meant, as a rule, a certain morphological scope with the implication that this scope tends to approximate a certain degree of phylogenetic differentiation and to include all animals related to one another in certain limits. This morphological scope may be almost entirely filled or exploited by known species if the genus has many (is a polytypic genus), or only one or a few species may be known, leaving much of the explicitly or implicitly assigned scope blank. The same considerations apply to all units above the specific level, which differ mainly in the assignment to them of increasingly larger scope as the hierarchy is ascended.

(3) What is the Scope of a Category? The question - How large is the scope of a genus, a family, or an order? - is not much more answerable than the question, How far is up? An effort is made to give approximately the same scope to groups of the same rank and to grade different ranks more or less evenly from species to kingdom. Nevertheless, this ideal is never fully attained even by one student within one group, and there is great variation between different students and different groups. This arises partly from current custom or fashion; genera are smaller units today than in 1858 and most of Linnaeus' 1758 genera are now families or even orders. Genera tend to be smaller in better-known than in little-known groups; to be smaller in families with many species than in those with few. Some students ("splitters") prefer genera small, with the extremists making a high proportion monotypic; other ("lumpers") prefer them large, and tend to unite the genera set up by other whenever a species showing intermediate or transitional characters is found. From the practical standpoint of usability neither extreme is desirable.

(4) Vertical and Horizontal Classification. The implication that members of a given group are more closely related than any of them are to members of another group gives rise to two kinds of problems in classification, the first and more difficult relating to the treatment of ancestral groups, the second and merely troublesome having to do with contemporary species.

(a) The Classification of Ancestors. In paleontology one deals both with ancestral groups and their separate and diversely modified descendants. In a phylogenetic sequence, is a group more nearly related to its ancestors, its descendants, or its contemporaries of like origin? Is a man more near-related to his father, his son, or his brother? Obviously there is no answer; but some practical solution must be sought.

In the simplest case, of an ancestral unit with two descendent lines, there are two systems in common use. (1) The name and concept of one of the descendent groups are extended to cover the ancestral group; or (2) the ancestral group is given a separate name and considered a group of the same rank as the two descendent groups. Both systems have their advantages but on the lower levels of classification the second seems more often useful. Thus, among the fossil horses, the group immediately ancestral to †Hipparion, †Pliohippus and other genera is also given generic rank and called †Merychippus.

Such simple cases are not very confusing, but analogous problems can be very intricate. Thus, among the Mammalia, the early carnivores were quite varied but apparently came from a common antecedent stock. One of the early groups, the †Miacoidea, survived and apparently gave rise to all the divergent lines leading to our modern terrestrial Carnivora. How shall this be treated? The †Miacoidea are ancestral to the later carnivores, the Fissipedia; but they are certainly equally nearly allied to the more ancient and archaic †Creodonta in the way often or customarily expressed by inclusion in one taxonomic unit, for they are derived from the same immediate ancestry. There are two sorts of affinity here, and following either one consistently through a classification is a practical impossibility. There are only two practical methods of dealing with the situation: (1) to place all the early carnivores including the †Miacoidea in the †Creodonta, separating the descendants of the †Miacoidea as Fissipedia; or (2) to place the †Miacoidea in the Fissipedia and nevertheless to lump all the other early lines in the †Creodonta. Neither is a clear expression of the phylogenetic affinities involved, but both solutions are equally valid, and both are in use, both in this particular instance and in many parallel ones.

The choice here is between so-called *horizontal classification* and *vertical classification*.

Horizontal classification separates ancestral from descendent groups, and unites contemporaneous groups, or those in a similar stage of evolution if they are derived from a common ancestry.

Vertical classification unites ancestral and descendent groups and separates contemporaneous groups that are diverging from a common ancestry.

These are often regarded as mutually exclusive principles and the assumption made that a classification should be based on one or the other; but in fact *neither can be followed consistently* and any classification necessarily combines both methods. The most ardent exponent of vertical classification finds it necessary to separate ancestral and descendent genera, for instance.

Advantages of horizontal classification: Usually easier and more objective. Applicable to groups whose ancestry is unknown. Likely to be more stable because less likely to be disturbed by later discovery. More in accord with conventional classification. [To illustrate: the earliest horses and tapirs have more in common than have the earliest horses and the latest ones. It is easier to define a group containing the earliest horses and tapirs (horizontal classification) than it is to define one containing all the horses and no tapirs (vertical classification).]

Advantages of vertical classification: More in accord with the whole evolutionary concept of descent with change. Sometimes called evolutionary or dynamic classification as opposed to pre-evolutionary or static classification, although in fact horizontal classification can be just as consistent with phylogeny as vertical, and neither can really express phylogeny.

Classification of successive stages in a phyletic sequence. A special and peculiarly confusing case of horizontal classification is continually presented to paleontologists who must classify the successive stages in unified or essentially unified lineages. Such a lineage or phyletic sequence is formalized as a succession of species, or on a larger scale a succession of genera, each of which gives rise to those which follow. From a genetical point of view, species, genera, or other units *in this sense* are totally different things from the horizontal units of contemporaneous faunas to which the same categorical names are applied. Thus:

(1) In *contemporaneous* (horizontal) species the very essence of the genetic definition is that interchange of heredity is possible throughout the group, but that established discontinuities prevent or restrict transmission to any other specific group. By contrast,

(2) In *temporally sequential* species (divisions of a "vertical" lineage) interchange of heredity is impossible throughout the species, if only because the later members cannot breed with those already dead;

and on the other hand, heredity is directly transmitted to what is defined as a wholly distinct species, the descendent species.

(3) The principle of nearness of affinity is also necessarily violated in all such cases. If one genus gives rise to another, the last species of the first genus will be more closely related to the first species of the next genus than to the first species of the first genus. Thus species placed in different genera sometimes are, and must be if the system is to be used at all, more closely related than species placed in the same genus.

[Note that this last type of difficulty besets all attempts to categorize unbroken sequences of any sort. We shall encounter it again at the subspecific level in horizontal classification, in relation to attempts to subdivide clinally varying species populations.

Despite these difficulties in theory, the direct use of inferred morphological groups and the principle of analogy of scope permit <u>workable practical solutions</u>. In paleontology, "vertical" lines are divided into species, genera, etc., such that the morphological scope of these units (in the "vertical" direction) is comparable with the scope of genetic species, genera, etc. (in the "horizontal" direction).

The horizontal lines drawn between "vertical" units are necessarily <u>arbitrary</u> when the sequence is unbroken. This does not mean that the resulting groups are "unnatural" or "unreal," any more than are the pieces cut arbitrarily from a continuous length of string. The severed pieces are still real, and each has natural continuity.

Such a system works better in paleontology than it does in dealing with subspecific variation, for several reasons. First, the necessity for some such convention is so evident in paleontology that no one argues the point, which is not true among neozoologists. Secondly, it is seldom in paleontology that the sequences are really so continuous and so uniformly graded that choice of the dividing lines is truly arbitrary; instead they are commonly made at present or former gaps in the fossil record, or where change is more abrupt, or at points where striking or important new morphological characters become widespread or universal in the evolving population. Independent workers would often choose the same divisions under these conditions.

(b) <u>Paradoxical situations in "horizontal" classification</u>. The general type of situation in which the morphological similarity, and by inference the genetic relationship, of two members of a single group is less close than is that of one or both of them to a member of some other group was exemplified in the temporal sequences discussed above. Analogous situations also occur in "horizontal" classification, both at the subspecific and higher levels.

1. <u>Continuous trends within species populations</u>. Populations showing clinal variation in one or more characters present the same problems for delimitation of subspecies as do continuous temporal lineages. Except where steps occur in the clinal gradient(s), and in all cases of non-coincident clines, any divisions are <u>arbitrary</u> both as to number and position, and as discussed under (a)(3) above they violate the principle of nearness of affinity. Zoologists are at odds over the desirability of attempting subdivision of populations under these conditions.

2. Relationships of species and genera. The type of situation diagrammed below, first in "horizontal" and then in "vertical" perspective, is so common that almost every practicing taxonomist has encountered many instances of it. It can be dealt with in several different ways, none very satisfactory.

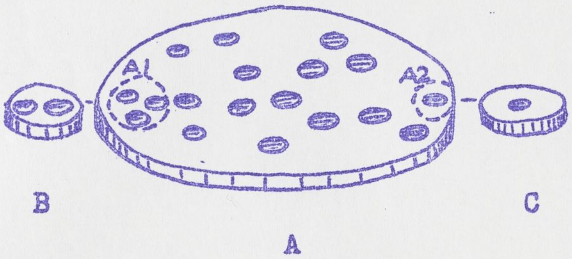


Fig. 4

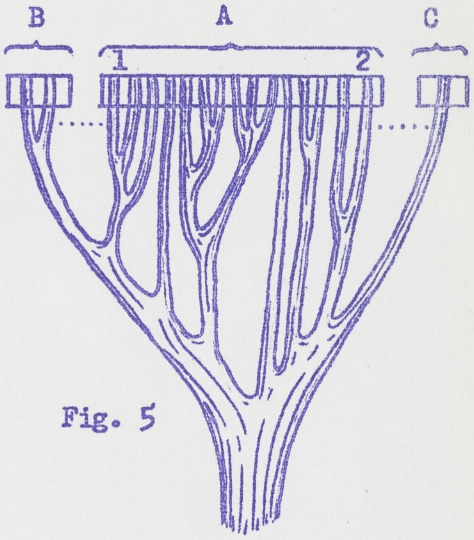


Fig. 5

Explanation of Figs. 4 and 5.

A is a large polytypic genus containing species groups but without good characters for separating it into smaller units; it is a tightly integrated complex.

B is a small genus of 2 species, which share nearly all their characters with the species of group A_1, but differ in a few very striking features which are incompatible with the morphological definition of genus A and in the opinion of specialists in the group warrent generic separation.

C is a monotypic genus which differs in a number of important respects from genus A but has its closest resemblance to monotypic species group A_2 of that genus.

Genus B shares more characteristics with species group A_1 (and hence is more closely related to that group) than group A_1 does with group A_2. The same is true of Genus C and species group A_2 as compared with group A_1.

Fig. 4 is the "horizontal" diagram of this situation, a slice of time cutting across the phylogenetic lines. Fig. 5 is the "vertical" view of the indicated phylogenetic relationships.

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(5) The Dimensions of Classification.

The problem of vertical and horizontal classification leads on to more general considerations of taxonomic dimensions, in a somewhat figurative sense. The morphology of an animal is literally 3-dimensional. When, for instance, two species are defined horizontally by differences in their (average) morphology they are distinguished in 3-dimensional space. This is the static procedure; but morphology as used in modern classification also has two kinetic elements, to some extent analogous with additional dimensions.

"In addition to its average, 3-dimensional condition, every morphological group has variation in two directions: (1) variation at any given time, and (2) variation between different times. These are not only essential qualities and quantities of group morphology, they are often the real crux of the problem of classification."

(a) *The Fourth Dimension*: Variation within a group at one time.

This is as much a character of the group as is any so-called constant characteristic, and may be much more important and more characteristic than any demonstrable constancy. The typical 3-dimensional statement of classifiers that, for instance, the skull of a given species is 60mm. long, 30mm. wide, and 15mm. deep, aside from being untrue (for it can apply only to an average in a sample or to one individual and cannot be true of the species) is wholly inadequate and misleading. In the species, each of these dimensions, or all 3 together, have another dimension, that of variation. This is more difficult to measure, and in fact cannot be measured in the real morphological or genetic species, but it can be estimated from a given sample (whatever the size of the sample). This estimate is an integral, or even the essential, part of the inference that is the thing really classified. *It cannot be too strongly emphasized that some estimate of variation is inherent in any valid classification. Classification is not concerned with individual organisms, but only with groups.*

(b) *The Fifth Dimension*: Variation in a group between different times.

Every group has duration and exhibits morphological differences in time as well as in space. In the definition of units that are notably "vertical" with a long extent in time, temporal variations or trends frequently become predominant. In such cases definition solely by 3-dimensional characters-in-common, or by these plus "horizontal" variation, is always inadequate and may be impossible. For example, the linking of *†Hyracotherium* with *Equus* in the Equidae is solely on the basis of temporal variation and is flatly contradicted by horizontal criteria. The fifth dimension is available for use only in groups with an adequate fossil record.

(c) *Dimensions and Hierarchical Categories.*

In *classical taxonomy* all categories were 3-dimensional only; from species to kingdoms, organisms were arranged by a given set of characters supposedly running through every member of the given group. This is still true of some parts of classification, and doubtless always will be, because we can never hope for enough data to put all of classification on the best possible basis.

In *modern taxonomy* the 4th and 5th dimensions are entering more and more into the characterization of the categories. They are affecting the various grades in somewhat different degrees.

1. *The Species.* In the great majority of instances species in modern classification are essentially 4-dimensional. They are defined by a set of morphological characters and by the horizontal variation of these. In exceptional instances a time element (5th dimension) also enters in, but this is usually minimized if present at all. Although the species is the basic unit of theoretical and genetic taxonomy (at least in zoology), it is a more multiform, fluid and dynamic entity than the genus because of the entry of 4th and sometimes 5th dimensional elements into its definition.

2. *The Genus.* This category tends more than any other to retain its classical, 3-dimensional status, and to be defined in practice as a group of species possessing certain characters-in-common. The elements of "horizontal" and "vertical" variation are, of course, operative in genera as in all other units; and by some authors or in some groups these may become essential in the generic concept. However, the present custom is usually to place contemporary or successive species in a given genus on the basis of their possession of a minimum set of diagnostic characters. This is classical 3-dimensional taxonomy.

This is the principal reason why, by and large, *genera are the most permanent units in modern classification.* This is to such an extent true that in much of taxonomy the genus can be considered to be the basic unit of practical and morphological taxonomy, in spite of the fact that in theoretic taxonomy it is the species which is the basic unit.

It requires less knowledge and skill to recognize units of a static category, especially when this is by intention a rather broad and definitely a group category, than to do the same when variables must be treated as such. This is particularly true in paleontology, for the dual reason that paleontological classification involves both 4th and 5th dimensional variation, and that the data for dealing with the variables are usually less adequate than those for modern groups.

3. The Subfamily. This, or some analogous category between genus and family, is being increasingly used as a unit whose greatest dimension is in time, and into the definition of which temporal changes or trends (5th dimensional elements) enter most largely. The extent to which the other taxonomic dimensions are employed differs as greatly as possible between different authors and to some extent in different parts of the classification.

(a) At one extreme is the primarily phylogenetic unit which has ideally only one dimension (the 5th), or variation in time. Such a unit is supposed to be a succession of actually ancestral and descendent individuals alike in character at any one time. However useful such a conception may be in theory, it is in most cases unattainable. This is fortunate, for in practice this conception of the subfamily (or an equivalent grouping) would lead to an arrangement in which the theoretically different grades of the hierarchy are coextensive—to genera each with one species, to subfamilies and families each with one genus, etc. Thus it defeats the whole purpose and use of hierarchic taxonomy.

(b) Somewhat broader and more rational is the conception of the fundamentally temporal subfamily unit as a succession of ancestral and descendent genera commonly with the implicit or even the unconscious proviso that only one genus in any one subfamily existed at one time or at least that little or no generic branching occurs in a subfamily. Such a classification is seen in Osborn's Monograph on the Proboscidea, for example. Even this conception of the subfamily leads to a great majority of monotypic subfamilies, which is certainly a drawback. There is no good reason to maintain a grade of classification and to remember a multitude of names in it if the grade usually has no greater scope than one below it in actual

(c) At the opposite extreme is the classic use of the subfamily as a smaller sort of family, without conscious attention to the temporal element. This is the way it is used by most zoologists, who deal with groups in which the fossil record is of little significance in classification. Even here, however, the time dimension does inevitably enter into the subfamily, as it does into all the higher categories, to a greater extent than it does into the species and genus. This is true whether it is recognized or not, and being true, it may be better to explicitly recognize the subfamily as a grade in which the time dimension is essential and is generally longer than the other dimensions (as far as such a comparison of incommensurate things can be made)—a category stressing phyletic relationships, although not in the sense that it must be purely monophyletic throughout.

Obviously such a definition of the subfamily could not be applied outside those groups in which the 5th or time dimension is accessible for study through fossils or dependable indirect evidence of phylogenetic trends. A grade so defined will obviously be more subject to fluctuation, impermanence, and inconsistency than almost any other, for phyletic theory is the most subjective element in taxonomy, the most influenced by differences of opinion, and the most liable to radical change with advance of knowledge. Hence there is an advantage to using the subfamily (and by extension, the tribe) as the grades in which to stress phylogeny. They are subsidiary grades, between the genus and the family deriving their names from those of genera, and capable of great flexibility and even distortion without seriously affecting the essential and obligatory grades of taxonomy. The stability of the whole system is improved by concentrating the instability-causing factors on these two grades.

4. The Family. The family is the lowest grade that in present-day classification tends to be well-rounded in all five dimensions in those groups where the available data make this possible. This is also true of all groups above the family; these higher units differ little in character except for their being larger and larger in scope as they bracket the lower units in ascending the hierarchy.

The family always includes, in theory, several distinct phyletic lines, with certain characteristic structures running nearly or quite through all, and with a certain characteristic sort and degree of variation embracing all, with characteristic differences in time within each, and (with some temporal differences) influenced by a common heritage manifested in many or in all. In practice some monophyletic families occur, but the assumption is that other lines existed but are not known. "It is not safe to assume, and it probably rarely happened, that a single phylum [lineage] in the most limited sense ever became so unlike its parent stock and its relatives as to be classed as a separate family without itself splitting up into more than one minor phylum."

Proponents of purely vertical, phyletic classification may apply this principle exclusively (as they all do in part) to almost any unit below the family; but somewhere they have to start horizontal grouping, to bring together quite distinct though related contemporaneous forms into one group. At present even the most ardent splitter and the so-called phylogenetic taxonomists usually start frankly horizontal grouping at about the grade of family; from this grade up the horizontal element of classification strongly predominates.

N.B. - Pages 21-33 of this outline are largely an abstract, rearrangement of, and exegesis upon Simpson's essay on the Principles of Taxonomy, Part I, of "The Principles of Classification and a Classification of the Mammals", Bull. Amer. Mus. Nat. Hist., 85 (1945). Many parts have been omitted, others have been quoted, and still others have been used as a point of departure for further development of an idea.

4. RULES AND REGULATIONS: NOMENCLATURE

These topics are covered in part 3 of Mayr, Linsley and Usinger. You should be acquainted with the material covered in Chapters 10, pp. 201-207; Ch. 11, pp. 212-218, 220-221; Ch. 12, 236-245; Ch. 13, pp. 246-248, 256-260; Ch. 14, pp. 261-266, 269-270; Ch. 15, pp. 271-275; Ch. 16. Refer also to Schenk and McMasters.

SYSTEMATICS AND BIOSYSTEMATICS

1. THE EVOLUTIONARY SYNTHESIS

In practice, systematics and taxonomy are essentially synonymous terms, both applying to the science and practice of classification. Attempts have been made to differentiate between them, making one apply to the principles and the other to the practice of classification, or one to include the other as being more comprehensive; but there has been no consistency or consensus in such attempts.

In recent years the rise of genetics and renewed interest in the problems of evolution have led to a reexamination of the problems of classification and to the development of new practical and theoretical approaches to the study of all three fields - or rather, of evolution in the widest sense as including genetics and classification. This modern synthesis has revolutionized the viewpoints if not the methods of systematics, has created new dilemmas while dissolving old problems, and has led to a great outburst of activity in systematics as well as in the related fields. This new synthesis has been called "The New Systematics" by Huxley (1940), and his term has been widely used by zoologists, in particular; but it is no longer so new, and the proposal of Camp and Gilly (1943) to call it biosystematics has much in its favor.

In biosystematics, genes, individuals, and populations are the units dealt with; the species is a concept based on that of populations, and one that must be defined for a particular set of circumstances, such as the mode or modes of reproduction, the level of organization of the individual, and other factors. Accordingly, there can be different kinds of species in different groups of organisms, or even in the same group; and the species is defined not by the possession of certain characters, but by the way it behaves as a population with respect to variation, adaptation to environment, and reproductive relations with other populations.

2. SPECIES CONCEPTS

Stebbins (1950) has pointed out that present knowledge does not confirm the opinion often expressed by experimental biologists that only individuals are real and the species is a man-made concept; but that it is nevertheless true that there are a number of equally "real" biological situations to which the traditional concept of species can be applied. "Our principal task should be to study these situations and to spend as little time as possible discussing the definition and application of terms....[Until we have a firmer basis of knowledge] the wisest course would seem to be to avoid defining species too precisely, and to be tolerant of the somewhat different species concepts held by other workers." Nevertheless we must have some idea of what the various species concepts are, in order to appreciate the alternatives of treatment that exist.

A. Kinds of Species: Major Categories

1. Biospecies. This is the species concept based on reproductive isolation, implicit in most discussions of biosystematics. It may be defined as a sexually reproducing, cross-fertilizing population or series of interbreeding populations existing at a given instant or brief period of time and during that time reproductively isolated from all other populations, if not completely then effectively so. The evidence needed to establish their separateness is that they are nearly or completely non-interbreeding populations, and no other form of evidence is a completely sufficient substitute in all cases.

2. Morphospecies. This is the species concept based upon morphological distinctness; a species possesses a constellation of characters which vary about a mean or typical condition, and is separated from other species by discontinuities in the variation of characters. It is a typological concept, generally applied to contemporaneous species of a given time level, but essentially without dynamic or temporal connotations.

3. Paleospecies. The organisms forming successive generations in a phyletic line, related to one another in the parent-progeny relationship, as well as the interbreeding individuals of a given generation, taken as a unit segment of the phyletic line arbitrarily delimited. As stated by Cain (1954) it is an unhappy attempt to impose a taxonomy of discontinuous groups on a continuous series. It is the unit of vertical classification, as the biospecies and morphospecies are the units of two different kinds of horizontal classification.
   Chronospecies.

B. Kinds of Species: Additional, Alternative, or Subsidiary Categories

4. Ecospecies. A population adapted to a particular set of ecological conditions and composed of freely interbreeding individuals producing vigorous and fertile offspring. Used chiefly in plants; cf. race.

5. Cenospecies. A population composed of one or more ecospecies so related that they may exchange genes among themselves to a limited extent through hybridization, but which in crossing with other cenospecies yields no or sterile hybrids. Used chiefly in plants; cf. polytypic species.

6. Monotypic and polytypic species. Species of uniform characteristics over the entire range, vs. species composed of differentiated geographic races or subspecies.

7. Ring-species. Polytypic species, the terminal subspecies of which are reproductively isolated from one another though connected by intergrading series of populations in another direction.

8. Sibling or Cryptic Species: Morphologically indistinguishable or very similar species shown to be distinct by genetic, physiological, ecological, or behavioral differences involving reproductive isolation.

EVOLUTIONARY MECHANISMS

1. THE GENETIC BASIS OF DIVERSITY AND OF EVOLUTION

In the modern synthetic theory of evolution the factors of the "genetics of the transmission of hereditary materials" are taken as established, and attention is given to the play of these factors in populations (the field of population genetics), and through time (the field of evolutionary genetics).

Among the best accounts of the genetic basis of evolutionary mechanisms is that given in Sinnott, Dunn and Dobzhansky, "Principles of Genetics", 4th ed. (1950). Especially valuable are Ch. 12, Genes in Populations, Ch. 13, Genetics of Race Formation, and Ch. 14, Genetics of Species Formation. Another work which is very stimulating and original in its approach is Darlington and Mather, "The Elements of Genetics" (1949). The flavor of the latter is given by the following quote from the preface: "There are two ways of attempting to describe a part of nature in scientific terms. One is to deal with the area which has been exactly mapped by experiment, with the ensuing generalizations and predictions, and to leave the rest empty. The other is to go further and use our knowledge of the mapped area to fill in the empty spaces according to the more likely assumptions. The first method is evasive, the second hazardous. We prefer the second method and have adopted it. .. We have tried to use what is known in order to find out what is unknown. As a consequence there stretches a complete range, in a gentle gradient or cline, from the old theories of Chapter 1, which are called Laws of Nature, to the new theories of Chapter 16 which are called Dangerous Speculations. The reader will don his doubting glasses at the point he feels proper. He will do well, however, to recollect that this is the first attempt to represent the whole scope of genetics, the whole of what has always been needed. In the past open hypotheses have been replaced by concealed assumptions and assumptions are far more dangerous than the statements we have laid before the reader in black and white." Particularly valuable parts of this book are Chapters 11 to 15 on Populations: Adjustment and balance, breeding systems, selection and variability, the breakdown of continuity, and the growth of genes.

The single most important reference on the genetic basis of evolution is Dobzhansky, "Genetics and the Origin of Species," which is now in its 3rd edition (1951). In this work the processes of evolutionary population genetics are seen as occurring at three levels: (1) The origin of evolutionary raw materials (variation) by mutations of genes and chromosomes; (2) Changes in populations by changes in the frequencies and combinations of mutations, chiefly through natural selection, and (3) The fixation of such changes by reproductive isolation. Each of these levels has its special basis in underlying factors derived from conventional genetics: (a) in the frequency and nature of mutations, (b) in the formal laws of of transmission of hereditary factors, and (c) in the mechanisms of hybrid sterility.

The following are some of the basic concepts and relations involved in any discussion of evolutionary mechanisms, which need definition here:

Mendelian population: A reproductive community of individuals which share in a common gene pool (Dobzhansky 1950). The integrating agent is the process of sexual reproduction, which establishes mating, parenthood, and progeny bonds between the component individuals. Such a population has a corporate genotype, which is subject to change under the influence of (1) mutation rate, (2) selection, (3) gene dispersion, and (4) changes in population size and structure.

Evolutionary statics: The factors which bring about changes in the genetic composition of the population.

These factors include the items listed under Mendelian populations above. Involved in evolutionary statics are the following concepts:

Genes: Molecules or molecular aggregates which are the units of self-reproduction and heredity.

Genotype: The sum total of the genes of an individual or a population.

Phenotype: The bodily forms resulting from the interaction of a genotype with various environments. A byproduct of the genotype.

Norm of reaction of the genotype: The total range of phenotypes which a given genotype can engender in all possible environments.

Genetic evolution: Change in the genotype of a population.

Phenotype and genotype in evolution: Phenotypes are selected. Their differences are adaptive in some environments and unfit in others. Elimination of some phenotypes eliminates the genes those individuals carried.

Modifications and morphoses: The survival values of the different phenotypes which can arise on the basis of a given genotype in different environments are often unequal. The phenotypes which develop in response to environmental influences which recur regularly in the normal habitats of a species are usually adaptive and conducive to survival (modifications—Schmalhausen); those reactions to environmental stimuli rarely or never encountered normally are seldom adaptive (morphoses—Schmalhausen). Every norm of reaction of genotype includes potentialities of numerous modifications and presumably of morphoses. Neither modifications nor morphoses influence the genotype, because they are conditioned by it, while the genotype reproduces itself regardless of what phenotype it evokes under particular circumstances.

Modifications maintain the normal equilibrium of phyiological processes in the body (homeostasis) as well as the harmony between the organism and the external world. Examples: seasonal changes in physiology, immunological reactions, healing of wounds, strengthening of organs with use and weakening with disuse, etc. All are phenotypic properties, but are conditioned by genotype. The success or failure of an organism is determined by its reaction norm, by the adaptedness of the modifications evolved in response to recurring environmental influences. [See Baldwin Effect]. Adaptive modifications = long selection.

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Morphoses are adaptively haphazard and often harmful. They represent new reactions which have not been sorted and ordered by selection.

Genetic Homeostasis: The fixity or plasticity of a trait with respect to environmental influences is determined by the genotype. The amplitude of the reaction norm is conditioned by the hereditary constitution. Schmalhausen (1949) has stressed the equilibrative properties (homeostasis) of the genotypes which are adaptively "normal" for the species, i.e., are widespread in the natural habitats. The normal patterns of the developmental processes are so buffered against the influences of recurrent environmental agencies that the outcome of individual development (ontogeny) is not unduly variable. Thus it is obviously important that the ♂ and ♀ genotypes produce normally functioning ♂ and ♀ individuals if the species is to be continued, and this is so buffered that such individuals are produced in spite of environmental variation. But in mutations that do not normally occur in the population there is no such buffering, and the phenotypes are often very unstable; temperature, nutritional changes, and most genetic modifiers do not affect the sex characteristics of wild-type Drosophila melanogaster, but produce gross changes in the reproductive organs of triploid intersexes.

Phenocopies: It is possible to produce, experimentally, variations in the phenotype which more or less closely resemble mutations. These require special environmental conditions to exist, while the mutants they resemble are the same in all known environments in which they can exist. Mutations change the norm of reaction, while in a phenocopy the norm of reaction remains unaltered.

Mutation: In the wide sense, changes caused by changes in single Mendelian units, losses or reduplications of parts of chromosomes, rearrangements of parts of chromosomes (inversions, translocations), and reduplications or losses of whole chromosomes or sets of chromosomes. Chromosome aberrations are classified as:

I. Numerical changes (genome mutations): affecting the number of chromosomes
    a. Haploidy: carrying only one of each kind of chromosome instead of the normal pair
    b. Polyploidy: carrying more than two sets of homologous chromosomes (triploids, tetraploids, heteroploids, etc.)
II. Structural changes (chromosome mutations): affecting the arrangement of genes in chromosomes
    a. Loss or reduplication of some of the genes
        (1) Deficiency (deletion). Section containing 1 or more genes is lost from a chromosome

(2) Duplication. Section of a chromosome present both at its normal place and elsewhere

b. Alteration of normal arrangement of genes

(1) Translocation: Two chromosomes may exchange parts

(2) Inversion: Location of a block of genes in a chromosome may be changed by rotation through 180°, inverting the order of the genes in that block.

Changes produced by mutation: Any morphological or physiological trait may be altered by mutation. So also may ethological traits (habits and behaviors). All changes must be mediated by physiological = biochemical processes. Single mutations never produce new species, genera, or families, since species populations always differ in many genes, and hence by summation of many mutational steps. No matter how extreme the mutant, it is still a member of its species population.

Pleiotropic genes: Although genes are named from the most striking phenotypic effects they produce, any given phenotype is the produce of a given gene in cooperation with all the other genes of the genotype, and it may be postulated that any gene change must have manifold effects. When such effects are evident or can be determined by experiment the gene is said to be pleiotropic (to have manifold effect). Differences between species and races frequently involve traits that appear to have no survival value, but these seemingly neutral characters may be incidental effects of pleiotropic genes which have important adaptive physiological effects.

Interdependency of genes: The position of genes in relation to other genes can modify their effects; translocations and inversions produce effects not expected as the basis of the classical gene theory, and which can only be due to alteration in gene order. Some translocations and inversions are lethal when homozygous and others produce morphological changes; in other instances genes lose dominance with change in position due to translocation. Evidently a chromosome must be considered a system of interdependent genes.

Population Statics and Dynamics

The Hardy-Weinberg Law: Also called the binomial-square law. The foundation of population genetics and modern evolutionary theory.

The frequency of a given gene and its allele in a population remains constant irrespective of the initial values of their absolute frequencies, under the conditions specified: (1) a relatively large, panmictic (randomly breeding) population in which there is no mutation in either direction (from either allele to the other) nor migration into the area, nor selection of one gene over the other; and (2) the original individuals with genotypes AA and aa are in the proportion of q and 1-q respectively, with the values of q and 1-q not approaching 0 or 1 closely. The formula under these conditions is, for the 2nd and all following generations:

$$q^2 AA : 2q(1-q)\,Aa : (1-q)^2\,aa$$

If there is some breeding preference, such as a tendency towards inbreeding or self-fertilization, the relative frequency of the homozygotes and heterozygotes will be modified but the gene frequencies, q and 1-q will remain constant, as it does under panmixis.

Factors that modify the Hardy-Weinberg formula:

a. Mutation pressure: Mutations are recurrent, the same mutation occurring over and over again. The rates vary widely; some computed rates are of the order of 1 in 10,000 to 1 in 10,000,000. The mutation pressure, A to a, if unopposed would eventually result in disappearance of A from the population. However, reverse mutations also take place, a to A. If both A to a and a to A occur, an equilibrium results that is dependent upon the values of the opposing mutation pressures. Since all of the genes in a population are subject to mutation, this process, if unopposed, would result in constantly increasing variability, wholly unrelated to the adaptability of any variant.

b. Selection pressure: When various alleles are present in a population, the several phenotypic expressions they produce are apt to have different survival values—to confer advantage, be neutral, or be deleterious under a given set of environmental conditions at a particular time and place. Selection pressure will be proportional to the degree of benefit or disadvantage shown by the phenotype expressing the given allele. This, of course, is subject to the limitations indicated under interdependency of genes above, since the effect of gene a may be advantageous in combination with bcdE and deleterious with BCDe or BcDe, in a given environment.

Even a very small selection pressure, unopposed or greater than an opposing mutation pressure, can more or less rapidly alter the genotypic ratio in a population.

c. Interference with free gene dispersal: Any barriers to free gene dispersal from one part of the population to all others will tend to make the gene ratios in the two parts diverge, since the effects of selection and mutation are almost certain to be different in any two parts of the population.

d. Population size and structure: An indicated above, interferences with free breeding preference will tend to alter the ratio of homozygotes to heterozygotes.

In very small isolated populations, genetic drift may operate. This is sometimes called the Sewall Wright effect, or scattering of the variability. It rests primarily on the fact that the mechanics of segregation and recombination involve a large element of chance, and that where there is a limited survival of zygotes chance alone will tend to eliminate some alleles and thereby fix (make homozygous) others. Wright has worked out the details under many hypothetical conditions: combined with and opposed to mutation, migration, and selection pressures of varying intensities and with populations of various sizes and breeding structures. Ford and Fisher contend that this factor is seldom if ever effective as contrasted with selection, and then only in extremely small and very probably doomed colonies. Its effect is certainly nil in large populations. Wright thinks its greatest effect may be (either alone or in combination with selection and mutation pressure) in causing change in many small isolated breeding groups within a large population, creating diversity between the various groups which is potentially capable of producing a variety of adaptive genotypes which may subsequently spread through inter-group competition.

Genetic Control of the Mutability: Mutations are only random in the sense that they occur without regard to the needs of the organism at a given time, and hence are far more likely to be deleterious than useful. But the kinds of mutation that a gene is capable of producing and the frequencies with which it produces them are determined by the structure of the gene itself and by the whole genetic constitution of the organism.

Mutation rates are higher in some strains of a species than in others, and in some instances this has been traced to modifying genes in particular chromosomes. Genetic variants that enhance or depress mutability are apparently fairly common, and under appropriate circumstances may be selected for or against like others.

Many, and perhaps all, genes may be changed in various ways, producing series of *multiple alleles* at the same locus. The rate of production of different alleles in a given strain of a species usually differs, and the rate of production of a given allele in different strains may also differ. The differences are sometimes due to a difference in the mutating gene itself, and sometimes to the presence or absence of modifying alleles of other genes, which can transform the mutating gene from a more stable to a less stable condition.

Potential Genetic Variability in Populations: Many mutants are recessive to the normal condition, and a "normal" individual may carry one or many recessive mutants in the heterozygous condition. Genetic analysis of wild populations by inbreeding and crossing with genetically known laboratory strains reveals the recessives such as lethals, semilethals, and genes producing visible characters or physiological effects in the homozygotes. Populations of *Drosophila* species prove to carry a profusion of recessive mutants concealed in heterozygous condition. In *Drosophila willistoni*, with three pairs of chromosomes (X, 2nd, and 3rd), the *% of the chromosomes* carrying concealed recessives was as follows: in the 2nd, lethals 29%, semilethals 13%, producing subvital homozygotes, 57%; producing sterility, 31%, slowing development, 32%, producing visible effects, 15%; accelerating development, ±1%; producing "supervital" homozygotes, ±1%. For the 3rd chromosome the figures are different but of the same general magnitude. From these data it can be taken as assured that very few individuals are free of at least one recessive abnormality in their chromosomes. The same is probably true of most populations, although the number of lethals varies markedly from species to species and from different parts of the same species population, as well as from season to season at the same place. The amount of concealed variability is probably controlled in part by the breeding structure of the species or population. Thus in species with haploid males there is no accumulation of lethals, which would be fatal to the males, except when there is a differential in the susceptibility of ♂♂ and ♀♀, or the gene is only lethal in double dose.

Polygenes: There is a great mass of variability stored in populations in the form of minor genetic variants controlled by multiple factors, termed *polygenes*. These give rise to changes less striking than those of the "major" mutants, but ones which affect very many traits. Here belong the subvitals and supervitals, the minor changes in developmental rate, minor variations in morphology, etc., varying in degree of expression from individual to individual as a more or less continuous rather than alternative phenotypic change. *This continuous, or polygenic, variability, is probably the most important in evolution.*

Polygenic inheritance favors storage of potential variability in populations. Thus, if size were controlled by 4 pairs of genes producing cumulative effects, with *A,B,C,D* adding equal increments, then *AAbbCCdd* and *aaBBccDD* will be alike in the phenotypic size; but upon crossing the F_2 generation will show a complete spectrum in size from the maximum produced by *AABBCCDD* to the minimum produced by *aabbccdd*. In such a way, natural populations may carry genes potentially capable of producing numerous and diverse new genotypes, if recombined in segregating hybrid progenies. The storage of potential variability is most efficient in linked polygene complexes carried in particular chromosomes.

The Role of Genetic Variability in Populations: A sexual species has been said *to be "like a sponge"* which absorbs and stores the genetic variability generated by mutation. The variants accumulate as a great store of potential change, carried mostly as a mass of recessive mutants in heterozygous condition. Yet most of the mutations are injurious, producing reduced viability, hereditary diseases, and monstrosities. It seems paradoxical that such a process can serve an evolutionary function. Furthermore, it appears to go against the trend of selection, which, since most of the mutants are injurious, should select strains in which the tendency to mutate is kept at a minimum.

The evolutionary advantage of this situation is that it preserves the plasticity of the species, enabling it to adapt to changing environments. A genotype adapted to one environment will not be fit to survive in another; with change in environment the species must either change or become extinct. Since mutations are not produced to order, only a store of multipotential variability can give a species the capacity to meet new conditions. Mutations which are unfavorable in one environment may be valuable in another; since selection operates not on genes but on phenotypes produced by the entire genotype in relation to environment, a mutation that decreases viability when combined with certain genes may increase it when combined with others in a different genetic background and selective environment. In a changing world, the species most likely to survive is not the one best adapted to present conditions, but the one best armed with potential variation against future changes. Possessing no foresight, selection always tends to suppress variability.

Natural Selection: In a population which is a mixture of genetically distinct types, some of them are likely to produce more surviving progeny than others. Certain genes, gene complexes, and chromosome structures will, then, become more frequent, and others less frequent, in succeeding generations. The gene frequencies, q and (1-q), will, accordingly, become altered.

The relative capacity of carriers of a given genotype to transmit their genes to the gene pool of the following generations constitutes the adaptive value, or the Darwinian fitness, of that genotype. The adaptive value is a statistical concept which epitomizes the reproductive efficiency of a genotype in a certain environment. This value is obviously influenced by the ability of a type to survive. That of a homozygous lethal is obviously zero. But the somatic vigor, viability, of the phenotype is only one of the variables which determine adaptive value. The duration of the reproductive period, number of eggs produced (fecundity), intensity of sexual drive in animals, efficiency of pollination mechanisms in plants, and a great many other factors are likewise important. Natural selection, then, includes anything and everything that interacts with the properties of the organism to determine the adaptive value as defined above. It need not necessarily involve any competition or conflict with other members of its own or other species; under some circumstances the effective selection may be entirely exerted by some element of the physical environment, of the genetic mechanism, or of a social relationship.

Selection Coefficients: The adaptive value of a trait is a continuously varying quantity, and the action of selection on a population is a statistical problem. Suppose that dominant gene A has the frequency q and its recessive allele a the frequency (1-q) in a sexual randomly breeding population. The population will then consist of three genotypes, AA, Aa, and aa, with frequencies respectively of q^2, $2q(1-q)$, and $(1-q)^2$. Let the adaptive values (W) of the dominants, AA and Aa, be equal to unity, and that of the recessive be equal to (1-s). In other words, for every unit of offspring produced by the dominants, the recessives produce (1-s) offspring on the average. The value s is called the selection coefficient.

In a population starting with A and a equal, and with aa having adaptive values (selection coefficients) of 0 (a recessive lethal), 0.4 (a semilethal), 0.9 (subvital), or 1.5 (supervital), the gene frequencies of gene A (originally 0.50) in the next generation can be calculated to be respectively 0.67 (an increase of 17%), 0.58 (8% increase), 0.51 (1% increase) and 0.44 (6% decrease). Because of the change in proportions, the progress of selection, rapid at first while the gene is frequent enough for producing numerous homozygous recessives, rapidly slows.

Interaction of Selection and Mutation: With mutation occurring, the process of selection may be either enhanced or slowed down; if mutation to an allele favored by selection takes place more frequently than away from that allele, the speed of the process is greatly accentuated in its initial stages. After the initial increase, the relative importance of the mutation declines, and further increase has to proceed by selection alone unless the mutation rate is very high. Thus, with an allele *A* mutating to *a* at a rate of 1 in 1,000,000, the change of the gene frequency from q = 0.000,001 to q = 0.000,002 is accomplished in a single generation, while a similar change without mutation requires 321,444 generations for a recessive type with a selective advantage of 0.001.

If the mutation is away from the allele favored by selection, the gene frequency will never reach 0 or 1, and a genetic equilibrium will be established instead. The population will consist of several genotypes which will occur in certain proportions; in other words, it will be more or less genetically polymorphic. The *proportions* of the *genotypes* in the population and of the *genes* in the gene pool *will remain fixed* as long as the mutation rates and the selection coefficient stay constant. Unfavorable recessives will reach equilibrium at a much higher level of occurrence in the population than will equally unfavorable dominants.

Environmental Modification of the Adaptive Values: Genotypes which are frequent in natural populations have reaction norms which have been molded by the evolutionary history through natural selection, and which are so adjusted as to produce adaptively valuable modifications in relation to environmental conditions commonly met by the species. Mutations create genotypes which have not gone through this process of adjustment. The overwhelming majority will be changes for the worse in terms of fitness to the existing environmental norms, but a few may be for the better. Since most mutations have appeared many times in the history of a species, most of those which improve "normal" genotypes have had an opportunity to become established, and those which have failed to become established are probably unfit in normal environments. However, a few of these recurring mutations or their combinations produce phenotypes which happen to be adaptively valuable in some of the environments encountered by the species in space and time. A mutation can be classified as beneficial or harmful only in relation to a particular genetic background and environment. Dobzhansky (1951) cites various instances of "neutral" or "harmful" mutations [judged by their value in "normal" environments] which could be beneficial under changed conditions: a mutation changing the temperature optimum of *Daphnia longispinosa* from 20°C to 25-30°C, which would enable survival in hot springs though it was lethal at 20°C; the mutant *eversae* in *Drosophila funebris*, which is inferior in viability to the wild type at low and high temperatures but superior at 24-25°C; mutant chromosomes in *Drosophila pseudoobscura* which increase or diminish viability according to the gene content of the other chromosomes with which it occurs; and various other examples.

The Effectiveness of Selection in Natural Populations: Responses of population to selection may be rapid when the coefficient of selection is high. Hydrocyanic acid gas fumigation of citrus trees for red scale in California was nearly 100% effective until a resistant strain appeared near Corona in 1914; this strain has since spread. Houseflies in many localities rapidly developed resistance to DDT, based on the selection of DDT-resistant strains which already existed potentially in the stored variability of the species. The same thing is true of many other insects against which DDT was at first thought to be the perfect control, and chlordane and other recently developed insecticides are likewise selecting out chlordane- and other insecticide-resistant pests. An interesting phenomenon is that some of the resistant strains selected by one insecticide prove to have resistant qualities in respect to other and chemically unrelated insecticides. Some of these instances may be due to the selection of individuals having reduced penetrability of the integument to poisons; others, like the DDT-resistance, represent selection of individuals able to break down the poison into harmless metabolic products.

"Reversion" or "deterioriation" of domestic breeds of animals and plants escaped from cultivation is rapid, and is probably the result of adverse selection in the wild against the traits for which man selects.

Correlated Responses to Selection: The differences observed between species and races of organisms very often involve characters the adaptive value of which is not evident. Some of these doubtless are adaptive; others seem to be neutral or sometimes even disadvantageous. Such characters are probably often the incidental accompaniments of pleiotropic genes which contribute to the adaptive value of the integrated genotype of which they are a part. As Dobzhansky points out, perfection of certain organs may confer so great an advantage on a species by making it the undisputed possessor of an ecological niche that other organs may undergo rudimentation. Thus, the species of Fregata (man-o'-war birds) are among the most common and successful of tropical marine birds; they are unsurpassed fliers, but are awkward out of the air because of their nearly rudimentary legs. When, as occasionally happens, they lose their balance while taking off and slide down among the branches of the trees where they roost, they die for inability to climb out to some jumping-off place; and if they fall in water they can neither swim nor rise into the air.

In ontogeny, the interaction of the genes results in integrated development, and a genotype adapted to produce such a norm of response, buffered against ordinary environmental variations, is the result of selection. In such a system, a change in one organ produced by selection is likely to result in correlated changes in others, which may or may not be adaptive. Furthermore, establishment of a genetic change in one organ may establish a selective premium on genes affecting other parts of the body in order to restore a balanced genotype. Thus Rensch has found that changes in size in both vertebrates and invertebrates are accompanied by diverse and often not evidently adaptive alterations in many features of the body——in cell size and cell numbers in various organs, differences in eye structure, and differences in relative sizes of some endocrine glands, in brain size of insects relative to size of head capsule, in spatial arrangement of thoracic muscles, in behavior and learning ability, and in various other items.

Many of the long-term trends shown in the paleontological record of phylogeny are probably the result of continued selection for some adaptively useful trait, such as progressively increasing body size, with which are correlated heterogonic and other effects which have no adaptive significance in themselves, but which are an incidental result of the "orthoselection" for the adaptive trait.

Selection for traits controlled by polygenes may lead to unexpected results; thus selection for high and low bristle numbers on abdominal sternites in Drosophila melanogaster resulted in various lines in sterility, abnormal number of spermathecae in the ♀♀, altered body pigmentation, altered eye form, and abnormal mating behavior. These results are explained as follows: The traits are determined by complexes of genes with small individual effects (polygenes), which are scattered at random in the chromosomes, and it often happens that polygenes which, for example, lower bristle number lie in the same chromosomes with polygenes which influence fertility, or spermatheca number, or mating behavior. A selection for low bristle number brings, therefore, unexpected correlated changes in these other traits which are not physiologically correlated with bristles.

In general, since natural selection operates on the phenotype, which is the product of the whole integrated genotype, it augments the adaptive value of the genotype as a whole; therefore neutral and even slightly deleterious traits may be promoted by selection if they happen to be connected with useful ones.

Cryptic and Warning Coloration and Resemblance; Mimicry; Regional Patterns. Inconspicuousness as a protection against destruction by predators is obviously an adaptive advantage, and is widespread in the animal kingdom as a result of selection. For animals which are slow-moving or spend much time at rest, resemblance to the general environment through color and pattern or form of body or both is common. Sometimes the resemblance to particular parts of the environment is amazingly close and detailed—to such a degree that many naturalists have in the past refused to concede that such resemblance could have been produced by selection of fortuitous variations. Examples are the leaf-resembling butterflies, walking-sticks and katydids, with a full complement of leaf-veins, marginal dentations, green, brown, or fungous-mottled colors, simulated feeding injuries, etc. All these insects behave in a fashion that makes the resemblance effective while they are at rest.

Many bizarrely formed and brightly colored animals which appear very conspicuous as specimens are actually inconspicuous in the natural habitat; this is true of many coral-reef fishes, many insects, and even some large mammals and birds. In animals which are in movement much of the time concealment is impossible, but conspicuousness may be reduced by countershading, or a predator may be confused by ruptive patterns that tend to break the outline, or by "eye-catchers" such as the actively vibrating white tips of the antennae of otherwise soberly colored insects. The variety of cryptic and confusing adaptations is endless, and no field naturalist can doubt their effectiveness or question, as some laboratory experimentalists have done, whether they are not purely coincidental.

Some animals are avoided by predators for one reason or another—powerful weapons such as poison fangs and stings, irritating skin secretions, offensive odor or taste, defensive structures such as quills, stinging hairs, or surface armor, etc. Predators are not born with the knowledge of what to avoid, but must learn. Often this involves the injury or death of the teacher. Anything that will increase the ability of the predator to distinguish and avoid the protected species will be of selective advantage to the latter, and this has led to the development of many forms of <u>warning</u> coloration and behavior—the bright colors and distinctive patterns of "protected" butterflies, the "flashing" of colored structures such as wings and inflatable skin pouches, the threatening attitudes of scorpions, spiders, snakes, and many higher vertebrates, etc. Some supposed examples of warning coloration, however, may not be such; the strikingly contrasted banding of coral snakes is claimed by some to be cryptic and ruptive in their normal habitat, and by others to be meaningless because of the nocturnal habits of the snakes and of their presumed predators. Others point to the fact that the chief predators of these snakes might be diurnal mammals turning over logs, and that the existence of "mimics" establishes a presumption that the pattern is a warning one.

Since there is loss to predators by protected species through the learning process, there would be a selective advantage in shared coloration and patterns extending over several or many protected species, among which the learning losses would be divided. This is the apparent explanation (plus a certain amount of parallelism in related groups of species) of the phenomenon called <u>Müllerian mimicry</u> - resemblance between protected species, related and unrelated, in a given region. This is well illustrated in many parts of the tropics by butterflies and other insects. There would also be an advantage to any unprotected species if it resembled a protected species or Müllerian group of such species, provided the unprotected species were not very numerous in proportion to the protected ones. It would share in their immunity, cheating the predators by its resemblance. This is called <u>Batesian mimicry</u> and is also common in tropical butterflies; it was first described in detail by Bates on the basis of his observations in the Amazon valley.

In one lecture examples were shown of the regional resemblances that tend to exist among numerous related and unrelated insects which do not appear to be protected but which live together in particular types of habitat. Thus, in the Philippines many wasps, flies, beetles, and some other insects will share a common pattern in the dense forests; another pattern will be prevalent in the grassy savannas. Related species or subspecies to some of those in these regional pattern groups will, in other regions, belong to other regional groups of quite different coloration. Thus in the United States, various species and subspecies of wasps go to make up a western group of prevailingly yellow coloration, while other subspecies of the same species, together with another assemblage of different species, has a prevailingly black color in the eastern United States. In general, each major habitat in each major region is likely to show a regional pattern among its day-flying insects of about the same size. The factors responsible for this condition are unknown, but there seems no doubt that it is the result of selection acting on some sort of advantage conferred by this common resemblance. Perhaps the advantage is no more than that it fuses all the diverse species sharing the pattern into an undifferentiated crowd, in which the most abundant (and most able to support predation) species at a given time carries most of the loss, while on another occasion it may be another species. Such an adjusted ecological system might be compared to an adjusted and buffered gene system.

The theory of protective coloration now rests on a firm observational basis, and although the conclusion that it results from natural selection is largely inferential, there is some experimental evidence (fishes, mammals, insects) that supports it. McAtee's (1932) conclusion, that because protectively or warningly colored insects were often found in birds' stomachs in proportions, as he thought, equal to the relative abundance of these and other insects in the birds' habitats, the whole idea could be dismissed as a myth, is an example of fallacious reasoning. It assumes, first, that only absolute immunity from attacks by predators can make natural selection effective, and second, that it is possible to determine on present knowledge what the relative abundance of the various insects actually is.

The Origin of Dominance and the Stabilizing Selection. From the standpoint of populations, the fact that among the genes normally present in the population certain alleles are usually dominant over others is important, because this permits the accumulation of variability in sexually reproducing populations. The dominant genes protect the recessives, in the sense that most recessives are deleterious in the homozygous state, but not in the heterozygous, as was stated above. The dominance of alleles which, in coordination with the other genes, produce an adaptive norm of response to the normal range of environmental conditions is therefore advantageous on two counts—stability of the norm of the species, and provision for retention of potential variability.

Most wild type alleles in Drosophila are dominant over mutant alleles which have arisen in the laboratory; when several such alleles are known for a single locus they do not usually exhibit dominance in heterozygotes carrying only such mutant alleles. The existence and degree of dominance of one allele over another have been found to be governed by the structure of the genotype as a whole. Thus alleles which behave as simple dominants in one genetic environment may show only partial or no dominance in another. There are apparently two chief causes for variation in dominance. (1) There may be several wild-type alleles at a locus, some more and some less completely dominant over recessive mutant alleles at the same locus. (2) The dominance of the "normal" over mutant alleles may be bolstered by a system of modifying genes at other loci. Such dominance modifiers are known in cotton, Drosophila, poultry, mice, and other forms. Some of them affect the expression of genes only in heterozygotes, others in both heterozygotes and homozygotes. These modifiers often have various effects of their own, aside from their influence on the expression of other genes. This is to say that dominance modifiers are not a special class of genes subsidiary to others, but merely pleiotropic genes which influence, among other things, the expression of certain alleles at other loci.

Dominance can arise, according to present theory, either through selection of modifying genes that tend to make mutant heterozygotes resemble the wild type, or by selection at each locus of potent alleles able to suppress in the heterozygotes the deleterious effects of most mutant alleles which arise at that locus. Whether by one or the other, the origin of dominance must be considered as a necessary step in the establishment of an integrated system of physiological reactions controlling development. Under normal environmental conditions the end result of development is the normal, or "wild-type" phenotypic condition. The reaction norms of the "wild" genotypes are such that the usual range of environmental variations evokes adaptive modifications, and insures the development of the necessary organs and traits. The development is buffered against environmental shocks by the ability of the genotype to produce modifications. The formation in evolution of genotypes with safely buffered reaction norms is due, according to Schmalhausen, to a form of natural selection which he calls stabilizing selection, and which he contrasts with dynamic selection which acts to produce genotypes adapted to new environments or to new ecological opportunities.

The genes guide development through production of enzymes; each gene must yield its normal quota; threshold reactions may frequently be involved, so that greatly increasing the effectiveness of a gene may result in no appreciable modification of the normal course of development, but having it may lead to retardation or arrest of the whole chain of reactions. Under such conditions, "wild-type" alleles with a "factor of safety" well above the minimum, will be advantageous; a mutation curtailing the activity of such a gene will, then, be recessive to the normal allele. Stabilizing selection favors alleles dominant over less effective mutants.

Genetic Polymorphism in Populations: In sexually reproducing, cross-fertilizing organisms, the things that exist in space and time are individuals and populations. Each individual carries a constellation of genes which is in all probability unique. Each population has a gene pool, from which the genes of the individuals spring and to which they are returned in the offspring. Gene frequencies and variances, rather than averages, characterize Mendelian populations. Morphologically considered, natural populations consist of somewhat variable normal, or wild-type, individuals, among which are scattered aberrant specimens, which owe their origin to mutation. Genetical analysis shows that the wild-type is a fiction like the morphotype of classical taxonomy. "Normal" individuals are actually a heterogeneous collection of genotypes, the common property of which is that they possess a tolerable adaptedness to the prevailing environments. When the heterogeneity happens to be striking to the eye in the phenotypes, or easily detectable by some method, it is referred to as polymorphism. If there are only two different phenotypic expressions the population or species is said to be dimorphic (sexual dimorphism is the commonest example but this is seldom what is meant when the term is used, sexual dimorphism being usually assumed by systematists and some other additional phenotypic difference forming the basis of the designation). All Mendelian populations are genetically polymorphic in some degree.

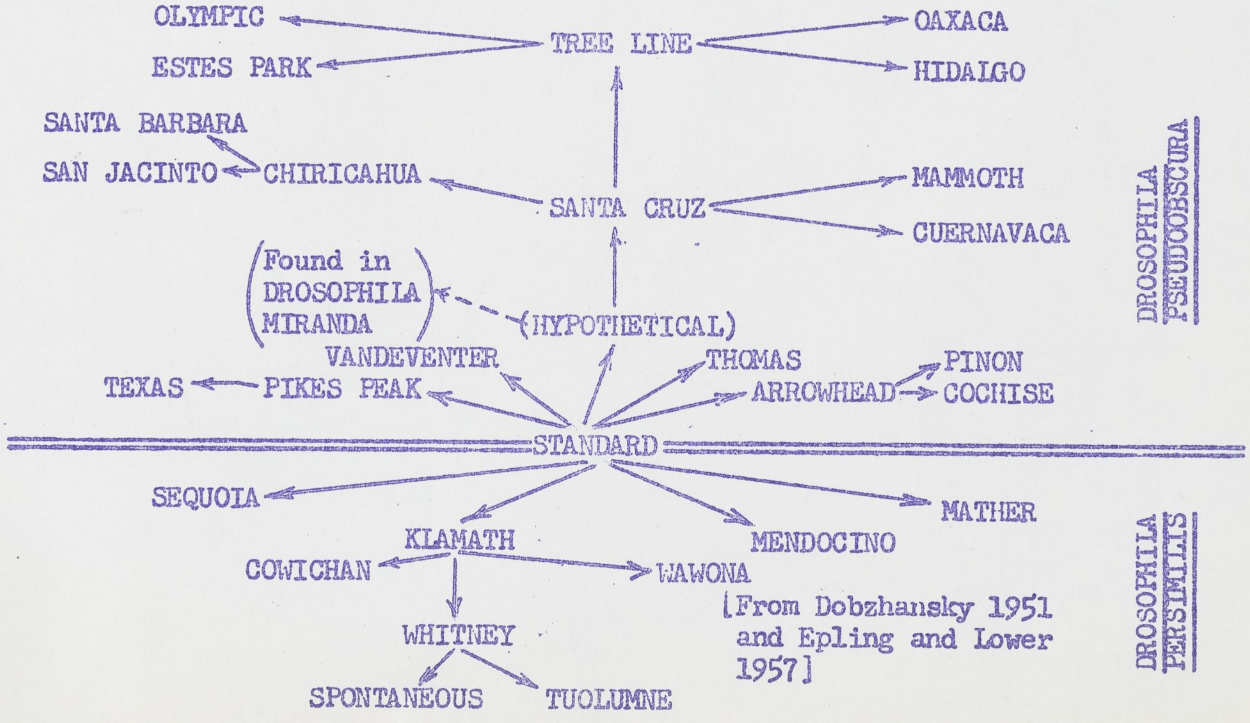
Gause's Principle: Two or more forms with identical ecological requirements cannot coexist indefinitely in the same environment, because one of them will in all likelihood be more efficient than the other(s), and will eventually outbreed and supplant its competitors. If the adaptive value of one form is 1, and that of the other 1-s, then, no matter how small is s, the less well adapted form will in time be eliminated. Although there may be apparent exceptions under special circumstances this principle holds in general.

Two species with ecological requirements of the same kind (herbivores, for example) can be sympatric only if the environment in a territory they inhabit is heterogeneous. The heterogeneity may be spatial or temporal. Two species, A and B, may be sympatric if they differ from one another in some aspect of their utilization of the habitat. A may depend more on one food, B on another; A may be better adapted than B in summer, B than A in winter; A may prefer the riffles of a stream, B the pools. Environments are always heterogeneous, though some are more so than others. This heterogeneity permits the development of sympatric diversity of organisms and hence of interacting ecological communities.

Polymorphism within a species (or any other kind of diversity of sympatric forms) increases the efficiency with which the species exploits the resources of the environment. The phenotypic products of a single genotype would all be alike, and no matter how much modification the genotype is capable of producing, it could hardly function with maximal efficiency in all environments. Hence, natural selection has preserved a variety of genotypes within the species population, more or less specialized to make the organism efficient in a certain range of the existing environments.

Chromosomal Polymorphism in Drosophila. By studying the various types of Drosophila chromosomes produced by inversion of sections of the chromosomes, and made accessible for detailed examination in the giant polytene chromosomes of the salivary glands of the larvae, a very complete understanding of polymorphism as it occurs in this genus has been obtained. It is known in natural populations of about 50 species of Drosophila. The inversions are easily recognized by the loops and other distortions formed by the pairing of the chromosomes of inversion heterozygotes. The giant chromosomes are also marked with stainable discs which may or may not correspond to genes, but which form a constant pattern which reflects the gene arrangement in the chromosomes. Because the inversions overlap, it has been possible to determine the sequence in which they must have arisen, to give an inversion history or chromosome arrangement phylogeny within single species and groups of closely related species.

In the two closely allied species, Drosophila pseudoobscura and D. persimilis, which are perhaps the best known of all from this standpoint, most natural populations are mixtures of individuals with different gene arrangements in their chromosomes. The gene arrangement is especially variable in one of the 5 chromosome pairs which these species have – the chromosomes of the third pair. Nineteen different gene arrangements are known in the 3rd chromosome of pseudoobscura and ten in persimilis; one of these, called Standard, is the same in both species. All must have arisen from one another through inversions of some sections of the chromosome, and nearly all are related to one another as overlapping inversions, making it possible to construct the following phylogenetic chart. Each arrangement is given the name of the geographic locality in which it was first discovered. Some of the arrangements (Santa Cruz, Tree Line) had been postulated theoretically as necessary "Missing links", and were subsequently found; one (Hypothetical) remains hypothetical so far as these two species are concerned, but what is essentially the same arrangement has been found in a related species, Drosophila miranda.



[From Dobzhansky 1951 and Epling and Lower 1957]

None of the gene arrangements of the above diagram occurs over the whole of the range of either species, and no natural population of either species contains all the arrangements known in that species. In some localities as many as 8 occur together, and in nature both inversion homozygotes (flies with different arrangements in the two chromosomes of the 3rd pair) are encountered. The chromosomal inversions thus give rise to a remarkable polymorphism in the populations with respect to chromosome morphology and presumably with respect also to manifestations of the genetic differences.

Laboratory experiments and field observations have shown that:

(1) There is a seasonal change in abundance in some of the arrangements.
(2) There are north-south and altitudinal clines in abundance of some of the arrangements.
(3) There are differences between local populations separated by only short distances.
(4) The system of frequencies in the population of Drosophila pseudoobscura in the San Jacinto Mountains, California, has had a certain stability over 100 generations (1939-1956), but each arrangement has fluctuated more or less independently of others, with several peaks and lows, over this period.
(5) The same inversions have arisen independently more than once in the phylogeny of the inversion system.
(6) Each gene arrangement is preserved by suppression of crossing-over in the heterozygotes, and this permits development of genetically different gene arrangements, each of which apparently makes a different contribution to the adaptedness of the populations in which it occurs.
(7) The adaptedness of the population appears to depend not simply on the aggregate of arrangements present, but also on their interchromosomal effects.

Balanced adaptive polymorphism: The essentials of the now well-established theory of balanced polymorphism are illustrated by the following example from Dobzhansky (1951): Suppose that in a population of Drosophila pseudoobscura a fraction, q, of the gametes carry the Standard (ST), and (1-q) the Chiricahua (CH) gene arrangement in the 3rd chromosomes. Suppose, further, that the flies mate at random with respect to the gene arrangement in their chromosomes, that the adaptive value of the inversion heterozygotes (ST/CH) is unity, and that the homozygotes (ST/ST) and (CH/CH) have, respectively, adaptive values of $1-s_1$ and $1-s_2$ respectively. The frequencies of the chromosomal types before and after selection will, according to the binomial square rule, be as follows:

GENOTYPE	ST/ST	ST/CH	CH/CH	TOTAL POPULATION
Adaptive Value (W)	1_2-s_1	1	$1 - s_2$	W
Initial frequency	q	2q(1-q)	(1-q)	1
Frequency after the selection	$q^2(1 - s_1)$	$2q(1-q)$	$(1-q)^2(1-s_2)$	$1-s_1q^2-s_2(1-q)^2$

The rate of change, delta q, of the frequency of ST in the population in one generation will be:

$$\text{delta } q = \frac{q(1-q)[s_2(1-q)-s_1q]}{1 - s_1q^2 - s_2(1-q)^2}$$

And, making delta q = 0 and solving for q, we obtain: $q = s_2/(s_1 + s_2)$. This means that q will not become either 0 or 1, and that in consequence natural selection will not eliminate either ST or CH chromosomes from the population, but will establish an equilibrium at which the population will be polymorphic and will contain the two kinds of chromosomes in the gene pool, with frequencies dependent upon the selection coefficients, s_1 and s_2. The results of experiment and observation bear out this theory, and show that under circumstances such as varying temperature, humidity, kind and amount of food, degree of crowding, etc., the values of s_1 and s_2 change, with corresponding changes in q.

Experiments have also shown that in Drosophila pseudoobscura and some other species, heterozygotes in which the two chromosomes came from the same or closely adjacent populations are superior in adaptive value to homozygotes (that is, show heterosis) as demonstrated by differentially greater survival, while those having chromosomes derived from geographically distant populations show no heterosis or are inferior in survival to both homozygotes. This indicates that the heterosis found in most natural populations is a product of genetic integration (adaptation) brought about by selection, a process which has not had an opportunity to operate on the hybrids produced by laboratory matings of flies from geographically separated stocks.

Brncic (1954) found heterosis in F_1 progeny of D. pseudoobscura from widely separated localities, all homozygous for Arrowhead, but in the F_2 and F_3 generations this disappeared, and viability was even inferior to that of the parents. This is attributed to crossing-over, destroying the integrated gene-assemblages of the parent stocks, and is further evidence of the role of the inversion system in maintaining particular gene-assemblages intact by preventing crossing-over.

The gene-complexes responsible for this high fitness or heterosis have been called by Darlington and Mather (1949) supergenes. Mechanisms for preserving them similar to those found in Drosophila are known in various genera of plants, but are apparently rare in animals; but other genetic mechanisms than inversion are capable of producing the same result and are probably widespread in both animals and plants.

Adaptive polymorphism and ecological opportunity: The hypothesis that adaptively polymorphis populations should in general be more efficient in the exploitation of ecological opportunities of an environment than genetically uniform ones, and conversely, that populations that occupy many habitats in a given territory are more genetically diversified than those which are restricted or specialized in their habitat choice, is borne out by observation and experiment in Drosophila and in mosquitoes.

Vavilov (1926) has suggested that genetic variability in populations is likely to be greatest in the region where the species arose and from which it has spread; there it has had most time to develop adaptive polymorphism, while on the peripheries it is likely to have a toehold in only a few ecological niches and to show limited adaptive variability. This hypothesis suggests one of Adams' criteria for determining "center of origin", and also Matthew's "center-fire" theory of distribution.

2. SPECIATION (EVOLUTIONARY CHANGE WITH SPLITTING)

It is evident that a population may change through the operation of mutation, recombination, and selection, while remaining a single population. If new species are to arise, it is necessary that differences develop between different parts of the population, and that these different parts diverge along separate evolutionary paths. In bisexual panmictic populations, and others approximating these conditions, the formation of two new species populations from a single ancestral one is completed when effective reproductive isolation is established between them. This is the concept of species implicit in the thinking of most zoologists about evolutionary systematics, because the great majority of species of multicellular animals are thus differentiated. It may, however, be regarded as a special case consequent on a particular mode of reproduction; a broader and more elastic species concept, or more than one kind of species, is required to cover all the varieties of situations encountered among plants and animals. Various species concepts and definitions will be considered after isolating mechanisms and hybridization have been treated.

A. Isolating Mechanisms. Dobzhansky (1951) has classified the principal isolating mechanisms as follows:

External Barriers

I. Geographic or Spatial Isolation. The populations occur in different territories, either within a continuously inhabited area, or separated by distributional gaps.

II. Reproductive Isolation. The gene exchange between species is restricted or suppressed owing to genotypically conditioned differences between their populations.

Barriers between the Parental Species

- a. Ecological Isolation. Representatives of the populations occur in different habitats in the same general region.
- b. Seasonal or Temporal Isolation. Mating or flowering periods occur at different seasons.
- c. Sexual, Psychological, or Ethological Isolation. Absence or weakness of mutual attraction between males and females of different species, due to any incongruity in behavior patterns preliminary to mating or to absence of some specific stimulus.
- d. Mechanical Isolation. In animals, inability to mate owing to differences in size, or non-correspondence of the male and female genitalia; in plants, differences in floral structures which prevent the formation of hybrids. Authentic instances of such isolation between closely related species are few.

Internal Barriers

- e. Gametic or Gametophytic Isolation. Spermatozoa, or pollen tubes, of one species are not attracted to the eggs or ovules, or are poorly viable in the sexual ducts or tissues of another species.

Barriers in the Hybrids

- f. Hybrid Inviability. The hybrid zygotes are inviable, or adaptively inferior to those of the two parental species.
- g. Hybrid Sterility. The hybrids fail to produce a normal complement of functional sex cells.
- h. Hybrid Breakdown. Inviability, or adaptive inferiority, of all or a part of the F_2 generation or of backcross hybrids.

Geographic isolation is on a different plane from all the reproductive isolating mechanisms, because it is independent of any genetic differences between the populations, while reproductive isolating mechanisms are necessarily genetic. Geographically isolated populations are also often reproductively isolated; but the fact that they may have become genetically distinct does not guarantee that they will have become reproductively isolated as well. Reproductive isolation between allopatric populations may develop incidentally to evolutionary divergence; between sympatric populations it is (in bisexual animal species) an essential condition for the existence of separate species, and a consequence of selection in its favor.

The Formation of Races: In a Mendelian population, or system of individuals united by mating and parentage bonds, the individuals are genetically diverse. Some of the genotypes are inadaptive products of the mutation process, which will be eliminated by natural selection; others are optimal for certain environments. If those environments recur regularly in the territory occupied by the organism, the adaptive combinations become normal and lasting components of the population and the species. Some of these genotypes occur together, sympatrically, while others are allopatric and live in different territories. Dobzhansky (1951) defines as sympatric those organisms which occur within the average distance intervening between the points in space at which an individual and its offspring are born, and as allopatric those which occur at greater distances.

Both sympatric and allopatric organisms encounter a variety of environments. Adaptation to these in sympatric members of populations gives rise to the intrapopulational polymorphism already treated. Adaptation to different environments of allopatric populations by genotypic differentiation gives rise to races, which, according to their size, degree of phenotypic distinctness, and relations to one another, as well as the conventions of classification prevailing in the particular group, may be called local forms or varieties, geographic races, or subspecies. If they occur throughout a common territory but with areal segregation by habitat they are often called ecotypes or ecological races. The great majority of geographic races, however, are adaptively adjusted to their environments, so that the distinction between them and ecotypes is merely whether they are geographically separated on a macro or micro scale; the term ecotype is therefore diminishingly useful.

Polymorphism and racial differentiation both rest upon the existence of gene alleles and chromosomal variants, and arise mainly through natural selection acting on the products of mutation. But in sympatric polymorphism the variant individuals are members of the same population; they interbreed, and their genotypes are formed and dissolved by gene segregation and recombination within the same gene pool. With races, on the other hand, the gene exchange between the allopatric populations is always more or less limited and may be altogether absent. Nevertheless the two phenomena are related; two geographic races may be characterized by differences in the proportions of gene arrangements common to both, as is true of the chromosomal races found in Drosophila pseudoobscura and other species. These races are characterized, not by being made up of individuals having exclusively one or another of the inversion arrangements possible in the chromosomes, but by differing combinations of arrangements in differing proportions in the gene pool. The populations so differentiated may form clinal chains in regions of gradual environmental change, or be sharply separated, as are those on either side of the Sierra Nevada mountain range.

Some racial variation is the result of differences in the ratios of alternative alleles at a single locus, as in the black and gray forms of the hamster in southwestern Russia, cited by Dobzhansky (1951). More often they are polygenic in nature and show various blendings in interracial crosses, with the progeny exhibiting about as wide a range of variability as the parents and including some individuals phenotypically indistinguishable from the parents, and with backcrosses to the ancestral races causing shifts of the mean condition in the direction of the parents.

The evidence for the adaptiveness of most geographic variation is somewhat clearer in plants than in animals, but has been demonstrated in enough instances, and is so reasonable a supposition, that it is now generally taken as presumptive in all instances. It is apparently the basis for the relations of populations to geographic distribution that are summed up in the so-called geographical rules, among which are the following:

(1) Gloger's rule, that races of birds, mammals (and other animals) inhabiting warm and humid regions are more darkly pigmented than are those of cooler and drier regions;
(2) A related rule that in insects pigmentation is darkest in humid and cool regions;

(3) In homoiothermal vertebrates races of cooler climates are larger than those of warmer climates (Bergmann's rule);
(4) Allen's rule, that length of appendages in warm-blooded animals diminishes from warmer to cooler regions;
(5) Rensch's rule, that birds with narrower and more pointed wings tend to occur in colder, and those with broader wings in warmer, climates, etc.

These rules are evidently of very unequal scope; the validity of the relationship expressed is not always sufficiently established; and the selective value of the changes is more often assumed than demonstrated. Some of the rules have recently been attacked on these and other grounds; but there remains a large residue of fact that most zoologists believe to be an expression of adaptive value.

Populations which are divided into more or less isolated demes with limited effective population sizes will tend to break up into more or less numerous genetically differentiated microgeographic races, of which a great many examples are known. There is a sharp difference between two schools of thought with reference to the importance of genetic drift in producing such races. Wright and others, among whom are Epling and Dobzhansky, have held that drift is often involved, and that the differences between the races are probably often not of adaptive significance. On the other hand, Fisher, Ford, Dowdeswell and Sheppard believe that most if not all differentiation of local populations is the result of selection. They point to the requirement of very small effective population size for the occurrence of drift at a significant rate, to the fact that many apparently non-adaptive characters are the incidental accompaniments of the selection of pleiotropic genes with other effects which are adaptive, and to the further fact that some supposedly non-adaptive traits prove to be adaptive when fully understood. The trend of the evidence and belief today seems to be to minimize drift and maximize selection as causes of local racial differentiation. (For statements of the opposing views, see: (1) S. Wright, 1951, Fisher and Ford on "The Sewall Wright Effect." Amer. Scientist, 39: 452-479; and (2) Sheppard, P. M., 1954, Evolution in Bisexually Reproducing Animals. pp. 201-218, in: Evolution as a Process, ed. by Huxley, Hardy & Ford, Allen & Unwin, London.

Races are populations, not assemblages of individuals showing certain characters. For this reason, it will often be impossible in practice as well as in theory to assign a particular individual to some race, without knowledge of what population the individual was a part of. An individual related by parentage to one race becomes by migration a member of another race to the gene pool of which it contributes. An individual phenotypically typical of one race may actually be a member of another race in which both its genotype and phenotype may be rare variants.

Race formation begins when the frequency of a certain gene or genes becomes slightly different in one part of a population than it is in other parts. If the differentiation proceeds, most or all the individuals of one race may come to possess certain genes which those of the other race(s) do not. If mechanisms which prevent interbreeding of the races develop, the originally continuous Mendelian population becomes divided, and when this process is complete separate species have been formed. The degree of "concreteness" or reality of a race depends upon the stage it has reached in this process.

The Role of Isolation: The genotypic complexes which represent species or races are genetically integrated and adaptively adjusted to the environments occupied by the species or races. They represent only a few out of multitudes of possible genetic combinations, nearly all of which would be adaptively inferior to the existing ones that have been put together through the agency of selection. Unlimited interbreeding of distinct species would submerge the harmonious gene combinations in a mass of recombinations. Some of these might be as good or better than the present ones, but the chances are greatly against it, and the result would be a vast wastage of individuals as a result of enormously increased adverse selection. Isolation is a device which insures protection of harmonious gene systems created by natural selection against disintegration through hybridization. Without it the ravages of natural selection would be too great. But too early and too rigid isolation may hinder the development of diversified and buffered genotypes capable of accommodation to varying conditions, and thus by limiting the organism to too narrow a range of environment and too specialized an existence may lead to extinction. As Dobzhansky states: (1) Favorable conditions for progressive evolution (improved adaptability) are created when a certain balance is struck; (2) Isolation is necessary, but it must not come too soon.

The Origin of Reproductive Isolation: Genetic situations which could serve as the material for development of isolating mechanisms have been demonstrated in natural populations. Among these are the following:

(1) Some strains of species X carry a dominant gene A which produces no visible effect in that species, but is lethal in crosses with species Y. Strains of species X homozygous for aa cross freely with species Y; strains of species X carrying gene A produce with species Y no offspring when the X parent was AA, 50% viable offspring when the X parent was Aa.

(2) Strains of species X, crossed to strains of species Y, produce a low-viability F_1 which rarely gives rise to an F_2. This results from the presense in these strains of complementary alleles or genes without visible effect except when present together. Other strains produce healthy hybrids. The strains in which these alleles are present occur in the region of overlap of the two species, and are almost entirely absent from the regions where only one of the species is found

(3) In species X there is a sex-linked gene which produces no visible effects but which in crosses with species Y acts as a dominant semi-lethal in the female hybrids.

(4) In Drosophila pseudoobscura and D. persimilis (and other species) males have different courtship patterns and mating success is determined by female preference; this preference for males of one or the other species is determined by a polygene complex, the constituent genes of which are scattered in apparently all chromosomes.

(5) Dominant genes for various pigment-cell distributions in the platyfish become lethal in crosses with the swordtail through causing cutaneous melanomas (cancers).

From a multitude of similar possibilities, isolating mechanisms have developed, probably through a process which may be generalized as the building up of systems of complementary genes. Assume that a population has the genetic constitution aabb, where a and b are single genes or groups of genes, and that this population is broken up into two allopatric, geographically isolated parts. In one part, a mutates to A and a local race AAbb is formed. In the other part, b mutates to B, giving rise to a race aaBB. Since individuals of theconstitutions aabb, Aabb, and AAbb interbreed freely, there is no difficulty in establishing in the population the gene A. The same is true for the gene or genes B, since aabb, aabB, and aaBB interbreed freely. But the cross AAbb × aaBB is difficult or impossible, because the interaction of A and B produces one of the various reproductive isolating mechanisms. If the carriers of the genotypes AAbb and aaBB surmount the extrinsic barriers separating them, they are now able to become sympatric, since interbreeding is no longer possible. In summary: Reproductive Isolation between pairs of sexually reproducing and cross-fertilizing species is produced usually by complementary gene complexes carried by the species concerned;

the minimum number of genes that can form a workable isolating mechanism is two. *Hybrid inviability* and *hybrid sterility* are caused by complementary genes or genetic conditions that act as dominants, and hence manifest themselves in heterozygotes.

The Theory of Allopatric Speciation. The essential points of this theory are two: (1) In sexual and cross-fertilizing populations the differentiation of races is due to modification of gene frequencies in allopatric populations by natural selection (aided to an undetermined amount by genetic drift, and quite probably by change of genetic environment following isolation). The environment is, in the final analysis, the directing agent, but it acts through interaction of the genetic mechanisms just named. (2) Allopatric populations attain the status of species by becoming reproductively isolated. Species may or may not become partly or wholly sympatric after the reproductive isolation has appeared.

Most zoologists are convinced that this is the normal course of speciation for bisexual cross-fertilizing animals, and that sympatric speciation, if it occurs at all, must be extremely rare, dependent upon very special circumstances, and not one of the important evolutionary processes. Not everyone agrees with this view, however, and the possibility of sympatric speciation is discussed in a subsequent paragraph.

In a recent, stimulating, and in part quite highly speculative paper ("Speciation in Animals," Australian Jour. Sci., 22 (1): 32-39, 1959), M. J. D. White reviews the case for allopatric speciation in the light of his studies in cytogenetics, and criticizes both the concept of sympatric speciation and some of the current hypotheses about the way in which allopatric speciation takes place. "In general, geographic isolation seems to be a prerequisite for the development of genetic isolating mechanisms [which is what we mean by speciation].... This means that speciation is seldom or never sympatric, that ecological separation of otherwise sympatric populations is hardly ever complete enough to lead to speciation, and that there is no reason to believe a highly polymorphic population is likely to split into a number of species.... We may distinguish between two extreme models of the speciation process" somewhere between which most instances of speciation probably fall:

I. *Splitting*. A large and originally continuous population becomes split into two geographically isolated populations by some geographic barrier. If this barrier is maintained for long enough, the two populations will become sufficiently different genetically that if they are brought together again, either naturally or in the laboratory, it will be found that genetic isolating mechanisms exist. In this model one cannot speak of one form as the "original" species and the other as the "new" species.

II. *Peripheral budding*. From a species occupying a large continuous range a small population lying on the periphery of the range is segregated off as an incipient species. Because every peripheral population faces novel ecological challenges which are lacking in the case of central populations, we must expect that genetic change will be more rapid in the initially small population that is "budded off" at the periphery. Other reasons for "genetic revolutions" have been discussed by Mayr (1954 - "Change of Genetic Environment and Evolution", in: Huxley et al., Evolution as a Process), who calls the striking deviations in morphological or ecological features which often distinguish such populations from the parental ones *typostrophic variation*.

Examples of the first model would be separation of a large island into two by submergence, or southward displacement of a northern species during a glacial maximum under conditions such that the originally continuous population is divided into eastern and western populations by an intervening north-south mountain chain or other barrier. In this model both parts of the specieshave a large breeding population at all times.

Most speciation probably takes place under conditions more closely approximating those of the second model. Several lines of direct and theoretical evidence support this conclusion.

"Budding off"

1. *Evidence from distribution*. Considering especially those groups of animals which are *less vagile* than birds, mammals and strong-flying insects, and less subject to accidental dispersal by air and water currents and other means than are many fresh-water and marine forms and some minute terrestrial animals, one encounters various patterns of distribution of related species. One of these patterns recurs with such frequency and in so many unrelated groups (small mammals, reptiles and amphibians, snails, flightless grasshoppers, crickets and katydids, ground beetles and crayfishes, to name only a few) that one must assume it to be the product of a frequently repeated evolutionary process leading to speciation. In a group of closely related species one will commonly be found to have a much more extended range than the others, which lie about the periphery of that range and are often isolated by some form of barrier from it. This observation conforms with but is not entirely comprehended by the so-called *Jordan's law* which states that the most closely allied forms occur not in the *same* nor in *distant* regions but in adjacent areas separated by some kind of barrier. Many examples could be cited; the following statement about the camel-crickets of the genus *Ceuthophilus*, written in 1936 (Hubbell, Monogr. Revision of *Ceuthophilus*) typifies *the pattern*: "In *Ceuthophilus* speciation seems usually to *have occurred* by the differentiation in *peripheral* areas or environments of specialized offshoots from a more generalized parent species. [In groups of related species] it is almost always the most generalized species which is most widespread, while the more specialized related forms occur about the peripheries or [in special restricted environments] within the limits of its range." This generalization holds for every one of the species groups in which the distribution has been well established, and for 14 pairs or triplets of geminate species. White's studies of grasshopper genera of the western United States and Australia demonstrate that this is the predominant pattern among the flightless or sedentary groups.

2. *Theoretical considerations*. The "budding" speciation model involves a stage in *which the "new"* species passes through a "bottleneck" in which its population size is small. The importance of this stage is emphasized by the following considerations drawn from population dynamics and relating to the "biological cost" of natural selection. This cost may be considered as a *load* or drain on the species.

a. *The cost of selection*. The basic evolutionary unit is the replacement of one *allele in a population* by another. If accomplished by selective mortality of immature individuals, each such elimination of an allele (or fixation of its alternative if only two are involved) has been shown to cause a number of deaths equal to between 10 and 100 times the total number of individuals in one generation (*n*). An average of 30n deaths may be assumed. If selection proceeds by way of *differential* fecundity rather than differential viability the ultimate effect is the same. It follows that *evolutionary rates are limited by the cost of natural selection*, and that *only a moderate number of alleles can be progressing toward fixation* at any one time; the larger the number, the slower must be the rate if the species is to survive. This is simply another way of stating the obvious but often forgotten fact that most populations which are evolving very fast are very ill-adapted to their environments, and that if sufficiently ill-adapted they face extinction. Thus Haldane found that in the moth *Biston betularia* in the smoke-polluted areas of England the light-colored *form (genotype cc)* has been replaced since 1800 by the dark-colored form (genotypes *Cc* and *CC*), the light-colored ones being more readily found and eaten by *birds*. Selection has been so intense that at times the frequency of *cc* individuals may be halved in a day. If selection were equally intense for *10* independently inherited genes, only $(1/2)^{10}$ or one in 1,024 of the original type would have survived, and extinction of the population would very probably result.

b. *Stabilizing natural selection*. Most well-established animal species carry a *load* of *balanced genetic polymorphism*, as we have seen, the function of which is to *buffer the species against environmental changes*. It generally favors heterozygotes at the expense of homozygotes (heterosis), and merely helps to maintain an equilibrium. It has a cost, which may be large or small; the extreme would be a balanced lethal system in which both homozygous genotypes are inviable, halving the reproductive capacity of the population. Such systems must be rare, though a close approach to one has been described in *Drosophila tropicalis* by Dobzhansky and Pavlovsky (1955).

c. *Progressive natural selection*. This is natural selection leading to *changes in the genetic composition of* a population; it corresponds to a situation of *transient polymorphism*. Most animal populations will carry both this and *the preceding kind of genetic* load, differing in relative amount in different species and under different conditions. In most well-established species, particularly those with numerous chromosome inversions or other rearrangements, the balanced polymorphism load probably greatly exceeds the transient polymorphism load, but this is not established as a general rule.

d. *The Evolutionary Advantage of the Marginal Population*. A population carrying *a very heavy balanced polymorphism load* may not be capable of bearing the additional burden involved in the genetic revolution which constitutes speciation. Acquisition of adequate isolating mechanisms probably always involves the fixation of some dozens of alleles at high selective cost. The cost may best be borne by populations with reduced balanced polymorphism loads, and it has been shown that this load is very often minimal at the edge of the species range (da Cunha and Dobzhansky, 1954; Carson, 1955). When this is the case it is there, rather than at the center of the range, that the population will be most capable of the evolutionary momentum required for the development of new isolating mechanisms and of the whole complex of new genetic equilibria and co-adaptations, which are surely involved in the attainment of species status.

A second reason why (apart from the situation envisaged in model I) speciation can only be expected to occur at the periphery of the range of the "parent" species is that it is only at the edge that populations possessing *the necessary degree of geographic isolation* can in general be expected to exist. *Any incipient trends in the direction of speciation*, any local reduction in the amount of balanced polymorphism, occurring in demes which lie well within the main distribution area of the species, are liable to be rapidly swamped by immigration from neighboring colonies.

e. *The Evolutionary Disadvantage of the Central Population*. The mere existence *of a species with a large population occupying an extensive* range is evidence that the species is well adjusted to conditions prevailing in at least the core area, and such adjustment can be assumed to involve a more or less heavy balanced polymorphism load. The situation at the center is the converse of that at the periphery; balanced polymorphism and potential variability may be maximal there, and at the same time the center, as far as evolution and speciation are concerned, is likely to be a "dead heart" because it does not provide the geographic isolation between local populations which is a necessary condition for the collapse of those polymorphisms.

An example cited by White (1959) is the little Australian grasshopper *Moraba scurra*, in which there is evidence that a particular type of chromosomal rearrangement (a dissociation of the large AB chromosome into two elements) has occurred several times within the main area of occupation of the species. But it seems that it was only when such a dissociation occurred in a peripheral (and presumably rather strongly isolated) colony that it could become an evolutionary success and give rise to a race with an increased chromosome number which spread out over an area previously uninhabited by the species.

According to this analysis, "a highly polymorphic population is not likely to be evolving fast and may be stagnating, while populations which show little evident polymorphism may be changing much faster. The idea that conspicuous polymorphism indicates active evolution is akin to the notion that rates of evolution are directly determined by mutation rates—and is equally or even more fallacious. Failure to appreciate the above principle is responsible for many mistaken ideas put forward by authors who have not considered evolution and speciation in terms of the actual processes of population genetics. Thus Brown (1957, Q. Rev. Biol., 32: 247-77) has evolved a whole theory of "centrifugal speciation" which emphasizes the center as the principal source of evolutionary change leading to "potent" new species and higher categories. There seems to be considerable merit in Brown's ideas on "the role of population density fluctuations in ... making and breaking the contacts between [central and peripheral] populations," provided that we reverse the parts which he believes the center and the periphery have played in progressive evolution. Again, Darlington (1958) has made the suggestion, quite unacceptable to the population geneticist, that *Drosophila robusta* "is likely to split into species in center where it keeps its stock of inversion hybridity"; this view largely or entirely neglects the need for geographic isolation during the speciation process.

f. Reduction of balanced polymorphism load in incipient species. Speciation would be an intolerably slow process (intolerable because of the probability of interruption of isolation and resultant swamping) if it did not draw to a considerable extent on the reserves of variability already in the parent species. Thus speciation must surely involve the fixation of a great many alleles that were previously floating in a state of polymorphism in the population; in other words, it is a process that must, in general, lower the level of genetic polymorphism, which has the effect of shedding a part of the genetic load borne by the population, at a cost. Once this has been accomplished, and genetic isolation has been completely attained, the potential for progressive evolution is greater than in the parent species or the incipient species at the beginning of its isolation, for it can stand the burden of more rapid progressive selection; it can also begin once more to build up its level of polymorphism to that permitted by its population dynamics.

g. The Prevalence of Peripheral Isolation. The very limited powers of dispersal of what may be a majority of animal species (especially among insects and other invertebrates) has not been sufficiently taken into consideration by many writers on evolution. In discussions on the theoretic aspects of evolution and speciation it is commonly assumed that gene flow within a species population is relatively unimpeded and continuous. Thus Fisher (1954, in: Evolution as a Process), while successfully defending the efficacy of natural selection, speaks of the "vast majority" of animal and plant species having a "constant interchange of germinal material, on a scale which ensures some community of ancestry between almost every two individuals, within a period no greater than a hundred generations".

Two examples, typifying extremely common situations, show how untenable this statement is as a generalization. Bateman (1950, Heredity, 4: 353-363) has pointed out that even though *Drosophila pseudoobscura* has greater powers of dispersal than many animals, it is inconceivable that average members of the species in the Puget

Sound area and in Oaxaca, Mexico, should have some common ancestors only 10 years removed. For one thing, this would imply that the same inversion sequences ought to be present in British Columbia and in Oaxaca, which is emphatically not the case (Dobzhansky and Epling, 1944, previously cited).

In the case of the Australian flightless grasshopper Moraba scurra, with annual generations, the power of dispersal is so limited that, although it is reasonable to think of individuals living a mile apart as having had a common ancestor 100 generations removed, it is certainly not possible to think of individuals living 10 miles, still less 100 miles, apart as having had a common ancestry as recently as the year 1859. There are two races of this species, one with 15 and the other with 17 chromosomes. In spite of widespread recent extermination of the species by destructive over-grazing of its habitat, enough remains to show that the zone of overlap between the two races (shown by the presence of chromosome-number heterozygotes) was 150 miles long and no more than a few miles or in places a few hundred yards wide. In one region where destruction of habitat has been less complete than elsewhere the width of the zone was 900 yards. Laboratory and field experiments show that the races can be crossed without difficulty; artificially established hybrid colonies at the end of 4 years are still polymorphic for chromosome number. If Fisher's estimate of community of ancestry were true for Moraba scurra the zone of overlap would be far wider, unless each homozygous genotype were sublethal in the territory of the other, which is absurd.

It is evident that the type of gene flow regarded by Fisher as the norm may be characteristic of many or even most species of birds and mammals, strong-flying insects, and other forms with considerable powers of dispersal. But Moraba scurra is typical of a very great number of species of invertebrates. It may well be that in the more vagile animals, especially the vertebrates, gene flow has been unduly neglected as a factor in evolution, as Mayr (1954) suggests. But if it were as free and unimpeded in most species as Fisher's statement suggests, it would make the existence of geographic races (that is, morphologically distinct local populations) almost impossible, since they could be maintained only by selection pressures of a most extreme kind.

Although Fisher has overstressed the community of ancestry in natural species and hence the amount of gene flow in their populations, the point he was making is one with which every modern evolutionist will agree: species have an objective reality because of their genetic continuity. However, most species are divisible into a great number of local geographic and microgeographic races, the existence of which is made possible by all sorts of geographic and ecological barriers. These barriers, although many of them are temporary or even ephemeral on the scale of geological time, lead to more or less complete isolation between these populations for periods of many generations. This whole situation is vastly more favorable for speciation than would be the case under the mating system considered by Fisher to be the norm.

In summary, it is evident that the principle of allopatric speciation is far more obvious in animals of low vagility, such as the flightless grasshoppers of the subfamily Morabinae, than it is in flying animals such as birds and Drosophila, where sibling or closely related species are frequently sympatric, no doubt as a result of range extensions after the establishment of genetic isolation.

h. Speciation Considered as a "Genetic Revolution." There is evidence that in Drosophila no two species (with the possible exception of the mulleri-aldrichi-wheeleri group) possess the same karyotype (chromosome complement including the characteristic numbers, forms, centromere and gene arrangements, etc. The same is apparently true of the Morabinae (the only other group of animals on which a comparably large number of observations has been made). It is a reasonable supposition that all animal species are karyotypically unique. If this is essentially true it prompts the question: Do chromosomal rearrangements play some special role in the speciation process? May they perhaps trigger off a series of genetic changes leading to speciation? White has developed the following hypothesis based on this assumption.

1. There may be two types of chromosomal rearrangements which establish themselves in evolution:
   - (a) Those capable of giving rise to long-lasting mechanisms of balanced polymorphism based on heterozygote superiority; and
   - (b) Those which either exhibit no superiority of the heterozygote or only a temporary or local one.

   To the first category belong the paracentric inversions (those not including the centromere region) in *Drosophila* and pericentric inversions in grasshoppers of the groups Morabini (Australian) and Trimerotropi (North America). With respect to rearrangements of this class, species populations may be polymorphic for the same inversion sequences over thousands of square miles.

   To the second category belong most chromosomal translocations, including centric fusions and dislocations, if the situation found in the Morabini is general. In this group, where at least 21 fusions and 14 dissociations have occurred in evolution, virtually no populations polymorphic for either of these kinds of changes are known. Also, whenever in this group a species includes geographic races differing in chromosome number, the zone of overlap or intergradation within which chromosome number heterozygotes would occur is now and probably always has been, extremely narrow. Low vagility is not itself sufficient to account for this; it is a sure indication of absence of heterozygote superiority.

2. Fixation of chromosome rearrangements of type 1b. In the Morabini it appears that certain types of rearrangements are able to establish themselves and reach fixation without necessarily conferring any advantage on the heterozygote. This probably occurs in rather strongly isolated populations, and seems to be what has happened in the case of the dissociation that gave rise to the 17-chromosome race of *Moraba scurra*. In this instance the two chromosome-number races are most likely incipient species, but insufficient time seems to have elapsed for the development of any strong isolating mechanisms between them. But the case is probably typical of a large category of instances in which rearrangements which do not possess significant adaptive superiority in the heterozygote have been able to establish themselves on the extreme edge of the natural range of a species. Support for this view is found in the situation in Rodentia, in which (1) chromosome numbers are very variable, closely related species frequently differing greatly in karyotype, and (2) chromosomal polymorphism for fusions and dissociations is very rare, having been only once reported. These apparently conflicting facts are reconcilable only on the hypothesis that fixation of rearrangements that do not confer heterozygotic superiority has been a frequent occurrence.

3. "Genetic revolution" accompanying fixation of chromosome rearrangement. Since alternative chromosome sequences (whether they have arisen by inversion, fusion, dissociation or in some other manner is immaterial) will always come to differ in respect to a number of genetic loci, any race or population in which a chromosomal rearrangement has reached fixation (that is, a frequency of 100%) has undergone a more or less profound genetic revolution. Many secondary and consequent genetic changes must be expected to occur, still further changing the population.

An inversion polymorphism which has been in existence for a long time has become an extremely important feature of the populations in which it occurs. Many genic polymorphisms on other chromosomes are likely to be adapted to it in the same kind of way as the inversions on two different chromosome pairs of *Moraba scurra* are co-adapted (White, 1958, Cold Spring Harbor Symposia, 23).

Loss of such a polymorphism is thus likely to lead to the collapse of other genetic polymorphisms adaptively linked with it. The general level of balanced polymorphism falls sharply, and with it the genetic burden.

4. *Resultant increased potentiality for progressive evolution.* Reduction of the balanced polymorphism load gives increased reproductive capacity, facilitating the establishment of entirely new polymorphisms and perhaps also making it easier for the population to invade a new area or a new ecological niche. Thus viewed, it seems likely that the fixation of chromosomal rearrangements may, in many groups of animals, play a rather special role in the speciation process. This role is not, however, the causation of intersterility at a single step, as some have naively assumed.

In summary, White's analysis of allopatric speciation is as follows:

1. The general theory of allopatric speciation is well established.
2. It may result from the splitting in two of the range of a species by some major ecological barrier (Model I).
3. Probably a much more frequent and important mode of speciation is the budding off of incipient species at the edge of a geographic range (Model II).
4. Peripheral budding usually involves a temporary reduction in the level of genetic polymorphism in the incipient species, a conclusion for which there is both direct evidence and theoretic basis.
5. There is reason to suppose that chromosomal rearrangements may often play a special role in this process.

Theories of Sympatric Speciation. The evidence for allopatric speciation in both plants and animals is overwhelming; the case for sympatric speciation in bisexual, cross-fertilizing animals is unconvincing to most modern workers, although there can be no doubt of the importance of such speciation in plants and in animals which are facultatively self-fertilizing, parthenogenetic, or asexual. Some recent authors (Huxley 1942, Thorpe 1945, Allee et al. 1949) think that under special circumstances incipient reproductive isolation may arise without geographic isolation, and may lead eventually to the splitting of the original population into reproductively isolated species. Supporting data are hard to find, and most of the examples that have been cited are susceptible to other explanation. Among such examples are the closely related insect species confined to different host plants, the so-called "species flocks" or "species swarms" in ancient lakes and on oceanic islands, and other instances of sympatric sibling species occupying different environments. In every instance the difficulty has been to show how the initial stages could be protected from swamping long enough to permit fixation of isolating mechanisms. Furthermore, analysis of the species-swarm of the Darwin's finches on the Galapagos Islands by Lack (1947) showed that an original immigrant species became divided into a number of different species on the various islands of the group, and that some of these reproductively isolated species were then able to spread to other islands, subdividing among themselves the available habitats and niches, and giving the appearance of having developed sympatrically through ecological isolation. In the large and deep Lake Baikal occur more than 300 species of shrimp; Brooks (1950, Speciation in Ancient Lakes. Quart. Rev. Biol., 25) showed that this is not an example of sympatric speciation, but that the species diverged while geographically isolated in different parts of the lake and at different depths. The tremendous amount of speciation found among the fishes of the African rift valley lakes (Victoria, Albert, Tanganyika and Nyassa) is probably to be explained in the same way. The situation with regard to related insect species on different host plants falls in a different class, and here the evidence for or against sympatric speciation is still inconclusive; Dethier (1954, Feeding Preferences in Insects. Evolution, 8) has reviewed the matter and suggested mechanisms which might bring about the necessary initial isolation. In general, however, the conclusions against the regular occurrence of sympatric speciation reached by Mayr (1947, Ecological Factors in Speciation. Evolution, 1) seem valid.

The Theory of Allochronic Sympatric Speciation. Numerous cases are known among insects in which closely related or sibling species are sympatric but are more or less completely reproductively isolated by having different times of sexual maturity. Doubtless many such instances are the result of allopatric speciation, followed by occupancy of common territory and selection for seasonal divergence. Recent studies on the cicadas and singing Orthoptera of the eastern United States, based in large part on analysis of song and other behavior, have greatly increased the number of sibling species known in these groups, and enabled their relationships to be determined much more precisely than could be done by morphological studies alone. In the field crickets of the genus *Acheta* one pair of species is of particular interest — *A. pennsylvanicus* and *A. veletis*. Alexander and Bigelow (1960) have shown that two distinct species populations have been grouped under the first name, one (*pennsylvanicus*) overwintering as a late instar nymph and maturing in the spring, the other (*veletis*) overwintering in the egg stage and maturing in middle or late summer. The only constant morphological difference between the two seems to be the average greater ovipositor/body length ratio in the females of the egg-overwintering population. No difference has been discovered in the songs of the two species, although the other eastern North American *Achetas* have individually characteristic songs. Diapause (the period of physiological inactivity and cessation of development, accompanied by maximum cold resistance) is evidently genetically determined, since it remains unaltered by laboratory rearing under varied conditions of temperature, etc. through successive generations. Although both *pennsylvanicus* and *veletis* are easily reared and produce very numerous offspring in the laboratory, the seasonal differences in time of maturation make crossing difficult, and such crosses as were attempted (using various methods) produced no offspring. Although both species occur in the very same spots, there is no evidence of any interbreeding in the field—the allochronic separation seems to be complete. Alexander and Bigelow suggest a mechanism by which these two species (and doubtless many others) may have speciated sympatrically. It may be outlined as follows:

A. Conditioning factors: Two stages in the life history are best able to survive the winter—the egg and the late instar nymph. The eggs are buried in the ground, the late instar nymphs burrow or seek shelter in holes. (Adults of *A. pennsylvanicus* also seek shelter in burrows or protected cavities, and may survive several killing frosts, but their tendency to be active in sound production, aggression, and sexual behavior, and the short adult life of about six weeks, makes this stage generally unsuited to overwintering. Very young juveniles are also ill-adapted for overwintering.)

B. *Initial Isolation.* A seasonal separation of breeding populations imposed by differential elimination of life history stages during winter could have been enhanced and reinforced by a gradual climatic change bringing longer and colder winters. This would have required no spatial isolation either macro- or microgeographic.

C. *Establishment of genetically determined isolating mechanisms.* Selection under the postulated intensification of winter cold would be expected to favor the fixation of genetic mechanisms for obligate physiological diapauses in the egg stage and late instar nymphal stage in the respective populations passing the winter in those stages. Such obligate diapauses not only increase winter-hardiness, but also aid in synchronizing the appearance of adults during the following seasons, both of which effects should have distinct selective advantage for the two incipient species.

D. Consequential Developments. Intensification of the burrowing habits of late instar nymphs of pennsylvanicus and elongation of the ovipositor permitting deeper placement of eggs by veletis are obviously adaptive modifications associated with the different times of obligate diapause. Occasional hybrids, if they occur, must certainly be less well adapted for survival than either of the stabilized parent types, and may well be inviable because of morphological or physiological incompatabilities in the egg or embryo. Failure of the two species to develop differences song may be taken as evidence (1) of the almost complete separation of the breeding periods, eliminating selection for reinforcement of behavioral isolating mechanisms, and (2) of the probable recency of the separation (Wisconsin glacial stage?) and lack of time for accumulation of slow incremental changes in song pattern.

Alexander and Bigelow call attention to the fact that a large number of the Orthoptera of the eastern United States consistently overwinter in either the egg or the late instar nymphal stage but not in both, and that other species pairs can be recognized which differ in this way (but none so close as pennsylvanicus-veletis. They believe that this type of sympatric speciation may be of rather common occurrence among insects and perhaps some other animals, in which the intrinsic and extrinsic factor permitting it happen to coincide.

Selection for Isolation. Not every race of a species is itself an incipient species. Race formation is a reversible process; race divergence under conditions of partial or temporary isolation may be replaced by race convergence and fusion when the isolation becomes less or ceases, as has occurred in man and probably is very frequent in other organisms. Races become species in the biological sense only if they develop reproductive isolation (although completely isolated populations that have not developed reproductive isolation may differ morphologically as much as or more than others which are so isolated). What causes reproductive isolation to develop in one instance and not in others? There are two general explanations, both based upon the concept that the functional genotype is not merely an agglomeration of unrelated genes, but an integrated system that functions as a whole through the interaction of its units.

1. Reorganization of the genotype. This may occur in either of two ways, or by some combination of them:

(a) By gradual accumulation of genetic differences in a split population as in Model I (p. 54 above). As this goes on in the two isolated populations the genes take on new functions and relations, and in time the gene systems become no longer compatible in hybrids. This may explain the inviability of hybrids of remotely allied species, and the breakdown observed in the F_2 and backcross progeny in other hybrids. It is well known, however, that the mere lapse of time and accompanying adjustments in the isolated genomes does not invariably result in reproductive isolation.

(b) By "genetic revolution" in small peripheral isolated populations as discussed for Model II (pp. 58 and 59 above). This may be expected to give rise much more rapidly to genetic incompatability giving incipient or possibly even complete reproductive isolation.

2. Selection for isolation. The genome of a species is an integrated system adapted to the ecological niche occupied by the species. Hybridization with

resulting recombination gives rise to discordant gene patterns that are adapted to neither of the ecological niches occupied by the parent species. Production of hybrids therefore reduces the reproductive potentials of both the interbreeding species; it constitutes a load or drain upon both species added to the normal loads due to stabilizing and progressive natural selection.

If mutations of any kind arise in either or both of two incipient species that are in contact and incompletely reproductively isolated, such that they make their carriers less likely to mate with the other species, selection will favor the spread and establishment of these mutations. This is because the mutants will breed only or mostly with members of their own species, while individuals not carrying the mutation will continue to produce hybrids as before and will end by having fewer descendants. The process is cumulative, since supplementary isolating factors will be similarly favored, and will end in producing complete reproductive isolation. Thus, in the instance of the field crickets *Acheta pennsylvanicus* and *veletis*, discussed above, reinforcement of the basic isolating mechanism (different obligate diapause periods) would be brought about by any genetic changes that reduced the amount of overlap in breeding periods, introduced behavioral differences that interfered with cross-breeding, or in any other way cut down the production of hybrids. (However, in this particular instance the time separation is already so nearly complete that selection for such supplementary factors may be very slight.)

This concept, for which Dobzhansky has been one of the principal proponents, is generally accepted as the principal mechanism by which reproductive isolation between species is made absolute. One of the lines of evidence in its support is the phenomenon called by Brown and Wilson (Systematic Zoology, 5 (2): 49-64. 1956) *character displacement*. It is a fairly common observation that the differences between closely related species tend to be maximal in regions where the two overlap or come into contact, which is what would be expected if selection against cross-mating occurs. Such maximization of specific differences in regions of overlap has been described in many groups of animals: for the camel-crickets *Ceuthophilus latens* and *pallidipes* and for *C. secretus* and *conicaudus* by Hubbell (1936), for the nuthatches *Sitta neumayeri* and *S. tephronota* by Vaurie (1950, 1951) and for many other birds, for the frogs of the genus Microhyla by Blair (1955), and for numerous other species. Brown and Wilson attribute the phenomenon in part to reinforcement of reproductive isolation, but also think that the process of *ecological displacement* may be of equal or greater importance in producing it. Although it is usually described in terms of the phenotypic characters employed in morphosystematics, it may affect any aspect of difference between species—morphological, ecological, behavioral, or physiological.

Recently, however, doubts have been expressed as to the importance of the role of selection for genetic isolating mechanisms. Species may be more strongly isolated genetically in their zone of overlap than elsewhere, but the opposite is sometimes true. It is a fact that genetic isolation between species can be increased in a population cage by removing the hybrids in each generation. But as Moore (1957, in: The Species Problem, Amer. Assoc. Adv. Sci. Publ. 50) has pointed out, neither of these lines of argument is a convincing proof that genetic isolating mechanisms always or even usually arise as a defense against hybridization. White (1959, cited above) evidently believes that the "genetic revolution" that constitutes speciation, especially of the peripheral type, is itself the cause of genetic isolation; he says: "The evidence for Dobzhansky's hypothesis seems rather weaker than it did twenty years ago, but it should perhaps not be abandoned entirely."

Character displacement: It is a fairly common observation that closely related species show maximum character-differences in regions where they come into contact or their ranges overlap; this phenomenon has recently been called character displacement by Brown and Wilson (Systematic Zoology, 5 (2): 49-64. 1956). It is probably a direct or indirect result of the action of natural selection *reinforcing reproductive isolation*, as just discussed. Such maximization of specific differences in regions of overlap has been described for *Ceuthophilus latens* and *pallidipes* and for *Ceuthophilus secretus* and *conicaudus* by Hubbell (1936), for the nuthatches *Sitta neumayer* and *S. tephronota* by Vaurie (1950, 1951) and for many other birds, for the frogs of the genus *Microhyla* by Blair (1955), for for many other animals. Brown and Wilson recognize that reinforcement of reproductive isolation is often involved, but think that the process of *ecological displacement* may be of equal or greater importance in bringing about this situation. Although usually noticed in relation to the phenotypic characters usually employed in systematic work, it may affect any aspect of difference — morphological, ecological, behavioral, or physiological.

B. *The Breakdown of Isolation.* It is common knowledge that animal species which in nature seldom or never interbreed may do so freely when caged together under artificial conditions. This does not mean that they are not distinct species or that they are not reproductively isolated, but only that the isolating mechanism(s) cannot operate effectively in the unnatural environment. Similarly, when man alters the ecology of a region by clearing, cultivation, irrigation, the planting of non-native crops, and other large-scale operations, he often may so change the distributional patterns and ecological relations of related species as to cause a breakdown of previously effective isolating mechanisms. The same thing may occur without man's intervention as a result of rapid climatic or other environmental change such as characterized the Pleistocene, but on a much more limited scale.

The breakdown of reproductive isolation between two sympatric species is not the same sort of phenomenon as the hybridization following the rejunction of incompletely isolated races of a species, such as must have occurred often after the recession of the Pleistocene glaciers. It is apparently commonest and has been most fully studied in plants, but comparable examples are not uncommon among animals. Edgar Anderson has called it *introgressive hybridization*, because it results in the somewhat limited and selective spread into the populations of the two species involved of genes from the other species. The limitedness and selectiveness result from the facts that (1) the hybridization is usually restricted to certain particular localities, (2) it involves a relatively small proportion of the individuals of the two populations, (3) reproduction of the hybrids is very largely by backcrossing with the parent species, and (4) survival of foreign genes is restricted by natural selection to those capable of harmonious or at least non-injurious interaction with the previously existing genotype. In plants, at least, the new combinations thus produced give new variability and new potentialities for the selection of adaptive characters; some of our more aggressive weeds are believed to have been produced from species modified by introgression. Anderson has called attention to the role of disturbed ecological situations as conducive to introgression, and has dubbed the process "*hybridization of the environment.*"

THE END

Zoology 245

Midterm Examination November 17, 1960

I. Distinguish clearly and concisely between the items listed in each of the following:

a. Standard deviation and standard error

b. Typology and the type method

c. Splitting and lumping in taxonomy

d. Polytypic species and sibling species

e. Diagnosis and description (definition)

II. Define each of the following:

a. Cline
b. Hypodigm
c. Sympatric
d. Nomen nudum
e. Phenotype
f. Coefficient of variation
g. Junior homonym
h. Syntype
i. Vertical classification
j. Parallel evolution

III. Discuss the concept of the species in modern biological thought.

IV. a. Construct a hypothetical dendrogram to ten genera (A-J) belonging to three subfamilies (Xinae, Yinae, Zinae) of a family.

b. Prepare a clear, "natural" key to these subfamilies and genera, employing brief hypothetical characters of your choice.

V. Spotted sunfish - Lepomis (Bryttus) punctatus miniatus (Forbes), 1884
(1) (2) (3) (4) (5) (6) (7)

In the name of the above animal there are seven elements designated by number. For each number identify the element and state briefly how it is handled in nomenclature.

VI. List, in sequence, the complete hierarchy of animal classification. Select an animal of your choice and give as much of its classification as you can.

Vincent

PAPER CHROMATOGRAPHY IN SYSTEMATIC STUDIES

Compiled by John B. Burch

December 1960

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* Good review

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Zoology 245 Systematics First Semester, 1960-61

TERM PAPER

The term paper will be due on or before January 17, 1961. You may choose either of the following:

I. Select some recent monograph or revision of a genus or higher category, preferably in a group in which you are interested. In making your choice ask advice of any of your professors or any of the museum curators. Write a critical analysis, answering the following questions so far as they are applicable:

1. At what general level(s) is the work done (alpha, beta, gamma); explain.
2. What kind(s) of species concepts are employed? What hierarchical systematic categories are used, and on what basis are the various taxa referred to them?
3. To what extent are typological, phyletic, and biosystematic concepts employed?
4. What relative emphasis is given to problems of nomenclature as contrasted with those of biology?
5. Are examples of the following included, and if so how much is each used and how important is it for the author's treatment? Polytypic species, subspecies, cline, deme, microgeographic race, ecotype, superspecies.
6. To what extent, and how, are ecology, geography, and geological history brought in?
7. To what extent, and how, are genetic and cytologic concepts and/or methods employed?
8. To what extent, and how, are quantitative biometric methods used?
9. To what extent, and how, are behavioral characteristics employed?
10. To what extent, and how, are theoretic concepts derived from work done on other groups of organisms used to explain situations in this study?
11. How much do you think subjective judgment entered into the taxonomic treatment employed?
12. Admitting that you may not be well qualified to judge, do you think, on the basis of your analysis, that this is probably good or poor work, useful or of little use (or perhaps even better unpublished), modern or old-fashioned, careful or careless? Remember that a work may be neither good nor poor, but mediocre, and that it may be both old-fashioned and useful, etc.

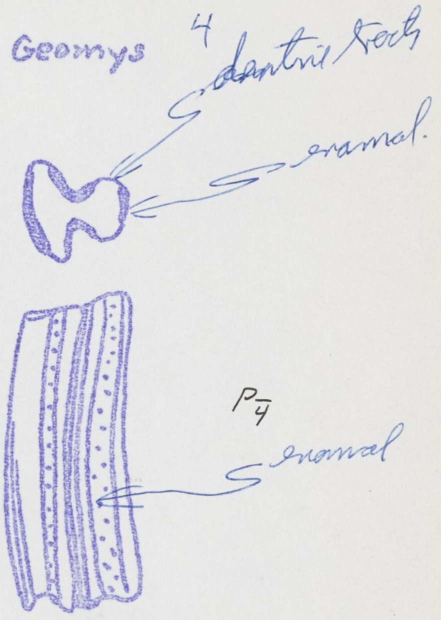
II. Select some pertinent topic in which you are interested, look up and read recent articles in journals dealing with it, and write a short review essay in a form suitable for publication, with bibliographic citations in proper form, etc. As examples of suitable topics (which are very numerous) the following are merely suggestive: Recent evidence bearing on the question of sympatric speciation in animals; the present status of systematics in the Mollusca; the species problem in the Protozoa; multiple character correlation and the use of punched-card machines in systematics; the history of the development of systematic nomenclature; an evaluation of paper chromatography as a systematic tool; etc. etc. etc. etc.

If you are interested in this choice, consult the instructor or any of your other professors for advice and pointers on how to go about it.

Vincent

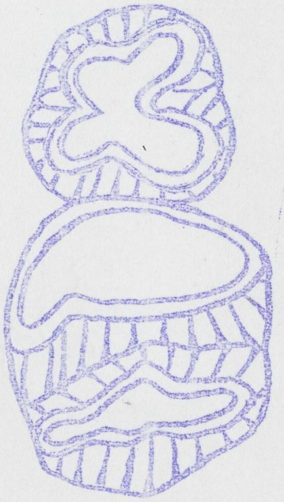
Perognathus hispidus
Recent

Geomys

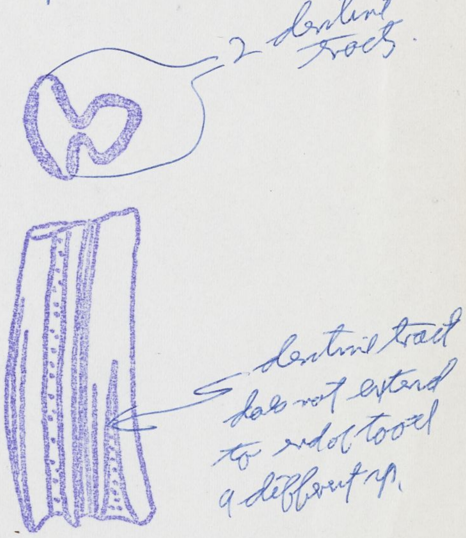


Perognathus rexroadensis
Upper pliocene

perognathus pearlettensis

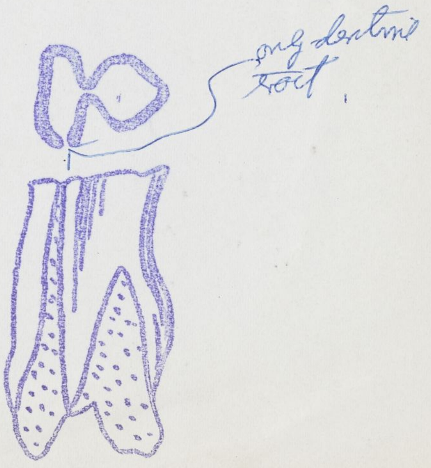


Geomys
pleistocene



Perognathus mclaughlini
Lower Upper Pliocene
X20

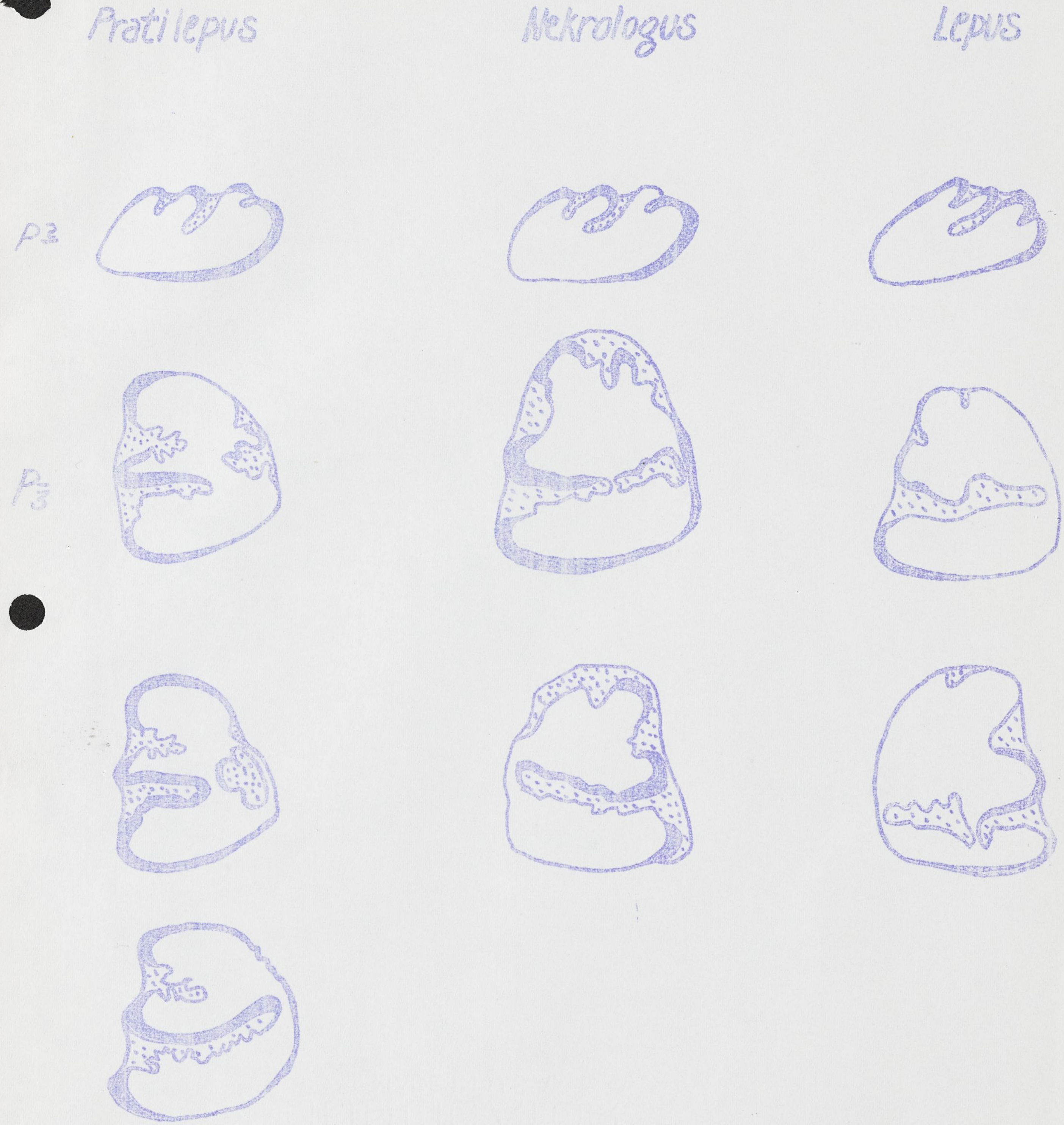
pliogeomys



Has roots was not a young tooth

X20

X7


Pratilepus
Nekrologus
Lepus
P^3
P_3

January 28, 1961

ZOOLOGY 245

Final Examination

18 1. Define the following:

a. Pleiotropic genes
b. Convergence
c. Beta taxonomy
d. Allopatric speciation
e. Polymorphism
f. Meristic variation
g. Standard error
h. Chronospecies
i. Hardy-Weinberg law
j. Introgressive hybridization

20 2. What literature sources could you consult to:

a. Determine the etymology of scientific names.

b. Discover whether or not your own last name has ever been used as the stem of a generic name of an animal.

Jaegers
Jaeger

c. Prepare a talk on principles of classification of animals.

d. Develop a list of the new species of the Tipulidae (crane flies) described since 1950. Zoo Record

e. Find graphical methods for the visual presentation of biological data.

Edgar Anderson,

f. Determine technical information on nomenclature of animals.

Del. of Int Zool. Congress.

g. Improve your comprehension of the genetic basis of evolution.

Dobzhansky,

h. Work out methods for solution of problems of treatment of quantitative data in taxonomy.

i. Compare prevailing concepts of species, subspecies, and genera among the groups of vertebrates. Evolution, Systematics,

j. Obtain a broad picture giving varied views on taxonomy and systematics.

Journl

Concur

20 3. Classify isolating mechanisms and discuss briefly.

Front

14 4. Discuss the concept of the species in current biological thought.

9 5. Cytogenetics, paper chromatography, electrophoresis and serology have been employed as procedures to aid in the solution of systematic problems. Discuss any one of them.

11 6. What are subspecies? What function, if any, do they serve? Can they be objectively defined and delimited? If so, how? Do they have importance in evolution? Discuss.

no appreciable statistically

Geo, Ecology

Yes, reversibly

Concur

Geo,

Reproductive
Ecolog
Temp
Behavior
morpho

Sometic, Hybrid

Zool. Record
zoological.