

A Comparison of Protozoan, Algal, and Metazoan Colonization of Artificial Substrates of Differing Size¹

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Abstract. The purpose of this investigation was to study the effect of island size on colonization of artificial islands by protozoa, algae, and micro-metazoa and to evaluate potential mechanisms for this effect. Four sizes of polyurethane foam (PF) artificial substrates, ranging from 1,000 to 200,000 mm³, were collected from a small pond after 1, 3, 7, 14, 21, and 42 days of exposure. Numbers of both protozoan and algal species increased asymptotically with time, but there was little relationship between the number of metazoan taxa on the substrates and time, suggesting that these organisms do not actually colonize and persist on substrates in this size range. There was a significant increase in the equilibrium number of species and the rate of species accrual with increasing substrate size both for protozoa and algae. Motile and non-motile subgroups within these two groups responded similarly to changes in substrate volume. The volume relationship found here is consistent with the null hypothesis for the species-island size relationship: larger islands passively collect more species than do smaller islands.

The structure of species assemblages on islands has been one of the most widely studied areas of ecology. Several models have been proposed to explain the dynamics of insular communities and their relationship to island size. The equilibrium theory of island biogeography (MacArthur & Wilson, 1963, 1967) predicted that the number of species present on an island would increase asymptotically to an equilibrium value determined by rates of species immigration and extinction. Rates of immigration decreased with increasing distance of the island from the species source pool. Extinction was dependent on island size: smaller areas should contain smaller populations and, therefore, enhance the probabilities of species extinctions. This would result in a decreased number of species at equilibrium with decreasing island size.

A second explanation, the "habitat-diversity hypothesis" (Williams, 1964), argued that species-area relationships were related to habitat heterogeneity: increasing the area sampled would result in the inclusion of an increasing variety of habitats and the species that live there. In this model, area is viewed as a confounding factor in the relationship between species richness and habitat diversity.

The preceding hypotheses can be considered as alternatives to a null hy-

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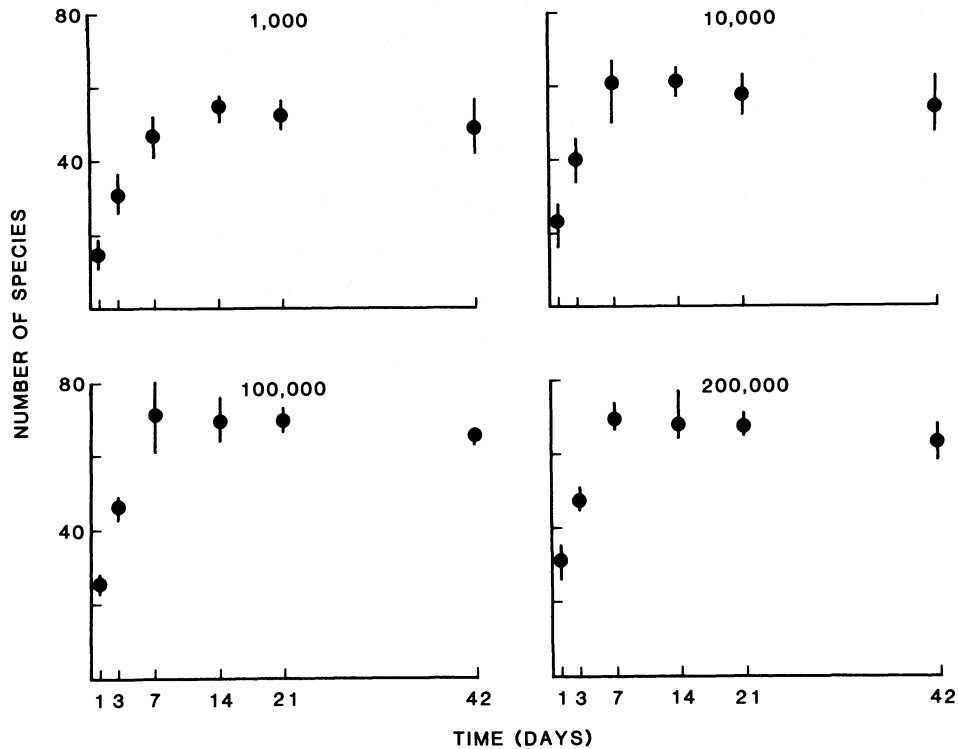


FIG. 1. Mean number of algal species observed over time for each substrate size. Error bars represent the ranges in number of species.

pothesis stating that species-area relationships are merely the result of a sampling phenomenon: as the area sampled is increased, a larger number of species from the source pool are found. This hypothesis invokes no biological explanation for the observed relationship and should be tested before more elaborate hypotheses are postulated (Connor & McCoy, 1979).

Few studies have investigated the relationship between substrate size and microbial colonization. Protozoan colonization of polyurethane foam (PF) substrates adheres to many of the predictions of equilibrium theory (Cairns et al., 1969), and the accumulation of species is positively related to substrate size below some critical volume (Cairns & Ruthven, 1970). The latter study sampled individual substrates repeatedly over time, whereas PF substrates are conventionally sampled destructively. Patrick (1967) found a strong area effect for diatom colonization of glass slides in streams in the United States and Dominica. Decreasing species richness with decreasing substrate size was attributable mainly to loss of rare species.

In many ecological investigations, the "community" under study is justified on taxonomic rather than ecological grounds. Close taxonomic affinity need not parallel strong ecological relationships (e.g., Brown et al., 1979). The utility of

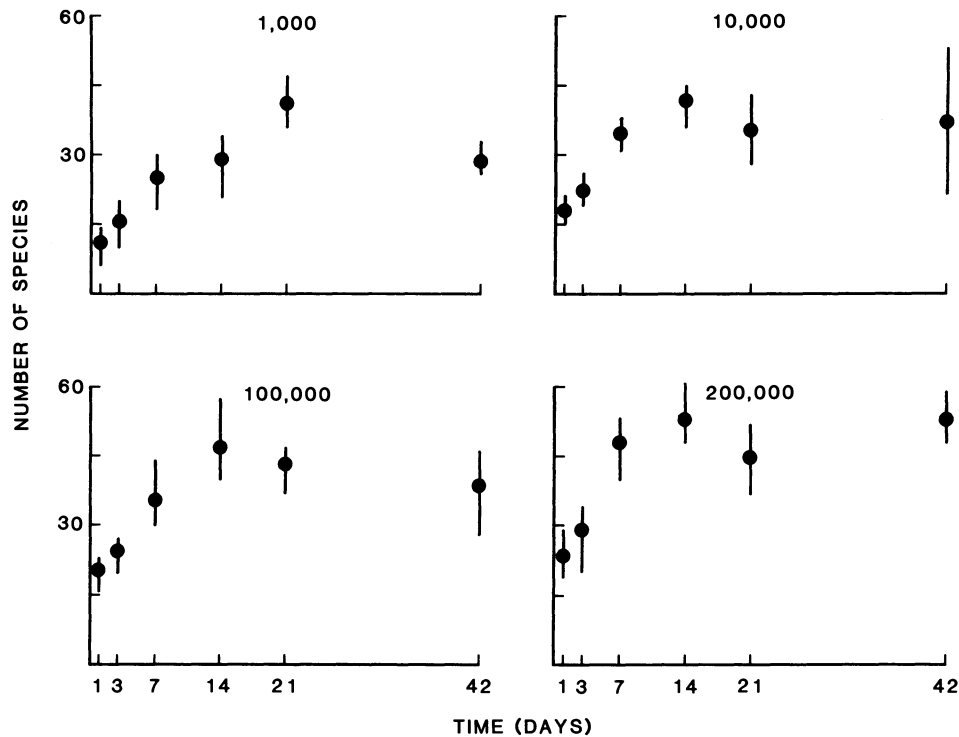


FIG. 2. Mean number of protozoan species observed over time for each substrate size. Error bars represent the ranges in species number.

delimiting ecological communities on the basis of phylogeny has been questioned (Bahr, 1982). Most substrates, both natural and artificial, collect a wide variety of organisms spanning several taxonomic groups. The PF artificial substrates have been used extensively in ecological and toxicological studies of protozoa (Cairns & Henebry, 1982; Cairns et al., 1986). These substrates also are invaded by other organisms, including most major groups of algae and several phyla of invertebrates. Relatively little is known about the colonization dynamics of algae and metazoa on these substrates.

The purpose of this experiment was to examine the effect of island size on colonization dynamics of several groups of microorganisms including protozoa, algae (including cyanobacteria), and microscopic metazoa.

MATERIALS AND METHODS

The experimental site used for this study was a small, soft-water pond in Montgomery County, Virginia. The "islands" used were PF artificial substrates cut into blocks of four sizes: 1,000 mm³, 10,000 mm³, 100,000 mm³, and 200,000 mm³. In November 1984, several substrates of each size were tied to two 5-m lines approximately 25 cm below the pond surface in the littoral zone. On days 1, 3, 7, 14, 21, and 42, four substrates of each size were collected and placed

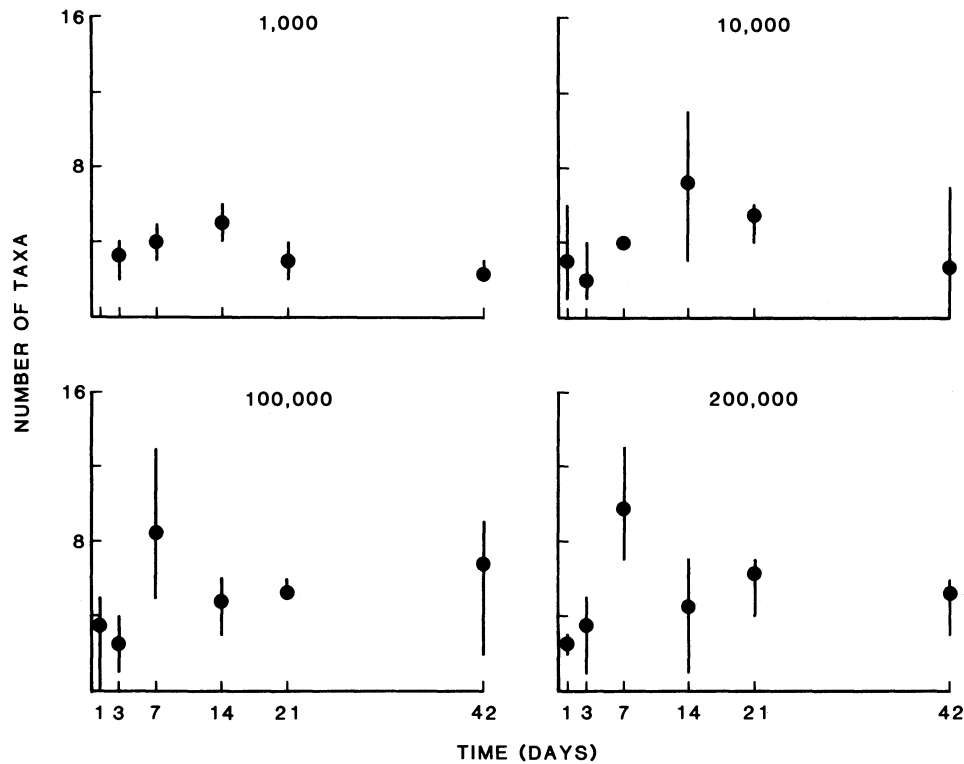


FIG. 3. Mean number of metazoan taxa observed over time for each substrate size. Error bars represent the ranges in number of taxa.

in sterile Whirlpak® bags. On their return to the laboratory, the contents of each substrate were squeezed into these containers and allowed to settle.

The number of protozoan species present in each sample was determined from live material at 100–430× within 8 h of sampling. Samples then were fixed in formalin (3% v/v) for the examination of algae and metazoa. In order to affix a particular species name to diatoms, samples must first be cleared of organic material and the silica frustules mounted. This was not done: (1) to ensure that only living diatom cells were considered in the analysis, and (2) because actual species identities were not of primary concern. Rotifers and cladocerans were identified to genus; other metazoan taxa included copepods and ostracods.

The species-time data were fitted to the MacArthur-Wilson species accrual model (MacArthur & Wilson, 1967)

$$S_t = S_{eq}(1 - e^{-Gt})$$

where S_t = the number of species present at time t , S_{eq} = the equilibrium number of species for the island, G = the rate of species accrual, and t = time using Marquardt methods of estimation (Draper & Smith, 1981) to obtain predicted species equilibrium (S_{eq}) and rate (G) values. Lack-of-fit tests (Klein-

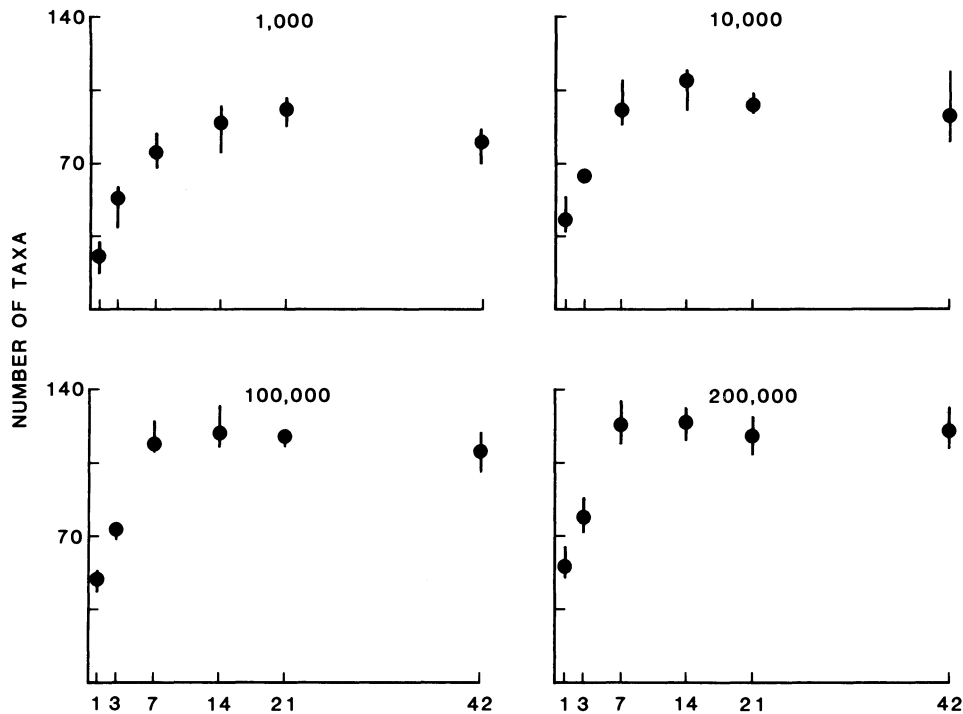


FIG. 4. Mean number of total microbial taxa over time for each substrate size. Error bars represent the ranges in species number.

baum & Kupper, 1978) were performed to assess the appropriateness of the model in explaining the observed data. This procedure was performed separately for each of the three taxonomic groups and for the total data set. Dummy variable analysis (Kleinbaum & Kupper, 1978) was used to test for significant differences ($p = 0.05$) in S_{eq} and G values among substrate sizes.

Patterns of colonization for subgroups within the three major taxonomic groups were investigated using the following classification: protozoa—autotrophic flagellates, heterotrophic flagellates, ciliates, sarcodines; algae—Chlorophyceae (non-motile), Cyanophyceae (these prokaryotes—cyanobacteria—are treated ecologically here as algae, the conventional “blue-greens” of the phycological literature), Bacillariophyceae; and micro-metazoa—rotifers, copepods, cladocerans, ostracods.

RESULTS

Although there was a significant lack-of-fit of the species accrual data to the MacArthur-Wilson model of colonization in most instances, the estimates of explained variation (r^2) were very large and highly significant ($p < 0.001$) for all groups except the metazoa (Table I). The data provided a qualitative fit to the species accrual model. The lack-of-fit results may be only an arithmetic artifact of low variability among species counts for any given sampling.

TABLE I

Estimates of colonization parameters for protozoa, algae, metazoa, and all taxa for four substrate sizes

Group	Vol (mm ²)	S_{eq}	G	r^2	p (lack-of-fit)
Protozoa	1,000	33.5	0.22	0.66	0.01 > p > 0.005
	10,000	37.8	0.39	0.59	0.25 > p > 0.10
	100,000	41.9	0.36	0.62	0.025 > p > 0.01
	200,000	50.1	0.39	0.71	0.025 > p > 0.01
Algae	1,000	52.5	0.31	0.91	0.50 > p > 0.25
	10,000	58.6	0.45	0.84	p = 0.10
	100,000	69.3	0.42	0.91	0.05 > p > 0.025
	200,000	66.8	0.52	0.87	0.01 > p > 0.005
Metazoa	1,000	*	*	0.01	0.005 > p > 0.001
	10,000	*	*	0.30	0.25 > p > 0.10
	100,000	*	*	0.16	0.10 > p > 0.05
	200,000	*	*	0.20	0.05 > p > 0.025
Total taxa	1,000	89.6	0.30	0.69	0.10 > p > 0.05
	10,000	105.9	0.38	0.88	0.025 > p > 0.01
	100,000	117.4	0.40	0.87	0.005 > p > 0.001
	200,000	123.5	0.43	0.83	p = 0.01

* Parameter estimates not analyzed due to low r^2 .

Numbers of algal species (Fig. 1) increased rapidly, leveling off within one week on all but the smallest substrates. Protozoan colonization (Fig. 2) was somewhat slower, but followed the same pattern. There was no strong pattern for metazoan accrual (Fig. 3), suggesting that the collected organisms were not true colonists of these substrates. The combined data for all three taxonomic groups were roughly asymptotic (Fig. 4).

There were significant differences in both the equilibrium number of species (S_{eq}) and the rate of colonization (G) within the substrate size range used (Table II). Equilibrium species numbers increased with increasing substrate volume. There was an inverse relationship between the rate of species accrual and substrate size. The estimated colonization parameters for metazoan taxa were not analyzed because of poor relationship of observed data to the asymptotic model.

Substrates of different size classes were similar with respect to the composition of the microbial association over time. Photosynthetic forms were always dominant, comprising 70–90% of the species. Diatom and non-motile chlorophycean species composed 30–40% and 15–25% of the community, respectively, over time. Autotrophic flagellates were important early species (27–29%) of the community, but quickly declined to less than 20% of the community. Most of the cyanophycean species observed during the experiment were present by day 3; as a result, the percentage of this group decreased from 5–6% to 1–2% by the end of the experiment.

Heterotrophic flagellates and ciliates showed small increases in importance during the experiment, composing 8–12% and 7–9% of the species in the community, respectively, by the end of the experiment. Sarcodines, mostly

TABLE II

Multiple comparisons of colonization parameters (S_{eq} and G) for the four substrate sizes and three taxonomic groups

	S_{eq}			
	1,000	10,000	100,000	200,000
Protozoa	_____			

Algae	_____	_____		

Total	_____	_____		

	G			
	1,000	10,000	100,000	200,000
Protozoa	_____			

Algae	_____	_____		

Total	_____	_____		

* Substrate sizes connected by a line are not significantly different from each other ($p > 0.05$) using dummy variable analysis.

naked amoebae, comprised only 1–4% of the community. Metazoan taxa never comprised more than 7% of the community, and this percentage fluctuated over time.

DISCUSSION

The relationship between species richness and habitat size is often cited as evidence for the existence of a causal biological mechanism, such as habitat diversity or area-dependent extinction rates. A much simpler explanation for such a pattern views the island as a passive collector of species; the larger the collecting device, the more rapidly it will receive organisms from a species pool. The species-volume relationship found here is consistent with the latter. The habitat homogeneity of a PF substrate is not affected by substrate size. Therefore, habitat diversity is not related to volume and cannot be proposed as a factor producing the observed relationship.

Because the sampling method used in this study was destructive, each “island” was sampled only once during the course of the experiment. Estimation of extinction rates would, therefore, require comparison of species compositions between different experimental units, and would introduce unknown experimental error into any statistical comparison of the resulting extinction curves. The equilibrium prediction of an inverse relationship between extinction and island size can be assessed indirectly from the species accrual data. Because all

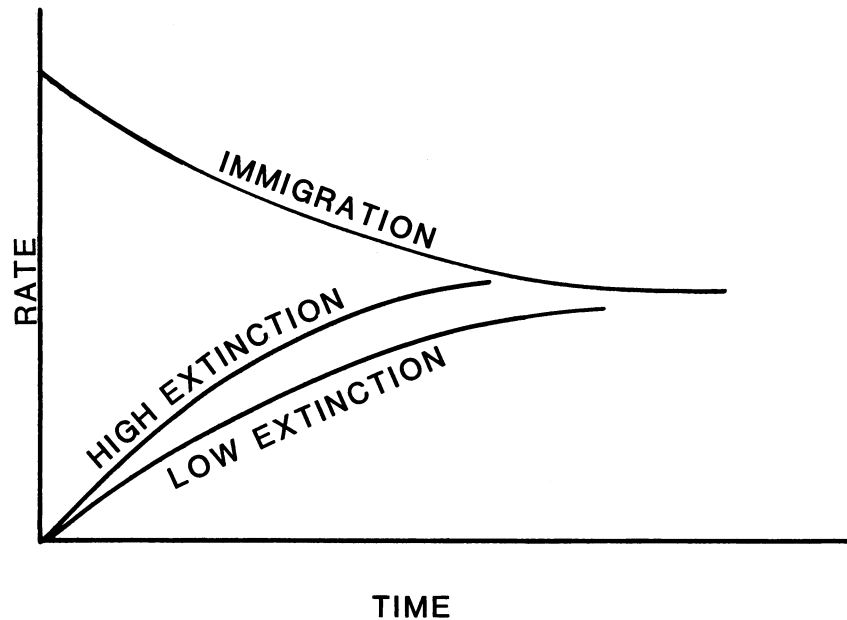


FIG. 5. Relationship between the rate of attainment of equilibrium (intersection of immigration and extinction rate curves) and extinction rate: assuming a constant immigration rate, the rate of species accrual (G) is positively related to the rate of species extinction. Adapted from MacArthur & Wilson (1967).

substrates were equidistant from the benthic species pool, rates of immigration should be equal according to equilibrium theory. Therefore, the rate at which an island achieves maximum species richness should be related positively to the rate of extinction for an island (Fig. 5). In this study, the number of species reached a maximum faster on larger islands, an observation that directly contradicts equilibrium theory. As a result, the null hypothesis of passive species collection cannot be rejected for the species-volume relationship.

Patrick (1967) reported a similar situation for diatom colonization of glass slides in a spring-fed stream. The numbers of diatom species reached an apparent equilibrium within four days on larger substrates (625 mm² and 36 mm²), whereas the number of species on smaller (9 mm²) slides continued to increase throughout the eight-week experiment. This experiment is comparable to the present study because the habitat diversity of glass slides, like PF substrates, should not increase with increasing size, and the distance from potential species source pools were the same for all substrates in the experiment.

The similarity in community composition among the different sized substrates suggests that substrate volume affects different groups in an equivalent manner. We might expect that there would be a stronger relationship between species richness and island size for non-motile groups: organisms capable of movement in the water column (e.g., flagellated and ciliated protozoa) should be capable of directed movement toward a benthic "island," thereby decreasing the rel-

ative importance of passive dispersal in the colonization process. Diurnal changes in vertical position have been well documented for planktonic organisms (Wetzel, 1983). The similar response of motile and non-motile groups of benthic microorganisms to substrate size suggests that passive movement through the water column via currents is the dominant mode of dispersal for most benthic protists.

In general, metazoa do not appear to persist on these substrates; either the substrate sizes used or, more likely, the pore diameter of the substrate material may be too small for the larger micro-metazoa to move and feed successfully. Moreover, many species in this group are truly planktonic and would not be expected to form an interactive component of the developing benthic community, although they may occasionally be collected from these devices. Apparently, colonization studies at this size level need not consider metazoan organisms as colonizing species in the analysis, but should view them instead as transient predators and competitors of colonizing protists, especially ciliates. However, small benthic rotifers may be true residents of "islands" in the size range used in this study.

Stewart et al. (1985) documented protozoan and diatom colonization in the autumn of 1983 for the same pond studied here. Although the results for the protozoa are comparable, the previous study found little relationship between the number of diatom species present on PF substrates and the time of exposure. In the present study, diatom species richness increased during the first week of colonization. Plankton tows (10- μ m mesh, 10 tows) taken on day 35 of the present study revealed only two diatom species in the plankton of the pond. By contrast, 27–34 species of diatoms were counted on material from PF substrates squeezed in the pond on day 1 of the previous colonization period. Quite likely, time of year may affect diversity of benthic microbes in the water column and, therefore, the rate of colonization by a certain group. Evidently, then, microbial colonization dynamics are dependent on several factors, many of which relate to dispersal potential of the organisms.

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Book Review

Morset, D. K. & Winer, J. A. 1986. *The Comparative Anatomy of Neurons: Homologous Neurons in the Medial Geniculate Body of the Opossum and the Cat*. (Advances in Anatomy Embryology and Cell Biology 97) Springer-Verlag, Berlin, Heidelberg, New York, Tokyo. 96 pp., illus. (\$31.50, paper)

The cytoarchitecture of the medial geniculate body of the opossum and cat is compared extensively using light microscopic methods of neurology. Golgi, Golgi-Cox, and fast Golgi preparations predominate in the presentation, but these are supplemented by a variety of other well-established neuroanatomical procedures, including experimental lesions. The monograph focuses on a comparative study of opossum and cat CNS structure, the brains of the two animals differing substantially in size, gross structure, and temporal development. There is a large evolutionary gap, in that the common ancestral line probably diverged in the early Cretaceous. Other mammalian material is included in the presentation, but in a more restrictive sense.

This is a specialized monograph directed to an audience of neuroanatomists and/or comparative neurologists. The work appears to have been executed in considerable detail. A number of similarities between the two animals emerges, thus documenting conservatism of neuronal architecture. However, there are obvious differences in details.

Clearly, this monograph embraces useful information for the specialist, but in the conclusion, one is struck by a need to know more about the detailed developmental history of the CNS in a comparative context, even between species as widely studied as these.—RONALD R. COWDEN, Department of Biological Sciences, Southeastern Louisiana University, Hammond, Louisiana.

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