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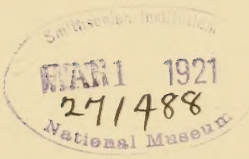
WILLIAM EMERSON RITTER
CHARLES ATWOOD KOFOID



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CONTENTS

PAGES

1. Mitosis in *Giardia microti*, by William C. Boeck; with plate 1; 1 figure in text 1–26
2. An Unusual Extension of the Distribution of the Shipworm in San Francisco Bay, California, by Albert L. Barrows 27–43
3. Description of Some New Species of Polynoidae from the Coast of California, by Christine Essenberg; with plates 2–3 45–60
4. New Species of Amphinomidae from the Pacific Coast, by Christine Essenberg; with plates 4–5 61–74
5. *Crithidia euryophthalmi*, sp. nov. from the Hemipteran Bug, *Euryophthalmus convivus* Stål, by Irene McCulloch; with 35 text figures 75–88
6. On the Orientation of *Erythropsis*, by Charles Atwood Kofoid and Olive Swezy; with 12 figures in text 89–102
7. The Transmission of Nervous Impulses in Relation to Locomotion in the Earthworm, by John F. Bovard; with 4 figures in text 103–134
8. The Function of the Giant Fibers in Earthworms, by John F. Bovard; with 1 figure in text 135–144
9. A Rapid Method for the Detection of Protozoan Cysts in Mammalian Faeces, by William C. Boeck 145–149
10. The Musculature of *Heptanchus maculatus*, by Pirie Davidson; with 12 figures in text 151–170
11. The Factors Controlling the Distribution of the Polynoidae of the Pacific Coast of North America, by Christine Essenberg; with plates 6–8; 2 figures in text 171–238
12. Differentials in Behavior of the Two Generations of *Salpa democratica* Relative to the Temperature of the Sea, by Ellis L. Michael; with plates 9–11; 1 figure in text 239–298
13. A Quantitative Analysis of the Molluscan Fauna of San Francisco Bay, by E. L. Packard; with plates 12–13; 6 figures in text 299–336
14. The Neurometer Apparatus of *Euplotes patella*, by Harry B. Yocom; with plates 14–16 337–396
15. The Significance of Skeletal Variations in the Genus *Peridinium*, by A. L. Barrows; with plates 17–20; 19 figures in text 397–478
16. The Subclavian Vein and Its Relations in Elasmobranch Fishes, by J. Frank Daniel; 2 figures in text 479–484
17. The Cercaria of the Japanese Blood Fluke *Schistosoma japonicum* Katsurada, by William W. Cort; 3 figures in text 485–507
18. Notes on the Eggs and Miracidia of the Human Schistosomes, by William W. Cort; 7 figures in text 509–519

Index 521–529

MAR 1921

INDEX*

Acanthias, 168.
  vulgaris, 152, 157.
Adinida, 404, 405.
Alaska, 175, 400.
"Albatross," U.S.S., expeditions, 172, 400; survey of San Francisco Bay, 299, 312, 313.
Allolobophora foetida, 106, 137.
Amphinomidae from the Pacific Coast, New Species of, 61; classification, 62; habitat, 63; bathymetrical distribution, 63; description of new species, 63–69.
Amphinomina, subfamily, 62.
Amphitrite, 213, 216.
Annelids, distribution of, 171, 172; Polynoidae, scaly annelids, 174; defensive organs of, 211; blindness of, 222, 223.
Antinoë anoculata, 183.
Aphrodita aculeata, 209.
Aphroditidae and Polynoidae, resemblance between, 46.
Arenicola, 127.
Arnold, A. F., quoted, 284.
Asterias ochracea, 213, 220.
  trochelii, 220.
Atkinson, E. L., cited, 487.
Autotomy in earthworms, 111.
Banyuls-sur-Mer, France, 97.
Barrows, A. L., 27, 397.
Bartsch P., acknowledgment to, 30.
Bergh, R. S., cited, 411.
Biedermann, W., studies on locomotion of earthworms, 105, 106, 119, 129, 130, 136.
Bispira polymorpha, 127.
"Blake," U.S. Survey Steamer, expeditions, 172.
Blanfordia, 487.
  nosophora, 487, 489.
Blastodinium, 405.
Blood fluke, Egyptian, 485; Japanese, 485, 486. *See also* Schistosoma haematobium; S. japonicum.
Boeck, W. C., 1, 145.
Bovard, J. F., 103, 135; acknowledgment to, 400.
Braune, cited, 380.
Brock, H., cited, 407.
Budington, R. A., cited, 120, 121.
Bullinus contortus, 488.
  dybowski, 488.
Burrage, G. H., U. S. N., member of board for survey of San Francisco Bay, 299.
Bütschli, O., 96; cited, 378.
California, 63, 489.
Calkins, G. N., cited, 370, 371.
Calonympha, genus, 383.
Carchesium genus, 350.
  polypinum, 380.
Cardium corbis, 303, 304, 307, 308, 312, 315, 320, 321, 322.
Carlson, A. J., cited, 122, 127.
Carquinez Strait, 315.
Carter, H. F., cited, 145.
Cawston, F. G., 488.
Centrodinium, genus, 416.
Ceratium, genus, 403, 416, 417.
  furca, figures of, 92, 93.
  gravidum, 91, figures of, 90.
Ceratocorys, genus, 440.
Cercaria of the Japanese Blood Fluke, *Schistosoma japonicum* **Katsurada,** 485; development of, in Katayama snail, 487; introduced into mice, 487; material studied, 490; method of study, 490; agreement with cercariae of other species, 491; structure of, 492–496, figures showing, 493, 497; excretory system, 494, figure showing, 499; oral sucker and cephalic glands, 496–501; activity of, 502–504.
Cercaria blanchardi, 488, 489.
Cercariae of human schistosomes, 491.
Cerebratulus, 127.
Cette, Biological Station, 400, 448.
"Challenger" expedition, 172.
Chemical composition of water, factor in distribution of Polynoidae, 209.
Chesapeake Bay, shipworms in, 37, 38; temperature of, compared with that of San Francisco Bay, 38.
Child, C. M., cited, 371, 372, 421, 463.
Chilodon, genus, 380.
Chione undatella, 308.
Chitin, or lime salts, effect of secretion of, on animal's habitat, 210.
Chloeia pinnata, 63.
Christiansen, E. B., 1, 21; cited, 366, 382.
Christineberg, in the Skagerak, 448.
Clam farming industry, 314, 315.
Claparède, D., cited, 172.
Clark, A. H., cited, 191, 209.

* Univ. Calif. Publ. Zool., vol. 18.

Cocaine, effect of on nerve cord of earthworms, 143.
Coccudina keromina, 338.
Cochlodinium citron, 93, 94.
pulchellum, 91.
Cockerell, F. D. A., cited, 205.
"Cold islands," 198.
Coleps, genus, 380.
Columbella gausapata, 303, 320, 321.
Commensal polynoids, 213, 216; advantages of, 219, 220; plasticity in, 224; adaptive variation in setae of, 224; variation in color, 225, 226; external changes, 227.
Conor, A., cited, 509.
Coreus marginatus, 79.
Cort, W. W., 485, 509.
Crepidula nivea, 303, 307, 320, 321.
Crithidia euryopthalmi, **sp. nov., from the Hemipteran Bug,** *Euryopthalmus convivus* **Stål,** 75.
Crithidia euryopthalmi, compared with C. lepticoridis, 76; infection of Euryopthalmus convivus by, 81, 83, 85, 87; life cycle, 82; infective and degenerative cycles, 87.
lepticoridis compared with C. euryopthalmi, 76.
Crockett, California, 30.
Cropper, J. W., cited, 145, 148.
Coyptochiton stelleri, 213.
Cysts in Giardia microti, 20, 23.
Cytoplasmic structures and changes, correlation of mitosis with, 18.
Daday, E., cited, 91, 92.
Daniel, J. F., 479.
Daboux, J. G., cited, 224.
Da Silva, M. P., cited, 488.
Davidson, Pirie, 151.
Dechant, E., cited, 129, 130.
Degenerative cycles in Euryopthalmus convivus, 87.
Delage, Y., cited, 96.
Diatoms, influence of temperature on, 200.
Delitzsch, Saxony, 401.
Didinium, genus, 381.
nasutum, 380, 384.
Differentials in Behavior of the Two Generations of *Salpa democratica* **Relative to the Temperature of the Sea,** 239.
Dinifera, 404, 458.
Dinoflagellata, morphology of, 89; Eryopthropsis admitted to, 96; relationship and morphology of, 400; habitat, 401; flagella of, 401; shell of, 402; protoplasm of, 403; asymmetry in, 403, 462; horns or spines in, 403.
Dinophysidae, 404, 405, 458.
Dinophysis, 405.
Diplodinium ecaudatum, 365, 366, 378, 379, 380, 381, 383, 384, 385.
Dufour, L., cited, 79.
Earthworm, description of locomotion in, 104–105; function of the nerve cord, 104, 105–106; effect of anesthetizing, 107–108, 109; tension, in etherized worms, 109, in locomotion, 112–118; locomotor impulses, limits of transmission, 118–122, rates of transmission, 122–125; giant fiber impulses, 125–128.
Earthworm, The Transmission of Nervous Impulses in Relation to Locomotion in, 103.
Earthworms, Function of Giant Fibers in, 135; theories regarding, 136; functions of the nerve cord, 136; experiments in transection of nerve cord, 137–138, in regeneration of, 138–142, in removal of, 140–142, with stovaine, 143; summary, 144.
Ectoparasitic polynoidae, 224.
Egyptian blood fluke, 485. *See also* Schistosoma haematobium.
Ehlers, E., cited, 62, 172, 204, 206.
Ehrenberg, C. G., cited, 338, 401.
Elasmobranch Fishes, Subclavian Vein in, and Its Relations, 479; material studied, 479; method, 480; observations on material studied, 481–482; discussion, 483.
Engelmann, I. W., cited, 356, 378, 380.
Entamoeba, 145.
Environment, effect of, on animal life, 173, 215, 216.
Enzymes, 226.
Epitonium hindsi, 303, 307, 320, 322.
savinae, 303, 307, 320.
Erythropsis, orientation of, 89, 92; transverse flagellum of, 93; ocellus, 94; prod (tentacle), 94; prod (tentacle), 94; girdle, 96; paradinial lines, 97; attachment area, 99.
agilis, 95; figures of, 98.
cornuta, figure of, 98.
Essenberg, Christine, 45, 171.
Eunoë, genus, 212.
barbata, 47.
caeca, 183.
Euperidinium, genus, 411.
Euphrosinidae, 62.
Euphrosyne aurantiaca, 64, 65.
calypta, 63–65; figures showing, opp. 72.
dumosa, 69.
kyllosetosa, 63, 68–69.
limbata, 69.

multibranchiata, 63, 65–66; figures showing, opp. 72.
pacifica, 67.
spirocirrata, 63, 66–68; figures showing, opp. 72, 74.
Euphrosynina, subfamily, 62, 63.
Euploea, genus, 338.
Euplotes, genus, 338, 339–340.
charon, 338.
harpa, 338, 340, 356, 378, 381.
longipes, 338.
patella, 338; preparation of for study, 341–343; illustrations of, opp. 392, 394, 396.
Structure, external features, 344; diverticulum, 347; ectoplasm, 348; endoplasm, 349; food vacuoles, 349; contractile vacuole, 350; nuclear structure, 350; macronucleus, 350; micronucleus, 351.
Motor organs and neuromotor apparatus, 351; cirri, 352; membranelles, 353; structure of neuromotor apparatus, 354; function of neuromotor organs, 359; figure showing, 356; evidence of neural function, 362.
Binary fission, 367–368; formation of new cirri, 372, peristome, 373, neuromotor apparatus, 375.
Fibrillar system in other ciliates, 378; neuromotor apparatus of flagellates, 381; homology of neuromotor apparatus in ciliates and flagellates, 383.
vannus, 339.
worcesteri, 339, 340, 344, 349, 350, 352, 353, 356, 368, 372, 373, 374, 375, 378, 381.
Euplotes patella, **Neuromotor Apparatus of,** 337; summary of conclusions, 386; literature cited, 388.
Euryophthalmus convivus, 75; flagellates infecting digestive tract, 76, 81, 83, 85, 87; morphology of digestive tract, 78, figures showing, 80.
Euryopthalmus convivus **Stål, the Hemipteran Bug,** *Crithidia euryopthalmi,* **sp. nov., from the,** 75.
Eurythoë, genus, 63.
californica, 67.
Exuviaella, genera, 404.
Exuviation in Peridinium, 417.
Factors Controlling the Distribution of the Polynoidae of the Pacific Coast of North America, 171.
Falk, H. O., acknowledgment, 69.
Farallone, San Francisco Bay, 63.
Fauna, oceanic, feeding grounds of, 212.
Fauré-Fremiet, E., cited, 92, 93, 94, 96, 97, 98, 407, 412, 434, 459.
Fowler, G. H., quoted, 285.
France, 96.
Friedländer, B., work on the movements of earthworms, 104, 105, 128, 130, 131, 136, 142.
Fujinami, A., cited, 486, 487; acknowledgment to, 489.
Function of the Giant Fibers in Earthworms, 135.
Fundulus, 214.
Gattyana amundseni, 203.
cirrosa, 203, 209.
senta, 206.
Gemma gemma var. purpura, 303, 320, 321.
Giardia, genus, 382.
intestinalis, 145; compared with G. microti, 5.
Giardia microti, 1; infection of hosts, 3; compared with G. muris, 3, 5; duodenum natural habitat of, 3; pathogenicity of, 4; morphology of, 4; morphological structures, 5; parabasal bodies, 8, function of, 9; figures of, opp. 10, 26; neuromotor apparatus, 19; cysts, 20.
Mitosis in, 1; phases of, 11–17, figures showing, opp. 10, 26; correlated with cytoplasmic structures and changes, 18; conclusions, 22.
muris, 5.
Glyphis aspera, 213.
Goniodoma, genus, 416.
Gonyaulax, genus, 205, 402, 416, 420, 427, 438, 459.
Goto, S., acknowledgment to, 400.
Gran, H. H., cited, 411.
Grassi, B., and Schweiakoff, W., cited, 21.
Griffin, L. E., cited, 344, 349, 350, 352, 353, 354, 356, 359, 367, 368, 370, 372, 374, 375, 378.
Grube, E., cited, 206.
Gymnodinidae, 404, 405.
Gymnodinioidae, 89, 91.
Gymnodinium, 405.
Halosydna californica, 183, 212.
carinata, 47, 212.
insignis, 175, 183, 212, 213, 216, 227; figures showing, 238.
interrupta, 183, 212.
lagunae, 47.
macrocephala, 48; description of, 53; comparison of, 54; occurrence, 55; plate showing, 60.
Hance, R. T., cited, 370.
Haptomonads, 86.

Harmothoë bonitensis, 48; comparison and description of, 48; occurrence of, 50; plate showing, opp. 58.
carinata, 47.
crassicirrata, 47.
forcipata, 184, 206.
fragilis, 177.
hirsuta, 177, 183, 206, 211; figures showing, 236, 238.
imbricata, 47, 174, 183, 211, 213.
johnsoni, 48; description of, 50; comparison of, 52; occurrence of, 53; plate showing, opp. 60.
lamellifera, 183.
multisetosa, 183, 203, 204.
triannulata, 177.
luta, 177, 206.
yokohamiensis, 206.
Hashegawa, T., cited, 486.
Helodrilus caliginosa, 106, 137, 142; experiments in anesthetizing, 106.
Hemipteran Bug, *Euryopthalmus convivus* **Stål,** *Crithidia euryopthalmi,* **sp. nov., from the,** 75.
Heptanchus cinereus, 152, 147.
maculatus, description of, 151; figures of, 155, 158, 160, 163, 164, 168, 169; subclavian vein, figures of, 480, observations and discussion of, 481–483.
Heptanchus maculatus, **Musculature of,** 151; pharyngeal musculature, 152; superficial circular muscles, 153; interarcuales, 158; subspinalis, 159; adductors, 159; hypobranchials, 161; musculature associated with organs of special sense, 162; appendicular, 163; of the trunk, 167.
Hérouard, E., cited, 96.
Hertwig, R., 94, 95.
Heterocapsa, genus, 416.
Heterodinium, genus, 416, 440, 445, 459.
Hexanchus, 165.
griseus, 152.
Hickey, J. P., acknowledgment, 509, 516.
Hickson, S. K., quoted, 284.
Hinnites giganteus, 303, 320, 321.
Hjort, J., cited, 202; quoted, 284.
Holcomb, R., cited, 516.
Holothuria californica, 220.
Holway, R. S., cited, 198.
Huffman, O. V., cited, 515.
Human schistosomes, method of transmission, 486; value of study of, 489; characters of cercariae, 491. *See also* Schistosoma, and its species.
Human Schistosomes, Notes on the Eggs and Miracidia of, 509.
Hypotricha, 350, 353, 371.
Ikeno, S., cited, 384.
Ilynassa obsoleta, 314.
Iturbe, J., 488.
Izuka, A., cited, 203.
Janicki, C., cited, 383.
Japan, 175.
Japanese blood fluke, 485, 486. *See also* Cercaria of the Japanese Blood Fluke; Schistosoma japonicum.
Japanese current, 208.
Japanese Islands, 203.
Jenkins, O. P., cited, 122, 127.
Joergersen, E., system of classification of Peridinium, 412, 413–428, 460.
Johnson, H. P., cited, 45, 218, 220.
Johnstone, J., quoted, 283.
Katayama nosophora, 487.
Katsurada, F., cited, 486.
Kerona patella, 338.
Kodiak Island, Alaska, 66.
Kofoid, C. A., 89; acknowledgment, 2, 45, 61, 108, 173, 300, 400, 489; cited, 1, 9, 21, 205, 330, 366, 340, 382, 383, 403, 405; member of board for survey of San Francisco Bay, 299.
Konno, F. F., acknowledgment to, 488.
Krakow, Poland, 401.
Krawany, J., cited, 127.
Krukenberg, C. F. W., cited, 105.
Kuno Siwo, or Japanese current, 208.
La Jolla, California, 69, 99.
Langdon, F. E., cited, 129.
Lebour, M. V., cited, 91.
Leiper, R. T., cited, 487, 488, 489, 514.
Leodocidae, 63.
Lepidasthenia gigas, 177, 183, 213, 218, 223, 224, 228, 236.
Lepidonotus caeloris, 47, 175, 183, 203, 204.
squamatus, 174, 184, 215, 228; figures showing, 236, 238.
Leptocoris trivittatus, 76, 79, 87.
Life zones on the Pacific Coast, 75.
Light intensity, effect of on deep sea animals, 223.
"Lightning" expedition, 172.
Lime salts, 210.
Limnoria, crustacean woodbores, 28, 29.
Literature cited, 24, 43, 56, 70, 88, 101, 134, 144, 149, 170, 231, 291, 333, 388, 466, 484, 505, 519.
Loeb, J., cited, 210.
Looss, A., cited, 485, 486, 514, 518.
Lucapina crenulata, 220, 225.
Lumbriconereis, 127.

Lumbrinereidae, 62.
Lunatia duplicata, 314.
heros, 314.
Lupinus arboreus, 75.
Lutz, A., cited, 488, 489.
Lygaeus militaris, 79.
Lysidice, 221, 226.
McClung, C. E., cited, 370.
McCulloch, Irene, 75; cited, 383.
McEwen, G. F., acknowledgment to, 173, 191, 208; cited, 241.
McGlashan, H. D., acknowledgment to, 32.
McIntosh, W. C., cited, 62, 63, 206, 209, 221, 227, 228.
Macoma balthica, 303, 304, 305, 307, 320, 322.
inquinata, 303, 304, 307, 320, 321, 322.
nasuta, 303, 304, 307, 312, 320, 321, 322.
Madeira Islands, 95.
Maier, H. N., cited, 353, 354, 357, 361, 378, 380.
Mangin, O., cited, 91, 450, 451.
Mare Island Navy Yard, California, damage done at, by shipworms, 29.
Marenzeller, E., cited, 174, 206.
Massachusetts, Commissioners on Fisheries and Game, cited, 309; clam industry in, 314.
Mastigophora, order, 400, 404.
Matsuura, U., cited, 486.
Matthews, J. R., cited, 145.
Maupas, E., cited, 353, 356, 378.
Maxwell, S. S., acknowledgment, 108.
Meadow mouse. *See* Microtus californicus californicus.
Metaperidinium, 412, 413, 421, 428, 429, 430, 431, 435, 438, 444, 445, 446, 447, 454, 460, 461.
Metschnikoff, E., 95.
Meunier, A., cited, 412.
Michael, E. L., 239; cited, 202, 282.
Microtus californicus californicus, 1; gas inflation in, 4.
Mitosis in *Giardia microti*, 1; phases of, 11, 16, 17, figures showing, 10, 26; correlated with cytoplasmic structures, 18; conclusions, 22.
Miyagawa, Y., cited, 486, 487, 491.
Miyairi, K., 486, 487; cited, 487.
Modiolus, cf. rectus, 303, 320, 321.
Molluscan Fauna of San Francisco Bay, A Quantitative Analysis of, 299; collection of material, and method of procedure, 300–301; general distribution, 301; species of, 303–308; economic considerations, 308; factors governing distribution, 317: depth, 318, type of bottom, 318, salinity, 322, temperature, 324, food supply, 327, biotic environment, 330; summary, 331.
Monaco, Oceanographic Institute, 400.
Monia macroschisma, 303, 320, 321.
Moore, J. P., acknowledgment, 47, 55, 172; cited, 206.
Murray, J., cited, 202, 210, 215; quoted, 284.
Musculature of *Heptanchus Maculatus*, 151.
Mustelus, genus, 167, 168.
antarcticus, 479, 481.
henlei, subclavian vein in, and its relations, 481–483.
Mya arenaria, 303, 304, 306, 307, 308–310, 311, 314, 315, 320, 321, 322, 331.
california, 303, 304, 307, 320, 322.
californica, 322.
Mytilus californianus, 311, 315.
californicus, 308, 311.
edulis, 303, 304, 305, 307, 308, 311, 313, 320, 321.
Naegleria gruberi, 381, 383.
Nakamura, H., cited, 486.
Nansen, F., cited, 198.
Naples, Zoological Station, 400, 448.
Narabayaski, F., cited, 486, 488.
Nassa fossata, 303, 307, 320, 322.
mendica, 303, 320, 321.
perpinguis, 303, 320, 322.
Nectomonads, 86.
Nereis, 127.
dumerilii, 207.
mirabilis, 207.
Neresheimer, E. R., cited, 378, 379.
Nervous Impulses, The Transmission of, in Relation to Locomotion in the Earthworm, 103; materials and methods of study, 106–107; statement of problem, 108; experiments with anesthetized worms, 108; free moving, 109; tension factor, 109; anatomy, 111; free nerve preparations, 112–116; limits of transmission, 118; dependence on nervous system, 120; locomotor impulses, 122; giant fiber impulses, 125; the nervous mechanism, 128–130; transmission by reinforced stimuli, 131; summary, 132–133.
Neuromotor apparatus, first use of term, 351, 378; parts of, 351; definition of, 352; description of motor parts, 352–354; structure of, 354–359; "motorium," 355, 359, 365, figure showing, 356; function of, 359; evidence of

neural function, 362; in flagellates, 381; homology of, in cilia and in flagellates, 383.
New International Encyclopaedia, quoted, 284.
Ocean currents, 207.
Ocean depths, 215.
O'Donoghue, C. H., cited, 479, 483.
Odostomia franciscana, 303, 320, 321.
Ogata, S., 488.
Oleum, California, 31.
Ophryodendron, 95.
Ophryoscolex purkyngei, 380.
Orientation of *Erythropsis*, On the, 89.
Ornithocercus, genus, 405.
Orthoperidinium, subgenus, 412, 413, 428, 431, 432, 433, 434, 435, 438, 444, 446, 447, 452, 458, 460, 461.
Ostrea elongata, 308, 311.
lurida, 303, 304, 306, 307, 308, 311, 316, 320, 321, 322.
Oxyrrhis, 405.
Pacific coast, life zones on, 175.
Packard, E. L., 299.
Palmiridae, 62.
Panope generosa, 308, 312.
Paphia staminea, 303, 307, 308, 310, 313, 314, 315, 320, 322.
Paramoecium bursaria, 341, 371.
Paraperidinium, subgenus, 413, 421, 428, 429, 433, 434, 435, 438, 444, 446, 449, 454, 458, 460, 461.
Parker, G. H., acknowledgment, 108.
Parker, T. J., cited, 479, 482, 483.
Pathogenicity of Giardia microti, 4.
Paulsen, O., cited, 412.
Pavillard, J., 96, 97; cited, 413.
Pecten, 312.
Perediniae, found at surface, 200.
Peridinidae, asymmetry in, 403, 443; member of Dinifera, 404; characters of, 405; skeletal variation in genera of, 408, 435, 458; major skeletal characters, 408–414; plate development in genera of, 416–419, 458; multiplication of plates, 419–423; origin of accessory plates, 439, of dorsal plate patterns, 442. *See also* Peridinium.
Peridiniella, genus, 416.
Peridinium, genus, 398, 399; skeletal variations, 403, 408; systematic position, 404, 408; nomenclature of the plates, 405–407.
Skeletal characters, 408–414, 459; antapical horn, 409; girdle, 411; plate patterns, 412, figures showing, 409; size, shape, surface, etc., 414, 459; plate relationships, 414.
Plate development, 416–419, 459; exuviation, 417; origin of accessory plates, 439, 459.
Skeletal variations, regions of, 423, 460; figure showing, 423.
Plate patterns, basis for subdivision, 426–428; origin of dorsal, 442, 443; paired area of change, 444; completeness of series of variations, 446–447; variations in length of critical sutures, 448–450; significance of variation in suture length, 450–456; mutations in, 456, 463; influence of environment on, 457, 465.
Subdivisions, 428, 435; definition, 436; regions of variation in shell of, 437, 444.
Peridinium achromaticum, 432.
aciculiferum, 432.
adriaticum, 430.
anthonyii, 431.
bipes, 431.
breve, 430.
brevipes, 430.
cerasus, 429.
cinctum, 431.
claudicans, 431, 432, 435, 450, 456, 458.
conicoides, 431.
conicum, 431, 442, 455.
crassipes, 410, 430, 442.
forma autumnalis, 430.
forma typica, 430.
cummingii, 410.
curvipes, 413, 429, 430.
depressum, 431.
divergens, 430, 435, 442, 448, 449, 450, 451, 452, 454, 463; charts and figures of plate patterns, 415, 422, 423, 425, 429.
excentricum, 419, 433, 447.
faeröense, 431.
globulus, 430.
granii, 429, 435, 450, 456, 457.
islandicum, 429, 443.
laeve, 432.
latum, 432.
lenticulatum, 430.
leonis, 431.
marchicum var. javanicum, 432.
marsonii, 434.
minutum, 432.
var. tatihouensis, 434, 459.
mite, 413, 430.
monacanthus, 430.
monospinum, 432.
multipunctatum, 432.
obtusum, 431.
oceanicum, 431, 435, 442, 450, 456, 457, 458.
ovatum, 429, 434, 450, 456.
pallidum, 429.

parallelum, 431.
paulseni, 433.
pellucidum, 429.
var. acutum, 429.
pentagonum, 431.
perrieri, 433.
punctulatum, 431.
pusillum, 432.
quadridens, 432, 441.
quarnerense, 430.
rectum, 413, 429.
roseum, 430.
spinosum, 429.
steinii, 410, 430, 445.
subinermis, 431.
tabulatum, 431, 443.
tenuissimum, 410.
thorianum, 403, 432.
tristylum, 429.
trochoideum, 432.
typus, 431.
umbonatum, 432.
var. elpatiewskyi, 433.
westii, 431.
wiesneri, 430.
willei, 431.
Placoides tenuisculptus, 303, 320, 321.
Phalacroma, genus, 405.
Pholadidea penita, 308, 312.
Pholas pacificus, 303, 320.
Physopsis africana, 488.
Phytoplankton, 200.
"Plankton concept," 240, 290; validity of, 281–287.
Planorbis bahiensis, 488, 489.
boissiyi, 488.
guadelupensis, 488.
olivaceus, 488, 489.
Plasmotomy in Giardia microti, 17.
Polinices lewisi, 314.
Polychaeta, 62.
Polymastix, 382.
Polynoë californica, 177, 213, 218.
complanata, 47.
filamentosa, 177, 183.
fragilis, 177, 213, 220; figures showing, 236, 238.
lordi, 177, 213, 224; figures showing, 236, 238.
ocellata, 218.
pulchra, 220, 224, 225, 226.
remigata, 177.
scolopendrina, 221, 226, 227.
Polynoidae, attributes of, 46; resemblance to Aphroditidae, 46; description, 46; definition of, 174; division of based on distribution, 174; modes of self defense, 211, 228; changes in, 217; power of regeneration, 217; muscular adapblance to Aphroditidae, 46; devantage of commensal habits, 219; adaptive coloration, 220, 225; abyssal species, 222; ectoparasitic, 224.
Distribution of, 46; tables showing, 176, 178, 184–190; bathymetrical, 179, 180, 181, 183; factors in, 191: temperature, 200, 206, ocean currents, 206, winds, 208, chemical composition of water, 209, plasticity (variability), 213; rôle of food in, 211.
Food habits, 47, 210, 211; influence of, on mode of life, 211–213.
Species of, number, 174; cosmopolitan, 174; littoral, 182; deep water, 183; commensal forms, 213, 215; influence on, of environment, 215, of depth, 215.
Polynoidae from the Coast of California, Description of Some New Species of, 45.
Polynoidae of the Pacific Coast of North America, Factors Controlling the Distribution of, 171.
"Porcupine" expedition, 172.
Port Erin Marine Biological Station, Isle of Man, 282, 400.
Pottschapel, Saxony, 401.
Pouchet, G., 96.
Pouchetia, genus, 405.
cochlea, 96, 97.
cornuta, 96, 97.
Prorocentrum, genus, 404.
Protoceratium, genus, 416.
Protoperidinium, genus, 411.
Protozoan Cysts in Mammalian Faeces, A Rapid Method for the Detection of, 145; description of, 147; value of, 148.
Prowazek, S. von, cited, 1, 256, 358, 378.
Prowazekella. *See* Prowazekia.
Prowazekia lacertae, 345.
Psephdia ovalis, 303, 320, 321.
Pyrocystis, genus, 405.
Pyrophacus, genus, 416, 420, 427.
Quatrefage, cited, 62.
Raia erinacea, 152, 157.
Ramsay, L. N. G., cited, 207.
Rankin, E. P., cited, 330.
Reed, A. C., cited, 489.
Retzius, G., cited, 129.
Ritter, W. E., acknowledgment, 241.
Robson, G. A., cited, 487.
Rodenwaldt, E., cited, 5, 21.
Row, R. W. H., cited, 145, 148.
Sacramento-San Joaquin river system, 32; tables showing discharges of, 32, 33.
Sagitta bipunctata, 202.
Salinity of San Pablo Bay, 33, 35, 39, 42. *See also* Teredo diegensis.
Salpa cabotti, 258, 259, 271.

Salpa democratica, distribution, control of, 240, 286, 290; questions on, 241; seasonal, 250, 288, vertical, 251, 288, surface, 252, 288; relations between temperature and surface distribution, 252–261, 288, 289, bearing of on morphology, 256, on locomotion, 261; existence of protruding chains, 258, 290.
life cycles, 241; relation between season and temperature, 262, between position and temperature, 265; viscosity theory, 269, 290; peculiarities in temperature relations, 274–281, 289.
locomotion, theory of, 271, 286; conditions deduced from, 276, 279, 280.
Salpa democratica, **Differentials in Behavior of the Two Generations of, Relative to the Temperature of the Sea,** 239.
Salpa fusiformis, 260, 272.
zonaria, 260.
San Diego, California, 68, 448.
San Francisco Bay, distribution of shipworm in, 27–43; temperature of, compared with that of Chesapeake Bay, 38; physical characters of, 301; temperature, 302, salinity, 302–303; diversified bottom, 303; molluscan fauna of, 303–308; economic considerations concerning, 308–317.
San Joaquin and Sacramento river systems, 32, 33.
San Pablo Bay, presence of shipworms in, 29–42; physical conditions of, 31; salinity of, 33, 35, 39, 42; temperature of, 36.
San Quentin, Point, 316.
Sars, M., cited, 172.
Sausalito, California, 431, 435.
Saxidomus nuttalli, 303, 308, 310, 313, 315, 320, 321.
Schistosoma haematobium, 485; intermediate hosts, and larval stages of, 488; cercaria of, 488; position of miracidium, 509; hatching of embryo, 516; excretory system of miracidium, 518. *See also* S. japonicum; S. mansoni.
Schistosoma japonicum, method of transmission, 486; discovery of intermediate host, 487; egg and miracidium of, 514–518; rudimentary spine, 514–515.
Miracidium, 515; extrusion of oil globules, 516; hatching of embryo, 516–517; cephalic glands, 518; excretory system, 518. *See also* Schistosoma haematobium; S. mansoni.
Schistosoma japonicum, **Japanese Blood Fluke, Cercaria of the,** 485.
Schistosoma mansoni, cercariae of, 488, 489; egg and miracidium of, 509–519; egg shell, 510; figure of egg, 510.
Miracidium, shape, 510; cephalic glands, 511; nervous system, 512; excretory system, 513; figures of, 517; flame cells, 513; symmetry, 514; figures of, 511, 512, 513; extrusion of oil globules, 515–516. *See also* S. japonicum.
Schistosomiasis, 487, 489.
Schizothaerus nuttalli, 303, 307, 308, 310, 314, 315, 320.
Schott, G., cited, 191, 200.
Schuberg, A., cited, 378.
Schurig, W., quoted, 283.
Schütt, F., cited, 411.
Scripps Institution for Biological Research (Marine Laboratory), 99, 151, 400.
Scyllium, genus, 168.
canicula, 479.
Scymnus lichia, 152.
Seligmann, C. G., cited, 516.
Setchell, W. A., cited, 175.
Sharp, R. G., cited, 350, 352, 366, 378, 379, 381, 384; quoted, 365.
Shipworm. *See* Teredo diegensis.
Shipworm in San Francisco Bay, California. An Unusual Extension of the Distribution of the, 27.
Sigerfoos, C. P., quoted, 37.
Siliqua nuttalli, 308, 311, 315.
Smith, A. J., cited, 516, 517.
Solen sicarius, 303, 312, 315, 320.
Soule, H. B., U.S.N., member of board for survey of San Francisco Bay, 300.
South Africa, 488.
Spinax, 168.
Spiraulax, genus, 416, 440, 459.
Spirostomum ambiguum, 380.
Spisula catilliformis, 303, 312, 320.
Squalus sucklii, figure showing subclavian vein and its relations, 480, 482, 483.
Stefanonympha, genus, 383.
Stein, F., cited, 368.
Stentor coeruleus, 371, 378, 379.
niger, 380.
Steuer, A., quoted, 282.
Sthenelais, 127.
Stockard, C. R., 210.
Stovaine, effect of, on nerve cord of earthworms, 116, 143.
Straub, W., cited, 120, 121, 136, 142.

Strombidium testaceum, 371.
Stylonychia, 341, 356, 378, 380, 381.
Styloplotes, genus, 338.
Subclavian Vein, The, and Its Relations in Elasmobranch Fishes, 479; studies on, in Heptanchus, Mustelus, and Squalus, 480–483.
Sumner, F. B., acknowledgment, 241, 300; member of board for survey of San Francisco Bay, 299.
Sumner, *et al.*, cited, 32, 34, 35; acknowledgment, 300.
Suzuki, M., 487; cited, 487.
Swezy, Olive, 89; acknowledgment, 2, 173, 340; cited, 9, 366, 382, 383.
Tellina buttoni, 303, 320, 321.
salmonea, 303, 320, 321.
Temperature in abyssal waters, 191, in the Pacific Ocean, 191, 192–197, off the Pacific Coast of North America, 199, 201; factor in distribution of fauna and flora, 200, 202, 203, 205. *See also* Salpa democratica; San Francisco Bay; San Pablo Bay.
Teredo diegensis, absence, and presence, in regions of San Francisco Bay, 27, 28, in San Pablo Bay, 29; activity of, 28, 40, 42; destruction done by, 29, 30, 37, 39; effect of salinity on, 36, 42; sensitiveness of, 41.
dilatata, 37.
navalis, 37.
Thais lamellosa, 303, 304, 305, 307, 320, 322.
Thelepus, 216.
Thon, K., cited, 380, 384.
Tivila crassatelloides, 308.
Tower, W. L., cited, 210, 225.
Tragosome harrisii, 205.
Transmission, The, of Nervous Impulses in Relation to Locomotion in the Earthworm, 103.
Treadwell, A., acknowledgment, 172.
Trichoda, genus, 338.
Trichomonas, genus, 382.
Tripsolenia, genus, 403.
Tsuchiya, I., cited, 486, 487.
Turbonilla franciscana, 303, 320, 321.
keepi, 303, 320, 321.
Turris, cf. incisa, 303, 321.
Union Bay, Alaska, 431, 457.
United States Bureau of Fisheries, Biological Survey of San Francisco Bay, 299.
Unusual Extension of the Distribution of the Shipworm in San Francisco Bay, California, 27.
Uronychia, 370, 371, 372.
Urosalpinx cinereus, 314, 330.
Venezuela, 488.
Vogt, C., 95.
Vorticella, 363.
Walcott, C. D., cited, 171.
Wallengren, H., quoted, 371.
Webber, H. J., cited, 384.
Wenyon, C. M., cited, 1, 21.
Werner, H., cited, 1.
Westwalde, Germany, 401.
Whiting, P. W., cited, 370.
Willemoes-Suhm, R., cited, 212.
Wilson, C. W., cited, 366, 381, 385.
Wooley, P. G., cited, 515.
Wyville Thomson's Ridge, 202.
Xylotrya gouldi, 37.
setacea, 27.
Yamamoto, J., cited, 486.
Yes Bay, Alaska, 429, 448.
Yocom, H. B., 337.
Zirfaea gabbi, 303, 304, 305, 307, 320, 321, 322.

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BY
WILLIAM C. BOECK

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CONTENTS

	PAGE
Introduction	1
Material and technique	2
Table of infection	3
Morphology	4
Parabasal bodies	8
Mitosis	11
Prophase	11
Metaphase	16
Anaphase	16
Telophase	17
Correlations of mitosis with cytoplasmic structures and changes	18
Neuromotor apparatus	19
Cysts	20
Conclusions	22
Literature cited	24
Explanation of plates	25

Introducton

The investigations of Kofoid and Christiansen (1915*b*) on *Giardia muris* showed that multiple and binary fission were carried on in the free state of the flagellates as well as during encystment, contrary to the conclusion of Wenyon (1907), Prowazek and Werner (1914) and others. Previous to this work, no evidence had been discovered for the occurrence of multiple fission either in the free state or during encystment. While the investigations on *Giardia muris* were being carried on, a new species, *Giardia microti,* was discovered in the meadow mouse, *Microtus californicus californicus* (Peale).

In order to affirm further the work of Kofoid and Christiansen with regard to binary fission occurring in the free state of the flagellate and also to set forth the process of mitosis, investigations were made upon this new species, *Giardia microti.*

I wish to acknowledge to Professor Charles A. Kofoid and to Dr. Olive Swezy my appreciation of the help given me in the various features of this research.

Material and Technique

The meadow mice were collected in fields about a mile from the University campus. These fields have an abundant growth of long grass in which the runways of these mice are easily found. In the afternoon the common "Catch 'em alive" traps were set in these runways, having been previously baited with crushed barley. The mice were collected the following morning from the traps.

Most of the trapping was done during the rainy season, characteristic of winter months around Berkeley, and as a result many of the mice were found dead from exposure in the traps. Often, however, I could not make an examination of these dead mice the same day I collected them, but waited until the second day; even then the parasites were often found to be living.

Ordinary smears upon cover-slips were employed. These were made by cutting out a piece of the intestine about five millimeters long, moistening it with normal salt solution, and smearing it over the surface of the cover-glass. This was done in order to obtain the flagellates which adhere to the mucous lining of the epithelium as well as those in the lumen. Thin smears were prepared from faeces in the rectum and colon, the material being rolled out upon the cover-slip, in normal salt solution.

The smears on the cover-slips were fixed in hot Schaudinn's fluid and stained in aqueous iron haematoxylin. Mallory's connective-tissue stain was also used. It was of importance in bringing out the neuromotor apparatus. The intracytoplasmic fibrils stain a bright red therein, but it was not satisfactory as a nuclear stain. Counter-staining with eosin made a clear differentiation between the cytoplasm and the chromatin, and enabled one to trace the course of the flagella, but upon the whole gave no advantage in the study of mitosis.

The data in this paper are based on the examination of twenty-three mice, all of which were *Microtus californicus californicus* (Peale). From the table given below, it will be noticed that four of the mice contained no parasites, but that these four had been dead several hours at the time the examination was made. The remaining nineteen mice were infected, thus making a very high rate of infection.

TABLE OF INFECTION

Series	Date	Condition of host	Slides prepared	Colon	Infection small intestine	Sex
1	11/1/15	Alive	8	.....	Slight	?
13	12/30/15	Dead several hours	7	.....	Slight	♂
14	12/30/15	Dead several hours	17	.....	Heavy	♀
15	12/30/15	Dead several hours	....	.....	.....	♂
16	12/31/15	Dead 2 days	23	.....	Heavy	♂
18	12/31/15	Dead 2 days	7	.....	Fair	♂
20	1/4/16	Dead several days	....	.....	.....	♀
21	1/6/16	Alive	62	.....	Heavy, (cysts)	♀
22	1/19/16	Alive	7	.....	Slight	♀
23	1/28/16	Dead 1 day	5	.....	.....	♂
24	1/28/16	Dead 1½ days	9	.....	Fair	♂
25	1/28/16	Dead 1½ days	13	.....	Fair, (cysts)	♂
26	2/13/16	Alive	17	.....	Fair	♂
27	2/28/16	Dead (time?)	....	.....	.....	♀
28	3/2/16	Alive	12	.....	Heavy	♀
29	3/4/16	Alive	36	Cysts	Heavy, (cysts)	♀
30	3/17/16	Alive	22	Not examined	Heavy	♂
31	5/1/16	Alive	6	*Hexamitus*	Slight	♀
32	5/1/16	Alive	12	Not examined	Heavy	♀
33	5/8/16	Alive	16	Very few cysts	Heavy, (cysts)	♀
34	5/16/16	Alive	2	.....	Fair	♀
35	5/16/16	Alive	5	.....	Heavy	♀
36	2/8/17	Alive	8	Not examined	Heavy, (cysts)	♀

It would seem from the data set forth in the table that these flagellates are very resistant to the degenerative conditions in the tissues of the host which ensue at the time of death. Of the twenty-three mice examined, ten were dead; of these, six still showed the intestinal flagellates present. In two instances the parasites were still living in great numbers, after the host had been dead two days. *Giardia microti* seems to differ from *Giardia muris* in resistance, the latter remaining alive for only a few hours, while the former lived for two days. Because of this characteristic hardiness, it seems as if they should thrive under cultural conditions.

Attempts were made to obtain cultures by placing some of the intestinal contents with normal salt solution in a cell slide sealed with vaseline. The parasites lived for only a short time in the preparations.

It will be noticed, from the table, that the duodenum seems to be the natural habitat of these flagellates. In series 29 and 33 a few were found just below the caecum, probably preparing for delayed encystment, or were there through contamination, some forms having remained on the forceps used in the making of previous smears from the duodenum. In series 21, 25, and 29 cysts containing only one

individual each (pl. 1, fig. 12) were found at the posterior end of the duodenum and close to the caecum; in series 29 and 33 the cysts were found not only in the small intestine but also in the colon and rectum, the smears having been made from the faeces. These cysts showed single individuals with two nuclei (pl. 1, fig. 12) and the so-called "copulation" types (Schaudinn, 1903; Rodenwaldt, 1911) with two individuals in the back-to-back, end-to-end position, and a total of four nuclei. The latter type is shown in plate 1, figures 13 and 16. In series 33 and 36, cysts with many nuclei (pl. 1, fig. 14) were very abundant in the small intestine, but only a very few were present in the colon.

With regard to the pathogenicity of these parasites, Kofoid and Christiansen (1915*b*) found that *Giardia muris* caused a chronic enteritis; that the walls of the intestine become orange or yellow in color, flaccid and often inflated with gas. In the case of the meadow mouse, a chronic enteritis accompanied by the erosion of the mucous lining, and the disintegration and falling away of epithelial cells and even of whole villi into the lumen, are the main visible pathogenic effects.

The gas inflation did not occur in mice examined by me; this condition as found in *Peromyscus* infected with *G. muris* is probably due to the presence of certain gas-producing bacteria and not to the presence of the flagellates. There is no evidence at hand that *Giardia microti* causes a dysentery in the meadow mouse as *Giardia intestinalis* causes in man.

That these parasites in turn undergo parasitism, which leads to deleterious results, is seen in the fact that they are at times covered with rod-like bacteria, many adhering to the flagella and some occurring as inclusions within the body itself (pl. 1, figs. 3, 15). The identity of these bacteria could not be determined. They occurred in only two series of preparations. They appear to be surrounded by a clear space, filled with a liquid and walled off from the rest of the body by a membrane, or they may be situated in a vacuole.

Morphology

The parasites were found to vary from 6 to 16μ in length and from 4.5 to 8μ in width. The body as seen from the dorsal or ventral surface is pyriform in shape, and, from a partial side view, the dorsal surface or back is arched (pl. 1, fig. 8). The anterior end of the parasite is semi-circular. Posteriorly the body tapers gently or abruptly to form the caudal area. This caudal area is well developed in this species,

and presents an appearance not unlike that characteristic of *Giardia intestinalis* (see Rodenwaldt, 1911).

The cytoplasm is finely granulated, sometimes appearing quite uniform in texture, except at the time of and during encystment, when some degree of coarseness is usually present. The cytoplasm in the area of the cytostome and in the triangular halo enclosing the caudal portion of the axostyle and bordered by the intracytoplasmic portions of the posterolateral flagella is of a still finer constituency and more finely granulated than that in the other parts of the body.

Compared with *G. muris,* the species found in culture mice and *Peromyscus gambeli* (See Kofoid and Christiansen, 1915*b*), *G. microti* is found to be from two to three μ longer, but somewhat narrower. Its caudal area is more tapering, resembling that of *G. intestinalis* as seen in the microphotographs by Rodenwaldt (1911). There is some indication that the cytoplasm of *G. microti* is more finely granulated than that of *G. muris.* The parabasal bodies in *G. microti* are usually slender, elongated bodies, lying dorsal to and across the axostyle, while in *G. muris* these organs are ellipsoidal bodies lying dorsolaterally on either side of the axostyle. The cytostome in *G. microti* is seen to extend more nearly to the periphery of the body than that in *G. muris.*

The body contains the following morphological structures: the *axostyle,* lying medially upon the ventral surfce of the body; two *nuclei,* in the cytostomal area and near the axostyle; a *centrosome,* embedded in the nuclear membrane at the anterior pole of each nucleus; the *rhizoplasts,* connecting the two nuclei with centrosomes and the blepharoplasts and within the nucleus with the central karyosome; and two *blepharoplasts* (united by an anterior commissure), situated on the anterior end of the axostyle. A temporary *paradesmose* stretches between the divided centrosomes of each nucleus at the time of mitosis. The *anterior chiasma* is the point of intersection of the two anterolateral flagella arising from the blepharoplasts. These flagella after leaving this point pass to the side opposite that from which they originated. The anterior and posterior *peristomal fibrils* border the periphery of the cytostome; the anterior right and left fibrils are thicker than the posterior fibrils. The *parabasal bodies,* composed of one or two bands of chromatic material, are situated in the posterior third of the body, and lie upon the dorsal surface of the axostyle.

There are eight flagella: a pair of *anterolaterals* which border the anterolateral edges of the animal; a pair of *posterolaterals* whose intracytoplasmic portions bound the outer limits of the clearer cyto-

plasm in the caudal area; a pair of *caudal* flagella which arise from the posterior tip of the axostyle or axostyles; and a pair of *free ventrals,* arising upon the axostyle a short distance back from the blepharoplasts. *Basal granules* are sometimes visible at the posterior end of the axostyle, and where the free parts of the anterolateral flagella emerge from the cytoplasm (pl. 1, fig. 2).

The separate structures enumerated above may now be treated more fully, as to structures, position, and possible function.

The two oval-shaped nuclei lie on either side of the axostyle in the cytostomal area. In the resting stage (pl. 1, fig. 1) each nucleus contains a central ovoid karyosome surrounded by a hyaline space, which in turn is enclosed by a very definite nuclear membrane. I could find no signs of peripheral chromatin in the nuclei. The major axes of the nuclei are slightly directed toward each other anteriorly. The karyosome is connected to the centrosome on the nuclear membrane at the anterior pole by a small intranuclear rhizoplast; and the centrosome in turn is connected with the blepharoplast by a small extranuclear rhizoplast (pl. 1, fig. 1). By means of these rhizoplasts and the anterior commissure, the nucleus, centrosome, blepharoplast, and flagella of one side are connected with those of the other side, thus forming one integrated system, designated by Kofoid and Christiansen (1915) as the neuromotor system.

The centrosome of each nucleus, previous to division, varies in size; it lies on the nuclear membrane at the anterior pole of the nucleus. The centrosome of each nucleus is connected by a slender rhizoplast with the nearest blepharoplast at the head of the axostyle. When the axostyle splits, the anterior commissure may for a time remain intact, thus connecting the blepharoplasts of each new axostyle head; and when the axostyle is not split it appears as a fibril making possible the establishment (pl. 1, fig. 1) of direct connection between the karyosome of one nucleus and the karyosome of the other nucleus. A *paradesmose* was best demonstrated with Mallory's connective tissue stain; this fibril connects the two divided centrosomes of each nucleus and always lies outside of but closely applied to the nuclear membrane (pl. 1, figs. 5, 6, 7). It is a recurrent cell organ in this species.

The two blepharoplasts united by a fibril, the anterior commissure, lie embedded in the material at the head of the axostyle. The blepharoplasts appear to initiate mitosis, for they are the first organelles to divide and are followed by the cleavage of the axostyle. That this is the case is evidenced by the large number of forms having a partial

separation of the axostyle, but as yet there is no mitotic change in the nucleus, or a cleavage of the centrosome. This, however, as will be shown later, is the final step of the preceding mitosis. When the blepharoplasts divide, resulting in two smaller blepharoplasts on each axostyle head, there may be also a splitting of the anterolateral flagella extending from the blepharoplasts to the anterior chiasma, although this condition is variable (pl. 1, figs. 9, 17).

Of the eight flagella, the anterolaterals, arising from the blepharoplasts, proceed anteriorly, cross each other to form the anterior chiasma, and then, going to the sides opposite to their place of origin, lie in the anterior peristome. The intracytoplasmic portions of these flagella fuse or partially coalesce with the anterior peristomal fibrils, and are seen to proceed backward, each one later emerging from a basal granule as a free flagellum. Often the anterolateral flagella fuse or partially coalesce with the anterior peristomal fibrils, thus causing these fibrils to be wider than in their usual state (pl. 1, figs. 1, 2, 7).

The pair of posterolateral flagella seem to arise, as has been said before, at a point on the axostyle a short distance back from the blepharoplasts. This is contrary to the findings of Benson (1908), who pictures each intracytoplasmic portion as having a special point of origin, a basal granule situated alongside of the blepharoplasts. But the evidence on hand in my material does not confirm his findings. As these flagella continue posteriorly in their course, they diverge from the axostyle at an angle of 20° to 30° in a lateral direction. The intracytoplasmic portion is more rigid and thicker than that part of the flagellum which continues outward as a free whip. There is no basal granule discernible at the end of the intracytoplasmic portion.

These intracytoplasmic portions of the posterolateral flagella are close to the surface of the cytoplasm. Observations of living forms show them to be active, as scull-like propellers in the locomotion of the parasite. They vibrate in a co-ordinated wavelike manner from side to side, the vibration starting at the origin of each intracytoplasmic portion and continuing outward to the end of the flagellum. This movement is possibly due to the extreme plasticity of the caudal area of the flagellate's body. At no time were the intracytoplasmic parts seen to be separated from the body.

The pair of free ventral flagella take origin at or near the same point at which the posterolateral flagella arise, but they have no intracytoplasmic portions. In locomotion they are seen to trail behind, and

like the other flagella vibrate in the characteristic wave-like manner, the waves always progressing anteroposteriorly.

The axostyle lies on the ventral floor extending from the caudal area anteriorly, well into the cytostomal area. It lies in the median plane. Bensen (1908*b*) describes the axostyle as double, composed of two chromatinic rods; the blepharoplasts situated at their anterior extremities, each rod continuing posteriorly in a free flagellum. But according to investigations of Kofoid and Christiansen (1915*a* and *b*) there is more evidence to show that the axostyle is a single rodlike structure and not a double one, for throughout their study of mitosis in *Giardia muris* they found that the axostyle split, forming new ones for the new individuals. In no case did they find four rods, as must be the result of splitting had the axostyle been composed of two rods as Bensen (1908*b*) believed. My work on *Giardia microti* confirms on this point the findings of Kofoid and Christiansen. The axostyle may now be said to consist of a single rod, terminating anteriorly with the two blepharoplasts and posteriorly with the two caudal flagella. It is but a single undivided rod except as mitosis approaches.

In many cases a basal granule can be seen at the point at which the posterior or caudal flagella take origin (pl. 1, figs. 2, 7). It would seem quite justifiable to regard the axostyle as the intracytoplasmic portion of the caudal flagella, and therefore probably of flagellar origin (Kofoid and Swezy, 1915). When the axostyle has completely split, one flagellum goes to each daughter axostyle (pl. 1, fig. 9); the continuity of the intracytoplasmic portions with each caudal flagellum is easily followed. The axostyle was never observed free from the body of the flagellate. It is very flexible and may bend upward and downward or to either side, acting in such a way as to direct the course of the flagellate in locomotion.

Parabasal Bodies

The parabasal bodies, composed of one broad, or two narrow bands of deeply-staining material which in some cases appear to be fused in one body, are situated dorsal to the axostyle and at the end of the anterior two-thirds of the body (pl. 1, fig. 1). These organs lie in a median plane, extending either to the right or left of the axostyle. In figure 8 it seems to lie directly upon the axostyle, or (as in figure 12) it may be connected with the axostyle by one or more slender fibrils. It plays no part in mitotic activity. The character of these bodies in *Giardia microti* has a striking resemblance to that of similar structures found in *G. intestinalis* (see Rodenwaldt, 1911). Rodenwaldt (1911)

expresses no theory as to the functions of these bodies, but believed their presence to be a criterion for determining the age of the flagellates. He says that the bodies are present in *old* forms and not in *young* forms. This conclusion, however, is unwarranted from the study of *G. muris* (Kofoid and Christiansen, 1915*b*) and from my study of *G. microti,* for both small and large forms may be found without this organ.

In another group of organisms, the trichomonad flagellates, the parabasal rod is correlated with the well-developed undulating membrane (Kofoid and Swezy, 1915). They found that "in the absence of such a localized area the parabasal body or homologue is often more condensed (not however in trypanosomes) and lies nearer the blepharoplast and nucleus, as in *Parajoenia.*" Their final conclusions, however, are that its function is "not primarily skeletal, or supporting, but rather connected with the metabolism of, and possibly also with the control of, the motor activity."

With regard to the function of the parabasal bodies in *Giardia microti* an hypothesis may be made based on the evidence revealed in the study of both the vegetative and encysted forms. From this study I am led to believe that these parabasal bodies are conveniences on the part of the flagellate for coping with the intestinal medium in which it lives; that they are connected with the motor activity and in relation to the metabolism of the flagellate.

Most vegetative forms have this organ well developed, but occasionally some will lack it and they may be either large or small forms (pl. 1, fig. 10); some forms show the organ to be small in size (pl. 1, figs. 4, 11). There are three explanations for these differences: First, an investigation of the parabasals during encystment reveals the evidence that at the end of encystment the bodies are very faint (pl. 1, fig. 14) or entirely absent (pl. 1, figs. 13, 16), so that when plasmotomy occurs the daughter individuals would lack this organ (pl. 1, fig. 13); this would explain the absence of this organ in small forms which recently have been the products of plasmotomy and have not had as yet sufficient time for the organization of these bodies. Secondly, the organ may be fading out due to exhaustion from excessive activity on the part of the host—either motor or mitotic activity in some cases (pl. 1, figs. 10, 11); this may be true in large individuals which may not show evidence of mitosis. Thirdly, its absence may be due to the non-absorption of the stain, due to the biochemical state the bodies were in at the time of the preparation of the material.

Figs. A–O. Mitosis in *Giardia microti* Kofoid and Christiansen. Diagrammatic presentation of the nuclei figured of the individuals illustrated in plate 1. × 11,000 approximately.

Prophase figs. A–K; metaphase fig. L; anaphase figs. M–N; telophase, figs. N–O.

Fig. A. Typical resting stage of nucleus; ellipsoidal karyosome with connecting intranuclear rhizoplast to centrosome.

Fig. B. Mitosis begun; karyosome elongated, extension of linin to posterior periphery of nucleus in the major axis.

Fig. C. Knotlike spireme formed by contraction of chromatin at various points, initiating the formation of chromosomes.

Fig. D. Spireme band, showing longitudinal split progressing anteriorly-posteriorly.

Fig. E. Each spireme strand segmenting into four chromosomes, the action progressing from the centrosome posteriorly.

Fig. F. Eight or tetraploid number of chromosomes completely formed.

Fig. G. Dispersal of chromosomes. Centrosome has divided, one portion migrating to posterior pole of nucleus; paradesmose on outside of nuclear membrane.

Fig. H. Dispersal of chromosomes, linin connecting fibril, paradesmose present.

Fig. I. Anterior chromosomes serially homologous, or sisters, pair with each other. Linin connecting fibrils and paradesmose still present.

Fig. J. Pseudosynapsis, in a side-by-side or parasynaptic union of sister chromosomes completed, forming four bivalent chromatinic masses. Linin suspending the four masses and paradesmose present.

Fig. K. Four chromatinic masses; paradesmose present; linin assuming spindle-like form.

Fig. L. Four chromatinic masses on spindle formed from linin. Chromosomes dividing apparently in a transverse plane, but in what probably marks the end of a longitudinal division; paradesmose no longer visible.

Fig. M. Showing chromosomes after their division on the spindle, beginning their migration to their respective poles of the nucleus.

Fig. N. Chromosomes at each pole fused into single mass; constriction of nuclear membrane.

Fig. O. End of mitosis; two rounded nuclei with central karyosome. Upper nucleus showing rhizoplast from centrosome to blepharoplast (not figured).

The evidence for the connection of the parabasal bodies with motor activity is mostly morphological in that this organ is found directly upon the axostyle, a unit of the motor apparatus of the free vegetative organism. Often these connections can be demonstrated in the cysts (pl. 1, fig. 12) ; here the connections are very slender fibrils.

By far the best evidence for the metabolic nature and relationship existing between the parabasal bodies and the organism as a whole is gained from a study of the cysts. It was found that all forms encysting had the parabasal bodies, but that they became very much hypertrophied (pl. 1, fig. 12). This is explained by the fact that by virtue of encystment all motor activity is slowed down or ceases, and so the draft upon the reserve food-supply in the parabasal bodies decreases or stops and the bodies temporarily enlarge until absorption of food is cut off by the cyst-wall. They then decrease slowly and even disappear. This view gains more evidence when it is found that in those cysts in which binary fission of the flagellate had been completed the parabasal bodies were lacking (pl. 1, figs. 13, 16) and also that in the multinucleate cysts these bodies were either very faint (pl. 1, fig. 14) or entirely lacking; in explanation, the bodies had become physically exhausted because of the metabolic activity which must necessarily have taken place in the cyst, while the original source of food-supply had been progressively cut off.

That these bodies are conveniences to cope with the varying intestinal medium would appear to be established since thus far it has been found that only the entoparasitic organisms have these parabasal bodies well developed.

MITOSIS

Mitosis in *Giardia microti* presents stages characteristic of the prophase, metaphase, anaphase and telophase which are in many respects homologous to these phases of mitosis in Metazoa.

Prophase

The prophase, in which the chromatin is getting ready for its equal division in the metaphase, is especially marked by the complexity of nuclear changes, most of which occur previous to the division of the centrosomes which is the forerunner and initiator of mitosis in the Metazoa.

At the time when the first mitotic activity occurs, the division of the blepharoplasts and the beginning of the splitting of the axostyle

has been completed (pl. 1, fig. 2), but these cytoplasmic changes have come about long before the division of the centrosome (pl. 1, figs. 5, 6, 7). The division of the blepharoplast in trichomonad flagellates initiates mitosis, and the question now arises as to the significance of this division in *Giardia microti* at the time when mitosis has begun, yet previous to the division of the centrosomes.

If we consider that *Giardia* has evolved as a two-celled individual from a unicellular trichomonad flagellate which had undergone mitosis but no plasmotomy or division of the cytoplasmic body, then this point can be easily explained. In the mitosis of trichomonad flagellates, as has been said before, the blepharoplasts initiate mitosis by dividing and forming a paradesmose between the two daughter blepharoplasts; these blepharoplasts become the poles of the spindle. They appear in function to be centrosomes as well. However, they still act as the central point at which the new undulating membrane and the new flagella will form and so must be considered blepharoplasts (see Kofoid and Swezy, 1915). It is very significant that in the anaphase these daughter blepharoplasts temporarily divide to form two smaller granules, one a "centrosome" and the other a "basal" granule or blepharoplast *with the paradesmose connecting the basal granules or blepharoplasts.* This paradesmose in all probability corresponds in part to the anterior commissure in *Giardia microti*, the fibril connecting the two blepharoplasts (pl. 1, fig. 1), which has here become a permanent structure. It is thus evident that *Giardia* is a two-celled animal derived from a trichomonad flagellate which had gone through mitosis but not plasmotomy. In the trichomonad flagellates these new centrosomes are only temporary structures and in the telophase the separated centrosome and blepharoplast reunite to become the permanent blepharoplast. Hence this blepharoplast contains the centrosome. In *Giardia* this fusion of the centrosome and blepharoplast has not taken place, but the separation is permanent, each centrosome occupying a position on the nuclear membrane at the anterior pole of each nucleus while the blepharoplast becomes a separate organ at the head of the axostyle (pl. 1, fig. 1).

Now then, when the axostyle does divide at the time of mitosis in the prophase in *Giardia,* this division represents only the delayed division of this part which would ordinarily have taken place in the trichomonad stage of the organism after the completion of mitosis. This structure is now divided to provide the two axostyles of the new daughter individuals which will later separate after mitosis by plas-

motomy. A large central, ellipsoidal karyosome, connected by an achromatic fibril, linin in nature, to the centrosome (pl. 1, fig. 1; text-fig. A) is characteristic of each nucleus in the resting stage. The first mitotic change in the prophase consists of the extension of this linin fibril posteriorly to a point on the nuclear membrane (pl. 1, fig. 1; text-fig. B) and the expansion of the chromatin of the karyosome to form a long, slender, ellipsodial karyosome.

It is to be noted that thus far the nuclear changes have been of such a nature as to make more pronounced a polarity in the nucleus. This is marked by the extension of the linin fibril posteriorly and the expansion of the chromatin anteriorly and posteriorly on it. This polarity of the nucleus can be followed in later stages. It is related to the polarity exhibited by the cytoplasmic structures, especially to the main axial structure, the axostyle, which defines the poles and main axis of the body of the organism itself, although the axes of the two nuclei are not quite parallel to this major axis of the body. The longitudinal and what appears to be an equivalent splitting of this spireme to form two single, somewhat ragged spireme strands in each nucleus soon follows (pl. 1, fig. 3; text-fig. D). The splitting begins in the area adjacent to the centrosome and proceeds posteriorly and completely through the spireme band. These two spireme strands in each nucleus soon show the beginnings of the differentiation of the chromosomes by localized knotting up of the substance, which exhibits itself first at the end nearest the centrosome (pl. 1, fig. 3, right nucleus; text-fig. D). Thus from this progressive action in the splitting of the spireme and in the formation of the chromosomes, the centrosome, the center of mitotic activity, exerts its influence on the mitotic process.

After the formation of the split spireme, localized contraction and tranverse segmentation of the chromatin on these strands ensues to form four chromosomes from each strand, or eight chromosomes for the tetraploid number of each nucleus (pl. 1, fig. 6; text-fig. F). An intermediate stage shows the chromosomes first completely formed nearest the centrosome, again giving evidence of the fact that mitotic activity proceeds from the still undivided centrosome, as though under its influence, towards the opposite pole. The chromosomes are seen to be connected end to end by linin fibrils, forming two chains of four chromosomes each. These chains are in most cases parallel to the major axis of the nucleus, thus maintaining the same polarity (pl. 1, figs. 4, 5, 6).

It is significant to note here that the chromosomes arrange themselves into two groups of four each and that the line of separation is at the equator of the nucleus (pl. 1, fig. 5; text-fig. F). This suggests the possibility of a biparental origin of the chromosomes, and indicates the probability of the occurrence of sexual reproduction in *Giardia,* but there is as yet no evidence for this assumption. The linin connecting fibrils between chromosomes are present at this stage of mitosis.

The chromosomes appear to be oblong in shape, about 0.3μ long and about 0.2μ in width. The chromosomes derived from a single spireme strand in a nucleus show immediately after their formation a tendency to pair off with the adjacent chromosomes derived from the other spireme strand of the same nucleus (pl. 1, fig. 5; text-fig. F). The chromosomes appear to be very much alike in shape and size. More evidence for polarity within the nucleus is displayed by the chromosomes in that their long axes are parallel to the long axis of the nucleus itself, as the chromosomes are differentiated in two linear axial lines in the nucleus (pl. 1, fig. 5; text-figs. F, G).

Thus far it must be noted that all these mitotic changes, including the formation of the eight or tetraploid number of completely divided chromosomes, have taken place *before the division of the centrosome* or any evidence of activity therein, and that throughout the process thus far all nuclear changes have consistently displayed a polarity related to that of the polarity of the nucleus itself and of the organism as a whole in the direction comparable to that of the axial gradient of Child.

On the division of the centrosome of each nucleus at this time, one daughter centrosome remains fixed while the other one migrates to a point on the periphery of the nucleus at the opposite pole 180° from its original situation, and here marks the posterior pole of the spindle to be formed later (pl. 1, fig. 5; text-fig. G). A paradesmose lying outside the nucleus but closely applied to the nuclear membrane is formed as a connecting fibril between the two daughter centrosomes.

The chromosomes at this stage, as has been previously stated, may often be seen to be still connected in an end-to-end manner by linin fibrils, but there is a tendency now for them to disperse throughout the nucleus; this progressive stage and the one preceding are often found in the two nuclei of the same individual (pl. 1, fig. 5). Because of this dispersal there is given the opportunity for a rearrangement of the chromosomes different from that of their first order, but there

seems, however, a tendency for them to return later to approximately the same position as that which they occupied in the split spireme when first formed. The uppermost chromosome of each spireme band comes to lie side by side with its mate of the opposite strand (pl. 1, fig. 6; text-fig. I). Lower chromosomes continue this pseudosynaptic side-by-side pairing. After this pairing a rather intimate lateral fusion of these pairs takes place. This is a fusion on a plane identical, or at least parallel, with that of their original separation. What is probably the beginning of this pairing and fusion of chromosomes number 1 is seen in the uppermost end of the left nucleus in figure 6 (plate 1), while the same chromosomes in the right nucleus also appear to be approaching each other. The end result of this fusion is four chromatinic masses, each composed of two chromosomes which have previously split and then fused (pl. 1, fig. 7; text-figs. J, K). Here again there is evidence that each one of these masses is so situated that its long axis is still nearly the same as that of the nucleus and approximately that of the whole cytoplasmic body. This is also true for plane of fusion, which is parallel to the plane which involves the long axis (pl. 1, fig. 7; text-fig. J).

The spindle is now formed from the linin of the nucleus. Just previous to spindle formation the linin is a central mass upon which the four chromatinic masses are situated (pl. 1, fig. 7; text-figs. J. K). Often it seems to be shaping itself into a spindle-like structure approaching prematurely the structure of the later spindle (pl. 1, fig. 7, left nucleus). The spindle may partially or entirely fill the nucleus (pl. 1, figs. 8, 9). The condition in which the spindle partially fills the nucleus is probably due to plasmolysis at the time of the fixation of the material.

With spindle formation, these four chromatinic masses come down into the equatorial plate (pl. 1, fig. 8; text-fig. L). On the spindle they appear to be elongated and to be getting ready for *tranverse* division in the metaphase. Because of the position of these chromatinic masses on the spindle it is probable that when the chromosomes previously fused side by side (pl. 1, fig. 7) they next began to pull apart at one end and this proceeded more and more until finally these chromosomal members of each chromatinic mass came to an end-to-end position, though still fused in that region and are shown in this stage (pl. 1, fig. 8) in the equatorial plate on the spindle ready for final separation at the close of the metaphase.

This pairing of chromosomes and their subsequent fusion might

be called a pseudosynaptic phenomenon. There is no evidence that a true synapsis occurs in any premitotic phases observed by me, moreover, thus far no sexual reproduction has been discovered in *Giardia*. Since, however, each chromosome seems to show a tendency in this stage in ordinary vegetative mitosis to fuse with the corresponding chromosome of its sister spireme strand, this relationship is strictly one devoid of all true synaptic relations, and so can be looked upon as wholly *pseudosynapsis*.

Metaphase.

The four chromatinic masses now at the equator of the spindle appear to divide by transverse constriction through the center of each mass (pl. 1, fig. 8; text-fig. J); the division is equal. It results in the re-formation of eight chromosomes, two each from the four masses formed from four chromosomes which had previously split and then come together and fused. But, as has been said before, this apparent transverse division of these four chromatinic masses is not true transverse fission, but is rather an end-to-end separation, the completion of a division along a longitudinal plane which is identical with the plane of fusion of the two chromosomes.

Again the chromosomes seem to be of uniform size (pl. 2, fig. 9) and there is evidence here of their recent separation from other chromosomes (pl. 2, fig. 9, left nucleus). For convenience we may consider the chromosomes in this nucleus in the right and left hemispheres. The two chromosomes above the equator in the right hemisphere were probably separated from the two chromosomes below the equator in the same hemisphere. Likewise the two chromosomes above the equator in the left hemisphere were separated from the other two chromosomes below the equator of the same hemisphere. It is possible that these four chromosomes in the left hemisphere which are farther separated from each other than those in the right hemisphere are the upper chromosome pairs, and that, as in previous stages they were formed first because of their proximity to the centrosome, so here, not for the same reason, but because of their holding on to their property of priority of change, they have been the first to become separated and already have migrated farther than those in the right hemisphere.

Anaphase

This phase is noted by the migration of the chromosomes to the poles of the spindle. The beginning of this phase shows the individual chromosomes near each other subsequent to the division in the metaphase (pl. 1, fig. 9; text-fig. M). Often inequality of nuclear changes

on the two sides of the organism occurs. This is exemplified in figure 9, where the left nucleus is in the anaphase, and the right nucleus displays the four chromatic masses previous to their arrangement at the equator of the spindle. Another case, earlier in mitosis, is seen in figure 5.

The chromosomes in the course of their migration fuse into two chromatinic masses, one mass going to either pole (pl. 1, fig. 10; text-fig. N).

Telophase

With the formation of each chromatinic mass produced by the fusion of four chromosomes at each pole, the nuclear membrane begins to constrict (pl. 1, fig. 10; text-fig. N). The completion of this process results in two daughter nuclei (pl. 1, fig. 11; text-fig. O) on each side of the body. The upper two may still be connected by the small extra nuclear rhizoplast to the blepharoplast nearest each centrosome; the intranuclear rhizoplast as yet has not been differentiated (pl. 1, fig. 11) but undoubtedly occurs later as an outgrowth from the linin supporting the karyosomes. The reconstruction of the nuclei except for this intranuclear rhizoplast is thus completed. The linin of the spindle has again collected to form the network upon which the chromatin of the karyosome is suspended. Mitosis is now completed and is to be followed by plasmotomy.

Plasmotomy

Plasmotomy, or the division of the parent cytoplasmic body to form two daughter individuals, is not well understood. Only two cases were found in my material, one of which is figured (pl. 1, fig. 15). But from the study of these two stages and from like study upon *Giardia muris* by Kofoid and Christiansen (1915*b*), the plane of cleavage appears to be longitudinal, and the last point of cohesion of the two daughter flagellates to be at their caudal areas. This would result in the equipment of each daughter flagellate with two of the daughter nuclei, an axostyle, and a complete peristome. Whether or not this is the method in the case pictured in this paper (pl. 1, fig. 15) cannot be definitely determined, for the anterior peristomal fibrils of the lower daughter flagellate are fainter than those of the upper but this may be due to the non-absorption of the stain. The division of the cytoplasmic body is not equal in this case, but this again is similar to cases found in *Giardia muris* (Kofoid and Christiansen, 1915*b*).

Correlation of Mitosis with Cytoplasmic Structures and Changes

That there are effects or changes possible in the cytoplasm which can be correlated with mitotic activity taking place in the nucleus is probably not doubted by any cytologist, but owing to the fact that this problem of finding these correlations in the cells of Metazoa and Protozoa alike is wrapped up with biochemical and physiological complexities, investigation in this field is attended with many difficulties. In the Protozoa, although the biochemical and physiological conditions are as complex as are those of metazoan cells, yet certain definite correlations between mitosis and cytoplasmic structures and changes can be the more readily detected because of the unusual development of cytoplasmic organs in these lower organisms.

The first change to be noted is the division of the blepharoplasts and axostyle at the beginning of the prophase. This division of the axostyle, as has been said in the discussion of mitosis, represents the delayed division of this cytoplasmic organ following and belonging to a previous mitosis. It is a cytoplasmic phenomenon which precedes or initiates the next nuclear divisions, although it is completely detached, except for the rhizoplast, from the centrosome.

The phenomenon of polarity exhibited by the chromatin in its arrangement during the prophase, as well as the direction of the major axis of the spindle, is very significant in that for the most part it is definitely related to the polarity of the body as a whole. Not only was the single knotlike spireme nearly parallel to the major axis of the nucleus, but also the two split spireme strands, and the major axes of the chromosomes when they were completely formed.

Very significant in importance is the seeming influence of the centrosome. It was previously noted under mitosis that in the prophase the distribution of the chromatin of the karyosome proceeded along the axis or rhizoplast originating in the centrosome and extended distally in this axis to the opposite pole to form the single axially located spireme. Again, when this spireme split, the split proceeded from a point in the chromatin nearest the centrosome posteriorly; likewise when the chromosomes were formed the first ones to be completed by segmentation of the spireme strands were located near the centrosomes. The centrosome, even before its division, by the behavior of the chromatin gave evidence of its potential influence over the mitotic process. The entire number of eight chromosomes was, how-

ever, completely formed previous to the division of the centrosomes, but their final separation, after the previous parallel fusion in pairs, came as it does in mitosis of Metazoa, after the centrosomes had divided.

The behavior of the blepharoplasts, and axostyle, the distribution of the chromatin in the nucleus, and the influence of the cytoplasmic structures, the centrosomes afford clear morphological evidence for the correlation of mitotic activity with changes in the cytoplasm.

Neuromotor Apparatus

The evidence of the presence of a unified system of structures which may be closely associated with the motor and sensory activities of *Giardia* was brought forward by Kofoid and Christiansen (1915*a*, *b*). They called this system the neuromotor apparatus.

In *Giardia microti* this same system appears, and here may be briefly described. Figure 1, plate 1, is indicative of what is present in all forms. The neuromotor apparatus may be conceived as constituting here a union of the fibrillar system with the nuclear system. As has been said before, the two nuclei are connected together by rhizoplasts, which on their route join the centrosomes and the blepharoplasts.

The blepharoplasts together constitute the center of the fibrillar system. Connected to the axostyle are the anterior and posterior peristomal fibrils, the posterolateral flagella by means of intracytoplasmic portions, then the free ventral flagella, the pair of caudal flagella, and the parabasal bodies. The anterolateral flagella arise from the blepharoplasts. Thus all the fibrillar and motor parts are connected directly to the blepharoplasts, or indirectly by means of the axostyle, and, since the blepharoplasts are connected directly with the centrosomes and nuclei, there exists a definite integration into a single system of both the nuclear and fibrillar structures. The greatest metabolic activity takes place in the cytostomal area, and here we find the neuromotor apparatus conspicuously in evidence by virtue of the continuous fibril (peristomal fibril) bordering this area. This condition is analogous to the condition found in metazoan animals, such as trematodes and cestodes, wherein we find the presence of nerve-rings associated with sucker-like organs of attachment. Because of the close association of this unified system with the areas of motor and metabolic activities, these regions presupposing the existence of structures for the accommodation of motor and possible sensory

impulses, this unified system has been compared to the nervous system of metazoans, and is probably more closely allied to the mechanism of the reflex arc, and therefore called the neuromotor apparatus. The fibrils stain red in Mallory's connective-tissue stain, which is characteristic of nervous fibrils in the Metazoa.

The neuromotor apparatus forms one entire integrated system for regulating and controlling the motor activities of the organism. The fibrillar division of this apparatus, composed of the eight flagella and their intracytoplasmic portions, are the organelles for locomotion. In the study of living forms all flagella are seen to vibrate synchronously and with the same rapidity when the flagellate lies upon its dorsum. The members of each pair of flagella vibrate together and at the same rate. The axostyle also undulates, as do the intracytoplasmic portions of the posterolateral flagella, the waves of vibration commencing at their proximal ends and continuing outward to the ends of the free flagella. When an increased rate of locomotion takes place it results from increased activity of all the flagella. It appears that the course of the animal in locomotion is directed by the tail, which acts as a rudder bending up and down, or from side to side. When the flagellate comes in contact with an obstacle the axostyle, because of its rigidity, serves as a lever to push away from the impediment.

The turning or rotating movement of the flagellate in locomotion is due to the combination of three factors—the concavity present between the intracytoplasmic portions of the posterolateral flagella; the action of the axostyle in bending up and down and from side to side; and the position and increased activity of the flagella; the direction of their stroke, whether straight back or oblique, is dependent on the position of the flagella, an oblique direction of the stroke tending to rotate the organism (pl. 1, fig. 8).

Cysts

The cysts of *G. microti* are ellipsoidal in shape, varying in size from 6.7×8.5μ to 7×13.3μ. In all cases these cysts are easily identified by the thick, firm cyst-wall and the scattered remains, now and then still intact, of the parabasal bodies and of the neuromotor apparatus. The cysts occur both in the small and large intestine, but predominantly in the latter. Many of the cysts show a condensation of the protoplasm and its withdrawal from the cyst-wall (pl. 1, figs. 13, 16). This is probably due to plasmolysis at the time of fixation in the preparation of the material.

These cysts of *Giardia* were identified very early by various workers, among them Grassi and Schweiakoff (1888), Wenyon (1907), Bensen 1908), and Rodenwaldt (1911). Because of the various morphological aspects which these cysts present during different stages in their development, certain stages have received names designating them as definite types of cysts.

Prior to the appearance of the paper "On Binary and Multiple Fission in *Giardia muris*" by Kofoid and Christiansen (1915*b*), only three types of cysts were identified. The first type, "single individual" cysts (pl. 1, fig. 12), was described by the early investigators, Wenyon (1907), Bensen (1908) and others. The second type, or "binary fission" cyst, contained four nuclei, and direct evidence for the cleavage of the body to form two individuals (pl. 1, fig. 16). The cysts containing four nuclei were seen by Wenyon (1907) and Rodenwaldt (1911). The third type, the "copulation" cyst, included those in which two individuals were found (pl. 1, fig. 13). These differed from the second type in that the organisms, although separate, appeared to be in a state of partial fusion, suggesting copulation. Schaudinn (1903), in a footnote, refers to *Giardia* cysts in which he found two individuals adhering to each other by their cytostomal areas, and interpreted this act as one of copulation. It is from this interpretation that this type has received the name of "copulation" cyst.

It was the prevalent view previous to the paper by Kofoid and Christiansen (1915*b*) that reproduction in *Giardia* took place only within the cysts, for no binary or multiple fission of these organisms had been seen in the free state. This paper, representing the results of work on *Giardia muris,* revealed evidence of the occurrence of binary and multiple fission in both the free and encysted states of *Giardia muris.* The work of Kofoid and Christiansen also disclosed another type of cyst which may be called the "multinucleate" cyst, for in it were found as many as sixteen nuclei. This type was also found in *Giardia microti* by the same workers (see Kofoid and Christiansen 1915*a*). The question was raised by these authors whether certain of these multinucleate cysts with unequal nuclei might represent possible maturation stages or whether the multinucleate condition present was due to "multiple fission of two individuals in the stage of advanced plasmotomy."

In the light of the evidence upon cysts gathered in my work on *G. microti,* the four enumerated types of cysts would seem to resolve

themselves into only three types. The first, that of the "single individual" cysts (pl. 1, fig. 12), the second, "binary" cysts (pl. 1, figs. 13, 16), and the last the "multinucleate" cysts (pl. 1, fig. 14). The binary cyst is in all probability the same as the so-called "copulation" cyst; in the latter case complete separation of the cytoplasmic bodies has occurred, while in the former the cleavage of the parent body is still in process.

In the results of my study of the "multinucleate" cysts there are no grounds for attributing maturation phenomena to the parasite after encystment. No evidence was found which could be interpreted as progressive fusion of two individuals in a cyst; and when nuclei appeared larger, it was because they had another division to undergo; furthermore, no evidence for a reduction of the four ancestral chromosomes to two chromosomes was ever found; the chromatin content appeared equal for all the sixteen nuclei.

The sixteen nuclei came, therefore, as a result of multiple fission, three progressive divisions having taken place.

Conclusions

1. Mitosis in *Giardia microti* presents phases characteristic of mitosis in Metazoa, viz., prophase, metaphase, anaphase and telophase. The normal number of chromosomes is four.

2. The nuclear membrane of each nucleus persists during the entire process of mitosis.

3. The prophase presents many peculiar and complex nuclear changes:

(a) The karyosome elongates to form a single spireme band supported by a linin-like substance in the main axis of the nucleus.

(b) The single spireme band in each nucleus splits longitudinally from the centrosome distally to form two spireme strands.

(c) Each spireme strand segments to form four chromosomes. The segmentation proceeds from the region of the centrosome posteriorly, due to the probable influence of the centrosome.

(d) Through all these stages the chromatin in its distribution on the spireme exhibits a polarity related to that of the body of the flagellate; the long axis of the chromosomes also shows this polarity.

(e) The eight chromosomes formed appear at first in two groups of four chromosomes each, one group above the equator of the nucleus and the other group below, suggesting biparental origin.

(f) The chromosomes are about 0.3μ in length and narrower in width, uniform in size and show little or no differentiation.

4. The centrosomes divide after the formation of the eight chromosomes; a paradesmose is formed between the daughter centrosomes, one of which migrates 180° and the other stays fixed at the position of the parent centrosome.

5. Dispersal of the chromosomes in the nucleus takes place, followed by their pairing in an order which seems to be that of their former splitting and constriction in the spireme strands. The uppermost chromosome of one spireme strand fuses with its mate of the sister spireme strand, etc. This is a pseudosynaptic phenomenon.

6. The four chromatic masses thus formed come down on to the spindle formed from the linin.

7. Later the chromosomes of each mass all appear in an end-to-end position before final separation in the metaphase.

8. In the metaphase, what is apparently a transverse division of the chromatic mass to form the equivalent and uniform chromosomes, is in reality the end of a longitudinal splitting which commenced previous to or at the time of the metaphase. The original plane of fusion becomes the plane of division in the metaphase.

9. In the anaphase the four chromosomes migrating to either pole in each nucleus fuse to form a chromatic mass near each pole of each nucleus.

10. Completion of the constriction of the nuclear membrane results in four daughter nuclei in which reconstruction has taken place.

11. The division of the axostyle prior to mitosis represents the cytoplasmic change of a previous mitosis.

12. All changes in mitosis are closely correlated with structural changes in the cytoplasm.

13. The cysts may be grouped under three types: (*a*) "single individual" cysts; *(b)* "binary fission" cysts; *(c)* "multinucleate" cysts; no stages were found in the material studied which were indicative of copulation on the part of the individuals and the fusion of their nuclei, or of maturative phenomena.

14. The organelles of the fibrillar system, together with the two nuclei and their related structures, present a single unified and integrated complex, which constitutes the neuromotor apparatus.

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EXPLANATION OF PLATES

All figures of *Giardia microti*, Kofoid and Christiansen, drawn with camera lucida from smear preparations as described in paper. Magnification ×2,750. Full length of flagella not shown in many figures.

PLATE 1

Fig. 1. Ventral view, trophozoite in resting stage; note basal granules of anterolateral flagella and the axostyle as a single rod.

Fig. 2. Ventral view showing elongated karyosome and linin extension; basal granules for caudal flagella.

Fig. 3. Ventral view, prophase—knot-like spireme, and split in right nucleus—stage previous to segmentation of spireme bands to form tetraploid number of chromosomes. Parabasal; bacterial inclusions.

Fig. 4. Ventral view, prophase—spireme of two strands; contraction of chromatin to form chromosomes, axostyle partially split, parabasal body.

Fig. 5. Ventral view, prophase—precocious splitting to form eight chromosomes or tetraploid number. In left nucleus separation of chromosomes to show possible ancestral origin. Linin fibrils between chromosomes; paradesmose.

Fig. 6. Ventral view, prophase—precocious splitting of double spireme band of each nucleus, forming tetraploid number of chromosomes, paradesmose

Fig. 7. Ventral view, prophase—four chromatinic masses resulting from fusion of the tetraploid number by pairs and their consequent contraction into single mass; centrosome divided; axostyle partially divided; basal granules.

Fig. 8. Lateroventral view, late prophase—four contracted chromatinic masses at the equator.

Fig. 9. Ventral view, metaphase—equatorial plate in right nucleus; eight chromosomes. Axostyle divided, blepharoplasts divided and formation of new anterolateral flagella as far forward as chiasma. Right nucleus in prophase.

Fig. 10. Ventral view, late anaphase or early telophase—chromosomes fused at poles. Nuclear membrane constricting. Axostyle almost completely split.

Fig. 11. Ventral view, telophase completed—four nuclei; small parabasal.

Fig. 12. Dorsal or ventral view, "single individual" cyst—large parabasals with connectives to axostyle.

Fig. 13. Lateral view, so-called "copulation" cyst, but in reality the end-result of binary fission. New organelles differentiating.

Fig. 14. Dorsal or ventral view, "multinucleate" cyst—sixteen nuclei; remains of two neuromotor apparatuses; parabasals.

Fig. 15. Ventral view, binary fission—axostyles partially split; anterior peristomal fibres of lower individual faint because of body being turned backward. Bacterial inclusions.

Fig. 16. Dorsal or ventral view, "binary fission" cyst—four nuclei; two sets of neuromotor apparatuses.

Fig. 17. Ventral view, metaphase—new anterolateral flagella as far as chiasma; splitting of posterolateral flagella; equatorial plate formation.

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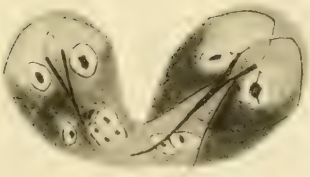
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16

17

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Index, pp. 545-558.

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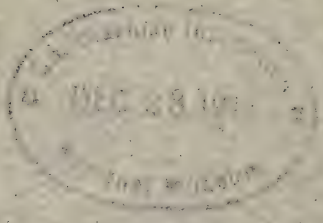

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AN UNUSUAL EXTENSION OF THE DISTRIBUTION OF THE SHIPWORM IN SAN FRANCISCO BAY, CALIFORNIA

BY

ALBERT L. BARROWS

CONTENTS

PAGE

Introduction and acknowledgments 27
General distribution of *Xylotrya* in San Francisco Bay 28
Recent incursion of *Xylotrya* into San Pablo Bay 29
Dikes at Mare Island 29
Wharf near Crockett 30
Wharf at Oleum 31
Physical conditions in San Pablo Bay 31
Discharge of fresh water into San Pablo Bay 31
Salinity of San Pablo Bay 33
Temperature conditions in San Pablo Bay 36
Relation of *Xylotrya* to salinity 36
Conclusions 41
Bibliography 43

Introduction and Acknowledgments

It is said that the shipworm was unknown in San Francisco Bay in the early history of the port, and that wood-boring molluscs did not become an extensive menace to marine woodwork here until some years after the great increase in the shipping entering the bay which followed upon the discovery of gold in California. Be that as it may, a species of the Teredidae, *Xylotrya setacea* Tryon, now thoroughly infests the main portion of the bay, and, as in other localities where shipworms are abundant, this borer is a constant cause of damage to marine timbering in this port. Another species of shipworm, *Teredo diegensis* Bartsch, has also recently caused damage in the upper part of San Francisco Bay.

For much of the material presented in this paper I am indebted to engineers of several construction and transportation firms of San Francisco and to engineers of the Union Oil Company. I wish also to acknowledge the great courtesy of officers of the Corps of Civil Engineers, United States Navy, stationed at the Mare Island Naval Station, in furnishing information upon damage caused by marine wood borers in wooden dikes about Mare Island.

General Distribution of Shipworms in San Francisco Bay

The part of San Francisco Bay in which shipworms are most active, to judge from their destructiveness, lies in the regions nearest the Golden Gate, where presumably not only the salinity of the water is most favorable, since it most nearly approximates that of the open sea, but where a suitable food supply of plankton is abundantly brought in from the ocean with the tides.

Engineers familiar with conditions in this bay have reported a certain falling off of the activity of shipworms in parts of the bay at some distance from the Golden Gate, and particularly in those regions where water from the open sea is not brought abundantly by the tides. Thus along the North Beach wharves of San Francisco, in the vicinity of Sausalito, in Racoon Strait, and about Angel Island and Alcatraz Island, shipworms are extremely active. Unprotected timber in these places is destroyed within a few months. On the Oakland side of the bay, however, the rate of devastation of marine woodwork by shipworms is said to be slower than in the localities just mentioned, and in the Oakland estuary the rate of activity of the borers is greatly diminished, unprotected marine woodwork being said to last from two to four years.

In these localities where the destructiveness of the shipworms is thus decreased, it is usually found that the size of the borer is also reduced from a diameter frequently of one-half inch for borers taken from the Golden Gate to a diameter of one-eighth inch or three-sixteenths inch for borers taken from parts of the Oakland estuary. In localities where the activity of shipworms is reduced, the crustacean wood-borer *Limnoria* is often increasingly destructive. Thus *Limnoria* seems here to be the more active in brackish water and teredine wood-borers more active in normal sea water.

Shipworms are conspicuously absent in San Francisco Bay from stagnant regions and from regions which are contaminated by sewage or by factory or refinery wastes. Except in a few such regions, prac-

tically all of the timbers used in marine woodwork in the main part of the bay are impregnated with creosote as a protection against shipworms as well as against *Limnoria.*

The northern portion of San Francisco Bay is called San Pablo Bay, and is separated from the main part of the bay by San Pablo Strait. It is generally believed that shipworms do not live in San Pablo Bay because of the reduction of the salinity of the water in this bay by the influx of a large amount of fresh water from the Sacramento and San Joaquin rivers emptying into the bay through Carquinez Strait. In spite of prolific activity on the part of shipworms in the main part of San Francisco Bay, the records of the Mare Island Naval Station, in the upper part of San Pablo Bay, do not mention the presence of marine wood-borers, either *Xylotrya* or *Limnoria,* prior to the discovery of shipworms in the Mare Island dikes in January, 1914. The experience of construction engineers in charge of numerous wharves from Vallejo Junction to Port Costa, at the head of San Pablo Bay, confirms this record for the practical absence of wood-borers from this locality.

Recent Appearance of Shipworms in San Pablo Bay

Dikes at Mare Island.—Mare Island is located at the head of San Pablo Bay, opposite Carquinez Strait, through which empty the Sacramento and San Joaquin rivers. Several wooden dikes have been built in the channel which separates Mare Island from the mainland and about the entrance to this channel in order to confine the currents and prevent the filling up of the channel by the deposition of silt. The longest of these dikes reaches southward into San Pablo Bay along the edge of the main ship channel through the bay for a distance of over 8000 feet, and is designed to prevent a back current in the shallow northern part of San Pablo Bay from carrying sediments into the shipping channel by which the naval station may be reached. In view of the usual limitation of the range of shipworms below San Pablo Bay, it occasioned great surprise when an examination of certain of these wooden dikes in January, 1914, showed extensive damage from the borers. It was found that the greatest damage had been done in the long dike which offered the first exposure to tide water coming up the bay, though damage had been done also in two shorter dikes at the entrance to Mare Island Strait.

In general the damage in the long dike was greatest on the side which faced the ship channel, where the water is deepest and where

it is presumed that the flood tide sweeps up the bay with the least reduction in salinity from the normal salinity of ocean water. On the back or western side of this dike damage was noted for only about 2000 feet from the outer end, while on the front or eastern side the damage extended for over 6000 feet shoreward from the outer end, indicating that the eastern or front side of the dike was exposed to water suitable for the existence of shipworms, while the water eddying over the wide mudflat behind the dike was largely unsuitable for them.

In the damaged portion of the dike the operations of the borers were more extensive in the brace piling, which extended out from the sheet piling at an oblique angle, than in the sheet piling, suggesting that a free circulation of water about the isolated brace timbers promoted the greater activity of the borers in these timbers. Much of the brace piling was more than half eaten through, whereas the shipworms had bored hardly more than an inch below the surface of the wood in the sheet piling. Further, the greatest damage in these dikes was found near the mudline, suggesting that the borers throve best in the denser water known to lie along the bottom of the bay. The species of shipworm in this case has been identified as *Teredo diegensis* Bartsch, by Dr. Paul Bartsch, of the United States National Museum, to whom I am indebted for this courtesy. It is a small species making holes averaging one-eighth or three-sixteenths inch in diameter.

The board of naval engineers which inspected the Mare Island dikes on the occasion of this damage reported that this unprecedented incursion of *Teredo* was due to an increase in the salinity of the water of that part of San Pablo Bay on account of the occurrence just previously of two dry years in succession in which not only was the rainfall and snowfall over the Sacramento-San Joaquin watershed less than usual but in which it was so distributed that the amount of runoff in proportion to the precipitation was also less than usual.

A repetition of damage to marine woodwork in this region, due to *Teredo,* was found in January and February, 1917, when sample piles showing renewed activity of *Teredo* were removed from a number of places in the outermost dike of the Mare Island Naval Station. The penetration of the *Teredo* in these cases was generally not over three inches in depth and the extent of damage caused at this time was not so great as that during the incursion of 1913–14.

Wharf near Crockett.—Another instance of damage due to shipworms in this vicinity came to light when in the spring of 1914 a

freight steamer, on attempting to make fast to a wharf about a mile above Vallejo Junction at the entrance of Carquinez Strait, rammed the wharf and carried away a number of piles. A pile pulled up for examination when this damage was repaired showed that the broken timbers had been weakened by the operations of shipworms. At Crockett, less than a mile above this point and well within Carquinez Strait, untreated piles are still in use which are known to have been in place for twenty-eight years.

Wharf at Oleum.—Damage due to wood-borers was also discovered in a third locality in this same general region when repairs on the wharf of the Union Oil Company at Oleum, less than a mile below Vallejo Junction and directly opposite the long Mare Island dike across the ship channel, revealed operations of wood-borers, the piles of the wharf being corroded by the shipworms for a depth of about one inch.

It thus appears that at three points located within two or three miles of each other at the head of San Pablo Bay notable damage was done during 1912 and 1913 by a dwarfed race of shipworms, *Teredo diegensis* Bartsch, in a region in which shipworms had not been known to cause damage previously, and that renewed activity of these borers was observed in the spring of 1916 and in the winter of 1916–1917, in the same region. The fact that the damage reported occurred at the head of San Pablo Bay may be explained probably by the location of most of the untreated marine timbering in this bay near the entrance to Carquinez Strait.

Physical Conditions in San Pablo Bay

Very fortunately for our present purpose definite information is available upon the physical conditions of the waters of San Francisco Bay (Sumner et al., 1914). This information includes observations upon the temperature and salinity of San Pablo Bay made during the two years preceding that in which the damage just described took place.

Discharge of Fresh Water into San Pablo Bay.—Though a number of small streams empty into San Pablo Bay besides the Sacramento and San Joaquin rivers, by far the greater amount of fresh water entering the bay comes from these two large rivers, both of which empty into the bay through Carquinez Strait. The approximate amount of fresh water discharged from the Sacramento-San Joaquin

river system for a series of ten years has been computed for the biological survey of San Francisco Bay (Sumner, et al., 1914, p. 77) by a summation of the measured flow of the principal tributaries of this system. Through the courtesy of Mr. H. D. McGlashan of the United States Geological Survey, who has furnished data for the years 1911–12 to 1914–15, it has been possible to complete these data for the years of the survey, and also for the two following years. Though not representing absolutely the total amount of fresh water passing through Carquinez Strait from these rivers, these data, compiled according to a uniform method for the fourteen years represented, furnish at least a fairly accurate picture of the relative variation above or below the average in the discharge of these rivers.

It is to be noted from the table below for the annual discharge from the Sacramento-San Joaquin river system that the years 1912 and 1913 were both years of unusually small discharge, the runoff amounting to less than half the average amount for the fourteen years for which acceptable data are available. In the season 1913–14, however, the discharge of fresh water was over 22 per cent more than the normal amount.

DISCHARGE OF SACRAMENTO AND SAN JOAQUIN RIVER SYSTEMS

In Acre-Feet, Based Upon Records For Fourteen Years[1]

Year[2]	Sacramento system	San Joaquin system	Combined flow
1878–79	26,387,000	7,090,000	33,477,000
1879–80	32,300,000	12,091,000	44,391,000
1880–81	32,000,000	9,916,000	41,916,000
1881–82	25,300,000	8,367,000	33,667,000
1882–83	17,800,000	6,361,000	24,161,000
1883–84	29,900,000	13,212,000	43,112,000
1907–08	15,291,000	4,023,000	19,314,000
1908–09	33,756,000	11,178,000	44,934,000
1909–10	20,705,000	8,106,000	28,811,000
1910–11	27,906,000	14,460,000	42,366,000
1911–12	11,372,000	3,797,000	15,169,000
1912–13	12,850,300	3,464,400	16,314,700
1913–14	31,442,000	10,366,000	41,808,000
1914–15	26,663,000	7,873,000	34,536,000
Average,	24,548,000	8,593,200	33,141,200

[1] Care has been taken to complete this table according to the same method as that employed by Sumner in compiling the data for the years 1878–79 to 1910–11 inclusive (Sumner, et al., 1914, p. 77).

[2] The runoff year is computed from October 1 to September 30.

The average monthly discharge from this double river system, which of course varies with the rainfall and melting of the snow over the watershed of the rivers, is given as follows (Sumner, et al., 1914, p. 78).

MEAN MONTHLY DISCHARGE OF SACRAMENTO AND SAN JOAQUIN RIVER SYSTEMS

BASED UPON RECORDS FOR TEN YEARS

Month	Runoff in acre-feet
October	527,356
November	748,586
December	1,352,997
January	3,728,103
February	3,453,295
March	4,710,754
April	6,137,662
May	6,467,948
June	4,854,338
July	2,027,965
August	766,125
September	490,364
Total,	35,275,493

The months of maximum discharge of fresh water are seen from this table to be April and May, and it is during these months that we should expect the salinity of San Pablo Bay to be at its minimum. The months of least discharge of fresh water are the fall months of August, September, October, and November, and it is during these months, constituting one-third of the year, that we should expect the salinity of this bay to be at a maximum. The seasonal increase in the amount of fresh water discharged and the corresponding decrease in the salinity of this part of the bay begins during December and becomes marked during the month of January. It is to be noted in this connection that shipworms were found dead in the later part of January, 1914, in certain test piles which had been taken up early in the month and moored for a few weeks alongside the dike which had been infested with the borers. This may have been due to the influx of a large amount of fresh water into this part of the bay during that month as the first of a discharge of considerably more than even the normal amount for that month during the rainy season of 1913–1914, or possibly to heavy jarring of the pile when removing it.

Salinity of San Pablo Bay.—From this varying discharge of fresh water into San Pablo Bay it has been found, as was expected, that the

salinity of the water of the bay was greatest during the fall months and least during the spring months. This is shown in the appended table of salinity measurements for three stations chosen at the head of the day and not far from the places where the *Teredo* had caused damage.

These stations may be described as follows (Sumner, et al., 1914, p. 153, pl. 4):

Station 4975. Tang. Crockett Whf., S 74° E; Carquinez St., N 50° W; Tang. Selby Whf., S 69° W. Well within the entrance to Carquinez Strait, near Crockett; depth 14½–12 fms.

Station 4976. Tang. Crockett Whf., S 76° E; Carquinez St., S 48° E; Mare Isl. St., N 27° E. In the middle of the ship channel, directly south of the southeastern end of Mare Island, and near the long dike; about 1 mile W by N from Station 4975; depth 10½–9¾ fms.

Station 4977. Carquinez St., N 71° E; Lone Tree Pt. Whf., S 36° E; Pinole Pt. Tang., S 53½° E. In the middle of the ship channel and about 1½ miles W by S from Station 4976; depth 5¾–5 fms.

In the following tables, compiled both for salinity and temperature from the published results of the biological survey of San Francisco Bay, "the 'surface' figure is the mean of the surface figure recorded during the flood-tide observation and that recorded during the ebb-tide observation. Similarly, the 'bottom' figure is the mean of the ebb and flood figures for the bottom" (Sumner, et al., 1914, p. 28).

SALINITY AT STATIONS IN UPPER SAN PABLO BAY

Parts Per Thousand

	Station 4975			Station 4976			Station 4977		
	Surface	Bottom	Diff.	Surface	Bottom	Diff.	Surface	Bottom	Diff.
Feb. 13–27, '12	10.46	15.61	5.15	13.63	17.54	3.91	13.23	19.71	6.48
Apr. 23–May 6	9.95	13.35	3.40	12.45	14.29	1.84	9.08	10.89	1.81
July 22–31, '12	12.55	16.74	4.19	11.35	16.11	4.76	17.62	19.50	1.88
Oct. 7–12, '12	17.40	19.14	1.74	16.93	18.99	1.16	20.53	22.55	2.02
Nov. 23–Dec. 5	13.82	18.89	5.07	14.18	17.82	3.64	17.43	22.52	5.09
Jan. 13–28, '13	12.48	17.30	4.82	14.00	15.92	1.92	14.84	20.27	5.43
Annual range,	7.45	5.79	.....	5.58	3.80	.....	11.45	11.66	.....
Av. for entire year,	13.21	17.27	4.06	14.23	17.16	2.93	15.46	19.25	3.79

From this table for salinity it appears that of the six periods of observation the greatest salinities at all three stations were observed both at the surface and at the bottom during the period October 7–12, 1912. This period corresponds in general with the period of least discharge of fresh water from the Sacramento and San Joaquin river system, and lags only a little behind the month (September) in which the average minimum monthly discharge is found to occur.

On the other hand, the lowest salinity observed occurred for all stations, with one exception, during the period April 23–May 6, 1912. This, again, corresponds in general, as would be expected, with the period of greatest discharge from these rivers, and precedes by only a few weeks the month of maximum average monthly discharge.

The lag just observed between the time of observation of greatest salinity at these stations and the month of minimum average discharge and the precedence of the time of observation of the least salinity before the month of maximum average discharge are probably to be explained by the arbitrary selection of observation periods which happened not to coincide precisely with the actual periods of greatest and least discharge from the rivers. This minor discrepancy, however, does not vitiate the general conclusions to be drawn.

In the following table (Sumner, et al., 1914, p. 83) the salinity, as observed at ebb tide, i.e., when it might be expected to be at a minimum, on March 5 and 6, 1914, is compared with the salinity observed at a corresponding period in 1912 for station 4975 and for station 4978, which lies in the ship channel about two miles west by south from station 4977, described above, and for station 4974, which lies below San Pablo Strait and is some fourteen miles from station 4975.

COMPARISON OF SALINITY AT SELECTED STATIONS AND PERIODS IN 1912 AND 1914

	1912			1914		
	Surface	Bottom	Diff.	Surface	Bottom	Diff.
4974	17.47	21.47	4.00	*	24.65	24.65
4975	13.91	18.55	4.65	*	3.77	3.77
4978	14.19	21.47	7.28	4.02	13.42	9.40

* "Surface samples from these stations gave chlorine percentages so low that the salinities could not be obtained from Knudsen's Hydrographic Tables. These samples have therefore been regarded as nearly pure river water." (Sumner, et al., 1913, p. 83.)

A difference of from 9 to 15 parts per 1000 is to be noted in the salinity of this part of the bay between observations during the flood seasons of these two years for which, as has been noted, the discharge of fresh water from the Sacramento-San Joaquin system differed so markedly. A point of greater significance, however, is the reduction of the salinity at station 4975 to practically nil at the surface and to 3.77 at the bottom during the flood season of the "wet" year 1914, whereas during the corresponding flood season of the "dry" year 1912 the surface salinity remained fairly high, 13.91.

Though we have but the single observation for these stations in 1914, it is presumable that the low salinity indicated on this occasion

may have been so frequently repeated during the later months of the flood season as the discharge of fresh water reached its height as to have presented salinity conditions during a considerable portion of the year which would be inimical to the life of *Teredo.*

Temperature Conditions in San Pablo Bay.—Since the temperature may in a general way be of influence in determining the rate of activity of these borers, the following table is appended of temperatures taken at the same stations and at the same times as the observations for salinity. It is not presumable, however, that a difference in temperature of less than a degree between the temperature at the surface and at the bottom at these stations should be sufficient to cause so marked a difference in the activity of the borers as has been noted. A difference of average annual temperature amounting to 5° C or more between this general region and some other region may, however, be sufficient to cause a marked difference in the activity of marine borers even if the same species of borer be present in both cases.

TEMPERATURE OF SELECTED STATIONS IN SAN PABLO BAY

In Degrees Centigrade

	Station 4975			Station 4976			Station 4977		
Date	Surface	Bottom	Diff.	Surface	Bottom	Diff.	Surface	Bottom	Diff.
Feb. 13–27, '12	12.18	12.16	.02	12.24	12.27	.03	12.52	12.37	.15
Apr. 23–May 6	14.24	13.87	.37	13.74	13.78	.04	13.66	13.67	.01
July 22–27, '12	12.82	18.81	.01	18.46	18.54	.08	19.10	18.51	.59
Oct. 7–12, '12	16.66	16.34	.32	16.63	18.54	.14	16.52	16.28	.24
Nov. 25–Dec. 5	11.55	11.73	.18	11.46	11.66	.20	12.02	11.95	.07
Jan. 13–28, '13	5.96	6.35	.39	5.96	6.10	.14	6.34	6.63	.39
Annual range,	12.86	12.46	....	12.50	12.44	....	12.76	11.88	....
Av. for entire year,	13.15	13.14	....	13.04	13.08	....	13.34	13.23	.11

Relation of Teredo to Salinity

It remains now to determine as closely as possible from these data, so fortunately available, approximately the conditions of salinity which seem to be required by this species of *Teredo.*

The lowest surface salinity observed at any of these stations during 1912 and 1913 was 9.08 parts per 1000 and the lowest bottom salinity was 10.89, both observations occurring during the period April 23-May 6 in the season of maximum discharge of fresh water for that year. While we do not have the actual observations upon the salinity at these stations for the full year 1913, it is presumable, since the total discharge of fresh water was about the same for both years, 1912 and 1913, that the salinity could not have fallen much lower at any time

during the year 1913 than it did during the year 1912, for which we have observations.

While it is not definitely known whether shipworms began their disastrous operations in San Pablo Bay in 1912 or in 1913, there are certain considerations which indicate that the primary infection by the borers in this attack may have occurred in the summer and fall of 1912, with probably a second infection following upon the breeding season of the following year. The breeding habits of certain species of shipworms have been observed by Sigerfoos in Chesapeake Bay, including *Xylotrya gouldi* Jeffreys and *Teredo dilatata* Spengler, which are very abundant there, and *Teredo navalis* Linnaeus, which occurs in that locality but rarely. Sigerfoos (1908, pp. 195–198) writes as follows concerning the spawning habits of these species:

> *T. navalis* retains its eggs in the gills during their embryonic development. . . . On the other hand . . . the eggs of the other two species are laid free into and fertilized in the water. . . .
>
> In association with their character of free development in the water, the eggs of the shipworm are very small and very numerous. While they vary somewhat in size, they have an average diameter of somewhat less than 1/20 mm. (1/500 inch). . . . In one case I estimated the number laid by a large female of *T. dilatata* to be one hundred millions. . . . Development is very rapid and on warm days the embryos become free-swimming within three hours after the eggs are laid. Within a day the shell has been formed and the typical lamellibranch veliger stage has been reached. . . .
>
> . . . What becomes of the larvae after hatching from the eggs, how and where they live, it is difficult to surmise. Though the developed larvae are settling on wooden structures constantly, I have not taken them and the intermediate stages in the tow-net, and where they develop I do not know. The rate of growth of larvae of the marine lamellibranchs, however, is slow, and I think the larvae of shipworms when they attach themselves must be at least a month old. They may be more, for at this time their development is quite advanced and their organization complex.
>
> The breeding season of *X. gouldi* and *T. dilatata* seems to extend throughout the warm season. I have found ripe sexual products of both species from early in May till the middle of August. At the latter time there seemed no abatement in their development. . . . Individuals become sexually mature in a month after they have attached, and those which attach in August must bear ripe sexual products later in the season, so that the breeding period would seem to extend throughout the warmer months. . . .
>
> The shipworm in its larval stages develops slowly, but once in the wood it grows with remarkable rapidity. . . . The newly attached larva is somewhat less than 0.25 mm. long. In 12 days it has attained a length of about 3 mm.; 16 days, 6 mm.; 20 days, 11 mm.; 30 days, 63 mm.; and 36 days, 100 mm. In a month specimens may contain ripe sexual products, though normally these seem to be retained till larger quantities of spermatozoa and eggs are stored for extrusion at one time.

Sumner (Sumner, et al., 1914, p. 55) gives the following comparison of the mean annual temperature of San Francisco Bay with that of the lower third of Chesapeake Bay, both bays being located in about the same latitude:

	Mean	Range
San Francisco Bay	12.91° C	8.35° C
Chesapeake Bay	14.38° C	22.12° C

Although it is possible that the species of shipworms found in Chesapeake Bay may not be able to live in San Francisco Bay because adapted to the particular conditions of the Chesapeake Bay, in the absence of definite knowledge of the breeding habits of the species found in San Francisco Bay we may assume that there is no very great difference in the general breeding habits of these two species. If there be any difference we may expect that in San Francisco Bay, where the temperature must fall off the less rapidly in the latter part of the year, the breeding season of the Pacific Coast species of shipworms may continue later than that of the Atlantic species, and that egg-laying may possibly begin earlier in the spring in San Francisco Bay than in Chesapeake Bay. The period of possible infection of timber on the Pacific Coast may therefore be longer than on the Atlantic Coast. Thus, it is not improbable that even in normal years *Teredo* larvae may be carried from the main portion of San Francisco Bay into San Pablo Bay by the tides of the late summer, and that they may acquire at least a temporary foothold in accessible submerged timber. It should be born in mind, however, that the data for rate of growth given by Sigerfoos are for shipworms living in that part of Chesapeake Bay where the salinity is not greatly reduced, and that these rates should therefore be compared with the rate of growth of shipworms in the main part of San Francisco Bay rather than with the supposed rate of growth of the shipworms found in San Pablo Bay.

The general conditions throughout a normal year at these localities in the upper part of San Pablo Bay seem to include a period in which the surface salinity, at least on certain tides, must be reduced to practically zero and the bottom salinity to but a few points above zero. Such a condition, which may be of annual recurrence in this vicinity, appears to be sufficient to kill all shipworms which may have taken hold of marine timber in these localities. This condition of greatly reduced salinity in the spring, moreover, probably obtains during an average year during so great a portion of the year as to effectually prevent the existence of shipworms long enough to do notable damage,

even if they should become attached to woodwork during the season when the salinity is high. If any larvae are brought up alive from the lower portion of the bay after the flood season and do become attached, they must usually be killed within a few months by the recurrence of the next flood season. Adult shipworms embedded in the wood might occasionally be able to endure the reduced salinity of a single ebb tide by tightly closing the entrance to their bore, as they are able to do, but they could not endure prolonged reduction of salinity.

On the other hand, the increased salinity of the water of San Pablo Bay during a year of unusually small discharge of fresh water from the Sacramento-San Joaquin river system may be such as to permit not only the continuance of living *Teredo* in this bay throughout the entire year but also much damage on account of increased numbers and activity of the borers under the conditions of increased salinity.

It is just possible that an infection of marine timber in the upper part of San Pablo Bay may have occurred in the fall of 1911, and that the shipworms entering the wood then may have continued to live through the months of minimum fresh-water runoff in the winters of both 1911–12 and 1912–13, and until the discovery of the damage found in December, 1913; but so early an infection seems improbable because the discharge of fresh water during the previous year was nearly 28 per cent more than the average annual discharge.

It seems on the whole more probable that the first infection of the attack in question occurred in the summer of 1912, because the falling off of the discharge of fresh water unusually early in the spring of that year must have lengthened the summer period during which San Pablo Bay may have been open to invasion by *Teredo* larvae, permitting thus an unusually heavy infection to gain a foothold. If this infection occurred then, the shipworms settling at that time must have been able to withstand a reduction of salinity of about ten parts per thousand during the spring freshets of both 1912 and 1913. Another infection in the breeding season of 1913 may have caused an acceleration during the fall of that year in the damage being done to the structures attacked.

The lowest surface salinity recorded during 1912 was 9.08 parts per 1000 and the lowest bottom salinity 10.89. The average annual surface salinity for the three stations referred to in the upper part of San Pablo Bay ranged during the period of observation from 13.21 to 15.46 parts per 1000 and the average annual bottom salinity from

17.27 to 19.25 parts per 1000. It seems probable, therefore, that *Teredo diegensis,* once established, can withstand for several weeks or perhaps months a reduction of salinity to about 10 parts per 1000, though perhaps thriving sufficiently to cause marked damage only in a region where the salinity of the water, except for a short period, must average at least 13 or 14 parts per 1000.

In common with a recognized biological principle, the adult shipworms, moreover, may be expected to be hardier and more resistant to adverse circumstances than the larvae. Thus the larvae might be able to invade San Pablo Bay only in the period of maximum salinity in the bay during the late summer and fall, but once established and developed into adult animals the shipworms might much better withstand the reduction in salinity of succeeding freshets of the winter and spring, if this reduction should not fall below a certain minimum limit.

It is possible also that *Teredo diegensis* may breed normally in localities where the salinity is lower than that which *Xylotrya setacea* can endure, and that damage to unprotected marine woodwork will occur in such localities of reduced salinity from increased numbers of native *Teredo diegensis* when, as occasionally happens in San Pablo Bay, a "dry" year permits the salinity to rise above the condition usually prevailing. In this connection a more extensive knowledge of the distribution of *Teredo diegensis* and of *Xylotrya setacea* in such a region as San Francisco Bay than is at present available is to be desired.

From the known rate of operation of shipworms of the small size of those found in San Pablo Bay in other parts of San Francisco Bay, it seems hardly probable that the extensive damage to the brace piling of the Mare Island dikes, in which many of the timbers were from one-half to three-quarters destroyed, could have taken place during the six or eight months following the falling off of the discharge of the Sacramento and San Joaquin rivers in the summer of 1913. The conclusion seems justified, therefore, that the damage reported in January, 1914, dates back to an infection during the summer or fall of 1912, at least a year and a half previously, but hardly to the fall of 1911, two years and a half before.

The general observation of engineers in San Francisco Bay is that the shipworm is much more active at or near the mudline than near the tide levels. This same difference in the level of the greatest activity of these borers was noted in the dikes of the Mare Island Navy Yard, also in the piles extracted from the wharf of the Union Oil Company

at Oleum. From the salinity table just quoted, the bottom salinity is seen to be consistently greater than the surface density, in one instance by as much as 6.48 parts per 1000. While *Teredo diegensis* will probably live in water of a salinity of 10 or 12 parts per 1000, a slightly greater density of a few points per 1000 seems directly or indirectly to attract greater numbers of the borers and to stimulate their greater activity. It is noteworthy that an average annual difference in salinity of from 2.89 to 4.28 parts per 1000 within but a few fathoms of depth should cause so distinct a difference in the abundance and activity of these borers as has been reported.

It is probable that there may be a direct physiologic adaptation between a certain degree of salinity and the wellbeing of these wood-borers, such as is noted in the case of most marine animals, and which effectually prevents their existence in water of either unusually low or high salinity. It is possible also that the relation of shipworms to salinity may be only an indirect one, and that the distribution of shipworms may be at least partly dependent upon some other cause, such as the presence of certain classes of plankton organisms, upon which the shipworm may feed to the best advantage, which are in their turn directly dependent upon water of a certain density for flotation or of a certain salinity for their own physiologic wellbeing.

That *Teredo diegensis* is extremely sensitive to the amount of water in circulation around the place where it may have settled appears from the fact that the damage to the Mare Island dikes was much greater in the brace piling, consisting of isolated timbers set at an angle away from the dike wall, than in the sheet piling which formed the face of the wall, although both the brace piling and the sheet piling were more or less infected for their full length. The water washing more freely around the isolated brace timbers than over the closely set sheet piles of the wall of the dike probably brought to the borers in the brace piling a much more abundant supply of food than to the borers located in the sheet piling, thus suggesting the close ultimate relation between boring activity and food supply.

Conclusions

1. It, therefore, appears that shipworms of the species, *Teredo diegensis* Bartsch, may be intermittent residents of the vicinity of Mare Island near the mouth of Carquinez Strait; that the excessive damage caused by these borers in 1913 came about through the

marked increase in the average salinity of the water of this part of San Pablo Bay, because of the comparatively small amount of fresh water which entered the bay during the two consecutive dry seasons of 1910–11 and 1911–12; that these borers may be killed off entirely by a season of unusually heavy rainfall, though a re-injection may occur during the next summer and fall; and that these borers may occur in this region in small numbers even in years of average rainfall.

2. A salinity of at least 10 parts per 1000 (approximately) seems to be required for the existence of *Teredo diegensis* at temperatures ranging from 6° to 19° C.

3. Damage may be expected at these temperatures from *Teredo diegensis* in regions where the average annual salinity is as much as 13 or 14 parts per 1000, provided that the salinity does not fall for any considerable period below 10 parts per 1000.

4. An increase in salinity of even 3 or 4 parts per 1000 above the minimum salinity tolerated by *Teredo diegensis* seems to be effective in considerably increasing the abundance of the borers and in stimulating their activity; hence their greater activity near the bottom than near the surface in such localities as those under observation here.

5. The activity of *Teredo diegensis* is thus, directly or indirectly, related to the salinity. It is possible, however, that the salinity itself may not be the only factor determining the vertical or horizontal distribution of these borers, but that some other condition may to a certain extent be the factor immediately controlling this distribution, such, perhaps, as the plankton food supply, which may be more delicately related to the salinity than the shipworm is itself.

6. Of the several major factors of the marine environment, such as temperature, salinity, depth, pressure, food supply, etc., salinity may usually be regarded as the variable factor most likely to determine, either directly or indirectly, the distribution of *Teredo diegensis* in bays where all these factors undergo greater variation than is common on the open sea-coast.

7. Other things being equal, *Teredo diegensis* seems to be most active in woodwork exposed to a good circulation of water; hence the greater damage to the brace piling than to the sheet piling in the Mare Island dikes. Thus, being apparently held in check by the minimum salinity which can be endured, the activity of *Teredo* when once located in timber under tolerable conditions of salinity may depend largely upon the amount of food material which the constantly moving current may bring to it.

8. In such a bay as that of San Francisco, which is infested in its main portion with shipworms, and in which the movement of the tide is strongly felt in many parts, the borers may be expected to take advantage very promptly either of any variation in salinity which will permit them to invade a previously unoccupied locality or of any change in current conditions which by bringing in a more abundant food supply than formerly will permit an increased rate of growth and of destruction of woodwork.

9. This unusual occurrence of shipworms in the upper part of San Pablo Bay is indicative not only of the avidity with which such an organism seizes upon every opportunity to extend its distribution into previously unoccupied localities but also of the great importance of even slight and relatively temporary variations in conditions of the environment in determining the limits of the distribution of the species, particularly upon the fringe of its range.

10. It is noteworthy in this instance that *Limnoria* is not reported to have invaded San Pablo Bay in company with *Teredo diegensis*, though in other localities in San Francisco Bay, especially in those in which the salinity is somewhat reduced, *Limnoria* constantly accompanies the shipworms, and in certain places almost altogether supersedes them as a wood-borer, as, for example, in the Oakland estuary, where conditions seem to be less favorable for the teredine borers.

Transmitted March 9, 1917.

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DESCRIPTION OF SOME NEW SPECIES OF *POLYNOIDAE* FROM THE COAST OF CALIFORNIA

BY

CHRISTINE ESSENBERG

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CONTENTS

	PAGE
Introduction	45
Acknowledgment	45
General description of the Polynoidae	46
Description of new species	48
Harmothoë bonitensis, sp. nov.	48
Harmothoë johnsoni, sp. nov.	50
Halosydna macrocephala, sp. nov.	53
Literature cited	56
Explanation of plates	58

INTRODUCTION

In 1897 Dr. H. P. Johnson reported that there were thirteen species of Polynoidae on the Pacific Coast. The number of species has increased since that time to about fifty. The purpose of this paper is to add to that list some species which have not been described by any of the previous workers.

ACKNOWLEDGMENT

The work was carried on in the Zoological Laboratory of the University of California. The writer wishes to express her sincere gratitude to Professor Charles A. Kofoid for his interest and valuable criticisms of this work.

GENERAL DESCRIPTION OF THE POLYNOIDAE

The Polynoidae are widely distributed, occurring in boreal, temperate and tropical zones; in shallow waters and in depths beyond 3000 fathoms. A few species are cosmopolitan, occurring in all oceans, but for the most part each particular area harbors its characteristic species; species common around San Diego Bay are not found in San Francisco Bay, but their place is taken by other species.

The Polynoidae were classified by the early workers as a genus or several genera of Aphroditidae. The recent workers, however, with a few exceptions, are following Kinberg's (1857) plan in classifying the Polynoidae as an independent family. The Polynoidae resemble the Aphroditidae in certain characteristics. In the first place, they bear scales, or elytra, which are arranged in the same order as in Aphroditidae, occurring on segments 2, 4, 5, and on all alternate segments to segment 23. Thence posteriorly the arrangement of elytra is less regular. In the second place all elytroferous segments are devoid of dorsal cirri. The peristomal segment bears the first parapodia. On the other hand, the Polynoidae differ from the Aphroditidae in some essential characteristics. The shape of the body of the Polynoidae is more oblong than that of Aphroditidae, varying in length in different species. The lateral and the felt fibers are absent in Polynoidae. The parapodia are biramous and distinct from the main body. The prostomium is bilobed and convex. The facial caruncle is absent. The eyes, instead of being borne on peduncles, are placed farther posteriad on the prostomial lobe. The base of the median tentacle is inserted in the anterior fissure of the prostomial lobe. Two additional lateral tentacles are present. The proboscis is muscular and exsertile with a chitinous armature. The chitinous jaws are strongly developed. The setae are of two or more kinds and are more complex than those of the Aphroditidae. The nephridial papillae open ventrally at the base of the parapodia.

The shape, size, and color of the body of the Polynoidae may vary according to the conditions and the environment in which the individuals live. Hence these characteristics do not always furnish a reliable basis for classification. The following may serve as an illustration. While at the Scripps Institution for Biological Research at La Jolla, I had opportunity to compare specimens of *Polynoë pulchra* which had been taken from different hosts. The specimens that came

from a holothurian, *Stichopus californicus,* were brown in color, while the specimens found on the key-hole limpet *Lucapina crenulata* were dark, with conspicuous black rings on the elytra. At certain times the body of the worm may be filled with ova and greatly expanded, giving the worm a different appearance. The elytra do not extend far enough in that case to cover the entire dorsum.

However, some characteristics are constant, furnishing a reliable basis for classification. Among these are the shape and the relative size of the prostomium, the size and location of the eyes, the relative length and structure of the cirri and of the palpi, the structure of the setae, the shape and relative size of the corresponding parapodia, and to some extent the number and structure of the elytra. The last characteristic may not be true of long worms, such as *Lepidosthenia gigas.* The number of elytra may vary in this case in different individuals.

The Polynoidae are voracious feeders, attacking one another when in captivity. The writer had a number of specimens of *Polynoë californica* in an aquarium, where the food supply was scarce. The worms attacked one another with their strongly developed jaws, displacing the elytra or removing entire posterior segments of their companions.

The material used in this work was from the annelid collection of the Zoological Museum of the University of California at Berkeley. In the material of that collection some species were found that had not been mentioned previously in Treadwell's (1914) summary of the polychaetous annelids of the Pacific Coast. These were: *Polynoë complanata* Johnson, which I found labelled *Harmothoë imbricata,* and a number of specimens of *Halosydna lagunae* Hamilton, which were labelled as *Lepidonotus caclorus. Halosydna carinata* Moore, reported by A. Treadwell (1914) as being in the collection, was not there; some specimens labelled *Harmothoë carinata* did not agree with the characteristics of *Harmothoë carinata.* The writer had the opportunity of comparing a specimen of *Harmothoë carinata,* which Dr. J. P. Moore had the kindness to send to us, with the specimens labelled *Harmothoë carinata* Moore, in the Zoological Museum at Berkeley. Some *Eunoe barbata* were found labelled as *Harmothoë crassicirrata.*

DESCRIPTION OF NEW SPECIES

The species of Polynoidae in these collections were mostly well known or previously described. The following species, *Harmothoë bonitensis, Harmothoë johnsoni,* and *Halosydna macrocephala,* are new.

Harmothoë bonitensis sp. nov.

Pl. 2, figs. 1–11

Description.—A rather small-sized polynoid; the 32 anterior segments measuring 25 mm. in length, and the width at the widest part of the body, between the tenth and twelfth segments, is 5 mm. The dorso-ventral diameter is 1 mm. The worm is very much flattened dorso-ventrally and rounded at both ends. The anterior parapodia are shorter than those toward the central portion of the body. Thus the anterior end appears narrower, increasing in width up to the twelfth segment, where the maximum width is reached. The width decreases then gradually toward the posterior end. The color of the body is yellowish gray. There are only 32 anterior segments. The extreme posterior segments are missing.

The prostomium (pl. 2, fig. 1) is deeply fissured, with prominent acuminated peaks. The length of the prostomium is two-thirds of the width. The four pairs of eyes are comparatively large. The anterior eyes are situated in the widest part of the prostomium near the dorso-lateral margin. They are pointed anteriorly and laterally. The posterior eyes are smaller and are situated near the posterior end of the prostomium. They are closer together medially, and look posteriorly and upward. The cirratophore of the median tentacle is prominent, inserted between the prostomial lobes. The style of the median tentacle is missing. In this specimen the short lateral tentacles arise from short cirratophores, ventrad and mediad of the acuminated peaks. Their length is about two-thirds that of the prostomium. The palpi are white, stout at the base, decreasing in diameter very gradually and terminating in fine tips. Their length is nearly five times the length of the prostomium. They are densely covered with club-shaped sensory cilia, which are arranged spirally. The cirratophores of the peristomial cirri are long, equal in length to the prostomium, but the styles are missing. The dorsal cirri of the other segments (pl. 2, fig. 5) are white, of medium length, their tips extending to

the tips of the longest setae, covered with short, club-shaped papillae. The ventral cirri are short and fusiform.

The parapodia (pl. 2, fig. 5) are biramous. Each ramus is supported by an aciculum. The ventral ramus is by far the more prominent, forming a triangle and ending in a narrow projection. The dorsal ramus or notopodium is less prominent, ending in a long, finger-like projection, through which the aciculum projects.

The neurosetae are very numerous, 40 to 50, varying in size and structure. The ventral-most setae (pl. 2, figs. 9 and 10) are the shortest, about one-half the length of the long setae, with less conspicuous serrations. The setae increase in length and complexity toward the dorsum. The long neurosetae (pl. 2, fig. 11) are slender and the serrations are conspicuous. The ventral setae have a strong subterminal tooth, and curved, pointed tips. The dorsal setae are also very numerous (about 50 or more). In their arrangement they give the appearance of a fan. They are arranged in six or more rows. The ventral setae are the longest, being about three times the length of the long notosetae, decreasing in length dorso-anteriorly. The setae are curved, ending bluntly, their distal ends, except the extreme tips, being covered with fine serrations, which are more pronounced on the convex side. The postero-ventral setae (pl. 2, figs. 6 and 7) are long and stout, about one-half the width of the body. The extreme dorso-anterior notosetae (pl. 2, fig. 8) are very short, strongly curved, with but a few serrations on the convex side. Between these extreme dorsal and ventral setae all gradations of size occur. The color of the setae is golden yellow. Their arrangement is such that in each succeeding row the setae curve in opposite directions. This arrangement may be of some service as a protection for the animal.

There are fifteen pairs of elytra (pl. 2, figs. 2 and 3) covering the greater part of the dorsum, except the narrow median line, which is partly exposed. They occur on segments 2, 4, 5, and on all alternate segments to 25; then on 26, 29 and 32. The first pair of elytra (pl. 2, fig. 2) are nearly orbicular; the rest are reniform. They are densely covered with brown, spinous protuberances (pl. 2, fig. 4). These protuberances are club-shaped and covered with secondary projections. Numerous soft, white projections are scattered over the elytra. These projections are of the same shape as the marginal fringes, many exceeding the latter in length. The marginal fringes are confined to the postero-lateral margin only. A few large, soft tubercles are found near the lateral margin of the elytra.

Comparison.—A single example of this species is in the Zoological Museum of the University of California. It bears some resemblance to *Harmothoë triannulata* Moore (1910). Especially the shape and structure of the elytra, as far as can be judged from figures and descriptions of J. P. Moore, have a great resemblance. There is also some similarity in the setae of the two species. There are, however, some characteristic differences in the general shape of the body, the shape of the prostomium, of the cirri, and of other structures. The body of *Harmothoë triannulata,* according to Moore's description, is deep, while in *Harmothoë bonitensis* it is very much flattened and thin dorso-ventrally. The palpi are comparatively short and smooth in *Harmothoë triannulata,* approximately less than three times the length of the prostomium; in *Harmothoë bonitensis* the palpi are long (about five times the length of the prostomium) and are covered with spirally arranged rows of spines. The dorsal cirri of *Harmothoë triannulata* are covered with more conspicuous spines resembling more the cirri of *Harmothoë hirsuta,* while in *Harmothoë bonitensis* the spines are inconspicuous. In *Harmothoë triannulata* the notosetae are "moderate in number, forming an inconspicuous, depressed whorl"; in *Harmothoë bonitensis,* they are very numerous, forming a conspicuous whorl (see pl. 2, fig. 3). The setae are somewhat similar in shape in both *Harmothoë triannulata* and *H. bonitensis,* except the short, strongly curved notosetae of *Harmothoë bonitensis* (pl. 2, fig. 8) have no representatives in the figures for *Harmothoë triannulata* given by Moore. The distal ends of the neurosetae of *Harmothoë triannulata* are more slender and uniform in diameter, while those of *Harmothoë bonitensis* decrease in diameter gradually toward the tips.

Occurrence.—The specimen was found near Bonita Point at Station D 5846 at lat. 89° N, in a depth of 45–50 fathoms in the collection of the Survey of San Francisco Bay, made by the United States Bureau of Fisheries, April 7, 1913. This description is published by the kind permission of the Commission of the United States Bureau of Fisheries.

Harmothoë johnsoni sp. nov.

Pl. 2, figs. 12–17; pl. 3, figs. 18–21

Description.—The worm is flattened, but comparatively deep dorso-ventrally, the depth of the body being 4 mm. The color in the alcoholic specimen is gray. The dorsum is covered with large,

widely overlapping elytra. The dorsal and ventral surfaces are convex and the thirty-seven segments are well marked. The length of the body is 35 mm., and the width, including the setae is 14 mm. in the widest part of the body between segments 15 and 16. From these segments the body alternates very gradually towards both ends, more strongly towards the posterior end. The width of the body, excluding the setae and parapodia, is about one-third of the entire width, the length of each parapodium including setae being equal to the width of the body, or the parapodia and setae make up two-thirds of the entire width of the body.

The prostomium (pl. 2, fig. 12) is deep and broad; the length of the prostomium being only about two-thirds of the width. It is deeply fissured with acuminated anterior peaks. There are two pairs of comparatively small and equal-sized eyes. The anterior eyes are anterior to the widest part of the prostomium, while the posterior pair are near the center of the prostomium, about two-thirds of the distance from the anterior margin. The style of the median tentacle is missing. The strongly developed cirratophore is deeply inserted between the prostomial lobes. The lateral tentacles arise from prominent cirratophores. The styles are very short, being only slightly longer than the cirratophores. The length of the lateral tentacles, including the styles and cirratophores is about one-third of that of the prostomium. The palpi are stout and uniform in width near the base attenuating very gradually toward the distal ends. They are round and perfectly smooth without any papillae or cilia, slightly longer than the peristomial cirri.

The parapodia (pl. 2, fig. 14) are long, their length being equal to the width of the body, biramous, each ramus terminating in a narrow, finger-like projection, and is supported by a strong dark brown aciculum. The cirratophores of the dorsal cirri are very long, their length being about one-third of that of the style. The latter decreases very gradually in diameter toward the distal end, terminating in a fine filamentous tip. The neurocirrus occurs on all segments and consists of a strong cirratophore and a fusiform style.

The setae are numerous, from 70–100 on each parapodium. They are distinctly of three kinds, with gradations between, in size, as well as in structure. They are longest towards the center, decreasing in length ventrally and dorsally. The neurosetae (pl. 2, figs. 16 and 17) are long and slender, the longest neurosetae being equal in length to that of the parapodium and are twice the length of the stout noto-

setae. The subdistal end is covered with strong serrations, while the slender extreme distal portion and also the greater part of the proximal end is entirely smooth without any serrations. The extreme ventral neurosetae (pl. 3, fig. 21) are very much shorter than are those near the center, being about one-half or less the length of the latter. They are strongly curved, with the fine distal end slightly bent, and the convex subterminal portion strongly serrated.

The notosetae are of two distinct kinds. There are about half a dozen or more of fine dorsal setae (pl. 3, figs. 19 and 20) near the neuropodium. They are about equal in length to the long neurosetae, curved, attenuating very gradually and ending in very fine, almost capillary tips. The distal convex side is covered with spinous roughenings (pl. 3, fig. 20). The notosetae of the other kind are numerous, arranged in rows, each row consisting of 6 to 10 setae thus making a total of about 50 or more notosetae on each parapodium. The dorsalmost rows contain the shortest setae. The length of the setae increases with each succeeding row ventrad, until the maximum length is reached in the last row nearest to the neuropodium, the setae there being about twice the length of the shorter setae from the dorsal most rows. The setae are stout, perfectly smooth without any roughenings or serrations, uniform in width, tapering very abruptly towards the distal end (pl. 3, fig. 18).

There are fifteen pairs of elytra occurring on segments 2, 4, 5 and on all alternate segments to 23, then on segments 26, 29, and 32. The elytra (pl. 3, fig. 13) are kidney-shaped, large, widely overlapping, and thickly covered with chitinous tubercles (pl. 3, fig. 15). Fine venations radiate from the elytrophore in all directions.

The nephridial papillae begin with the sixth segment, occurring thence posteriorly on all segments. They are short, inconspicuous, and uniform in diameter.

Comparison.—The polynoid bears some resemblance to *Harmothoë complanata* Johnson (1901), and might even be considered as a subspecies of the latter. It differs, however, from *Harmothoë complanata* in the shape, and the relative dimensions of the body, the shape and the size of the prostomium, the shape of the parapodia and in the structure of the notosetae. In *Harmothoë complanata* the breadth of the body including the setae, is two-sevenths of the length, while in *Harmothoë johnsoni* the breadth including the setae is one-third of the length. The prostomium of *Harmothoë complanata* is equal in width and length, in *Harmothoë johnsoni* the prostomium is decidedly

broader, the length being two-thirds of the width. The parapodia also differ in shape in the two species. In *Harmothoë complanata* the dorsal ramus or the notopodium is very much shorter than the neuropodium, having about less than one-half of the length of the neuropodium, while in *Harmothoë johnsoni* both rami are almost equal in length (pl. 2, fig. 14). The stout dorsal setae of *Harmothoë complanata* are serrated, those of *Harmothoë johnsoni* are perfectly smooth. The nephridial papillae in *Harmothoë complanata* have acuminated tips; they are uniform in width ending abruptly in *Harmothoë johnsoni.* The color of *Harmothoë complanata* in the alcoholic specimens is reported by Johnson (1901) to be pale brown and a specimen in the Zoological Museum of the University of California is also of a brown color, while the color of *Harmothoë johnsoni* is light gray. The color, however, is not of great importance in classification.

Occurrence.—The single specimen which is now in the Zoological Museum of the University of California, was given to the writer by Mr. H. O. Falk, who had found it December 4, 1915, at a low tide on the beach off La Jolla, near San Diego, California.

Halosydna macrocephala sp. nov.

Pl. 3, figs. 22–33

Description.—The shape of the body is flattened and uniform in width, narrowing gradually toward the posterior end, rounded at both ends. The two specimens are 40 mm. and 25 mm. long, and 10.5 and 7 mm. wide respectively, with 5 mm. between parapodia. The dorsum is covered with widely overlapping elytra.

The prostomium (pl. 3, fig. 22) is unusually broad, the width being more than twice the length. It is very convex, forming a deep median fissure and sloping down abruptly on both sides. Of the two pairs of eyes those of the anterior are considerably larger and are situated near the lateral margins in about the widest part of the prostomiums. The posterior eyes are smaller, nearer together, and are situated at the extreme posterior margin of the prostomium, so that they are partly concealed by the peristomial fold. The strongly developed cirratophore of the median tentacle is inserted between the anterior cephalic prolongations. The style of the median tentacle is lost in both specimens. The stout lateral tentacles, arising from the anterior prostomial prolongations are about one-half of the length

of the palpi. They are uniform in diameter with subterminal enlargements ending then in filamentous tips. The palpi are very stout at the base, decreasing in diameter gradually and ending abruptly in filamentous tips; they are deeply grooved and covered with rows of prominent cilia. The peristomial cirri arising from strong cirratophores are of equal length with the palpi. The styles of the peristomial cirri are long, uniform in width, with subterminal bulb from which filamentous tips project.

The biramous parapodia (pl. 3, fig. 25) are comparatively stout, bearing two dark aciculi. The neuropodium has numerous (40–60) amber-colored setae, varying in shape and size. There are about twenty supra-acicular setae (pl. 3, fig. 30) with prominent serrations and a strong subterminal tooth. The 30 to 40 subacicular setae (pl. 3, fig. 33) differ slightly from the supra-acicular in that the subterminal tooth is smaller or rudimentary. The notopodium is inconspicuous and bears two kinds of setae; about 12 to 15 short, strongly curved setae, covered with strong serrations and ending bluntly with the proximal end and the extreme distal end smooth or free from serrations (pl. 3, fig. 31), and about 20 to 30 long, fine setae, densely covered with serrations, more or less curved and terminating in a fine point (pl. 3, figs. 26 and 27).

The setae from the second parapodium differ from those of other parapodia in their shape and also by being more strongly serrated. The notosetae (pl. 3, figs. 28 and 29) are about equal in size to the neurosetae (pl. 3, fig. 32). They are also nearly alike in shape and structure.

The nephridial papillae begin on the fourth segment, being situated at the dorso-lateral margin near the base of the parapodium and occurring thence posteriorly on all segments. The first or anterior papillae are short, increasing considerably in length dorsad.

There are eighteen pairs of elytra (pl. 3, fig. 23) occurring on segments 2, 4, 5, and on all alternate segments to 27, then on segments 28, 30, 31 and 33. They are comparatively thin and smooth, with but a few small, scattered papillae and are mottled with dark brown or black pigment (pl. 3, fig. 24). There are no marginal cilia. Fine venations radiate from the elytrophore in all directions. The dorsal cirri are equal in size and shape to the peristomial cirri.

Comparison.—The species resembles *Halosydna carinata* Moore (1903) in some respects and this is specially true of the broad prostomium and the conspicuously grooved palpi. The chief difference

lies in the shape of the parapodia and in the number and shape of the setae. In *Halosydna carinata,* of which Dr. J. P. Moore kindly loaned to me an imperfect specimen for comparison, the notopodia are small but prominent, being distinctly differentiated, while in *Halosydna macrocephala* the notopodium is inconspicuous and hardly differentiated. The neurosetae in *Halosydna carinata* are few, 10 to 20. They are strongly serrated, the plates with the serrations extending to the tip of the subterminal tooth; in *Halosydna macrocephala* the neurosetae are more numerous, (40 to 60) the subterminal tooth is less prominent and the serrations do not extend nearly to the subterminal tooth, leaving a considerable portion of the distal end of the setae smooth. The notosetae in *Halosydna carinata* are few, only 3 to 4, short, barely reaching to the tip of the notopodium, curved and ending bluntly. In *Halosydna macrocephala* the neurosetae are numerous, (30 to 40) of two kinds, and long, reaching nearly to the tip of the neuropodium. The 12 to 15 short setae are strongly serrated, curved, and end bluntly (pl. 3, fig. 31). The twenty or more fine notosetae are covered with fine serrations and are terminating in a fine capillary tip.

The setae of *Halosydna macrocephala* resemble those of *Halosydna californica,* Johnson, but the shape and the relative size of the prostomium and the deeply grooved palpi of *Halosydna macrocephala* distinguish the species from *Halosydna californica.*

Occurrence.—The locality of the type is unknown. Two incomplete specimens, the paratypes were found July 17, 1901, off San Diego, lat. 33° 36′9 N; long. 118° 14′7 W, at a depth of 39–51 meters, on rocky bottom.

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EXPLANATION OF PLATES

PLATE 2

Harmothoë bonitensis, sp. nov.

Fig. 1. Prostomium. × 10.
Fig. 2. Fifth elytron. × 10.
Fig. 3. First elytron. × 10.
Fig. 4. Portion of elytron. × 310.
Fig. 5. Fourteenth parapodium. × 15.
Fig. 6. Tip of long notoseta. × 310.
Fig. 7. Tip of long notoseta. × 75.
Fig. 8. Tip of short notoseta. × 160.
Fig. 9. Tip of short notoseta. × 75.
Fig. 10. The same. × 310.
Fig. 11. Tip of long neuroseta. × 310.
Fig. 12. Prostomium. × 20.
Fig. 13. Fifth elytron. × 10.
Fig. 14. Eighteenth parapodium. × 10.
Fig. 15. Tubercles of elytron. × 160.
Fig. 16. Portion of long neuroseta. × 310.
Fig. 17. Tip of long neuroseta. × 75.

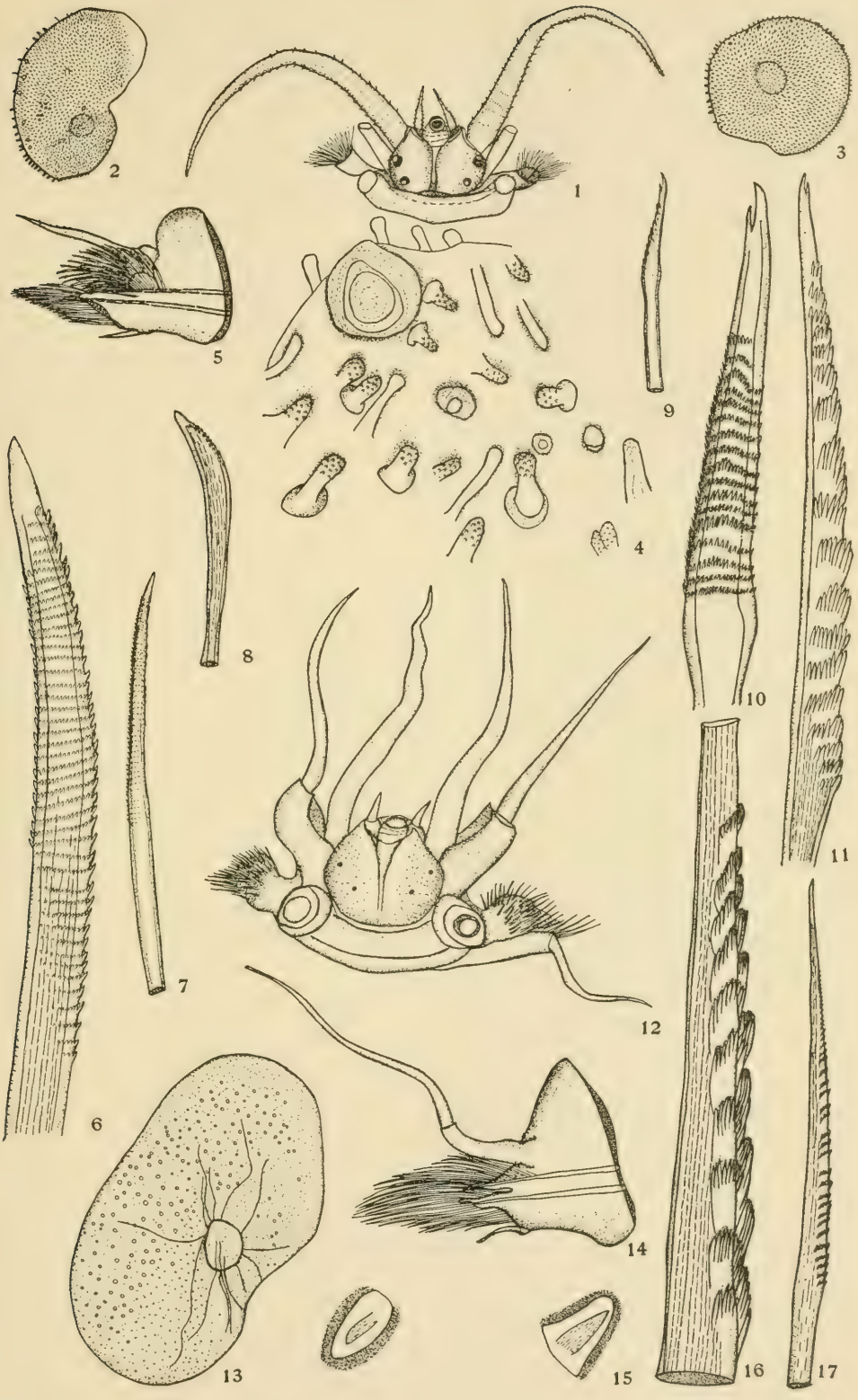
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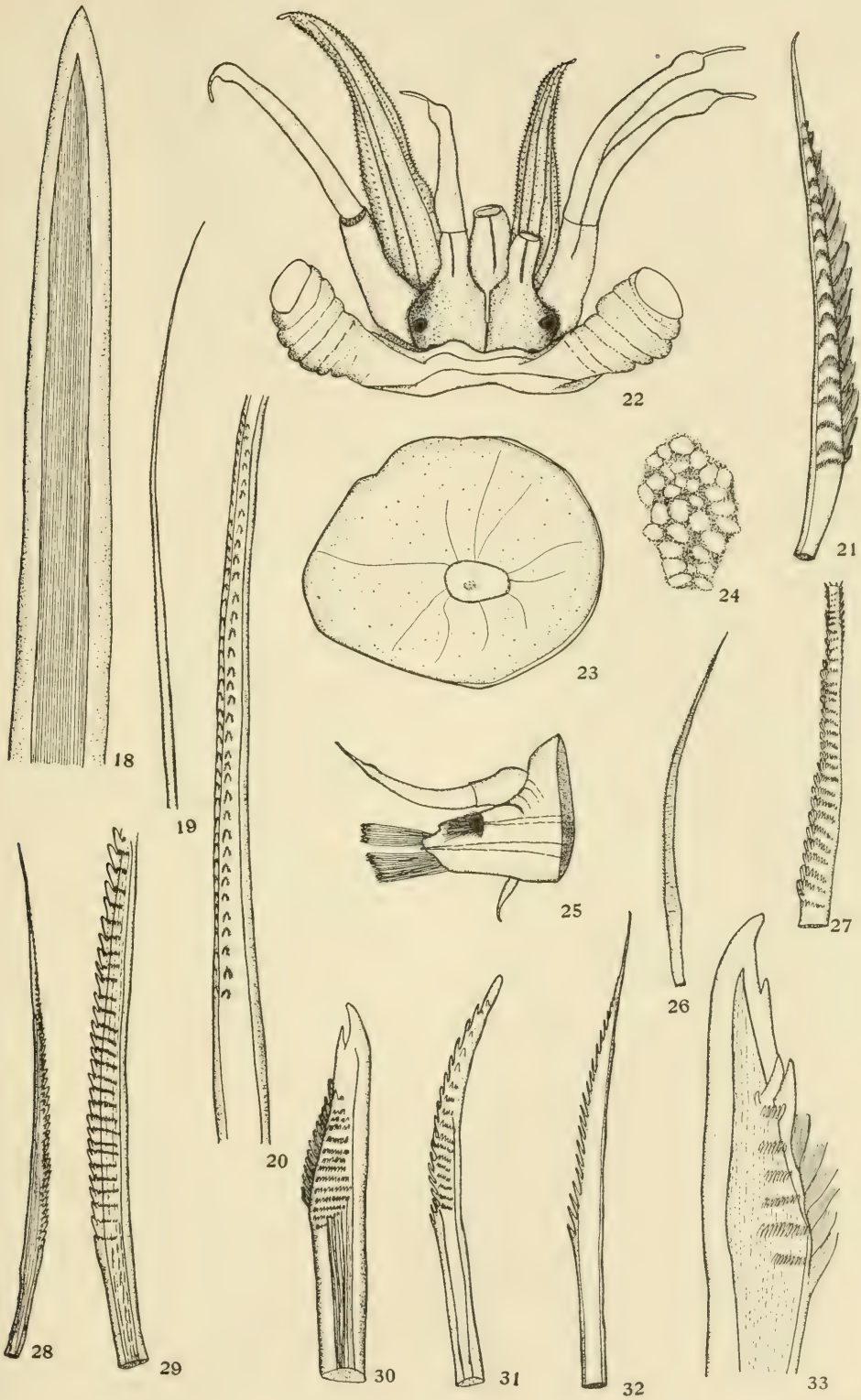
PLATE 3

Harmothoë johnsoni, sp. nov.

Fig. 18. Tip of short notoseta. × 310.
Fig. 19. Tip of fine notoseta. × 45.
Fig. 20. Portion of the same. × 310.
Fig. 21. Tip of short neuroseta. × 160.

Halosydna macrocephala, sp. nov.

Fig. 22. Prostomium. × 20.
Fig. 23. Elytron. × 10.
Fig. 24. Portion of elytron. × 75.
Fig. 25. Fourteenth parapodium. × 10.
Fig. 26. Tip of long notoseta. × 75.
Fig. 27. Portion of the same. × 310.
Fig. 28. Tip of notoseta of first parapodium. × 160.
Fig. 29. Portion of the same. × 310.
Fig. 30. Tip of supra-acicular neuroseta. × 160.
Fig. 31. Tip of short notoseta. × 310.
Fig. 32. Neuroseta from first parapodium. × 160.
Fig. 33. Subacicular neuroseta. × 310.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Vol. 15. Introduction. Dependence of Marine Biology upon Hydrography and Necessity of Quantitative Biological Research. Pp. i-xxiii. June, 1916 ..... .25

1. Hydrographic, Plankton, and Dredging Records of the Scripps Institution for Biological Research of the University of California, 1901 to 1912, compiled and arranged under the supervision of W. E. Ritter by Ellis L. Michael and George F. McEwen. Pp. 1-206, 4 text figures and map. July, 1915 ..... 2.25
2. Continuation of Hydrographic, Plankton, and Dredging Records of the Scripps Institution for Biological Research of the University of California (1913-1915), compiled and arranged under the supervision of W. E. Ritter, by Ellis L. Michael, Zoologist and Administrative Assistant, George F. McEwen, Hydrographer. Pp. 207-254, 7 figures in text. November, 1916 ..... .50
3. Summary and Interpretation of the Hydrographic Observations made by the Scripps Institution for Biological Research of the University of California, 1908 to 1915, by George F. McEwen, Hydrographer. Pp. 255-356, plates 1-38. December, 1916 ..... 1.00

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Nos. 2 and 3 in one cover. November 1915 ..... .30
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7. On a New Trichomonad Flagellate, *Trichomitus parvus*, from the Intestine of Amphibians, by Olive Swezy. Pp. 89-94, plate 12.
Nos. 6 and 7 in one cover. December, 1915 ..... .25
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9. Three New Helices from California, by S. Stillman Berry. Pp. 107-111. January, 1916 ..... .05
10. On *Trypanosoma triatomae*, a New Flagellate from a Hemipteran Bug from the Nests of the Wood Rat *Neotoma fuscipes*, by Charles Atwood Kofoid and Irene McCulloch. Pp. 113-126, plates 14-15. February, 1916 ..... .15
11. The Genera *Monocercomonas* and *Polymastix*, by Olive Swezy. Pp. 127-138. plates 16-17. February, 1916 ..... .10
12. Notes on the Spiny Lobster (*Panulirus interruptus*) of the California Coast, by Bennet M. Allen. Pp. 139-152, 2 figs. in text. March, 1916 .15
13. Notes on the Marine Fishes of California, by Carl L. Hubbs. Pp. 153-169, plates 18-20. March, 1916 ..... .15
14. The Feeding Habits and Food of Pelagic Copepods and the Question of Nutrition by Organic Substances in Solution in the Water, by Calvin O. Esterly. Pp. 171-184, 2 figs. in text. March, 1916 ..... .15
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3. Description of Some New Species of *Polynoidae* From the Coast of California, by Christine Essenberg. Pp. 45-60, plates 2-3. October, 1917 ..... .20
4. New Species of *Aphinomidae* From the Pacific Coast, by Christine Essenberg. Pp. 61-74, plates 4-5. October, 1917..... .15

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NEW SPECIES OF *AMPHINOMIDAE* FROM THE PACIFIC COAST

BY

CHRISTINE ESSENBERG

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NEW SPECIES OF *AMPHINOMIDAE* FROM THE PACIFIC COAST

BY
CHRISTINE ESSENBERG

CONTENTS

PAGE

Introduction 61
Acknowledgments 62
General description 62
Description of new species 63
Euphrosyne calypta sp. nov. 63
Euphrosyne multibranchiata sp. nov. 65
Eurythoë spirocirrata sp. nov. 66
Euphrosyne kyllosetosa sp. nov. 68
Literature cited 70
Explanation of plates 72

INTRODUCTION

The present paper is a continuation of two previous papers on the polychaetous annelids. The study of these annelids was begun and carried on for some time in the Zoological Laboratory of the University of California at Berkeley and was completed at the Scripps Institution for Biological Research at La Jolla.

ACKNOWLEDGMENTS

The writer avails herself of the opportunity to express her hearty thanks to Professor Charles A. Kofoid for his encouragement and for his valuable suggestions and criticisms in this work.

The material used in this work was obtained largely from the annelid collection of the Zoological Museum of the California University at Berkeley, of which a revision is being made, and from private collections.

OCT 30 1917
National Museum

GENERAL DESCRIPTION

The Amphinomidae are interesting in many ways. They have been a problem to the various workers as to their place in the polychaeta group and the question has not been definitely settled yet. Some authors as Quatrefage (1865), have separated this family from the Aphroditidae by the Palmiridae, Leodocidae and Lumbrinereidae. Others, as McIntosh (1900), disapprove of this division, claiming that anatomical differences are not sufficient to justify it. Further disagreement prevails among the various workers as to the classification of this group. Some, as Ehlers (1864), deal with the Amphinomidae as one family. A number of other workers treat them as two independent families, Amphinomidae and Euphrosinidae. McIntosh in his first work (1885) treats the Amphinomidae as two independent families, but in his later volume (1900) he places the subfamilies Amphinomina and Euphrosynina under the one family Amphinomidae. I am inclined to follow the latter plan of classification. Besides the various other characteristics common to both subfamilies of the Amphinomidae, the presence of a dorsal caruncle and the location of the mouth, which is removed ventrally from the usual position at the tip of the snout, distinguish the Amphinomidae from all other families of the Polychaeta.

The chief characteristics pertaining to both subfamilies are as follows: The body is oblong or ovate-oblong. The cephalic lobe is rounded or compressed and coalesced with the caruncle. The caruncle extends over several segments. Of the two pairs of eyes both pairs may be situated dorsally, or one pair may be situated ventrally and the other dorsally. In the family Amphinomidae, there are two lateral tentacles and one median. The latter, however, may be absent. The mouth is removed from the anterior end ventrally and is surrounded by specially modified segments. The proboscis is protrusible, devoid of papillae and of chitinous jaws. The parapodia are biramous and peculiarly modified. The notopodium extends on the dorsum and is coalesced with the latter. It bears setae, branchiae and cirri, arranged in transverse rows, frequently covering the entire dorsum of the worm, except a narrow mid-dorsal line. The setae are usually of two or more kinds; they are tubular, calcareous, very brittle, simple, capillary, unequally bifurcate or serrate. The branchiae are arborescent or pinnate; dorsal in Euphrosynina, marginal in Amphinomina. The ventral cirri are single, the dorsal, single or double.

The members of the family Amphinomidae are confined mostly to tropical and subtropical waters, but a few species of *Eurithoë* have been reported from the lower boreal regions, and some species of *Euphrosynina* have been found in the temperate zones.

The species in the collection of the Zoological Museum of the University of California are from the waters of the coasts of California, except two specimens, of which one is from the Hawaiian waters, the other one from the sub-boreal waters. The Amphinomidae have a varied bathymetrical distribution, ranging from the littoral zones to depths of 2000 fathoms. They have been found on the surface of the water attached to buoyant substances such as logs or weeds. They are frequently found on kelp between tide-marks. Some of the species live as commensals on sponges and are noted for their remarkable adaptive coloration (McIntosh, 1900).

DESCRIPTION OF NEW SPECIES

The species of Amphinomidae of the University collection have been enumerated by Treadwell (1914). On the following pages the following new species are described which may be added to his list: *Euphrosyne calypta, Euphrosyne multibranchiata, Eurythoë spirocirrata,* and *Euphrosyne kyllosetosa.*

To the list of the Amphinomidae in the annelid collection of the University of California may also be added *Chloeia pinnata* (Moore), of which fourteen specimens were found in the Survey of San Francisco Bay on October 21, 1912, at Station D5788, near Farallone, lat. 11° 30′ N., at a depth of 68 to 60 fathoms, in very fine green sand.

1. **Euphrosyne calypta** sp. nov.

Pl. 4, figs. 1–3, 6–7, 13–14

Diagnosis.—Body elongated, rounded at both ends. Dorsum slightly arched with segmentations definitely marked on dorsal and ventral surfaces. Caruncle bilobed, extending to the fourth segment. Six pairs of three- to four-lobed branchiae. Dorsal cirrus between second and third gill-trunks.

Description.—The species is comparatively small in size. The two specimens, type and paratype, measure 10 and 11 mm. in length, respectively, and 6 mm. in width. The body is ovate-oblong, uniform in width, rounded at both ends. The slightly arched dorsum is covered

with transverse rows of branchiae and setae except a narrow mid-dorsal bare line. The ventral surface is convex. The segmentation is well marked by transverse folds. The corresponding numbers of segments of the two specimens are 20 and 28. The caruncle (pl. 4, fig. 1) is coalesced with the prostomium and is dorso-ventrally bilobed. The posterior free end of the caruncle extends almost to the posterior margin of the fourth segment. The anterior end of the caruncle bears a tentacle consisting of a heavy basal portion and a prominent style, about the same length. At the base of the tentacle is a pair of large dorsal eyes. Another pair of smaller eyes is situated ventrally between the peristomial parapodia (pl. 4, fig. 7).

The parapodia are of the usual kind. The dorsal and ventral rami are distinctly separated. The dorsal ramus or notopodium merges into the dorsum, extending nearly to the mid-dorsal line, covering with its numerous setae and branchiae the greater part of the dorsum. There are three cirri, one ventral and two dorsal. The ventral cirrus is inserted between the ventral setae, its distal end reaching to the tips of the ventral setae. One of the two dorsal setae occurs on the dorsum immediately posteriad of the first dorsal trunk of branchiae. The second cirrus is situated between the second and third gill-trunks (counting from the dorsal extremities of the series). The dorsal cirri are stout, slightly tapering toward the distal ends. They are of about equal length with the branchiae, and about one-half of the length of the dorsal setae.

There are six main trunks of branchiae on each parapodium. Each trunk is subdivided into three or four finger-like projections (pl. 4, figs. 13–14). Anterior to each transverse row of branchiae is a row of numerous brown, forked setae (pl. 4, fig. 2). They are bifid, long, tubular, and hollow, with the distal end of the longer projection slightly tapered and the tip slightly curved. One type of dorsal setae only is present, although the setae vary in size. The ventral setae are similar in shape to the dorsal. They are long, one-half the width of the body, hollow, brittle, with the tips obtusely rounded (pl. 4, fig. 3). The setae and the branchiae incline anteriorly near the anterior portion of the body (pl. 4, fig. 1), and posteriorly on the posterior portion of the body.

The buccal region extends to the fifth segment (pl. 4, fig. 7). The caudal cirri (pl. 4, fig. 6) are fleshy and obtusely rounded.

Comparison.—This species has been previously classified by Treadwell as *Euphrosyne aurantiaca* Johnson. It resembles the latter at

first sight in the general appearance, but differs from it in some essential characteristics. The setae in the two species differ in color and in structure. The setae are brown and only of one kind in *Euphrosyne calypta;* they are white in *Euphrosyne aurantiaca,* and the dorsal setae are of two distinct kinds. Further differences are in the location of the cirri. In *E. calypta* the mid-dorsal cirrus is between the second and third gill-trunks; in *E. aurantiaca* the cirrus is between the third and the fourth gill-trunks, counting from the dorsal line. *E. calypta* has six pairs of three- to four-lobed branchiae on each segment; *E. aurantiaca* has seven pairs of seven-lobed branchiae on each segment.

Occurrence.—The type is a dark gray color in alcohol. It has been found in the channel off Santa Barbara. Further data lacking. The other specimen is tan-brown in color. Its locality is unknown.

2. **Euphrosyne multibranchiata** sp. nov.

Pl. 4, figs. 4–5, 8–12

Diagnosis.—Comparatively large-sized worm. Body elongated obtusely rounded at both ends. Dorsal and ventral surfaces convex; setae long and brittle; caruncle bilobed and long, extending to the seventh segment.

Description.—The classification of this species is based on a single specimen. It is a large worm, for this genus. The length of the body is 40 mm., the width in the widest part of the body (between segments 26 and 29) 13 mm., exclusive of the setae. From these segments the width of the body decreases towards both ends. The body is elongated, slightly wider in the center, very gradually decreasing in width toward the ends, which are obtusely rounded. The dorsal and the ventral surfaces are convex and the segmentation is well indicated on both sides by transverse ridges. The number of the segments in this specimen is 45. Except for the narrow mid-dorsal bare line, the dorsum is covered with rows of branchiae and setae. The color of the worm is grayish-brown with ventral setae light yellow, almost white.

The prostomium is deeply sunken between the peristomial parapodia and fused with the dorsally located bilobed caruncle. The caruncle (pl. 4, fig. 11) is long with its free end extending to the seventh segment. It is bilobed dorso-ventrally. The dorsal lobe is grooved and evidently longer than the ventral, for it is coiled in a

zig-zag line. The median tentacle consists of a long, heavy basal portion and a short style about one-fourth the length of the former. At the base of the tentacle on each side of it are a pair of eyes partly covered by the tentacle when the latter is bent posteriorly. The ventral eyes (pl. 4, fig. 12) are small, flanked on each side by very small antennae. The palpi are broad and flat, divided longitudinally by a median cleft. The mouth (pl. 4, fig. 12) is bordered posteriorly by the fifth segment.

The parapodia are typical of the genus, with the notopodium merging into the dorsum. The setae are of two kinds. The ventral setae (pl. 4, fig. 4) are long, one-third of the width of the body, slender, hollow, and very brittle, of straw color with a subterminal spur. The dorsal setae are similar in shape (pl. 4, fig. 5) but they are much shorter and stouter than the ventral, slightly surpassing the length of the branchiae (pl. 4, fig. 10).

There are ten to eleven pairs of branchiae on each segment. The main trunks of branchiae (pl. 4, figs. 8, 9, 10) are subdivided into smaller finger-like projections, the number of which may vary according to the size of the trunk. The finger-like ramifications are usually about 10 to 12 on a trunk, but some of the gill-trunks of the anterior end have only about 5 or 6 ramifications.

There are two dorsal cirri and one ventral. The short and heavy ventral cirrus (pl. 4, fig. 12) is situated at the posterior edge of the neuropodium on the ventral surface. The two dorsal cirri are short, stout, attenuating toward the end, terminating bluntly (pl. 4, fig. 10). The dorsal cirrus is posteriad of the last dorsal gill-trunk. The lateral cirrus is between the fifth and the sixth gill-trunks, counting from the mid-dorsal line. It is short, reaching only halfway the length of the branchiae.

The single specimen in the collection is from Kodiak Island, Alaska. Further data unknown.

3. **Eurythoë spirocirrata** sp. nov.

Pl. 4, figs. 15–17; pl. 5, figs. 18–23

Diagnosis.—Body long, slender, gray in alcohol. Dorsal surface slightly convex. Ventral surface strongly convex. Sides between parapodia vertical and flat. Branchiae marginal. Two cirri on each parapodium. Caruncle broad, smooth, extending to fourth segment.

Description.—The species is a typical representative of the genus *Eurythoë*. The body is long, somewhat uniform in width, very grad-

ually attenuating toward the posterior end and with both ends obtusely rounded. The dorsal surface is almost straight and only slightly arched. The ventral surface is strongly convex. The length of the body is 55 mm., the width, in the widest part of the body (about segments 29 and 30), 13 mm. The segmentation is well shown on the dorsal and the ventral surfaces, as well as on the vertical sides. The number of segments is 66. The caruncle (pl. 5, fig. 18) is coalesced with the prostomium. It is broad and smooth without any grooves and extends to the fourth segment. It has one short median tentacle. The posterior end of the caruncle is narrow and cleft. The prostomium bears two pairs of cirri. No eyes are visible on this specimen. The buccal region extends to the fifth segment (pl. 5, fig. 19). The cirri are spirally constricted. The parapodia (pl. 4, fig. 17) are made up of two widely separated rami. The ventral ramus bears a spirally constricted cirrus and a fascicle of comparatively short setae about one-half the length of the cirri (pls. 4 and 5, figs. 17, 19). The ventral setae (pl. 5, figs. 22, 23) are light yellow, hollow, brittle, with a subterminal prong, ending bluntly. The dorsal division bears a ramose gill (pl. 4, figs. 15, 16, 17). The gill-branches increase in complexity toward the median and posterior portions of the body. The dorsal setae are of two types. One type (pl. 5, fig. 20) is strongly serrated, ending bluntly; the other, very fine, straight, the distal end slender and pointed, with very minute serrations above the prong (pl. 5, fig. 21).

Comparisons.—The worm was labelled as *Eurythoë californica.* It differs from *E. californica* Johnson by the shape of the caruncle, which is narrow and twisted in the latter species, with the prostomium bounded anteriorly by a peculiar crescent-shaped margin. In *Eurythoë spirocirrata* the caruncle is smooth and broad. Further differences are evident in the setae, which are entirely different in the two species. The ventral setae differ in shape, and the two kinds of serrated dorsal setae present in *E. spirocirrata* are represented in *E. californica* by perfectly smooth, straight setae without any serrations. The cirri are spirally twisted in *Eurythoë spirocirrata;* they are straight in *E. californica.* Comparing the illustrations as well as the specimens of both species, one can see at once the characteristic differences.

Eurythoë spirocirrata resembles *E. pacifica* Kinberg more in general appearance and in the shape of the body. It differs from the latter in the broad shape of the caruncle, by the spirally twisted cirri,

by the absence of eye-spots and by the shape of the setae. In *Eurythoë pacifica* the ventral setae are more strongly bifurcated with a few serrations on the concave side of the longer fork.

The habitat of the worm is unknown. Most probably it comes from the vicinity of San Diego.

4. **Euphrosyne kyllosetosa** sp. nov.

Pl. 5, figs. 24–31

Diagnosis.—Body ovate-oblong. Dorsum arched and covered with branchiae and setae. Naked mid-dorsal line about one-fifth of the width of the body. Caruncle bilobed, long, extending to the fifth segment. Branchiae 6 to 7 pairs on each segment. Dorsal setae of two kinds, unevenly bifurcate smooth; and strongly bifurcate serrate.

Description.—It is a comparatively small worm measuring 11 mm. in length and 6 mm. in width including setae. The respective number of segments in the two specimens, type and cotype, are 31 and 32. The dorsum is convex, densely covered with branchiae and setae, except a narrow mid-dorsal line about one-fifth of the width of the body which is bare. The prostomium is coalesced with the peristomium and is partly concealed by the long bilobed caruncle dorsally. The crest of the caruncle (pl. 5, fig. 24) is marked by longitudinal grooves. The median tentacle consists of a long basal portion and a style of equal length. The whole tentacle is about one-half of the length of the caruncle. At the base of the tentacle is a pair of eyes. The caruncle is comparatively long, with its free end extending to the fifth segment. The palpi are broad, flattened pads (pl. 5, fig. 25). continuous by their anterior ends with the peristomial parapodia. The mouth is bounded anteriorly by the palps, and posteriorly by a V-shaped furrowed lip. The buccal region extends to the fourth segment. The ventral eyes (pl. 5, fig. 25) are small. The biramous parapodia are of the kind characteristic to the genus. The notopodia are sessile, merging into the dorsum; the neuropodia lateral, slightly projecting lamellae. The cirri are about equal to the gills in length, stout, slightly tapered. The notocirrus is situated mediad of the setae palisade and a little anterior to the branchiae. The lateral or middle cirrus is in line with the notocirrus and is between third and fourth gill-trunks, on the anterior segments, between the second and third gill-trunks (counting from the dorsum). The neurocirrus is similar in shape, situated within the postero-ventral margin of the neuropodial fascicle of the setae.

Branchiae occur on all setigerous segments, usually six pairs on a segment, but there may be only five pairs on the few extreme anterior segments, and seven pairs on the median segments. Each gill-trunk consists of a stem dividing dichotomously several times. The gills vary in size, the individual projections ranking from four to eight in number on each gill-trunk (pl. 5, figs. 31, 32).

The notopodial setae (pl. 5, figs. 26, 28, 29) are arranged in a long palisade of two rows along the entire length of the gill-series. They all are hollow, calcareous, translucent and yellowish-white. They are comparatively short, some projecting slightly beyond tips of the gills. The serrated bifid dorsal setae (pl. 5, figs. 28, 29) are narrow, enlarging near the place of forcation. Both forks are slightly bent, strongly serrated along the inner borders, and are covered with fine asperities. The serrated dorsal setae are more numerous on the anterior portion than on the rest of the body. The dorsal setae of the second row (pl. 5, fig. 26) are of the simple form, incompletely bifid, one of the forks being much longer, about three times the length of the shorter fork, with almost straight, smooth tips. The neuropodial setae (pl. 5, figs. 27, 30) arise in several rows from an elliptical area. They are similar to the smooth dorsal setae but are much stouter and longer than the latter. The length of the ventral setae varies, those in the dorsal part of the fascicle being the longest (about 1 mm.), the setae decreasing in length as they proceed ventrad.

Comparison.—The species resembles somewhat *Euphrosyne dumosa* Moore (1911), but differs from it in the lesser number of gill-trunks and in the shape of the setae. *Euphrosyne dumosa* has 10–11 pairs of branchiae on each segment; *E. kyllosetosa,* 6–7 pairs. The setae differ considerably in the two species. The distal ends of the notosetae as well as of the neurosetae are more slender in *E. dumosa* than they are in *E. kyllosetosa,* and the shorter fork of the non-serrated setae is very short, almost rudimentary, in *E. dumosa.* Other minor differences may be found in the shape of the branchiae and in other characteristics.

The two specimens, type and cotype, were collected between tidemarks from drifting kelp near La Jolla, California, and were kindly presented to me by the collector, Mr. H. O. Falk. They are now in the annelid collection of the University of California in Berkeley. Five specimens of *E. limbata* Moore have been given to me by the same collector and are now in the annelid collection of the Zoological Museum of the University of California at Berkeley. They were collected on December 4, 1915, from kelp holdfasts off La Jolla.

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EXPLANATION OF PLATES

(All figures drawn with camera lucida)

PLATE 4

Fig. 1. Dorsal view of anterior portion of *Euphrosyne calypta.* × 10.

Fig. 2. Tip of dorsal seta of *Euphrosyne calypta.* × 160.

Fig. 3. Tip of ventral seta of the same. × 160.

Fig. 4. Tip of ventral seta of *Euphrosyne multibranchiata.* × 160.

Fig. 5. Tip of dorsal seta of *Euphrosyne multibranchiata.* × 160.

Fig. 6. Posterior segments of *Euphrosyne calypta,* showing caudal cirri. × 10.

Fig. 7. Ventral view of anterior end of *Euphrosyne calypta.*

Fig. 8. Branchiae of *Euphrosyne multibranchiata.* × 20.

Fig. 9. A branch of the gills of *Euphrosyne multibranchiata.* × 20.

Fig. 10. Three gill-branches of *Euphrosyne multibranchiata,* showing the dorsal cirrus and the setae in their relative positions. × 20.

Fig. 11. Caruncle of *Euphrosyne multibranchiata.* × 10.

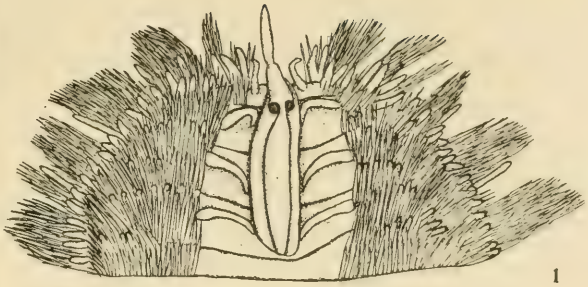
Fig. 12. Ventral view of anterior end of *Euphrosyne multibranchiata.* × 10.

Figs. 13–14. Branchiae of *Euphrosyne calypta.* × 75.

Fig. 15. Branchiae of *Eurythoë spirocirrata.* × 10.

Fig. 16. A branchlet of the preceding. × 20.

Fig. 17. Twentieth parapodium of *Eurythoë spirocirrata.* × 20.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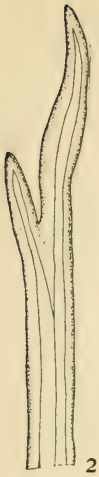
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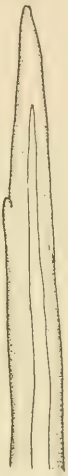
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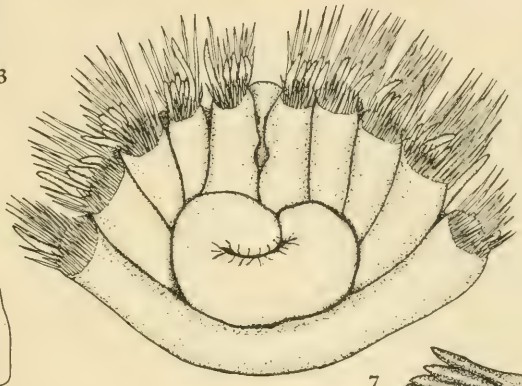
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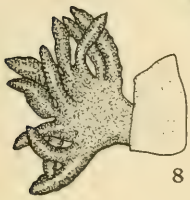
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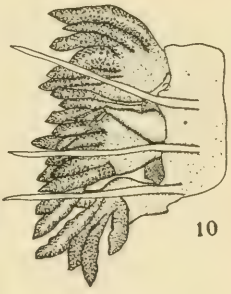
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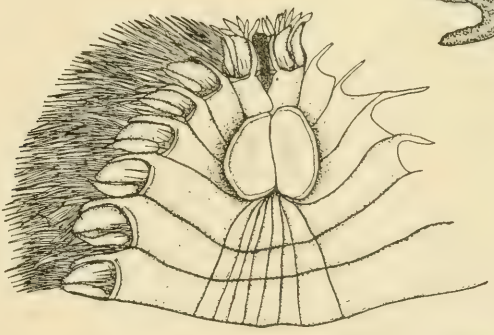
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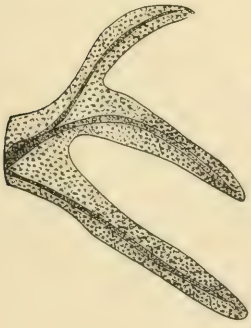
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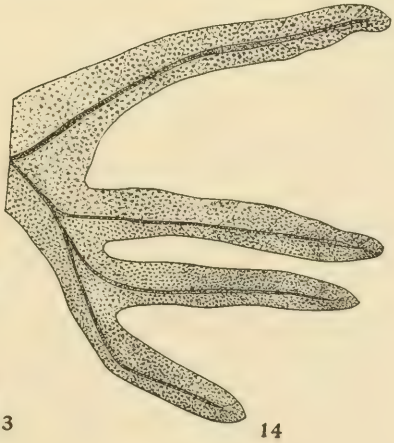
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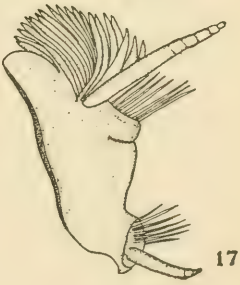
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PLATE 5

Fig. 18. Dorsal view of anterior portion of *Eurythoë spirocirrata*, showing relative position of caruncle. × 10.

Fig. 19. Anterior ventral view of *Eurythoë spirocirrata*. × 10.

Fig. 20. Tip of stout, serrated dorsal seta of *Eurythoë spirocirrata*. × 160.

Fig. 21. Tip of fine dorsal seta of *Eurythoë spirocirrata*. × 160.

Fig. 22. Tip of smaller ventral seta of *Eurythoë spirocirrata*. × 160.

Fig. 23. Tip of stouter ventral seta of *Eurythoë spirocirrata*. × 160.

Fig. 24. Caruncle of *Euphrosyne kyllosetosa*. × 20.

Fig. 25 Ventral view of anterior end of same. × 10.

Fig. 26. Tip of dorsal seta of *Euphrosyne kyllosetosa*. × 320.

Fig. 27. Tip of ventral seta of *Euphrosyne kyllosetosa*. × 320.

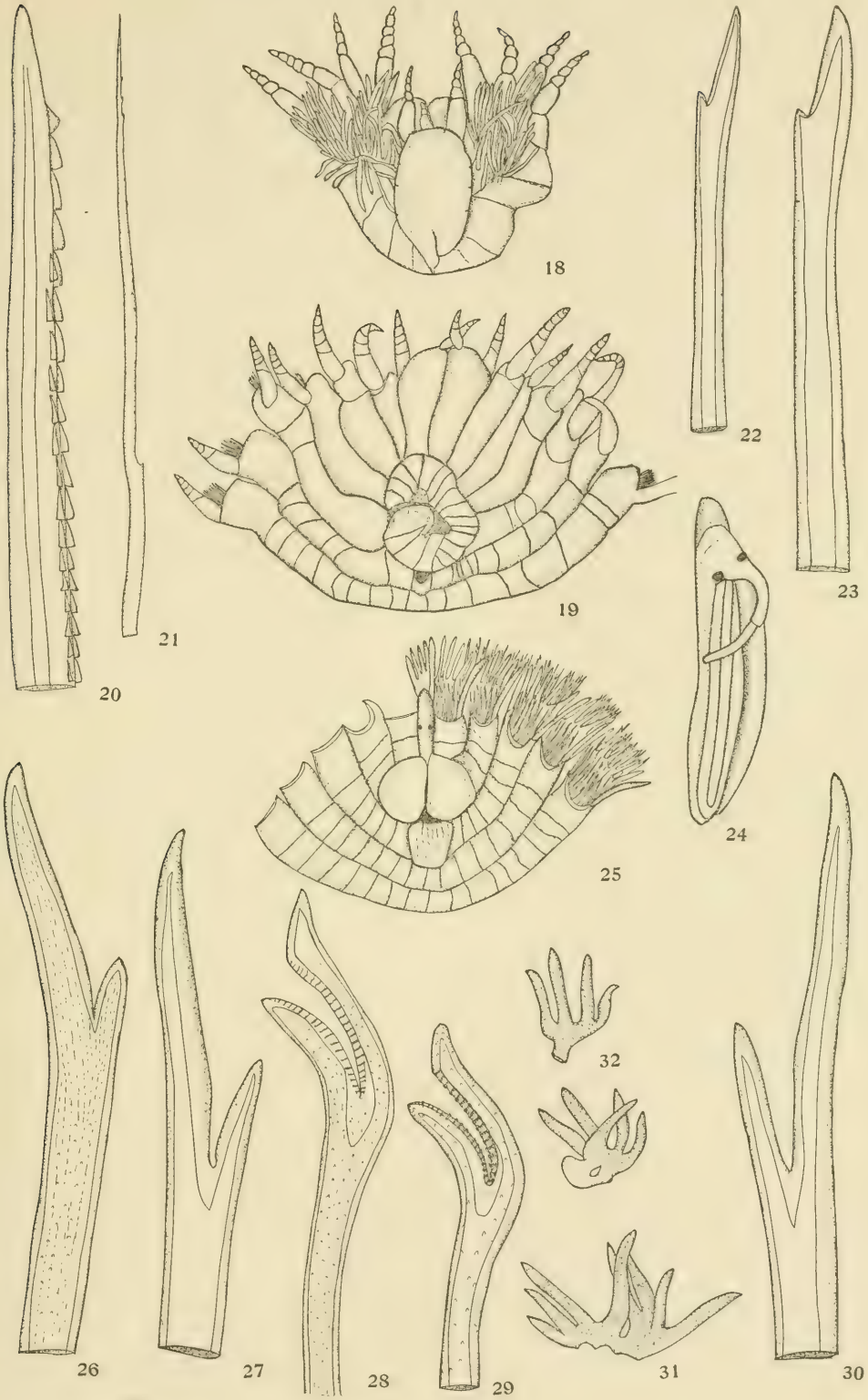
Fig. 28. Tip of serrated dorsal seta of same. × 320.

Fig. 29. Same.

Fig. 30. Tip of ventral seta of *Euphrosyne kyllosetosa*. × 320.

Fig. 31. Branchiae of the same. × 40.

Fig. 32. Branchlets of the same. × 40.


18
19
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21
22
23
24
25
26
27
28
29
30
31
32

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CRITHIDIA EURYOPHTHALMI, SP. NOV., FROM THE HEMIPTERAN BUG, *EURYOPHTHALMUS CONVIVUS* STÅL

BY

IRENE McCULLOCH

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IRENE McCULLOCH

CONTENTS

PAGE
Introduction 75
Comparison of *Crithidia leptocoridis* and *C. euryophthalmi* 76
Morphology of the digestive tract of *Euryophthalmus convivus* 78
Infection of the digestive tract of *Euryophthalmus convivus* by *Crithidia euryophthalmi* 81
Life cycle of *Crithidia euryophthalmi* 82
Forms from the crop 83
Oval spore forms 83
Developing crithidial stages 83
Multiple fission 83
Somatella 83
Internal or endogenous budding 84
Binary fission 84
Forms from the mid-stomach 85
Forms from the pyloric expansion 85
Nectomonads 86
Haptomonads 86
Rectal forms 86
Infective and degenerative cycles 87
Summary 87
Literature cited 88

Introduction

During the late summer and early fall, large numbers of *Euryophthalmus convivus* can be found feeding upon *Lupinus arboreus* Sims, one of the common lupines growing on the sand dunes of San Francisco near Golden Gate Park. Many bugs can also be detected

readily in the grass, dead leaves and sand beneath the bushes. The adults are protected in part by their coloration which is a dusky black with dull yellow wing-markings. The young, on the contrary, are conspicuous objects because of their shiny, steel-blue color. The tendency, also, of the nymphs to remain for some time in a compact mass increases the conspicuousness of their coloration.

An examination of the contents of the digestive tract of these insects revealed in eighty per cent a heavy infection of flagellates in certain portions of the mid gut, namely: the crop, the mid-stomach, and the pyloric expansion (fig. 1, *cr., mid., stom., pyl. ex.*). Close observation of these parasites at once placed them in the genus *Crithidia*. At first it was thought that they belonged to the species of *Crithidia* previously described by me (1915) as *Crithidia leptocoridis*. However, further investigation of the morphology and life cycle of both flagellates has presented sufficient evidences to justify the placing of the two flagellates in distinct species. Accordingly, the flagellate parasitic in the digestive tract of *Euryophthalmus convivus* has been called *Crithidia euryophthalmi*, sp. nov.

Comparison of Crithidia leptocoridis and C. euryopthalmi

A tabular comparison of these two species of *Crithidia leptocoridis* and *C. euryopthalmi*, from the plant-feeding bugs, *Leptocoris trivittatus* and *Euryopthalmus convivus*, respectively, will now be given.

	C. leptocoridis	*C. euryopthalmi*
Size		
	Length 20μ to 40μ. Width 1.5μ to 3μ.	Length 10μ to 30μ. Width 1.7μ to 2.5μ.
(A) Location of parasites		
(1) Stomach		
(*a*) Crop	Abundant infection present at certain periods. Few spore forms have been found.	Abundant infection containing many spore forms at certain periods. Wide range of forms including, possibly, two types of multiple fission.
(*b*) Mid-stomach	No division comparable to this in *Leptocoris*.	Usually infected with spore and flagellated stages of the parasites.
(*c*) Pyloric expansion	No division comparable to this in *Leptocoris*.	Exceedingly heavy infection nearly always present in adults. Stages here are comparable to those of the rectum of *Leptocoris*.

(2) Intestine Infection here somewhat comparable to that of the mid-stomach of *Euryophthalmus convivus*. Spore forms are seldom found here.	No infection has been found in the intestine.
(3) Rectum Heavy infection usually present in adults. Spore forms not common. The stages found here are comparable to those of the pyloric expansion of *Euryophthalmus*.	Spores only have been found in the normal preparations of the rectum. Two preparations only from fifty insects showed infection.
(B) Myonemes Usually present in a definite number and position on the body.	Not readily found and probably occur in no definite position on the body.
(C) Parabasal body Noticeably bilobed along anterior edge in nearly all of the crithidial stages.	Seldom shows any indication of the bilobed appearance.
(D) Parabasal rhizoplast Fan-shaped mass made up of numerous, colorless, thread-like fibers.	Outline of fan-shaped parabasal rhizoplast clearly defined but no internal structure has been discerned.
(E) Blepharoplast Some forms show an enlargement at the base of the flagellum. This stains lightly and can not be defined as a definite basal granule or blepharoplast.	Little evidence to show that there is normally any enlargement which could be regarded as blepharoplast from a purely structural standpoint.
(F) Nucleus The nucleus not commonly found with a chromatin encrusted membrane and a central karyosome. The chromatin is frequently broken up into several granules.	Nucleus as a rule shows a chromatin encrusted membrane with a central karyosome.
(G) Degeneration Shown by numerous chromidia in cytoplasm, broken up chromatin granules and vacuolated cytoplasm.	Shown chiefly by vacuolated cytoplasm. Entire nucleus may be diffused, but the chromatin is most frequently in the form of a central granule. Chromidia are not numerous.
(H) Spore forms Few preparations show spore forms.	Almost all of the preparations show a few or many spore forms.

(I) Binary fission More abundant in the crop and rectum.	Found in the crop and pyloric expansion, but it has not yet been found in the rectum.
(J) Multiple fission	
(1) Somatellae Somatellae have not been found showing flagellated zooids.	A few cases have shown somatellae in the crop. These are spherical in shape containing a variable number of flagellated zooids.
(2) Internal budding Process comparable to that of *C. euryophthalmi* results in a formation of numerous small non-flagellated zooids within the body of the parent.	A variable number of non-flagellated zooids are formed within the body of the flagellates in the crop. The parent body degenerates setting free the numerous small spore-like forms or zooids.

From the above tabular comparison, it will be noticed that in general the differences between the two species are of two types, morphological differences of minor importance, and developmental differences, seemingly of great importance, especially from the standpoint of transmission of the flagellate. Certain small, non-flagellated forms (figs. 11, 19, 27, 35) are constantly present in the life cycle of *C. euryophthalmi*. However, further investigation of the morphology and life cycle of both flagellates may prove the separation of these two species to be untenable. It is possible that more knowledge of the structural modifications of these parasites due to food and digestive juices of the host will account for all the differences above tabulated. It must also be taken into consideration that these flagellates are microscopic forms with few characters and that the differences existing between the two species of this group will be necessarily slight as compared with differences between two species of Metazoa.

I am indebted to E. P. Van Duzee of the California Academy of Sciences for the identification of this insect; and to Dr. C. A. Kofoid for suggestions and criticism of this work.

Morphology of the Digestive Tract of Euryophthalmus convivus

The alimentary tract of the bug, *Euryophthalmus convivus* has three divisions, the fore-, mid-, and hind-gut.

The Fore-gut.—The fore-gut as indicated in the diagram (fig. 1, *oes., prov.*) shows the two parts, the oesophagus and proventriculus. The foregut consists of the mouth, pharynx, and oesophagus (fig. 1, *oes.*). The oesophagus is a short, delicate tube of thin, white, almost transparent tissue. Following the oesophagus is the anterior end of

the crop into which projects the cardiac valve. This portion of the crop is of smaller calibre than that posterior to it and usually appears to be invaginated into the main cavity of the crop.

The Mid-gut.—The mid-gut of *Euryophthalmus convivus* is relatively much more complex than that of *Leptocoris trivittatus* or of the Heteroptera in general. One of the early investigators (Dufour, 1833, pl. 2, fig. 13) figures in *Coreus marginatus* a digestive tract with similar parts but the nomenclature for these parts has not been definitely established. The digestive tract of *Lygaeus militaris* (Patton, 1908) is somewhat like that of *Euryophthalmus convivus.* His use of the term *mid-intestine* is questionable; hence we have preferred to use the word intestine (fig. 1, *int.*), believing that the anterior three parts of the mid-gut are all parts of the stomach proper. Accordingly these three parts have been designated respectively, as the crop, the mid-stomach and the pyloric expansion.

The crop is the first division of the mid-gut and is characteristically of a light yellow color. This portion of the gut presents an ellipsoidal shape, more or less irregularly lobed, and capable of great dilation. During the fasting period this region is filled with gas.

Immediately posterior to the crop is another enlargement of the mid-gut which we have designated as the mid-stomach (fig. 1, *mid-stom.*). This enlargement occurs regularly, and is of a yellowish brown color which is due almost entirely to the contents. The size of this portion varies from one-half to one-third of that of the crop. The mid-stomach and the next enlargement, the pyloric expansion, may contain equal amounts of the contents, or either one may be greatly distended at the expense of the other, depending upon the stage of digestion.

A narrow tube connects the mid-stomach with the pyloric (fig. 1, *pyl. ex.*). This pyloric division is a symmetrical bulb-like enlargement filled with a dark brown liquid giving to this part of the tract a blackish appearance.

The last division of the mid-gut is a unique structure which we have called the intestine (fig. 1, *int.*) with a continuously attached intestinal gland (fig. 1, *int. gl.*). The canal or intestine passes through the center of the ruffle-like band of white, almost transparent, glandular tissue (fig. 1, *int. gl.*). The intestine and gland of the intestine are approximately equal in length to the anterior three portions of the mid-gut just described. A similar structure was described by Dufour (1833, pl. 2, fig. 13) in the hemipteran bug, *Coreus marginatus.*

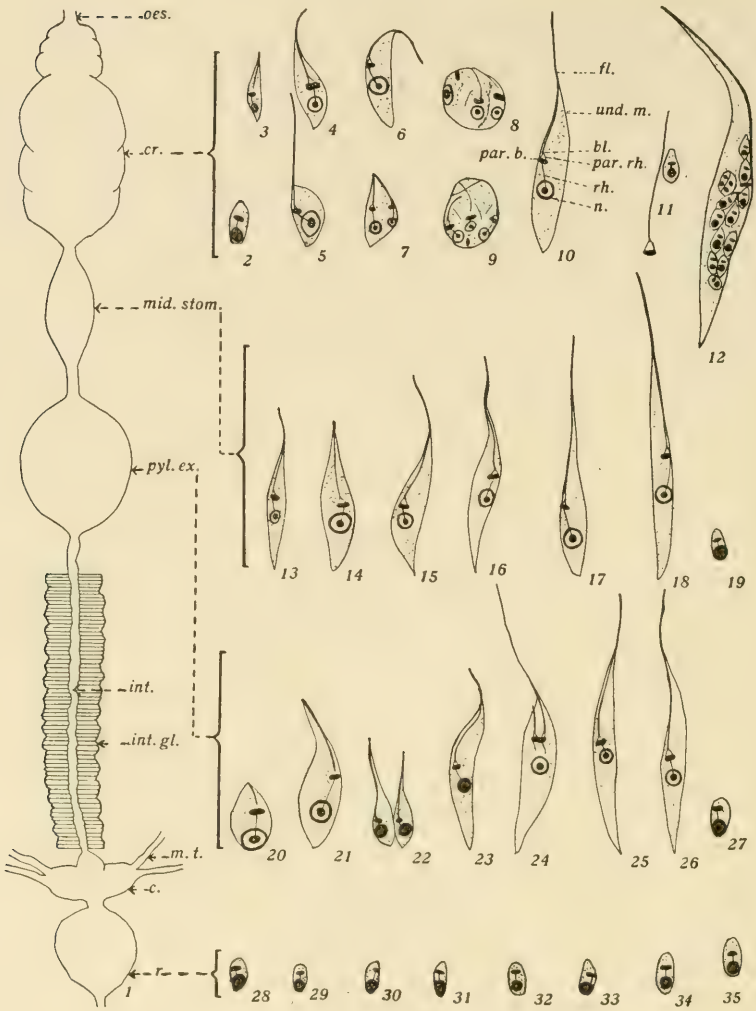

Fig. 1. Diagram of the digestive tract of *Euryophthalmus convivus,* including the portion between the oesophagus and anal opening. Accompanying this diagram is a series of outline drawings (figs. 2–35) of the characteristic forms of the flagellate, *C. euryophthalmi,* found in the several positions of the digestive tract. *Oes.,* oesophagus; *cr.,* crop; *mid. stom.,* mid-stomach; *pyl. exp.,* pyloric expansion; *int.,* intestine; *int. gl.,* gland of intestine; *m. t.,* malpighian tubules; *c.,* colon; *r.,* rectum. × 1750.

Figs. 2–3. Forms from the crop. Fig. 2. The initial infective spore.

Figs. 3–6. Developing crithidias.

Fig. 7. Binary fission in non-flagellated forms.

Figs. 8–9. Multiple fission in form of a somatella containing zooids.

Fig. 10. Elongate flagellate showing structures common to these forms: *fl.*, flagellum; *und. m.*, undulating membrane; *bl.*, blepharoplast; *par. rh.*, parabasal rhizoplast; *par. b.*, parabasal body; *rh.*, rhizoplast; *n.*, nucleus.

Fig. 11. A discarded flagellum and parabasal body with one of the zooids showing the results of the internal budding process of figure 12.

Fig. 12. Modified form of multiple fission designated as internal budding, flagellum and parabasal body present, zooids in the parent body.

Figs. 13–19. From near the entrance of the pyloric expansion. Fig. 13. An attached or haptomonad form found on wall near entrance to the pyloric expansion. Figs. 14–15. Nectomonad or free forms. Figs. 16–18. Haptomonad forms. Fig. 19. Oval spore form.

Figs. 20–27. Forms from the pyloric expansion. Figs. 20–22. Haptomonads or attached forms. Figs. 23–26. Nectomonads or free forms. Fig. 24. Binary fission form. Fig. 27. Oval spore form.

Figs. 28–35. Oval spore forms from the rectum. Probably the infective forms of *C. euryophthalmi*.

The Hind-gut.—The hind-gut is composed of two parts, the colon and the rectum. The colon is a thin, transparent, three-lobed structure (fig. 1, *c*). Into each of the two lateral lobes opens one of the malpighian tubules (fig. 1, *m. t.*), while the apex of the middle lobe is joined to the intestine.

The rectum is an almost transparent, ovoidal structure with the larger end toward the colon. It gradually tapers down to a narrow tube leading to the anal opening. The rectum is found either collapsed, or greatly distended with a clear brown liquid.

Infection of the Digestive Tract of Euryophthalmus convivus by C. euryophthalmi

Three parts of the digestive tract, the fore-, mid-, and hind-gut, were carefully examined, each part separately, for flagellates. The examination of the several parts of the fore-gut, namely: the oesophagus and proventriculus, has always yielded negative results. The hind-gut has shown a slight infection in the rectal portions in a few instances, but the mid-gut has in almost every case shown a heavy infection of *C. euryophthalmi* in one or more of its several parts. This heavy infection may be either in the crop, the mid-stomach, or in the pyloric expansion. Few adults are free from great masses of attached parasites completely covering the inner surface of the pyloric expansion. When this condition exists there is little evidence of an epithelial lining to be found in this division of the mid-gut.

The study of the stages of the life cycle of the flagellate shows that those stages normally found in the rectal portion of other Hemip-

tera are here found in the pyloric expansion of the mid-gut. This may be due in part to the presence of the intestinal gland and in part to certain chemical or physiological conditions within the several parts of the digestive tract. The investigation thus far indicates that probably only resistant spore forms succeed in reaching the rectum through the intestine. However by means of pressure upon the abdomen some of the contents of the pyloric expansion can be forced through the intestine and ejected through the anal opening along with the rectal contents. These contents from the pyloric expansion are usually swarming with free, flagellated parasites.

Life Cycle of C. euryophthalmi

In the life cycle of *C. euryophthalmi* in *Euryophthalmus convivus* there are present the following types in the stomach proper which is made up of three parts, the crop, the mid-stomach and the pyloric expansion. It must also be emphasized that the whole life cycle of this flagellate occurs in the several parts of the stomach.

(1) Oval spore forms (fig. 2) in the initial infective stages in the crop.

(2) Developing crithidial stages from the non-flagellates (fig. 2, 4–5) present in the crop, which migrate posteriorly into the mid-stomach and pyloric expansion.

(3) Multiple fission forms, probably of two types (*a*) a somatella (figs. 8, 9); (*b*) a modified type designated as internal budding (fig. 12). These have been found only in the crop.

(4) Binary fission forms in the crop (fig. 7), and in the pyloric expansion (fig. 24).

(5) Crithidial stages from the crop, which become free forms in the mid-stomach and pyloric expansion, called *nectomonads* (Minchin and Thomson's terminology, 1915).

(6) Crithidial stages from the crop, which become attached forms in the mid-stomach (fig. 13) and pyloric expansion (figs. 21–23), termed *haptomonads*.

(7) Final spore stages are found in both the mid-stomach and the pyloric expansion. Some of these succeed in reaching the rectum through the intestine. The staining capacity of these indicate that they probably become more resistant to destructive agencies by forming a protective covering.

Forms from the Crop

Oval Spore Forms.—In the crop of approximately twenty per cent of the nymphs and two per cent of the adults oval spore forms together with the developing forms can be found. The oval spore forms have been regarded as the infective spore taken up casually with the food by the host. They are 3.2μ long and 7.4μ wide (fig. 2). The anterior end is slightly pointed while the posterior is blunt. They have a very characteristic shape and retain the haematoxylin stain for a longer period than the other forms of the flagellate. Internally the nucleus and parabasal body are relatively large. These two deeply staining structures are connected by the nuclear rhizoplast which retains enough of the stain to make it readily visible under a high-power binocular microscope. The oval spore forms with their characteristic staining capacity, size, and nuclear structure can be pointed out among the parasites of the mid-stomach (fis. 1, 19) and of the pyloric expansion (fig. 27). The development of these oval spore forms into flagellates has been followed in part in the living material. The several stages in development have not been followed for the same individual, the process having been studied in a disconnected manner.

Developing Crithidial Stages.—The oval spore form begins to unfold slightly at the anterior end. The flagellum is bent back along the body as far as the parabasal body. This straightens out anteriorly and accompanying this change there is an elongation of the posterior end (fig. 3). The whole series of developing forms gradating from the non-flagellated forms (fig. 2) to the large elongated flagellates can be found readily in almost all preparations of the infected crops.

Multiple Fission—Somatella

In four instances out of two hundred crops examined, spherical forms were found showing a variable number of nuclei and parabasal bodies together with a multiplication of the number of flagella. The flagella may project from spherical surface in various directions. The origin of the several nuclei and parabasal bodies within this plasmodial mas has not been followed in detail; at the present time these spherical forms are regarded as somatellae which are common to many of the flagellates. There is little evidence to show that this process of multiple fission is of any importance in the multiplicative phase of the parasite, since it occurs so rarely. Its relation to a

possible sexual phase as yet undetermined may be suggested, but no proof is as yet available of the validity of this hypothesis.

Internal or Endogenous Budding.—Under multiple fission also the process which we have designated as *internal* budding has been included since it is regarded as a modified form of multiple fission (fig. 12). In this large flagellated form a number of small zooids can be counted. It was of the greatest interest to find that such a flagellate containing numerous zooids still retained intact its parabasal body. Neither the original parabasal nor the flagellum enters into the formation of the zooids. On the contrary, preparations are in hand showing fields wherein numerous discarded flagella usually bearing the parabasal body still attached can be found. Along with these detached flagella (figs. 1, 10) are myriads of small zooids resulting from the process of internal budding. The zooids are not all of the same size. Many minute forms are found containing the two deep-staining structures, the nucleus and the parabasal body. Between these minute forms and the oval spore forms previously described is a complete series of forms varying slightly in size. The cytoplasm of the small forms called zooids differs from that of the oval spore forms in its staining capacity. The zooids do not retain the haematoxylin as long as the oval spore forms. This is true of the zooids and oval spore forms in the crop, mid-stomach, and the pyloric expansion.

Previous to the discovery of sufficient stages in this internal budding process to determine its nature, the appearance of so many zooids was most puzzling. Preparation after preparation was examined showing the field literally covered with the minute forms with no clue as to their origin. This is explained by the fact that out of two hundred preparations of the crop only three show the early or beginning stages of the process of internal budding. A knowledge of the feeding habit of the bug and of the time necessary for the ingested spores to develop into mature flagellates would undoubtedly greatly facilitate the investigation of this process. A more detailed discussion of internal budding together with the figures showing the process in all the stages will appear in a later paper.

Binary Fission.—Binary fission occurs among the zooids (fig. 7) in the crop and among the flagellated forms in both the crop and pyloric expansion (fig. 24). It probably occurs in the mid-stomach but no record has been made of its occurrence there. If the number of forms in binary fission found in the living material or stained

preparations can be used as a definite evidence, this process does not play an important part in increasing the numbers of flagellates. The small number of preparations of the crops which show an infection leads to the conclusion that the developing flagellated forms and zooids pass back into the mid-stomach and into the pyloric expansion after a very short period of development in the crop.

Forms from the Mid-Stomach

The series of forms found in the mid-stomach are shown in figures 13–19. These may be divided into three classes: (1) the small oval spore forms (fig. 19) and small zooids, (2) nectomonad or free flagellated forms (figs. 1, 4–18), and (3) haptomonads or attached forms (fig. 13). Owing to the relatively small percentage of infection of the preparations in the mid-stomach as compared with that of the preparations from the pyloric expansion, there is probably a migration of the parasites from this portion of the mid-gut into the pyloric expansion.

The *oval spore forms* and zooids occur very frequently in the preparations from the mid-stomach. The question as to whether they normally develop into flagellates in this region can not be answered as yet. The serial sections of the region show these non-flagellated forms in the lumen when few or no nectomonads can be detected.

The *nectomonads* of the mid-stomach do not show any signs of degeneration, the nucleus has the characteristic chromatin, encrusted nuclear membrane and central karysome (fig. 17). The cytoplasm also is normal in appearance. The study of these forms indicates that the first signs of degeneration of *C. euryophthalmi* are to be found in the cytoplasm. The external surface of the body is likewise free from adherent bacteria.

The *haptomonads* (fig. 13) are attached to the epithelial cells in the posterior portion of the mid-stomach. The haptomonads, or attached forms are elongate, slender flagellates which resemble the free nectomonad forms. The serial sections of this region show epithelial cells lining the lumen to be intact. The cell walls are clearly outlined with the fringe of parasites on the outside. The cytoplasm of these epithelial cells is vacuolated but other than this there is little indication of any degeneration of this epithelial lining.

Forms from the Pyloric Expansion

In the pyloric expansion of the stomach proper the same forms just described in the mid-stomach are to be found, namely: the oval

spore, small zooid forms, the nectomonads or free flagellated forms and the haptomonads or attached forms. The infection of this division of the digestive tract is much greater than of any other part. It is in this part that the infection is retained after the first infection. The oval spore forms and zooids are readily found in nearly all the preparations of this division of the mid-gut. There is no evidence thus far to indicate that either the spore forms or the zooids develop into flagellates.

Nectomonads (figs. 23–26) are found in large numbers in the pyloric expansion. Binary fission forms (fig. 24) are found frequently and this probably accounts for the reduced size of such free forms as figures 23 or 24, and the production of the long, slender haptomonads which will be described shortly. Figure 23 shows a different type of nucleus which can not be regarded as being characteristic of the free nectomonads. It is doubtless a sign of degeneration but in these parasites it is not the most prevalent indication of degeneration. The preparations frequently show nectomonads with a sticky periplast. As a result of this the individuals adhere to each other and collect many bacteria on the body surface. Many others show the vacuolated cyotplasm or one stage farther wherein the cytoplasm has completely degenerated leaving only the nucleus, parabasal body, the rhizoplasts and the flagellum still attached to each other

Haptomonads are of two general types in the pyloric expansion. In the upper or anterior part there are found the attached, elongate, slender forms (fig. 23) like those which occur in the posterior portion of the mid-stomach. Gradually gradating from these long forms to the small pear-shaped forms (figs. 20–22) are the intermediate forms. No evidence has been found to show that the haptomonad forms become detached and encyst to form the oval spores. On the contrary the cytoplasm of the haptomonad forms like that of the nectomonad forms is vacuolate and degenerative in structure. Furthermore there is no evidence that any of these nectomonads or haptomonads normally succeed in reaching the rectum through the intestine of *Euryophthalmus convivus.*

Of the three forms which migrate into the pyloric expanse the oval spore forms are probably the true infective agents while the nectomonads and the haptomonads are forms in degeneration.

Rectal Forms

In a few cases the preparations made from the rectum and contents have shown a few oval spore forms (figs. 28, 35). The origin of these is not clear but it is possible that they are zooids which have been somewhat protected by a thicker membrane and consequently are more resistant. As previously mentioned they retain the haematoxylin stain relatively longer than any of the other forms or zooids in particular. Whether these spore forms become protected by a thick membrane through which the stain does not readily penetrate is an open question. Some spore forms found in rectal preparations do not take the stain.

Infective and Degenerative Cycles

The question regarding the part played by the small zooids which arise from the process of internal budding in the life cycle is of great interest. Do they develop into flagellates or do they remain zooids, migrating back to the posterior parts of the intestinal tract to form the rectal spores? Preparations show that the zooids are exceedingly numerous in the mid-stomach and pyloric expansion. Because of their numbers and the same characteristic structure found throughout, the zooids are regarded as infective forms. They become deeper-staining upon reaching the rectum. All the forms which do not remain as non-flagellated forms constitute what we have designated the degenerative cycle. The flagellates of the mid-stomach and of the pyloric expansion show signs of degeneration. They become vacuolate. The nucleus may show a diffuse structure. Bacteria may adhere to the sticky periplast or the cytoplasmic part may disappear entirely leaving only the skeleton of the nuclear structures. No stages of encystment of haptomonads have been observed. All the nectomonads and haptomonads become degenerate. Flagellated forms in *C. euryophthalmi* do not become spores in so far as our investigation has gone.

Summary

1. The differences existing in the morphology and life cycles of the two flagellates found in *Leptocoris trivittatus* and *Euryophthalmus convivus* have been deemed sufficient to justify our classifying them as two distinct species, namely, *C. leptocoridis* and *C. euryophthalmi.*

2. The digestive tract of *Euryophthalmus convivus* consists of fore-gut divided into oesophagus and proventriculus; the mid-gut,

divided into crop, mid-stomach, and the pyloric expansion; intestine and gland of the intestine; and hind-gut, divided into colon and rectum.

3. The infection by flagellates usually occurs in the mid-gut in the crop, mid-stomach, and pyloric expansion. The rectal portion of the hind-gut has been found infected in a few instances, with spores.

4. Multiple fission is present. A few somatellae have been found along with internal or endogenous budding.

5. The life cycle of *C. euryophthalmi* may be divided into two parts, the infective cycle and the degenerative cycle.

6. The infective cycle consists of ingested spores which develop into large flagellates. These undergo a process of multiple fission designated as internal or endogenous budding. Numerous small zooids result, which migrate posteriorly and become rectal spores.

7. The degenerative cycle is made up of flagellated forms of various sizes. Both free and attached forms from the mid-stomach and pyloric expansion are included in this cycle.

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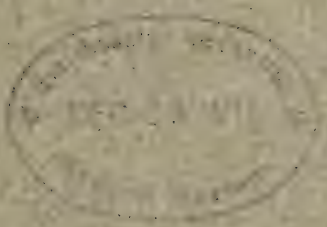

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10. Note on the Medusan Genus *Stomolophus*, from San Diego, by Henry B. Bigelow. Pp. 239-241. September, 1914 ..... .05

11. A Study of the Structure of Feathers, with Reference to their Taxonomic Significance, by Asa C. Chandler. Pp. 243-446, plates 13-17, 7 text-figures. April, 1917 ..... 2.00

12. Anatomical Adaptations in the Thoracic Limb of the California Pocket Gopher and Other Rodents, by Charles Daniel Holliger. Pp. 447-494, plates 38-39, 20 text-figures. March, 1916 ..... .45

13. The Inheritance of Extra Bristles in *Drosophila Melanogaster* Meig., by Edna M. Reeves. Pp. 495-515, 1 figure in text. December, 1916 ..... .20

Vol. 14. 1. A Report upon the Physical Conditions in San Francisco Bay, Based upon the Operations of the United States Fisheries Steamer "Albatross" during the Years 1912 and 1913, by F. B. Sumner, G. D. Louderback, W. L. Schmitt, E. C. Johnston. Pp. 1-198, plates 1-13, 20 text figures. July, 1914 ..... 2.25

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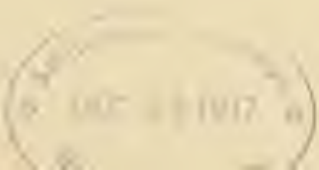
ON THE ORIENTATION OF *ERYTHROPSIS*

BY
CHARLES ATWOOD KOFOID AND OLIVE SWEZY
(Contribution from the Zoological Laboratory and the Scripps Institution of Biological Research of the University of California)

The dominating factors in the morphology of the Dinoflagellata and in their evolution as a group are the two flagella. The location of their points of origin upon the surface of the body determines the ventral surface. The course of the transverse flagellum which pursues a spiral direction in the girdle about the body delimits the epicone and hypocone in the Gymnodinioidae and in the thecate forms separates the epitheca from the hypotheca. The plates of the theca form zones above and below this girdle. The proportions of the body are profoundly influenced by the direction (ascending or descending), and steepness of the spiral and the amount of torsion of the body which has been developed in the direction of the stress which the activity of this powerful flagellum creates in the girdle.

The transverse flagellum lies in a depression or girdle which has one general direction on the body of the dinoflagellate, namely, that of a spiral from its point of origin at the anterior flagellar pore at the anterior junction of the girdle with the sulcus on the midventral face, transversely across the left side, thence across the dorsal surface and around upon the ventral face to the reunion of the girdle with the sulcus. If this reunion at its distal end is posterior to the origin the spiral is a descending left one. If it is anterior to the flagellar pore the girdle forms an ascending left spiral. If there is no anterior or posterior displacement the girdle forms a circle instead of a spiral, a condition rarely realized. The direction here described from the ventral face to the left of the body and over dorsally to the right, is universal in dinoflagellates above the Prorocentridae.

There are, in literature, seeming exceptions to this generalization.



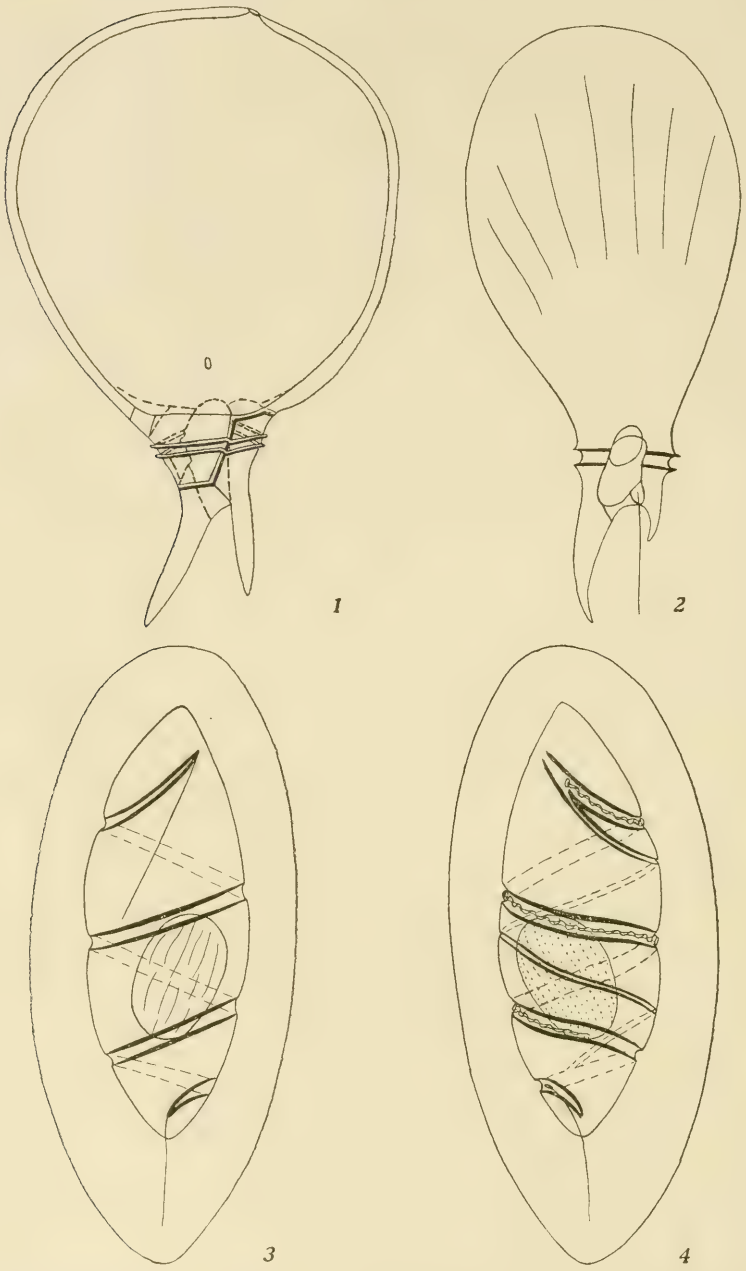


Fig. 1. *Ceratium gravidum.* Original. Dorsal surface as seen from the dorsal side. The outlines of the ventral area and other ventral structures seen through from the dorsal side are shown in dotted lines.

Fig. 2. The same, after Daday (1888, pl. 3, fig. 9). × 600. Showing the

ventral surface drawn as though on the dorsal side with resulting reversal of symmetry as determined by the relative sizes of posterior horns.

Fig. 3. *Cochlodinium pulchellum* Lebour, after Lebour (1917). × 964. Note that the direction of the spirally twisted girdle is from the left side of the body across to the right, that is, the girdle forms a descending right spiral. The sulcus is only partially and incorrectly drawn.

Fig. 4. *Cochlodinium pulchellum* Lebour, correctly drawn from life. Original.

For example, Daday (1888) described and figured *Ceratium gravidum* with a girdle having the opposite course. This, however, is due merely to an inadvertent oversight in observation and drawing. The ventral area of *Ceratium* is usually deeply impressed into the ventral face. Viewed dorsally its outline becomes distinct as one focuses down to secure an optical section of the midbody. If the outline of the body is then drawn from the dorsal side and the ventral plate also drawn, the symmetry of the organism is reversed and the girdle appears to pass from its proximal end distally on the ventral face to the right of the body over dorsally to the left, thus forming a right spiral instead of a left one.

Another example of reversal of symmetry by drawing the lower surface of the body as though it were the upper is found in Miss Lebour's figure (1917) of *Cochlodinium pulchellum* in which the direction of the girdle is reversed although in the description of the species no notice is taken of this profound structural modification. It appears to be only an inadvertent lapse in drawing. We have found that this species has the normal structure at La Jolla and offer for comparison a figure with the customary presentation of the upper surface (fig. 4) in which there is in consequence no reversal of symmetry.

During the examination of many thousands of dinoflagellates we have found not a single instance critically determined of such reversed symmetry in nature, although one easily falls into the trap of making such reversed drawings and failing to note the fact at the time. No such reversals should be accepted as valid unless critically verified on the living specimen showing the flagellum in action, and even then one should be on the lookout, in Gymnodinioidae, for transverse flagella thrown out of place into the anterior extension of the sulcus. It is, of course, possible that such reversals of symmetry might occur in nature, but evidence of their occurrence is lacking.

The so-called dextral and sinistral forms, described by Mangin (1911) do not involve the reversal in direction of the transverse flagellum and girdle above noted, but only the change from a descending to

an ascending spiral. It is not therefore such a reversal as that noted in the figures of Daday (1888) and Lebour (1917) and involved in the orientation of *Erythropsis* proposed by Fauré-Fremiet (1914).

The transverse flagellum and the girdle have important and fixed relations to the process of binary fission. The fission plane passes

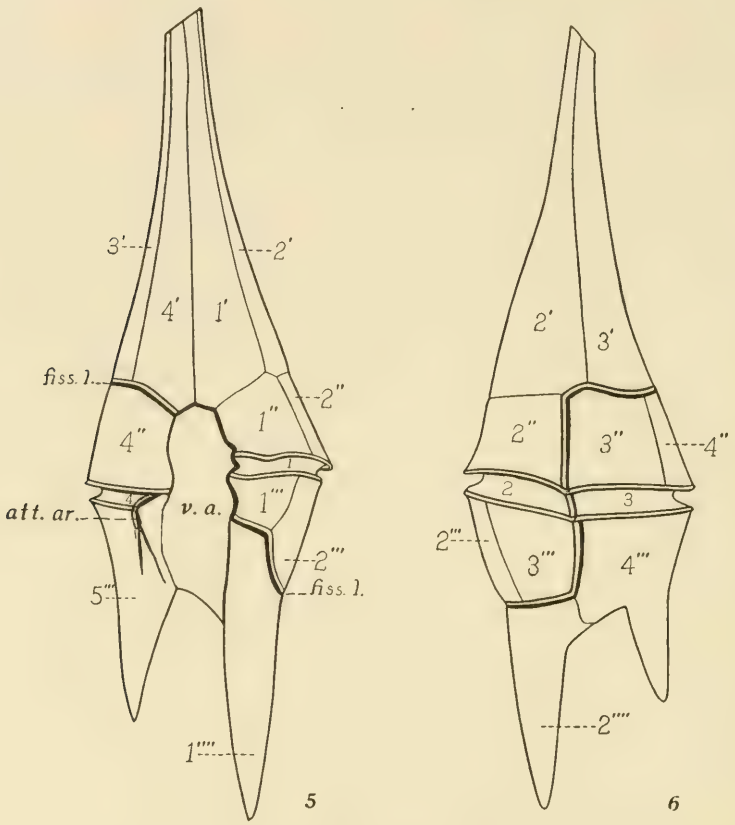


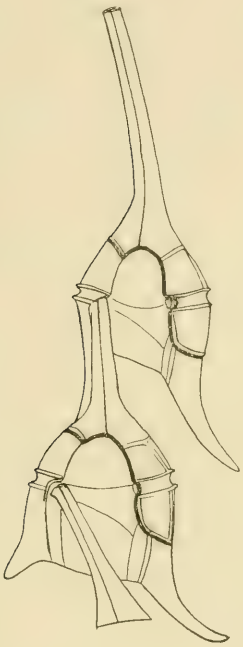
Fig. 5. Ventral view of *Ceratium furca*. × 706. In this and the following figure the apical plates are numbered 1′–4′, the precingulars 1″–4″, the postcingulars 1‴–5‴, the antapicals 1⁗–2⁗, and the girdle plates 1–4; *att. ar.*, attachment area; *fiss. l.*, fission line; *v. a.*, ventral area.

Fig. 6. Dorsal view of *C. furca*. × 706.

through the point of origin of the transverse flagellum and cuts across the girdle obliquely from the right anteriorly to the left posteriorly, parting the theca along definite suture lines (figs. 5, 6).

This plane has this oblique position in the dinoflagellates generally except in the Prorocentridae and the Dinophysidae. A reversal of

symmetry such as that induced by a change in the direction of the girdle as described above must be accompanied by an internal reorganization of the nucleus, mitotic figure, and fission plane, as well of of the exoskeleton and furrows. This reorganization would involve a shift of axes and attendant internal morphogenic factors of about 90° from the left over to the right.



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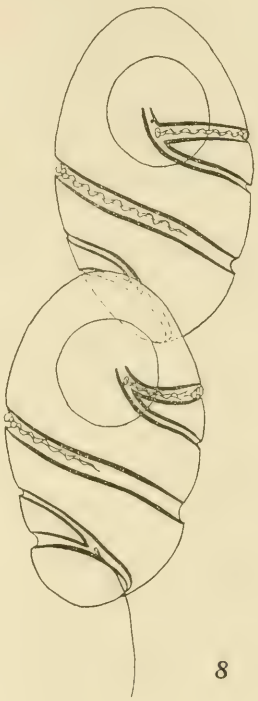

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Fig. 7. Ventral view of two schizonts of *Ceratium* in chain. After Kofoid (1909, pl. 1, fig. 1, two anterior schizonts and apical horn of the third). Note apical pore of horn of posterior schizont lodged against the attachment area of the anterior schizont. × 405.

Fig. 8. Daughter schizonts of *Cochlodinium citron* sp. nov. in chain, with apical region of the posterior schizont applied to the region of the end of the girdle of the other. × 937.

Such a profound reorganization as this should be proven beyond suspicion before it may be accepted. The place of origin and direction of the transverse flagellum in *Erythropsis* as figured by Fauré-Fremiet (1914), if the body is oriented as it is by all other observers of this organism, presents just such a reversal of symmetry.

A second feature of the relations of this girdle to the organization of the dinoflagellates is the fact that the point of contact of anterior and posterior schizonts in chain formation, or at binary fission, is at the distal end of the girdle of the anterior cell and the apex of the posterior one (figs. 7, 8). The apical pore at the anterior tip of the posterior daughter cell is thus in direct protoplasmic continuity with the anterior cell at the distal end of the girdle. Its shaft lies in a channel below the girdle and its tip is thrust against the anterior shelf or lip of the girdle. When the schizonts part, this depression persists for some time as an attachment area (*att. ar.*, fig. 5) but may ultimately fade away. It appears that Fauré-Fremiet (1914) has interpreted this attachment area, or a region near it, at the distal end of the girdle as the flagellar pore of its proximal end in *Erythropsis*. The apical horn of *Ceratium* is modified to fit the attachment area (fig. 7) and this modification persists for some time after the detachment of the schizonts. The apex of *Erythropsis* is homologous to this apical pore of *Ceratium* and may be expected to detach from the attachment area at binary fission, as well as to undergo some readjustment after detachment.

The relationships of two schizonts in chain in *Cochlodinium citron* are shown in figure 8. In case of the reversal of symmetry and orientation proposed by Fauré-Fremiet (1914) for *Erythropsis*, the adjustments necessitated in chain formation would be considerable. The proposed orientation provides neither attachment area nor apical point.

It has not infrequently been the fate of rare and at the same time peculiar or novel organisms to be strangely or even absurdly misinterpreted. Thus Nitzsch (1817) described a *Ceratium* as a *Cercaria* and Uljanin (1870) interpreted *Polykrikos* as a Turbellarian, and the larva of the Syrphid fly *Microdon* was described as a mollusk.

Such misfortune has attended few organisms so persistently as it has the ill-starred *Erythropsis*, a unique genus of the Dinoflagellata, in which there has developed a remarkable stigma or ocellus with amoeboid melanosome, hyaline laminate lens, and pigmented sensory (?) core or end organ, as well as a highly specialized, remarkably active, protrusible and retractile prod (tentacle, Hertwig (1884), dart, Fauré-Fremiet (1914)), directed posteriorly from a ventro-posterior recess (figs. 11, 12).

Up to the time of Fauré-Fremiet's observation (1914) only six individuals of the remarkable genus had been reported. In most, if

not all, of these cases the period of observation was brief in as much as the animal quickly drops its prod and undergoes cytolysis shortly thereafter, when exposed to the stimulus of the brilliant illumination of the microscope.

The first individual was found by the eminent Russian biologist, Élie Metschnikoff, who found it amid plankton débris taken off Funchal in the Madeira Islands in 1872. In a brief note (in Russian) he (1874) called attention to its possible relationships to the Suctoria, but neither described nor figured it. Ten years later the greatest of German protozoologists, Professor Richard Hertwig, then of Bonn University, found a single individual in the plankton of the Mediterranean at Sorrento. It dropped its prod soon after its capture, but was thereupon fixed in osmic acid and preserved in mutilated and distorted form as a microscopical preparation. From this abnormal fragment Hertwig (1884) described "*Erythropsis agilis*, eine neue Protozoe," making the comparison of the prod to the stalk, and noting the similarity of its anterior part to the peristomal region of a vorticellid ciliate. However, he explicitly notes the absence of cilia and the presence of a spiral filament wound about the anterior end. He did not, however, suggest any relationship of his unique organism to the flagellates or to the Dinoflagellata.

Immediately upon the publication of Hertwig's account, the veteran zoologist, Carl Vogt, of Geneva, attacked (1885*a*) the validity of the organism and called upon all zoologists to deny it admission to the category of beasts on the ground that it was only a detached zooid of a marine vorticellid, *Spastostyla sertulariarum* Entz, which had eaten the eye of a medusa, *Lizzia* or *Nausithöe*. Hertwig replied (1885) clearly setting forth the characters of *Erythropsis* which made Vogt's interpretation untenable; but the latter was unconvinced, returning (1885*b*) to the fray with a deadly array of parallel figures in which he reproduced Hertwig's figure with the evidence of the error by Hertwig made the more convincing by the substitution in his copy of the figure of *Erythropsis* of a row of membranelles for Hertwig's spiral thread and the introduction of an axial fibre in the stalk-like prod or tentacle.

This discussion brought Metschnikoff (1885) to the support of Hertwig who recalled his brief note (1874) on the organism of a decade prior, expressed his confidence in the authenticity of the organism and allied it with the suctorian *Ophryodendron*.

The cloud of suspicion thus cast upon *Erythropsis* may or may

not have been responsible for its subsequent complete disappearance from the literature of protozoology. The articles pertaining to it were in part published in the *Zoologischer Anzeiger,* the most widely distributed zoological journal in the world. But Bütschli in his *Thierreich* monograph of the Protozoa, then in process of publication (1883–1889), omits all reference to *Erythropsis.* Pouchet who published in France a series of papers on dinoflagellates and rediscovered the ocellus in organisms now referred to *Pouchetia,* a genus closely related to *Erythropsis,* makes no note of Hertwig's species. Neither does Schütt in his Plankton Expedition monograph (1895) note its existence, although he describes, as *Pouchetia cornuta* and *P. cochlea,* two species which belong to the genus *Erythropsis.* This relationship, however, was in part obscured by the reduction or absence of the prod in Schütt's specimens. The ocellus, it would seem, was sufficient to have established the relationship. In his later (1896) assemblage of the genera of the "Peridiniales" in Engler and Prantl's *Pflanzenfamilien, Erythropsis* is again missing.

It was not until Delage and Hèrouard (1896) assembled the Protozoa in their *Traité de Zoologie Concrète* that the genus was recognized as valid and placed in its true relationship. These authors, impressed by its similarity to *Pouchetia,* cautiously admitted it into an appendix to the Dinoflagellata.

They fell, however, into one misrepresentation of Hertwig's figures, which affords the starting point for Fauré-Fremiet's later erroneous allocation of the flagellum. In discussing the girdle and its flagellum they state:

> Le filament en ressort à boudin n'a rien de commun avec une zône adorale tandis qu'il représente exactement le fouet transversal d'un Peridinien (il faut noter cependant que Hertwig n'est pas très affirmatif sur la question de savoir si la portion qui occupe la gouttière est ou non continue avec celle qui est logée dans la partie supérieure du sillon longitudinal, et que ce fouet, par une exception unique, suivrait le sillon de gauche à droite. Enfin le gros appendice serait le fouet vertical).

The basis for this interpretation is not clear as will be seen in our reproduction of Hertwig's (1884) figures (figs. 9, 10). In so far as the main encircling spiral filament, as shown in the figures, is concerned, it might run in either direction around the body, for as a matter of fact, neither end is figured, and the short strand seen in one of Hertwig's figures (pl. 6, fig. 2, reproduced in our figure 10), may be the amoeboid uppermost end of the sulcus and not a flagellum connected with any part of the girdle.

In the previous year Schütt (1895) had figured two species which he called *Pouchetia cochlea* and *P. cornuta*. Both had the ocellus, as have other species of *Pouchetia,* but in neither one did Schütt detect the prod, although he figures it in *P. cornuta* as hidden in the posterior recess, but leaves it unnamed and unnoted. Owing to this record and to his discovery of the paradinial lines (fig. 12, *par. l.*) along the girdle, not seen by Hertwig (1885) but now known to be characteristic of the genus, his figures of *P. cornuta* have been referred to *Erythropsis* by Pavillard (1905) and Fauré-Fremiet (1914).

Schütt's figures (1895, pl. 26, figs. 96, 1, 2, reproduced in our figure 12), continue and confirm the previous confusion regarding the location of the anterior flagellar pore. In these figures the girdle, instead of arising at a junction with the sulcus above the ocellus, comes down from the apical horn. The upper end of the sulcus is thus confused with the proximal end of the girdle.

In 1905 Pavillard had the opportunity to inspect for a brief period another specimen which he referred to Hertwig's *Erythropsis agilis* and presented for the first time an adequate sketch from life of the entire animal, but he also figures the transverse flagellum as running up this apical horn.

Collin (1912) records the discovery of another specimen of *Erythropsis* in the student laboratory at the Biological Station at Cette and Fauré-Fremiet (1914) states that Chatton had seen another at Banyuls-sur-Mer.

Thus up to the time that Fauré-Fremiet (1914) saw his "vingtaine" of specimens at Croisic on the west coast of France in the summer of 1913, not more than six specimens of this peculiar and puzzling organism had been seen.

Whatever doubt and suspicion may have persisted as to its validity had been made entirely untenable by Pavillard's account, but the point of origin and the course of the transverse flagellum were still undetermined, and the presence or not of a longitudinal flagellum in addition to the prod was problematical. A peculiar stout flagellum-like structure was figured by Schütt (1895) for *P. cornuta,* but the presence of a prod or tentacle in this species was not clearly established.

In 1913 Fauré-Fremiet published a brief note recording *Erythropsis* from the west coast of France and followed this with a fuller account than anyone has yet made of this remarkable organism. In his later paper (1914) he orients it (fig. 11) with the prod anterior, the ocellus directed posteriorly, and the apical end as the antapical.

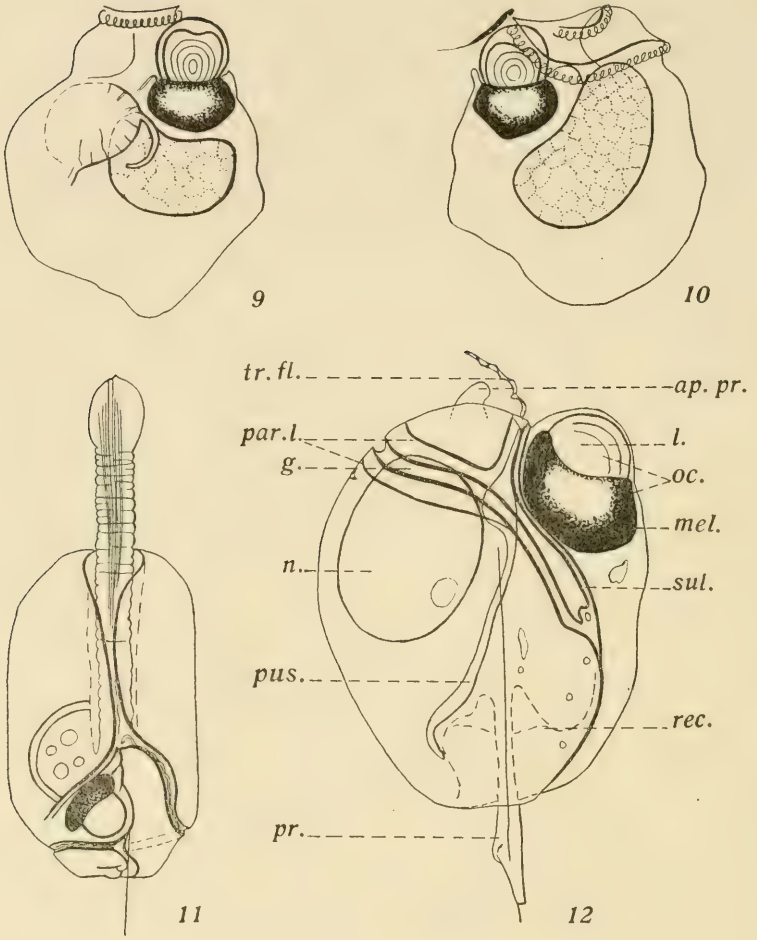

Fig. 9. Ventral view of *Erythropsis agilis* Hertwig. After Hertwig (1884).

Fig. 10. Dorsal view of *Erythropsis agilis* Hertwig. After Hertwig (1884).

Fig. 11. Ventral view of *Erythropsis agilis* Hertwig. After Fauré-Fremiet (1914, fig. 1*a*). Orientation as proposed by Fauré-Fremiet.

Fig. 12. Ventral view of *Erythropsis cornuta* (Schütt). × 530. Original. Orientation based on locomotion. *ap. pr.*, apical process; *g.*, girdle; *l.*, lens; *mel.*, melanosome; *n.*, nucleus; *oc.*, ocellus; *par. l.*, paradinial lines; *pr.*, prod; *pus.*, pusule; *rec.*, recess for prod; *sul.*, sulcus or longitudinal furrow; *tr. fl.*, transverse flagellum.

He furthermore concludes that the transverse flagellum takes its orgin at the region which we interpret as the attachment area. If we orient the body in the usual position the girdle and flagellum would thus form an ascending right spiral instead of a descending left one and the symmetry of these two fundamental structures, the girdle and flagellum, would be reversed.

The grounds upon which this interpretation rests appear to be "logical" rather than observational. There is no evidence in Fauré-Fremiet's account that he had correlated his orientation with the locomotor activities of the animal. He does not state that he has seen it advance prod first and with the ocellus directed posteriorly. He figures (fig. 1*a*, reproduced in our fig. 11) a small longitudinal flagellum emerging from the apical process, but states in his text "les données relatives à son existence elle-même sont malheureusement insuffisants."

During the past summer we have seen at the Marine Laboratory of the Scripps Institution at La Jolla, California, in the plankton taken five miles off shore a number of individuals of *Erythropsis* and have noted its mode of progression and its orientation. The animal progresses mainly in anti-clockwise circles with some rotation about its major axis. During locomotion its prod is directed posteriorly; the ocellus anteriorly. Moreover, the transverse flagellum (fig. 12) takes its origin at the flagellar pore at the point where the girdle joins the sulcus anteriorly and passes in the usual direction of a descending left spiral about the body in the transverse furrow. As cytolysis approaches, it shortens up and may be thrown out of the furrow towards the apex. It does not arise at the distal end of the girdle as figured and described by Fauré-Fremiet. There is, however, at the distal end on the anterior margin of the girdle a notch with a pit-like depression which we interpret as the attachment area. It is not a flagellar pore either posterior or anterior.

The longitudinal flagellum does not emerge at the apex although the transverse one may be temporarily thrown towards that region, and the area itself at times may appear to have local amoeboid movements in the region of the tip of the sulcus which passes anteriorly upon the epicone. The longitudinal flagellum is found, as figured by Schütt (1895, pl. 26, fig. 96), emerging from the posterior chamber or recess surrounding the base of the prod. From this region, as also from the anterior flagellar pore there passes into the cytoplasm the characteristic pusule.

Summary

We conclude therefore on the basis of the examination of the evidence from the comparative structure of *Erythropsis* and other Dinoflagellata that the prod of *Erythropsis* is directed posteriorly, not anteriorly, that the girdle is anterior, not posterior in location, and that the ocellus is directed anteriorly, not posteriorly. Likewise that the transverse flagellum takes its origin at the anterior junction of girdle and sulcus at the proximal end of the girdle and not at the attachment area at its distal end.

We also confirm Schütt's (1896) findings as to the presence of a posterior flagellum in addition to the prod, arising in the chamber about the base of that organ and projecting posteriorly. These conclusions from the standpoint of comparative anatomy are supported by our observations on the locomotion of the living organism. Fauré-Fremiet's (1914) orientation of the animal with the prod anterior and his account of the origin and course of the flagella must be rejected as untenable.

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Zoological Laboratory,
University of California,
Berkeley, California.

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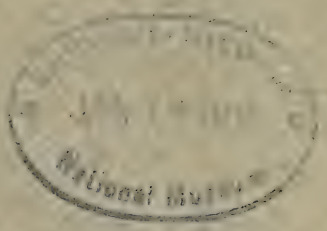
BY
JOHN F. BOVARD



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CONTENTS

PAGE
Introduction 104
I. Work of Friedländer 104
II. Anesthesia experiments of Krukenberg 105
III. Work of Biedermann 105
Materials and methods 106
I. Materials 106
II. Methods 106
1. Biedermann's method 106
2. Anesthesia method by ether and nitric acid 107
State of anesthetized area 107
The problem 108
Acknowledgments 108
Experiments with anesthetized worms 108
I. Free moving animals 109
II. The tension factor 109
III. Autotomy 111
IV. Free nerve preparations 112
1. Dissection experiments 113
2. Graphic records 114
3. Effects of stovaine 116
V. Limits of transmission 118
VI. Dependence on the nervous system for transmission 120
VII. Rate of transmission of locomotor impulses 122
VIII. Rate of transmission of giant fiber impulses 125
Theoretical considerations 128
I. Review of anatomy 129
II. Theory of reinforced stimuli 131
Summary 132
Literature cited 134

INTRODUCTION

The normal creeping movements of the earthworm proceed as follows. The first movement is a contraction of the circular muscles of the first few segments. This causes an extension of the anterior end. The chaetae now become directed backwards and take hold on the substrate while the longitudinal muscles begin a contraction which draws the next few segments forward. The circular muscles in each segment contract, one segment after another beginning at the anterior end and proceeding posteriorly. Immediately following the circular muscle action the longitudinal muscles contract so that a wave of extension followed by a shortening can be seen to traverse the whole animal. After the first wave of muscular activity is well started posteriorly another may be initiated and at any one time several of these contraction waves may be seen in a normally creeping worm.

Some years ago Friedländer (1894) showed that in the normal creeping of an earthworm the nervous system played only a small part. When a section of the nerve cord containing ten to twelve ganglia was removed, the movements of the parts of the worm were still perfectly coördinated. The most important part of the activity was the "pull" which the contraction of each segment as the wave progresses gave to the succeeding segments. The wave-like motion of the contractions proceeding down the length of the animal was due, first, to the pull of segments on each other, and, secondly, to the sequence of reflex actions of the nerves in each segment, which are such that the longitudinal muscles follow the contractions of the circular muscles. This nervous mechanism is, according to Friedlander, concerned with each segment alone, and there is no passage of impulses up or down the cord. No attempt was made by him to analyze the matter of tension or pull, or to determine whether coördination would proceed without this factor.

In order to show that the nervous system was entirely secondary, Friedländer cut a worm into two pieces and then joined these two with a thread. The creeping movements of the anterior piece gave the necessary pull on the posterior piece through the thread, and the two parts crept along in perfect coördination. In certain special cases, when the nerve cord was destroyed for a short distance without transection of the body, the parts anterior and posterior to the cordless region moved together with perfect coördination. According to this

view, then, the nerve cord is supplementary and concerned only with those short reflex paths which are mediated by a single ganglion. Previous to the year in which Friedländer published his analysis of the movements of earthworms, Krukenberg (1881) showed, in some work on leeches, that the middle section of the animal could be anesthetized with the result that the parts anterior and posterior to this region still acted in perfect coördination. In these animals, however, the nervous system differs structurally from that of an oligochaete. In leeches the nerves run from the anterior to the posterior end, while in the oligochaetes the only long nerves are the giant fibers, the other fibers in the cord being those of short neurones extending at most from one ganglion to the next. The anesthesia in leeches affects only the peripheral nerve endings, while the trunks connecting anterior and posterior portions are not affected.

The more recent work of Biedermann (1904) becomes particularly interesting, however, as it gives some new light on the function of the nerve cord of the earthworm. In this work on the comparative physiology of peristaltic movements he compares the locomotor action in earthworms to the rhythmic movements found in smooth muscle. Biedermann discovered that if worms were placed in seven per cent alcohol for a few minutes until they became motionless and then the middle region of several segments was anesthetized with nitric acid or pure chloroform for a few seconds, the muscular activity of the section was destroyed and all response to stimulus failed. He then had a worm with active anterior and posterior parts connected through the anesthetized area by a nerve cord. In creeping movements, the anesthetized area, or dead area, acted as one piece. It transmitted no rhythmic movements, while the posterior part still acted in perfect coördination with the anterior part.

In further tests by Biedermann of the transmission of impulses through the cord over more than one segment, he pinned such anesthetized specimens to a cork plate by needles through the dead muscular area and found that the posterior part still moved in perfect coördination with the anterior part. With regard to the limits of this transmission through the cord, and the speed of the impulses, it is stated in his paper (1904, p. 493) that the transmission often runs 2–3 centimeters in 4–5 seconds.

In the interpretation of these experiments Biedermann accepts the theory proposed by Friedländer, except that in order to explain the coördinated movements of posterior pieces when a certain part was

anesthetized, it is necessary to assume that the impulses run through the cord for a considerable distance rather than through one ganglion as Friedländer supposed.

MATERIALS AND METHODS

Materials.—Several species of worm were used for these experiments. The large garden worm, *Helodrilus caliginosa,* was favorable material owing to its size. The small dung worm, *Allolobophora foetida,* was also very convenient material because of the ease of obtaining the material during the winter. No difference was observed in the reactions in these worms. Unless specially noted the experiments recorded will refer to the larger worm, *Helodrilus.*

Methods.—Biedermann's (1904) method of anesthetizing a certain portion of a worm by use of nitric acid or chloroform, as described, had the effect of killing any peripheral nerve endings present in the part and of impairing the muscle cells. It left the anterior and posterior portions connected, however, by a functioning nerve cord, still intact, except that no stimuli applied to the treated epithelium were effective in setting up reflexes.

It was suspected by Biedermann that as locomotion took place the posterior part was acting in coördination, not only because it was connected to the anterior, as Friedländer might have supposed from his string experiment, but that there was some real nervous influence transmitted by the cord in the inert middle section. In order to test this point fully, he pinned the middle anesthetized portion to a cork plate to remove the factor of tension, when it was found that the posterior portion still made movements coördinated with those of the anterior piece. This established beyond a doubt that transmission did take place over a longer section of the cord than the earlier investigators had deemed necessary and showed the more important part played by the nervous system.

In developing a method of anesthesia to test farther the matter of transmission, it seemed to me desirable to find some means of blocking reflexes in the *middle area,* and yet it was also quite necessary at the same time to leave the muscle tissue and the central nerve cord intact, only the peripheral nervous system being eliminated. The method developed was quite different from that of Biedermann. The worm was placed on a glass plate slightly moistened with water, so that it was slippery. A small four-drahm homeopathic vial containing some

cotton soaked with ether, was then turned down over the worm so that the mouth of the bottle covered the middle section of the worm. It was possible to hold this in place over the squirming worm until the middle part was anesthetized. Owing to the slipperiness of the plate, the worm could get no hold and autotomy was very rare. When, however, as occurred in early experiments, this method was tried on a cork plate, autotomy of the anterior or posterior part was frequent because of the hold the chaetae were able to take on the cork and so the worm could pull itself in two. Exposure of two minutes to ether fumes was sufficient for complete anesthesia, but had little effect on the muscle tissue itself. The worms usually recovered completely from the effects of the treatment in from ten minutes to an hour. During this time a stimulus to the muscle in the anesthetized area called forth a direct response but started no reactions in the untreated parts of the worm.

In using some of the larger worms this simple method was varied by treating the etherized area with six per cent nitric acid for ten seconds, then washing the whole worm in water; this made certain that the sensory nerve endings, of this part, were rendered functionless. In cases where nitric aid was used the worm never recovered from the treatment, and in a few cases where the worms were kept for a few days they autotomized the posterior and middle sections. This method was used where only a nerve bridge was desired between the active anterior and posterior parts, as in measuring the speed of transmission of impulses in the nerve cord.

STATE OF THE ANESTHETIZED AREA

For a very short period after treatment, the anesthetized section looks whitish and gives off a great deal of mucous, but later the appearance is much the same as that of the rest of the worm, except for an increase in diameter. As the worm begins active movement, this middle piece decreases in diameter, due to stretching, for it acts much like a rubber band, extending and then contracting with each creeping movement. However, no waves of muscular contraction run along its length, as in the anterior and in the posterior parts, or from the former to the latter.

Stimulation of a quiescent worm in the anesthetized and live regions respectively gives a marked difference in response. If the anterior part is touched lightly the response is an increase in diameter due to a reflex stimulation of the longitudinal muscles, but a stimu-

lation of the middle area results in a constriction, due to the contraction of the circular muscles with no reflex to the longitudinal muscles. In recovery from the ether treatment the longitudinal muscles recover and reassume normal functions first and the circular some minutes later. In creeping movements the middle section shows that the longitudinal muscles recover their nervous connection first, for they begin to contract in coördination with the anterior part, some time before the circular muscles begin any active participation in the general movement. This condition is due no doubt to the fact that the longitudinal muscles lie deeper than the circulars and so are less affected by the anesthesia. In addition to this the position of the longitudinal muscle is closer to the general blood supply, which would be advantageous in the removal of waste products and the bringing in of new materials.

THE PROBLEM

The problem then suggests itself: how is this transmission through a number of segments accomplished? (1) Does Biedermann's discovery necessitate the existence of long fiber tracts in the cord? or, (2) Can it be explained on present knowledge of the neurones? (3) Are there any limits to the transmission through anesthetized areas? (4) Can the speed of such impulses be measured, and how do they compare with the speed of nerve impulses in other annelids?

ACKNOWLEDGMENTS

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EXPERIMENTS WITH ETHERIZED WORMS

Problem.—Will it be possible to get transmission of locomotor impulses through an anesthetized area in both directions, from anterior to posterior and also from posterior to anterior?

Discussion.—If a worm is etherized by the vial method and allowed to creep on a damp surface, such as moist filter paper, it will be seen to act like a normal worm in every way, except that the middle or etherized portion takes no part in the contractions. With each pull of the anterior piece it will stretch and passively contract as the posterior piece moves up, without showing the normal waves of muscular contraction seen in the active portions.

A worm, that is moving anteriorly, will reverse its direction and creep posteriorly if stimulated on the anterior end. Stimulation of the posterior end reverses the direction again. This indicates that nerve impulses may pass up or down the nerve cord and that these impulses may change the direction of the creeping movement, but it does not indicate that the impulses responsible for the actual creeping pass through the nerve bridge. There is still the fact that the muscles in the etherized section attaching the anterior to the posterior part may act as the "string" in Friedländer's experiment and give the necessary pull which keeps the two parts working in coördination.

Conclusion.—These simple experiments only show that there may be transmission of locomotor impulses in both directions through the nerve cord in an anesthetized region of the worm.

Tension

(*a*) *Experiments with Etherized Worms*

Problem.—To what extent is the factor of tension or pull responsible for normal locomotor reactions?

Method.—By the use of ether in anesthesia we are able to test out the importance of the matter of tension or pull in the transmission of locomotor impulses. It will be remembered that the etherized part acts as one piece. No waves of contraction pass up or down this part. A small piece of cork was glued to a glass plate and the glass plate kept wet. A worm prepared by etherizing ten segments in the middle portion was pinned to the cork so that the anterior and posterior parts were free to move, but the middle part was fixed.

Discussion.—Under these conditions no movements of the anterior part could exert any pull on the posterior piece. In all such experiments the worms behaved as Biedermann (1904) reported, the posterior piece responding with locomotor reactions in perfect coördination to all attempts of the anterior piece to make creeping movements. These movements could not be accomplished because of the slippery

glass surface and the pinning down of the middle section, but the wave of contraction, as in normal creeping, can be easily observed (fig. 1).

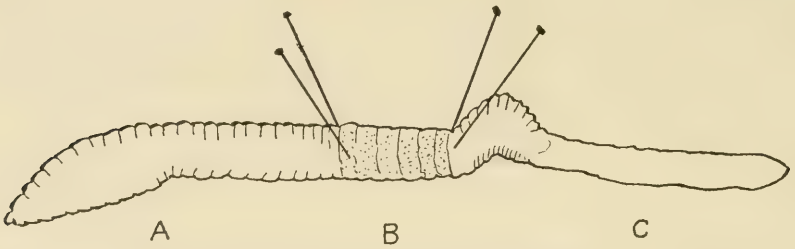


Fig. 1. This shows the method of pinning the anesthetized region of the worm. Region *A* has just made an anterior creeping movement and region *C* can be seen making a coördinated movement. On account of being pinned through region *B*, the anterior part of *C* is forced to buckle.

The reversal of the direction of these movements is also possible. Stimulation of the anterior end will cause the posterior end to attempt creeping posteriorly with the anterior piece acting in perfect coördination.

If, now, the nerve cord be severed in the middle region without disturbing the muscular connections a great deal, the coördinated movements of the two ends cease and become independent each of the other. It is possible when a worm is pinned and the continuity of nerve in the anesthetized area is broken, that the anterior and posterior ends may each be making locomotor movements in opposite directions, showing an independence of action even though joined by a muscular connection. There can be, therefore, no doubt that the nerve cord carries, for some distance, impulses which are responsible for locomotor movements. By pinning the worm to the cork, the matter of tension has been eliminated and by cutting the nerve, the transmission through the nerve cord has been removed and coördinated movements cease entirely.

When such a worm with transected nerve cord and anesthetized middle section is released from its cork plate and allowed to creep freely, it is found that the coördination of anterior and posterior parts is perfect. In this case, however, there is an entirely different explanation. The coördination of the posterior end can not be due to any nerve impulses from the anterior end, but each forward movement of the anterior section causes a pull on the posterior piece and this starts a chain of reflexes at the anterior end of the posterior piece which run the length of this part of the worm and give rise to the muscular contractions which normally would give rise to locomotion.

In worms in which the entire dorsal wall, the lateral muscles, and the intestine of the etherized part were dissected away and the nerve cord freed from the ventral muscle by cutting the lateral roots, the coördination continued perfect in function between the anterior and posterior portions. It was observed that such specimens, in creeping, did not move with the middle section tense, as a string connecting the two parts, but that often the posterior part moved along rapidly, causing the middle part to buckle so that under these circumstances no pull could possibly have been exerted on the posterior part. When the anterior part was pinned down, the posterior piece still continued its coördinated movements and "telescoped" anteriorly into other parts.

Conclusion.—Tension or pull, while important in normal creeping movements, may be eliminated and the locomotor stimulus will still pass on down the nerve cord for some distance.

(*b*) *Autotomy*

In the course of administering the anesthesia to the middle portion of the worms, it sometimes followed that the strong contractions would break the muscular walls of the body, a condition of incomplete autotomy. If the animal was released in time the anterior and posterior ends would remain connected by the intestine and the nerve cord (fig. 2).

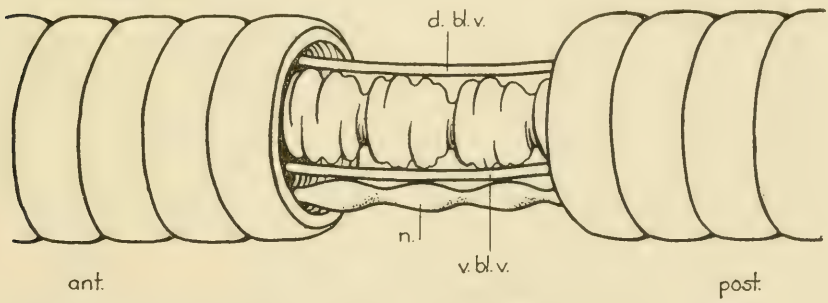


Fig. 2. This shows the nervous bridge as made in an incompletely autotomized worm. The break in the musculature occurs between the segments. The intestine (*int.*), with the dorsal and ventral blood vessels (*d.bl.v.* and *v.bl.v*) and a portion of the ventral nerve cord (*n.*), may be seen.

Problem.—Is the nervous bridge made by incomplete autotomy between anterior and posterior ends of the worm capable of transmitting locomotor impulses in both directions as in the etherized worms?

Discussion.—Under these circumstances the reactions of the partially autotomized worms are the same as in etherized ones; creeping anteriorly and posteriorly can be induced by stimulation. If the anterior end is pinned, the posterior part will still act in coördination; in this case the only possible way for the transmission to take place would be through the nerve cord. Microscopical sections of such cases as these showed that the nerve card was quite normal in structure and still intact.

Friedländer (1894) laid such stress on the matter of tension, the pull of one part on the next succeeding segment, that the behavior of the worm under these conditions of anesthesia becomes particularly important as bearing on the correctness and completeness of his explanation (fig. 3).

Fig. 3. An illustration of Friedländer's experiment which shows the anterior and posterior parts of the worm tied together with a thread. The movement of the anterior piece pulls on the anterior end of the posterior piece and starts the locomotor reactions which are coördinated with those of the anterior half.

Conclusion.—In cases where the tension is eliminated by pinning the worm to a cork on glass, the posterior part can be seen to begin rhythmical movements of contraction coördinated with those of the anterior part. If this anesthetized portion is composed of but few segments, then the coördination is most perfect and the beginning of the movement of the posterior section follows in shorter time than when this portion of the worm includes many segments. It is possible to anesthetize a section of such length that no coördination is carried on and the posterior part lies entirely inert. In *Helodrilus* transmission of impulses was effective through 20 segments, rarely through 28, and never through more than 30 segments.

Nerve Free Preparations

Problem.—The fact that the worms perform autotomy and that the anterior and posterior parts are then connected with each other only by a simple nerve bridge and the intestine, suggested the possibility of dissecting away all the connecting muscle between the anterior and posterior parts. Could the nerve cord be dissected free for a distance exposing several ganglia and could locomotor impulses be transmitted through such a cord?

Methods.—(*a*) *Dissection.* All the muscle in the anesthetized region was cut away after the worm had been pinned to a cork plate. Owing to the fragility of the nerve, it was easily broken and in cases where it was not broken it was easily impaired by stretching, so that particular care had to be taken with the preparations made. Here, as in the experiments discussed above, where transmission was over a few segments, the coördination was good and as the nerve bridge was lengthened the coördination was less complete and finally failed. Such an operation must have a decided "shock" effect on the animal and it does not behave as would be expected under more normal conditions, consequently the length of the nerve does not represent the limits of transmission, as will be shown in some experiments to be discussed later.

In all these cases it was necessary to keep the worm pinned, for if allowed free creeping the anterior part would move more rapidly than the posterior, the nerve was not strong enough to drag the weight of the posterior part and so the nerve was promptly broken.

In my first dissections all of the musculature in the anesthetized region was removed, so that the nerve cord was the only connection between the anterior and posterior parts of the worm. Later I modified this so that the nerve cord, while entirely free for several segments, was not allowed to touch the cork plate but was kept in its own body fluids on a piece of muscle (fig. 4). All the muscle on the dorsal and

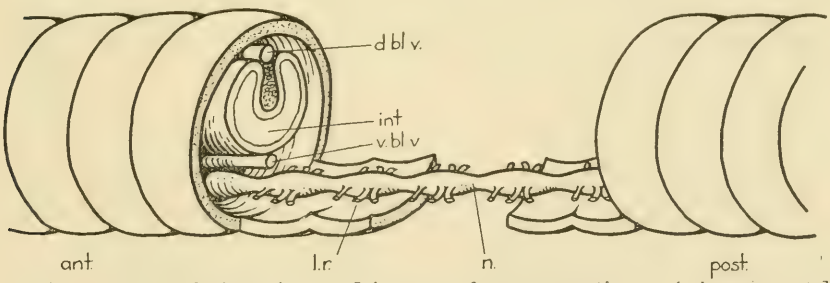


Fig. 4. Type of dissection used in nerve free preparations. (*n.*) nerve cord with lateral roots cut (*l.r.*), intestine (*int.*) and blood vessels (*d.bl.v.* and *v.bl.v.*) cut away.

lateral walls was dissected off. The intestine was removed. This left the nerve cord attached to the ventral plate of muscle. A sharp flat stylet was introduced under the nerve cord and all the lateral roots severed. A transverse cut was then made across the ventral muscle so that no muscular connection remained between the two parts of the worm. When this type of operation was used much more uniform

results were obtained than where the nerve was allowed to come in contact with the cork of the dissecting tray. Garrey and Moore (1916) used a method similar to the earlier method that I used with the same general results.

(*b*) *Graphic Records.* Apparatus. As a check on the observations just described, it became desirable to find some way in which to make a graphic record showing the part the nerve cord plays in the transmission of locomotor impulses. The movements of the anterior and posterior ends of the worm, while the middle part was fixed to a cork plate glued on glass, suggested that if levers were attached to these moving parts a record could be obtained on a kymograph. It was necessary in order to obtain good records to have the levers as light as possible and to have them move with very little friction. This was accomplished by making the levers of aluminum wire, number 22. A desired length was inserted in a cube of cork. Through the cork a small glass capillary tube was thrust which made the bearing for the axle of the lever. A very fine needle was then fitted into the glass capillary and the needle stuck into a firm support. This sort of a bearing allowed the lever to move with little friction and also was

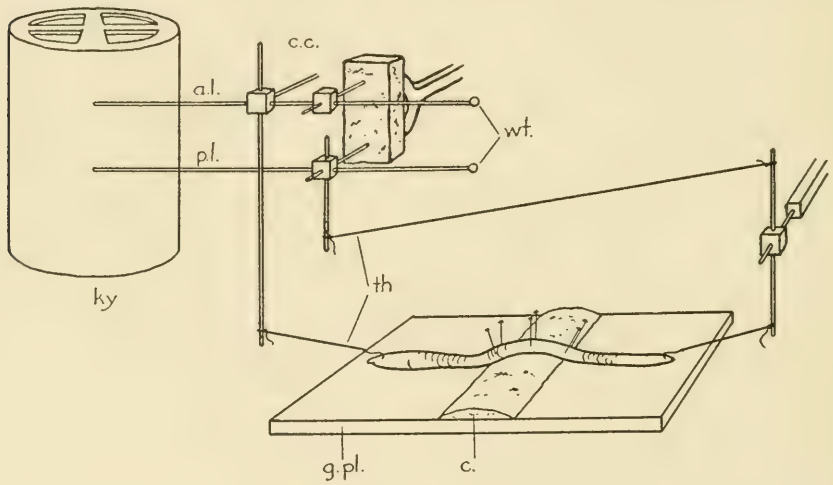


Fig. 5. The general arrangement of the apparatus for recording movements of the anterior and posterior parts of the worms. Method used at Harvard, 1914–1915.

a.l.—Aluminum wire lever connected to anterior end of worm by hook and thread; *c.*—Cork plate glued to glass for pinning the middle anesthetized portion; *c.c.*—Cork cubes through which aluminum wires run; *g.pl.*—Glass plate to which a little water was added to allow the worm to slide back and forth when pinned; *p.l.*—Aluminum wire lever connected to posterior end of worm by hook and thread; *ky.*—Drum of kymograph for taking tracings on smoked paper; *wt.*—Counter balance weights.

advantageous in that it allowed little side lash. Various forms of levers could be built up by means of extra cork cubes and short sections of aluminum wire, as in figure 5, *a.l.* and *p.l.*

The levers had to be weighted slightly so that the worm would be kept in a straight line on the glass plate or else the curves recorded would be exceedingly irregular (fig. 5).

If now a worm is prepared with the middle part anesthetized and arranged to record movements, the movements of the posterior part should show a perfect coördination with those of the anterior part (fig. 6).

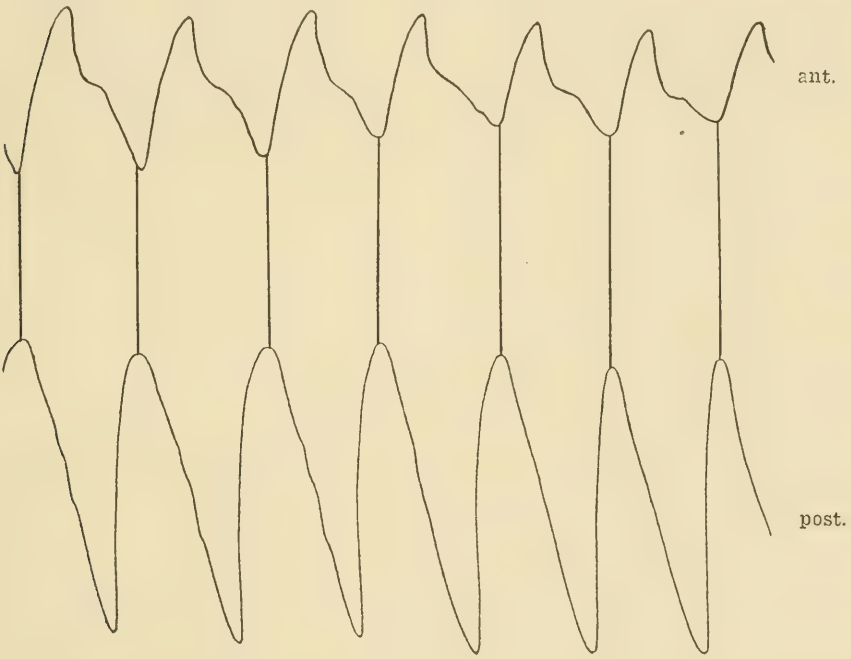


Fig. 6. Experiment 143. A record showing perfect coördination between anterior and posterior parts with a middle area of eight segments anesthetized and musculature cut away. The upper curve represents the movements of the anterior end and the lower that of the posterior end. Transmission of impulses mediated through the nerve cord only.

The method of preparation of the middle portion varied. In some cases the worm was treated with ether by the vial method, and then triple-pinned to the cork plate. In other cases, in addition, the dorsal musculature was cut away, the intestine removed, exposing the nerve cord, and the lateral branches of the nerve cord transected. In still other cases the musculature was cut in the middle region but not

removed, so the nerve could rest on its own body fluids. In all these cases coördinated movements of anterior and posterior portions were shown. The best records were obtained when the least dissection was used.

The clinching argument, however, was obtained when during the course of such experiments the nerve cord is cut. In all such cases, no matter what type of dissection was used, non-coördinated movements were shown when the cord was transected (fig. 7).

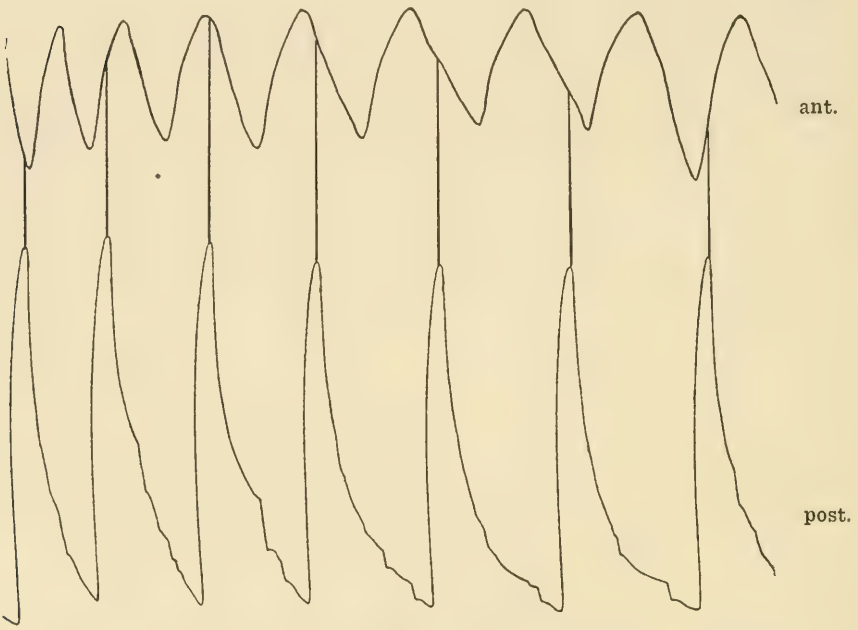


Fig. 7. Experiment 143. Explanation of the curves here the same as in figure 6. The nerve cord connection between anterior and posterior has been cut. Notice the lack of coördination between the movements of two portions of the worm.

(*c*) *Stovaine.* Should any doubts still remain concerning transmission of impulses for locomotor movements over long sections of the nerve cord, the action of stovaine will set these completely at rest. If stovaine be injected into the body cavity of the worm it acts as a block to the nerve cord over four or five segments and allows no impulses to pass up or down through the segments containing the anesthetic. The records will show that there is a lack of coördination and suppression of movements of the posterior end while the drug is effective (fig. 8),

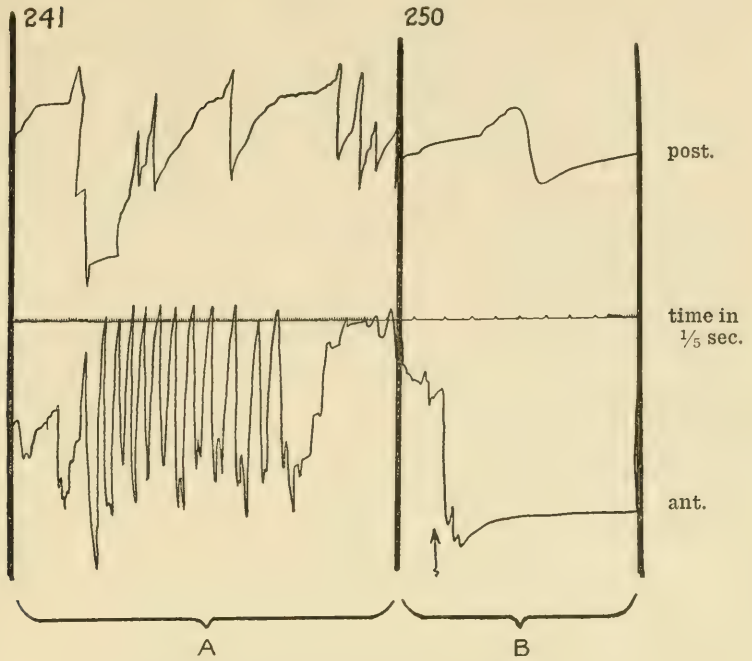


Fig. 8. Experiment 190. Stovaine injected into middle section of worm, four segments affected. Lower curve registers the movements of anterior end and upper curve those of the posterior end. At 2:41 P.M. the coördination between anterior and posterior parts is not normal, and at 2:50 P.M. the giant fiber action is lost. Stimulation at the arrow fails to give a reaction in the posterior part.

A represents ordinary locomotor activities.
B represents giant fiber action.

but as soon as the effects begin to wear off, the coördination between the two parts becomes more and more complete until finally the anterior and posterior parts are again acting in perfect rhythm (fig. 9).

The supposition in this case is that stovaine acts on tissue of earthworm as it does in the vertebrates, where it has no effect on muscle or nerve endings but acts only as a "block" on nerve fibers. The effects of the drug were kept localized to small sections while anteriorly and posteriorly all the normal reactions could be obtained.

Conclusion.—The nerve-free preparations, the graphic records of movements before and after the nerve was cut, and the physiological block established by stovaine, all go to show that the locomotor impulses travel considerable distances in the cord. This work confirms the results obtained by Biedermann but by quite different methods. The most important aspect of these results is the demonstration that

locomotor impulses are not "short relays" depending on a stimulus from each segment, but are capable of running a number of segments with no stimulus from the outside.

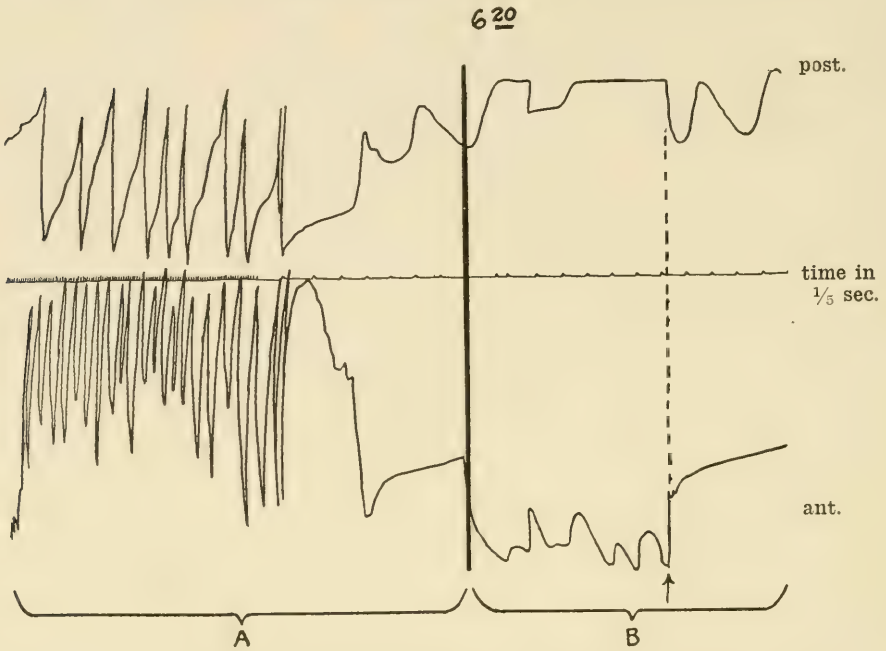


Fig. 9. Experiment 190. Continuation of experiment shown in figure 8. At 6:20 P.M. the worm had recovered from the effects of the stovaine. Normal coördinated movements are being made (*A*) and the giant fiber action has returned (*B*). Stimulation of the anterior end at the arrow shows a response in the posterior end.

Limits of Transmission

Problem.—How far will these locomotor impulses travel in the cord? Can a middle area of sufficient length be anesthetized so that no impulses from the anterior piece can get through to start locomotion in the posterior part?

Discussion.—It was soon discovered that transmission was best shown when it was concerned with few segments and that, as the number of ganglia through which the impulse must pass was increased, the coördination became less and less perfect. No sharp limits could be determined. When the nerve cord was dissected free from muscle, the most severe type of dissection, the transmission seemed to be limited to eight free ganglia. In one case, coördinated movements were obtained when ten ganglia had been freed, but this was unique.

When the length of the free nerve contained four ganglia, transmission was easily demonstrated.

In those cases where the dissection included the removal of the dorsal wall, intestine, and the transection of lateral nerves, the transmission easily ran for more than ten segments, but never for more than twenty-eight.

It has been demonstrated by Biedermann (1904) and confirmed by my own experiments, that the impulses run long distances in the cord when the worms are anesthetized in the middle region which is afterwards treated with six per cent nitric acid. In such cases, records of transmission were obtained when twenty segments intervened between the still active anterior and posterior ends. Failures came more often as the length of this etherized part was increased. One record was obtained with the large *Helodrilus* where coördinationed movements appeared in the posterior part when twenty-eight segments were etherized and their muscles killed with nitric acid.

These results fall somewhat short of the cases reported by Biedermann, where coördinated movements were obtained through anesthetized parts two to three centimeters long, but the number of segments is not stated. The greater part of my records were obtained on *Helodrilus*, where twenty segments of the body, in the part measured, approximated two centimeters. While this does not show a great discrepancy, my results are apparently nearer the lower figure quoted by Biedermann.

We can establish, then, no absolute limits, except to say that transmission is fairly well accomplished over ten segments, may run to twenty and even to twenty-eight, but that the longer the nervous bridge the greater the difficulty. No records have been obtained where thirty segments were concerned.

One factor which makes the determination of any such records very difficult is that impulses from normal stimuli in normal worms starting down the length of the worm do not necessarily continue to the end. The dying out of an impulse is quite a usual phenomenon seen in the contraction waves that run only part way down the animal. One of these impulses may start into the cord of the etherized part and never reach the other end of the etherized part of the worm. This does not mean that no impulses can come through, and so no limit can be determined by this failure, but it does indicate a dying out of this particular impulse somewhere in transit. Therefore, in the experimental determination of the limits to transmission, as long as impulses

come through the etherized part we are still within the limits of transmission, but as soon as failures become frequent it is evident that the limits have been approached. More refined methods may be able to determine these limits closely. My records can be considered only as approximations.

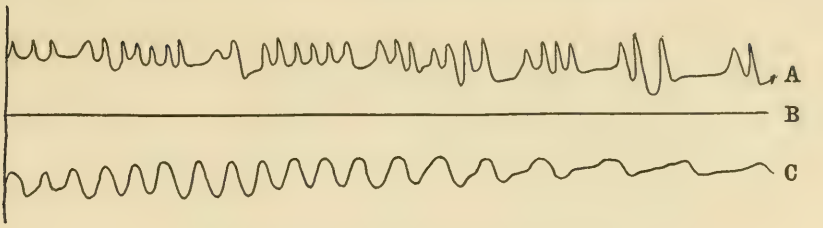
One other difficulty arises in making these determinations. Summation of stimuli has been shown by both Straub (1900) and Budington (1902) for annelid muscle. Weak stimuli adding themselves together will sooner or later give a contraction. There is the possibility that, in observations on these reactions, failures have been recorded, where, in reality, weak stimuli did get through. However, any errors so made would be on the conservative side.

Conclusions.—The results of these experiments show that no absolute limits can be set, the impulses travel short distances in the cord very readily and that the longer the section of cord to be traversed the greater the difficulty. In *Helodrilus* twenty-eight segments was the limit for the distance locomotor impulses would travel in the cord when the superficial nerves were anesthetized.

Dependence on Nervous System for Transmission

Problem.—While the nerve cord is capable of transmitting locomotor impulses for considerable distances is it possible for the muscles to carry on rhythmical movements without the aid of the nervous system?

Discussion.—If a short section of a worm containing about twenty to thirty segments is prepared in such a way that it will give a record of contractions of the longitudinal muscles on a moving drum, and the lever is slightly weighted so the piece will be kept straight but not stretched, it will be found to make rhythmic contractions. Straub (1900) and Budington (1902) show this characteristic of annelid muscle but disagree in the interpretation. Straub claims that strips of the muscles, both with and without nerve, will give rhythmic contractions. However, regions of the worm from which the nerve had been removed must be given several (eight) days for recuperation and then they would give contractions comparable to those of the regions of worm with nerve intact. Budington found that when care was used to remove all nervous tissue by using only pieces of worm in which the whole ventral muscle had been removed, that such pieces gave no rhythm; while pieces containing even a small amount of nerve gave a regular rhythmic curve (fig. 10).



A = Short piece of whole worm with nerve cord.
B = Dorsal longitudinal half without nerve cord.
C = Ventral longitudinal half with nerve cord.

Fig. 10. Experiment 104. Curve *A* is made by a short piece of worm attached to a writing lever. The piece was normal in every way and gave rhythmical contractions. Curve *B* represents a curve made by the dorsal half of a short piece of a worm that had been split in two longitudinally. This piece contained no nerve cord. Curve *C* was made by the ventral half of a short piece of a worm that had been split in two longitudinally. This piece did contain the ventral nerve cord and did give rhythmic contractions.

My results agree entirely with those of Budington. It is quite possible that the findings of Straub may be due to a factor that he overlooked, the matter of regeneration. As I shall show in a later paper, regeneration is exceedingly rapid and there is a possibility that nerves have grown into the operated portion, and the probability is that Straub was really dealing with pieces in which nerve fibers and cells had regenerated.

As further evidence of this dependence upon the *nerve cord* for transmission it will be noted that when a worm is pinned in the middle portion to a cork plate and the anterior and posterior ends are registering coördinated movements on a revolving drum, if the nerve be cut in the pinned region the rates of contraction of the two parts will be immediately changed. In this case, the muscle is disturbed as little as possible and only the nerve cord is cut (fig. 11).

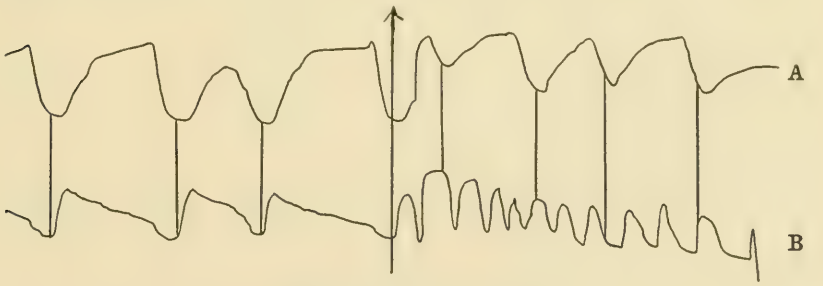


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Fig. 11. Shows how the posterior half of the worm changed its rhythm after the nerve cord had been cut. The upper line represents the movements of the anterior (*A*) half and the lower line the posterior (*B*) half. The nerve cord was cut without cutting any but a small portion of the ventral muscle.

Conclusion.—From the work just cited, it is quite certain that spontaneous movements are dependent on the nervous tissue and that

the muscle has no property of rhythmic contractility. While this does not show that transmission of impulse passes over many ganglia in locomotion it strengthens the work of Biedermann (1904) and Budington (1902) who hold the theory of nervous control.

Rates of Transmission of Locomotor Impulses

Problem.—The fact that locomotor impulses could be transmitted through a portion of the nerve cord isolated from segmental muscle connections led to the query, what is the speed of these impulses? If the speed were rapid it would mean that there were some fairly long neurones in the cord, and if the speed were slow it could be interpreted on the basis of short neurones and many synapses. This study should throw some light on the structural basis of transmission.

Discussion.—Jenkins and Carlson (1903) measured the rate of nerve impulses in several species of annelids. The rates were found to be exceedingly variable, from 89 centimeters in *Nereis* sp. to 694 centimeters per second in *Bispira polymorpha.* The question these investigators raised was whether they were dealing with simple continuous nerve fibers or with a very complex nervous tract. While the anatomical connections of neurones in the cord have been worked out to some fair degree of certainty, no long connections have been established in the cord, except by the giant fibers. Jenkins and Carlson left the question open as to whether their measurements were those of a direct nervous path or an indirect one.

After observing a very large number of experiments on the transmission of the impulses as they pass through the etherized section of the worm, and noting the slow progress of these as compared to the quick end to end jerk of the worm when stimulated, there is little doubt in my own mind but that the cord has two kinds of transmission of nerve impulses. First, the very rapid impulses through giant fibers, which result in vigorous contractions, as in the jerking back into their burrows of the worms when strongly stimulated; and the second type, the impulses in the short fibers in the middle of the nerve cord, which offer a complex path and so transmit impulses slowly down the cord.

My records for the speed of impulses in the giant fibers agree quite well with the speed recorded by Jenkins and Carlson (1903). The method which these workers used was such that only the action of quick contractions was recorded and no attempt was made to separate this phenomenon from that of the locomotor impulses. As has been shown, these latter impulses run but short distances in the cord unless

reinforced by outside reflexes; and so, unless special methods are used, the reactions of these short fiber systems would not be observed.

A frequent observation on the locomotor habits of worms is that the wave of contraction runs for a short distance and then disappears. This was a source of great inconvenience in determining the rate of impulse down the cord. A method was devised whereby electric contacts were successively made as the wave of contraction passed along the worm. These were recorded on a drum from which measurements were easily made and speeds computed (fig. 12).

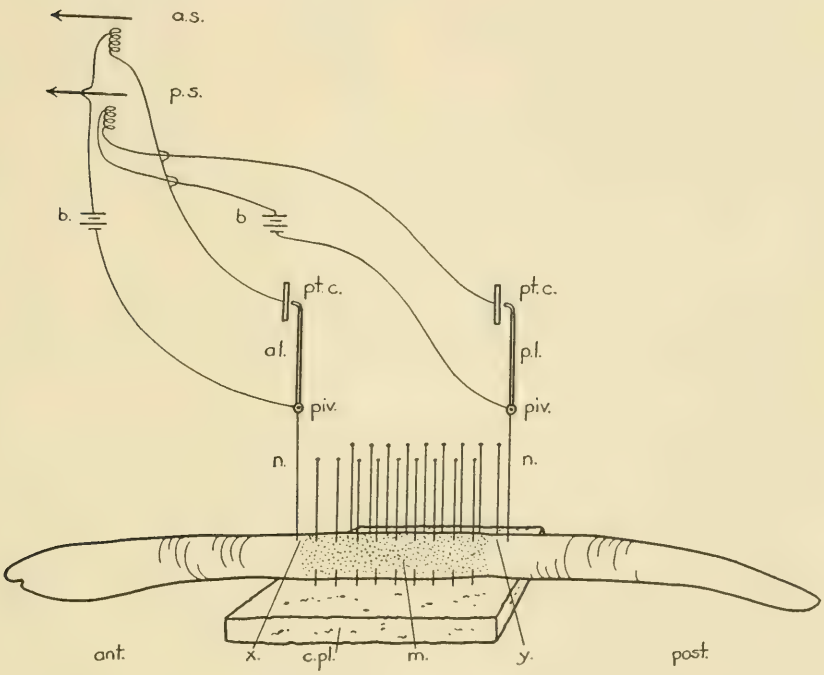

Fig. 12. The apparatus for measuring the speed of nervous impulses through the nerve cord in an anesthetized region was as follows: *a.l.* and *p.l.* are levers pivoted at *piv.* The lower part of the lever *n* is a sharp, very fine needle. One of these is thrust into the muscles of the first segment in front of the anesthetized part *m.* and the other into the muscles just behind this region *m.* The upper ends of these levers is quite long so that very slight movements of the lower part will produce considerable movement in the upper part. Platinum contacts were provided at *pt.c.* and each lever was connected by battery to signal magnets, *a.s.* and *p.s.*, which gave a record on a smoked drum of a kymograph. When the locomotor movement of the anterior part of the worm had reached the muscles at *x.* the electrical contact would be made in lever *a.l.*, which registered on a fast revolving drum at *a.s.* Now when the nervous impulses had passed through the anesthetized area *m.* and reached the muscle *y.* another electrical contact was made by lever *p.l.* and registered by signal magnet *p.s.* The speed of the drum being measured, the speed of the impulse could be calculated.

The very noticeable result of this series of experiments was the great variability in the speed, which seemed to depend on the state of irritability in the worm.

Another important fact seemed evident from these measurements; namely, the longer the section of nerve measured the slower the rate recorded.

Time Taken to Travel Over Certain Lengths of Normal and Anesthetized Worms

	Experiment 180 [1] 3 live, 20 etherized segments	Experiment 162 11 live, 20 etherized segments	Experiment 162 19 live, 20 etherized segments
1	.26 seconds	.90 seconds	.68 seconds
2	.44	.50	.65
3	.24	.64	.70
4	.21	.60	.90
5	.25	.34	.70
6	.35	.34	.82
7	1.02	.30	.92
8	.72	.25	.75
9	.13	.40	.72
10	.08	.25	.72
Average	.370	.452	.760

[1] These figures are calculated from experiment 180, a series different from that in columns 2 and 3.

The method for making these records was not refined and the times recorded can only be approximations. The table will show that where the length of the portion of the worm measured is increased the time of transmission increases, but not proportionately. The full significance of this fact and its relation to transmission and a new theory of locomotion will be brought out in a later part of this paper.

In measuring the speed of the impulse through the nerve cord in a section where the muscle had been anesthetized, the electric method of measurement was quite effective. Records of slight movements of the segments just anterior to the inert section were followed by the registration of movements beginning in the part immediately behind this portion. Here again we meet great variability, depending on the state of excitement in the worm. If the etherized section is greatly increased in length the point will eventually be reached when no impulse comes through. Records through more than twenty segments were frequent, but when more than twenty segments were used, failure resulted more often than in fewer than twenty. Measurements were recorded over twenty-eight segments but these seemed to be exceptional

cases. For the most part, impulses passed along the cord at the rate of about 25 millimeters per second. This represents the mode of a series of ninety-one measurements. Several observations showed good transmission at the rate of 60 millimeters per second, and a few were recorded in which the rate was very low, *10* millimeters per second (fig. 13).

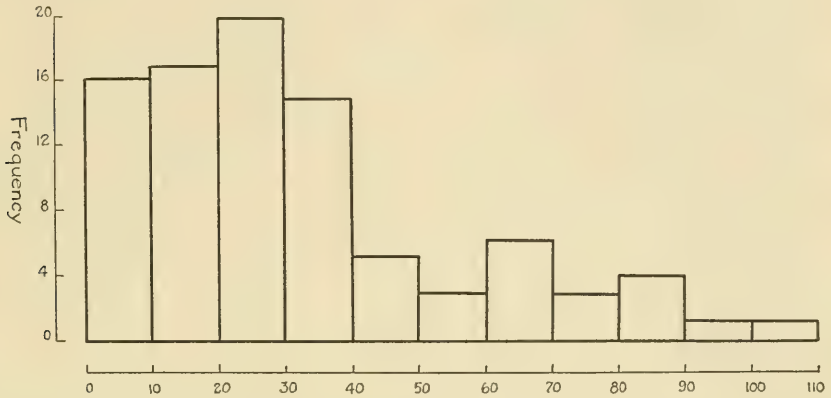

Fig. 13. The frequency polygon which shows results of ninety-one measurements of the speed of locomotor impulses through the nerve cord when the peripheral nerves have been anesthetized. The mode lies between 20 and 30 millimeters per second.

Conclusion.—The locomotor impulses show no definite speed. The most interesting feature is the extreme variability of this movement. In those cases where strength of stimulus is sufficient and other conditions are right the speed may be as fast as 100 millimeters per second, and again the speed may be so slow that it will die out in the nerve cord without ever emerging from the anesthetized region. I have taken the mode of the frequency polygon as against the average which shows that ordinarily the speed is about 25 millimeters per second. The slowness and variableness are the two main characteristics.

Rate of Impulses in the Giant Fibers

Problem.—How does the rate of transmission of locomotor impulses compare with that of the giant fiber? Are the rates such that these two phenomena can be ascribed to quite different systems of neurones?

Discussion.—The method used to measure the rate of transmission of impulses in the giant fibers was practically the same as that used in measuring locomotor transmission, except that in this case it was

possible to use the full length of the worm. One characteristic of this type of action is that it seems to be related solely to the longitudinal muscles in contrast to that of the locomotor nerve fibers which set up complex reactions in both circular and longitudinal muscles.

Responses resulting from stimulation of these large fibers are always exceedingly rapid as compared with other movements of the worms. The reaction may be slight or violent, according to the amount of stimulus applied, but any response travels the length of the worm in a very short time. It is interesting to note the antagonistic relations of the innervation of muscles when a quiescent worm is stimulated lightly, with a sharp needle, at the anterior end; immediately there is a response by a relaxation of the circular muscles near the posterior tip so that this part is flattened and enlarged. If the stimulus is made stronger, this reaction will be followed by a jerk of the longitudinal muscle and when the stimulus is moderately strong the contraction of the longitudinal muscle is so quick and extensive that no reactions of the circular muscle can be detected.

A number of determinations for speed of this rapid action are recorded in the accompanying table. The range of variation is large, due in part at least to the methods of measurement and the inaccuracies of the apparatus (fig. 14).

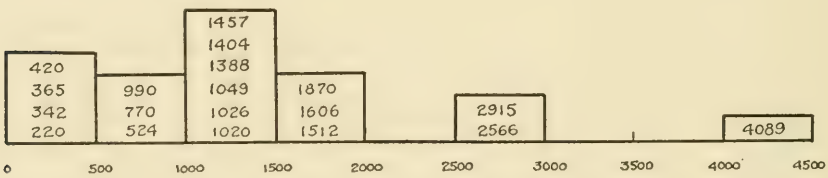

Fig. 14. Frequency polygon which shows the speed of impulse through giant fibers. The figures represent millimeters per second. The mode is between 1000 and 1500 millimeters per second.

All of these measurements were made on the large garden worm, *Helodrilus caliginosa*, and as nearly as possible under the same conditions. The interesting feature of this array of figures is that they are high compared to those obtained in locomotor transmission. Ordinarily they can be said to be fifty times faster, and may even be one hundred times faster, than the other type of transmission. The mode for these few measurements is around 1500 millimeters per second. While this is not so rapid as some recorded by Carlson and Jenkins (1903) (table 1), in measurements on marine annelids, it is certain that it belongs in the same class of phenomena as they were

TABLE 1

SUMMARY OF RATES IN WORMS—CARLSON AND JENKINS

Species	Direction		Centimeters per sec.
Cerebratulus	P	A	5.4– 9.0
Aulastoma lacustre	P	A	56.0
Cirratulus sp.	P	A	90.0
Arenicola sp.	A	P	120.0
Bispira polymorpha	P	A	694.0
Aphrodite sp.	A	P	54.0
Polynoe pulchra	P	A	293.0
Sthenelais fusca	P	A	205.0
Eunice sp.	P	A	466.0
Nereis sp.	P	A	165.0
Nereis virens	P	A	89.0
Nereis virens	A	P	73.0
Lumbriconereis sp. (*a*)	P	A	45–241.0
Lumbriconereis sp. (*b*)	P	A	49–937.0
Lumbriconereis sp. (*c*)	A	P	42–160.0
Glycera rugosa	A	P	433.0
Glycera rugosa	P	A	435.0

measuring. None of my measurements approached the highest speeds in these marine forms, such as that in *Bispira polymorpha*, viz., 6940 millimeters per second, or even in *Lumbriconereis* sp., viz., 9370 millimeters per second, nor on the other hand did I find any as slow as that in *Cerebratulus* at 54 to 90 millimeters. Several worms, *Nereis*, *Arenicola*, *Sthenelais*, give averages about the same as that which I found for *Helodrilus*.

Jenkins and Carlson used *averages* in obtaining the figures above, when it would seem such a variation in measurements occurred that the mode is more nearly the correct expression. I have used this in both series, that on locomotor transmission and on giant fiber action.

One feature of giant fiber action that is easily noticed is, that, once started, it always goes through to the posterior end; it never dies out in transit as the locomotor waves do. In cases where the nerve cord has been severed, the impulse runs as far as the cut, and never beyond.

Krawany (1905) in his discussion of the elements in the central nerve cord describes the relations of the giant fibers to the association cells in the cord. These large fibers pass from end to end of the nerve cord and in each ganglion send out branches which are intimately in connection with processes from association cells in the middle group. These cells which thus synapse with the direct fibers never have cross-over connections but seem to be entirely homolateral.

The physiology of these reactions is correlated with the anatomy of these fibers. The path is a direct one and the speed of their impulses is fast, 1500 millimeters per second compared with 25 millimeters per second for locomotor reflexes. The connections are simple and the reactions are concerned largely with the contractions of but one set of muscles, the longitudinal muscles. The fibers run the full length of the cord and so reactions are concerned with the whole animal. They are single fibers and produce a single action. There is no wave motion nor evidences of loss as the stimulus passes down the cord.

There is no reason to suppose that these fibers have anything to do with locomotor reflexes or transmission; everything points to a separate function for these large long fibers.

Conclusion.—We have taken for granted that Friedländer's (1894) suggestion that the end to end movements are due to impulses carried by the giant fibers. The results of this work on rates of transmission seem to justify this supposition. No theory allows a nerve to have for itself more than one rate of transmission. The speed of one type of action and the slowness of the other would necessitate two kinds of fibers. The anatomical conditions and the physiological reaction are easily correlated. The large giant fibers are continuous structures running the full length of the worm and capable of carrying the impulses swiftly from end to end at a normal rate of 1500 millimeters per second, while in the center of the nerve cord are numerous short neurones running short distances up and down the cord, giving a complex path, with slow speed of transmission, normally 25 millimeters per second, such as would be expected on account of the multiplicity of synapses.

THEORETICAL CONSIDERATIONS

The Nervous Mechanism.—Some of the most salient facts brought out in the study of transmission are: the nervous system plays an essential part in the movements of locomotion; the impulses responsible for the waves of contraction are capable of running for considerable distances in the cord and are not confined to one or two segments, as indicated by Friedländer; transmission may extend over as many as twenty segments without intervening muscular activity, the rate of transmission is a variable one becoming slower as it pro-

ceeds. The giant fibers have little to do with locomotion and are specialized for rapid, end to end contractions.

The excellent work of Krawany (1905) on the neurones of the central system of the worm and the researches of Dechant (1906) on the peripheral nervous system, together with the great amount of work done by the older writers, such as Bethe (1903), Rhode (1887), Apathy (1897), Retzius (1900), Biedermann (1904), Smirnow (1894), and others, have demonstrated that the nervous system is compounded of many short neurones. The longest elements are some few large fibers from the anterior end of the cord which arise in the sub-esophageal ganglion and run posteriorly to the terminal segment, but Krawany (1905) shows that for the most part the other nerve fibers run only from one ganglion to the next.

Sensory nerve fibers originating in the epidermis pass down through the main nerve trunks to the ganglion where they branch as T- or Y-shaped bifurcations immediately on entering. These run but short distances before ending in fine arborizations. Krawany (1905) was unable to demonstrate that these passed into ganglia anterior or posterior to the segments of entrance, but was inclined to think that they remained within the ganglion entered. No demonstration of neuro-muscular end organs has ever been made in the smooth muscle of earthworms. Retzius (1895) and Langdon (1900) have shown, by using Golgi methods, that nerve fibers are in among the muscle cells, but Dechant (1906) by using methylene blue was unable to differentiate any definite end organs. Many nerve fibers parallel to muscle can be seen, showing the presence of abundant nervous tissue, but all fibers which looked like end organs proved to run only short distances and could not therefore be true nerves. While free sensory endings in the subepithelial regions are not yet demonstrated, Dechant believes they are undoubtedly there.

After entering the cord the sensory nerves bifurcate, one branch passing up and another down the cord on the same side as they enter. They may then form synapses with neurones of motor ganglia in the anterior, middle, or posterior groups of nerve cells. These large cells send out neuraxes which may or may not cross to the opposite side, where they leave by one of the three lateral roots.

Within the cord, however, there are still other paths open to impulses entering by the sensory paths. The large multipolar cells are the association cells which show an arrangement into three groups, an anterior, a middle, and a posterior group. Their function is to connect

more or less distant parts of the ganglion and to interpolate themselves between the sensory and motor elements. Many of these are homolateral and some are contralateral. The greater number of these association cells are intraganglionic, i.e., never leaving the segment; but a few in the anterior and posterior groups send processes into the next ganglion and so connect up the ganglia segment to segment.

The most interesting feature is that in this nervous system there are no long nerve tracts, the giant fibers excepted. Impulses that run the length of the cord must find their way over a complex route and be necessarily slow. We have then a nervous system made up of many short units. Each ganglion is a complete relay station capable of receiving sensory and giving out the motor impulses necessary for the functions of each particular segment. The only connections between the succeeding segments are association fibers in the nerve cord and a few motor fibers which Dechant (1906) shows. These motor fibers take their origin from a nerve arising from the posterior root and pass laterally around the muscular wall near the intersegmental furrow and at intervals give off five branches which pass into the segment behind. Without these two connections, one in the cord and one peripheral, there would be no nervous connection from segment to segment of the worm.

Friedländer (1894) laid particular emphasis on the "pull" of one segment on the succeeding ones and that coördination was accomplished even though the nerve cord were cut. The experiment of cutting a worm in two and attaching a string to each part resulting in coördinated movements indicates that pull certainly does play an important part. Undoubtedly the tension or stretching stimulates the nerve and starts the reflex movement. The succeeding movements then are due to both pull and nerve impulse. If part is etherized, it ceases contractions although it responds to direct stimulus. The nerve reflex has been broken. Again, if tension be eliminated by pinning experiments, coördinated movement proceeds; but if now the nerve be cut, coördination ceases. So while tension is important in supplying a stimulus to the nerve mechanism, it is not wholly sufficient.

Biedermann (1904) showed that these reflexes can travel considerable distances in the cord. The interpretation of this might demand that there be present in the nerve cord longer systems of neurones than had been previously reported. However, it can be shown that no such supposition is necessary. The present knowledge of the neurones can be used to explain the facts at hand.

Transmission by Reinforced Stimuli

There is one other point of great importance in the analysis of locomotion in the earthworms and one which has not been heretofore mentioned. This is the variability in the rate of the impulse along the cord. Experiments have shown that the transmissions over short distances are much faster than those over longer distances, and this agrees with a phenomenon easily observable in the movements of worms, i.e., the dying out of waves of contraction. One can watch a wave of contraction start down the length of the worm and become more and more feeble until it is lost at the middle region. The distance the wave runs seems to depend on the force of the wave at the start. A strong wave runs further than one with a weak start. A glance back at the charts of the speeds of impulses passing through the etherized portion of a worm will show that there is a great variability. One has but to observe a single worm under the experimental conditions to become convinced of this without the figures.

Any theory that accounts for locomotion must take into consideration the short unit system of the nervous system, the transmission of locomotor impulses over long sections of the cord, and the variability in rate of the speed of these impulses.

Friendländer (1894) likened the locomotor mechanism to a system of telegraphic relays. Each contraction of the circular muscle elongated the segment and stretched the longitudinal muscle. This stretching caused a stimulus to pass along the nerves to the cord, where a reflex gave a contraction of the longitudinal muscle. The contraction of the longitudinal gave the pull which caused the circular muscle to contract and so on down the length of the worm, each segment with its own reflex, but progression of the wave of contraction due to the pull of contracting parts on succeeding segments.

A short unit nervous system is all that is necessary for such an explanation. But when transmission of locomotor impulses can pass along the cord this relay system in each segment is not sufficient. If, however, we suppose that the association fibers transfer stimuli from one ganglion to the next, then we have a means for explaining Biedermann's experiment. One of the characteristics of this transmission was that it varied considerably in rate. When the worm was in an excited state or stimulated, the impulses passed through an etherized section faster than otherwise. If we suppose that with each contraction reflexes are set up in each segment and that these stimuli entering the cord reinforce the locomotor stimuli passing along in the short

association tracts, and that if these stimuli are heavy they add to the strength of stimulus passing along, or if weak add little or nothing at all, then we have a basis for explaining the variations in rate. In each ganglion there will be at least one and maybe two synapses to be passed, each with a certain resistance which will tend to cut down the force of the stimulus and its power to get through. Each synapse in each segment resists the passage of the locomotor impulse but in ordinary locomotion each well coördinated contraction wave reinforces the loss and the movement runs the full length of the worm. The uncertain limit of such transmission then can be understood for many factors may come in to change the force of the stimulus; the stimulus may have started in a weak contraction—outside conditions may have altered the amount of reinforcement—internal conditions in the cord itself may have demanded a more complex path in one case than in another, or even the physiological condition of the worm may have had some effect on the resistance in the synapses.

SUMMARY

1. When a worm is anesthetized in the middle area and the peripheral nerves are rendered useless, locomotor impulses may be transmitted in both directions through the nerve cord of this middle region from anterior to posterior, and posterior to anterior.

2. Tension or pull, while important in normal creeping movements, may be eliminated and the locomotor stimuli will still pass up and down the cord for some distance.

3. Nerve free preparations show that locomotor impulses may travel considerable distances in the cord. Under such conditions the anterior and posterior parts act in perfect coördination. When the nerve is cut such coördination ceases. Stovaine when applied to the nerve cord blocks the passage of locomotor impulses up and down and the coördination of anterior and posterior parts is lost; as soon, however, as the effects of the drug are removed impulses again pass freely in the cord and coördination returns.

4. The results of measuring the limits of transmission of the locomotor impulses shows that no absolute limits can be set. The impulses travel short distances of ten segments very readily but when required to traverse a longer section of twenty-eight segments the difficulty is great. No records show impulses passing through as many as thirty segments.

5. Spontaneous rhythmical movements are dependent on the nervous system and the muscle tissues do not possess the property of rhythmic contractility. This strengthens the theory that locomotion is under nervous control.

6. The speed of locomotor impulses is quite variable. The mode that expresses the normal rate is about 25 millimeters per second. The rate may be increased or decreased in transit from segment to segment.

7. The rate of the transmission of giant fiber action is very rapid when compared to that of the locomotor impulses. The mode for a number of measurements shows the speed to be about the rate of 1500 millimeters per second. The wide gap between these two types of nervous activity, the slow locomotor on the one hand and the rapid giant fiber action on the other, indicates that these impulses are mediated by two quite different kinds of nerve elements.

8. The anatomy of the nerve cord as shown by Krawany and Deschant has in it no long neurones. The processes may join successive ganglia but none extend through the cord for a great distance except the larger giant fibers, which run the full length of the cord.

9. The peculiarities of the locomotor impulses in transmission, such as the variability in rate of speed, and the slowness of it, can be accounted for on the basis of the structure. The impulse to make its way down the cord must pass in each ganglion at least one synapse, and the possibility is that there would be more than this. Each synapse would not only cut down the strength of the impulse but would also slow down the speed because of the time consumed to cross the gap between neurones. In normal creeping the impulses travel regularly down the cord because each contraction of circular and longitudinal muscle in each segment sends in locomotor impulses which reinforce the impulse passing down the central nerve cord, and any loss through the synapse is made up in this way. If for any reason the muscular activity fail or if the nervous connections to the cord be destroyed the locomotor impulse traveling down the cord in this region would decrease in strength and decrease in rate because of the lack of reinforcement.

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THE FUNCTION OF THE GIANT FIBERS IN EARTHWORMS

BY
JOHN F. BOVARD

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CONTENTS

PAGE
Introduction ... 136
I. General functions of the nerve cord ... 136
1. Biedermann's theory ... 136
2. Muscle not responsible for rhythmic movements ... 136
3. Friedländer's theory of giant fiber action ... 136
Materials and methods ... 137
I. Material used ... 137
II. Methods used ... 137
1. Simple transection ... 137
2. Removal of short sections of the cord ... 137
3. Effects of the operation and recovery ... 138
Regeneration experiments ... 138
I. Effects of simple transverse section ... 138
1. Recovery of activity of locomotor fibers ... 139
2. Recovery of activity of giant fibers ... 139
II. Removal of short pieces of the cord ... 140
1. Recovery of locomotor fiber activity ... 141
2. Recovery of giant fiber activity ... 142
III. Comparison of results with those of Straub and Friedländer ... 142
Experiments with stovaine ... 143
I. Methods ... 143
II. Recovery from effects of drugs ... 143
1. Behavior of the locomotor fibers ... 143
2. Behavior of the giant fibers ... 143
Summary ... 144
Literature Cited ... 144

INTRODUCTION

In the analysis of the locomotion of the earthworm Friedländer (1894) showed that worms made well co-ordinated movements even after considerable portions of their nerve cords had been removed. He concluded that the nervous system served simply as a medium for very short relayed reflexes and played a secondary part in locomotion. Biedermann (1904) extended this idea by showing that stimuli could run long distances in the cord, and in my recent paper (1918) I was able to show something concerning the limits of this transmission and also the rate at which such impulses travel in the cord when not reinforced from without.

Straub (1900) claimed that the spontaneous contractions of short sections of earthworm were due to inherent qualities of the muscle; at least they were not due to the nervous system present. My own experiments seemed to show a contrary result, and in all cases rhythmic movements were only in pieces containing nerve cord.

The results of these experiments just cited were obtained on worms from which the nerve cord had been entirely taken away. It occurred to me, therefore, to study the effects of regenerating nerve cord on locomotor movements. It is well known that the nerves do not all regenerate in the same time, and this, then, would give me some clue as to which fibers carried locomotor responses and which the end to end collapsing movements. Friedländer (1894) suggested that the quick jerks which take the animal back into its burrow were due to impulses carried by the giant fibers. This has been accepted as most probable, but has not been demonstrated. If, then, a regeneration of the nerve cord would give a differential healing, it would be probable that the giant fibers would unite sooner or later than the transmission nerves, and we would have some definite proof for Friedländer's contention.

The effects of simple transverse sections of the ventral cord were studied and later short portions of the cord were removed. Drugs, such as stovaine, were also tested, because they have the effect of "blocking" the nerve cord, which is practically the same as removal of ganglia for a brief time. Drugs have the added advantage of losing their effect quickly, and so the changes in nerve reactions during development and recovery from the anesthesia could be watched.

MATERIALS AND METHODS

Material.—Both the common *Allolobophora foetida* and *Helodrilus caliginosa* were used in these experiments. Similar results were obtained with each, but in general the larger worm was the easier to work with, especially when operations were made for the removal of sections of cord.

Methods.—In all cases where operations were to be performed the worms were kept for at least twenty-four hours in clean moist cloths, so they would clear themselves of dirt and grit. Worms that were kept in moist filter paper usually ate large quantities of this, which made the cutting of sections quite difficult.

The transecting of the nerve cord was a simple operation. The worm was held tightly on a moist surface and a transverse cut made with a safety razor blade. A single stroke was usually sufficient to cut both ventral muscle and the nerve, and if care were exercised there was little danger of cutting too deep. The cut was examined with a hand-lens to make certain that the cord had been cut.

A simple physiological method of determining whether the cord had been sectioned, and a method that proved a check on all experiments, was as follows: Examination of the worm immediately after the operation showed that the muscles posterior to the cut had lost their tone, giving an increase in the diameter of the part. This condition did not extend for any great distance, but was usually confined to from three to five segments. If the nerve had not been severed, this effect wore off after the first day of regeneration; otherwise it remained enlarged until physiological continuity was re-established.

In operating on *Helodrilus,* a simple transverse cut with a razor blade usually only severed the musculature. The cord adheres very closely to the intestine and comes away from its ventral muscles very readily. In these cases it was necessary to cut the cord with a pair of fine scissors, making a simple snip. Where care was not used and the ventral blood vessels were cut also, the animal bled profusely, and in many cases died or autotomized the posterior piece.

When necessary to remove two ganglia, the worms were anesthetized in a 5 per cent alcohol solution for fifteen minutes to one-half hour, in all cases until they were motionless. Under a dissecting microscope, a transverse cut was made in the ventral muscles. The opening was stretched and pinned back with clean, fine needles. The nerve cord and bloodvessels then could be easily seen. Great care

had to be exercised to prevent cutting any blood vessels. The cord was lifted up with fine forceps, and a cut made anteriorly. The cord could then be pulled forwards and a cut made posteriorly. The segment, which was removed, was then put into 95 per cent alcohol and examined later to ascertain the exact amount of nerve substance removed.

After the operation the worms were placed in small 8-ounce jars with some moist cloths over them and put away in a dark cabinet. It was not found necessary to keep the worms in a particularly cool place as long as the jars and cloths were kept scrupulously clean. The temperature was the ordinary room temperature during April and May in the Harvard laboratories. The only cases where worms died during these experiments were those which bled profusely after the operation due to rupture of the large ventral blood vessel. The loss was surprisingly small.

By the following day the worms appeared normal, the wound had healed over and they could be seen creeping about in the jars. Usually, however, they were not very active in the cramped quarters of their jars.

Effect of Transverse Sections of the Cord

The result of simply transecting the cord was the loss of transmission and of the animal's power to reverse its direction of creeping on stimulation. Stimuli applied at either end ran as far as the cut, but failed to pass across the break in the cord. Earthworms often respond to strong stimuli given to the anterior end by certain lashing movements and side to side jerks. When the cord was severed these lashing movements could be induced in the anterior portion of the worm without producing any effect on the posterior part behind the cut, which might lie quiet during this movement. Giant fiber action induced either from the anterior or the posterior direction was effective as far as the cut only. The quick, end to end action never succeeded in starting the same kind of a movement in the portion of the worm on the other side of the break opposite to the point stimulated.

The effects on the musculature were particularly noticeable. Immediately behind the cut region the worm showed an enlargement of the segments. Here the circular muscles seemed to have lost their tone. As the worm crept along the posterior part acted in co-ordination with the anterior, but these few segments behind the cut took no part. The length of this inactive part varies from three to five

segments. Behind this, normal creeping movements were seen as the nerve regenerated and the lost function was restored. This appearance of the cut region disappeared as the normal reactions returned.

REGENERATION

The regeneration of the nerve was remarkably rapid. Sections of a worm (*Allolobophora foetida*) prepared after two days of regeneration showed that the nerve fibers had penetrated into the regenerating tissue and had formed across the gap. And on the third day the physiological reactions were being transmitted up and down the cord. The reversal of the direction of creeping was easily possible on stimulation. The giant fiber reactions, however, were not yet possible. Any stimuli which called out such reactions in the anterior part of the worm ran only as far as the cut, and the same is true of reactions started in the posterior part. However, on the fourth day and fifth day the giant fiber action was restored for the entire worm, which in all respects gave normal reactions.

In the large *Helodrilus,* the same relations were found, except that the period of regeneration was a little longer. The return of the locomotor transmission occurred usually from the fourth to sixth day after the operation and the giant fiber action on the following day. The regeneration of nerve cord in this large worm shows a very interesting thing in this return of the activity of the giant fibers. Twenty-four hours after the return of locomotor transmission, one can look for giant fiber action. This makes its first appearance as an impulse traveling from anterior to posterior, and it is not until some hours later, usually the following day, that this action is transmitted in the opposite or postero-anterior direction.

In testing worms for the return of locomotor transmission through the cut area it will be noticed that in the early stages posterior creeping may not be the response on stimulating the anterior part. However, if several stimuli are given, summation takes place and a posterior movement takes place. At other times the result of a stimulation may be shown in the contraction of the circular muscles and elongation of the posterior tip, a movement preparatory to creeping, without the movement being completed by a well organized reaction.

The first indication of the return of giant fiber transmission is a condition that shows the antagonistic innervation of muscles that has been shown for vertebrates.

The following table, no. 182, shows a series of worms and regeneration of nerve cord as expressed by the return of physiological activity.

Experiment 182—Regeneration of Nerve Cord After a Simple Transvese Section

Time in days when impulses are again possible in Transmission Fibers and Giant Fibers

Worm	Locomotor trans. A P	Locomotor trans. P A	Giant fiber A P	Giant fiber P A
A	3	3	3	....
B	3	3	....	....
C	3	3	4	5
D	3	3	5	6
E	3	3	4	5
F	4	4	5	6
G	4	4	5	7
H	4	4	5	6
I	4	4	5	5
J	4	5	8	10
K	4	4	5	5
L	5	5	6	6
M	5	7	10	....
N	5	5	6	8

A P = transmission from anterior end to posterior end.
P A = transmission from posterior end to anterior end.

Stimulation of the anterior end causes the end to end jerk of muscles as far as the cut, but behind this no such movement arises. With each stimulus there will be seen, in the posterior tip, a relaxation of the circular muscles and a dorso-ventral flattening. The chaetae will be projected and directed forwards, but there is no movement of the longitudinal muscles. A few hours later the same movement will be accompanied by a distinct jerk of the longitudinal muscle, and the next day a well co-ordinated, end to end contraction will be added to the reaction.

Removal of Sections of the Cord

When small sections of the cord were removed, as shown in the following table, the return of physiological activity was in the same order as when simple transverse sections were made. The time for regeneration and complete recovery was lengthened, but was still surprisingly short.

EXPERIMENT 191—REGENERATION OF NERVE CORD AFTER REMOVAL OF SHORT SECTIONS OF CORD

Worm	No. of ganglia removed	Trans. locomotor A P	Locomotor trans. P A	Giant fiber A P	Giant fiber P A
A	2	6	6	9	9
B	1½	4	4	10	11
C	2	....	Dead	....	....
D	2½	....	Dead	....	....
E	1½	4	4	5	6(?)9
F	2	4	4	9	9
G	1½	....	Dead	....	....
H	1	9	9	12	13
I	1½	4	4	5	6
J	1	....	Dead	....	....
K	1	....	Dead	....	....
L	2	9	9	10	11
N	2	4	4	5	6(?)9

A P refers to locomotor impulses passing from anterior to posterior.
P A refers to locomotor impulses passing from posterior to anterior.

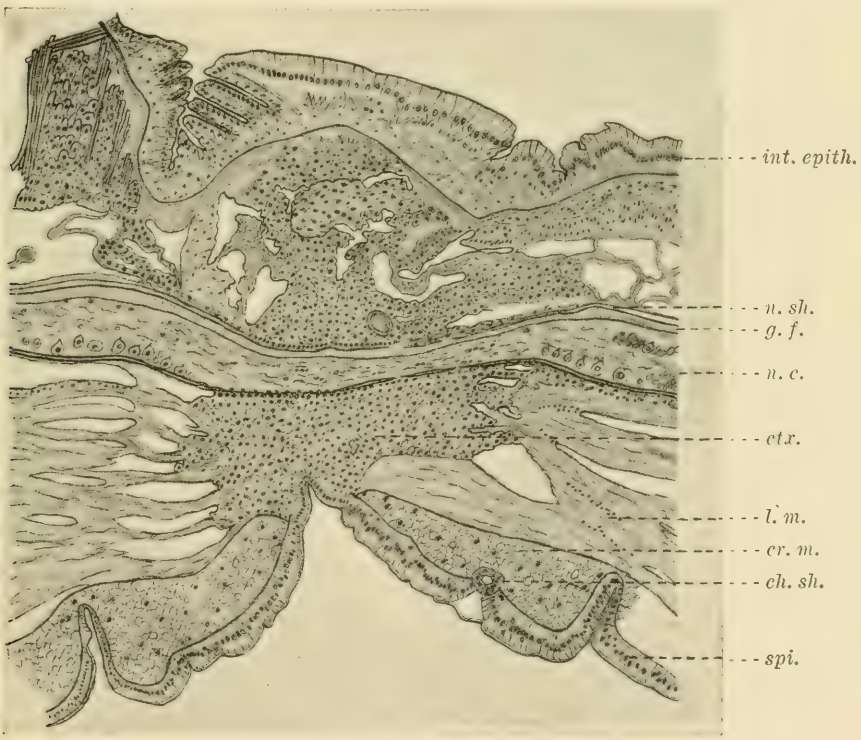

Fig. 1—A camera lucida drawing showing the union of the cut ends of the ventral nerve cord. × 42. Experiment 191, line 1. In this worm two ganglia had been removed and nine days given for regeneration. Normal locomotor transmission and giant fiber action had returned. *ch. sh.*, chaeta sheath; *cir. m.*, circular muscle; *ctx.*, cicatrix tissue; *epi.*, epidermis; *g. f.*, giant fiber; *int. epith.*, intestinal epithelium; *l. m.*, longitudinal muscle; *n. c.*, nerve cord; *n. sh.*, nerve sheath.

Figure 1 shows a longitudinal section of a worm that showed normal locomotor transmission and giant fiber action after nine days of regeneration. Two ganglia had been removed. In some cases the regeneration was more rapid and in some slower, so this figure represents a typical case.

It was expected that the removal of short sections of the cord would lengthen the time between recovery for locomotor transmission and giant fiber action. But this was found not to be the case, for, in general, the responses of end to end contractions recur about twenty-four hours after the locomotor transmission reappears. Here, as in the regeneration from simple transection, the giant fibers gave impulses in the antero-posterior direction in advance of those in the opposite direction. While removal of short pieces of cord lengthens that period of regeneration in which no transmission of impulses is possible, it changes very little the order and time of events after the union of the cord is established.

The remarkable facility with which these worms regenerate lost sections of nerve cord has an interesting bearing in the experiments of Friedländer (1894) and Straub (1900).

After the removal of ten to twelve ganglia from the nerve cord, Friedländer (1894) allowed the worm two to four weeks before he discarded them for use in his experiments. My results would indicate that he was not dealing with segments entirely free from nervous transmission, for, while the nerve cord may not have entirely regenerated, it is certain that it could have grown considerable distances into the region, even if it had not grown across the gap. This would make a marked difference in interpreting experiments of co-ordination of anterior and posterior pieces, especially if nearly four weeks had been given for regeneration.

Straub (1900) claimed that annelid muscle would give rhythmic contraction if the nerve cord were dissected out. In this case, sections of twenty to thirty ganglia were removed and the worms given eight days to recuperate. In this short time the nerve probably could not grow the length of such a gap, but could grow into the area for a considerable distance from the end of the nerve stump. When he cut out the operated part and used this to show rhythmic contractions, it is just possible these segments may have contained some regenerated nerve elements. Budington (1902) has shown that segments of worms containing even small fragments of nerve will give these rhythmic contractions, but when the ventral wall is removed no such contractions can be induced.

EFFECT OF DRUGS

If small quantities of cocaine or stovaine are injected into the body cavity of the worm the drugs act as a block on the nerve and affect the transmission through the nerve cord. Cocaine has a more general effect on the worm and produces in many cases very irregular behavior, but stovaine gives very consistent results. The first effect was the loss of giant fiber action through the region. Transmission was perfect above and below the point of injection. As the effect of the drug worked deeper into the cord the transmission of locomotor impulses became more irregular and in some cases was lost altogether. As recovery took place the return of activity was just the reverse. The locomotor impulses became more and more regular until perfect co-ordination was set up. Then the giant fiber action began to show transmissions. Here, too, the same phenomena were seen as in the case of regeneration. Just before giant fiber impulses showed normal, end to end responses, the stimulation of the anterior end showed the characteristic relaxation of the circular muscles in the posterior tip. Very soon after this the end to end movements occur in response to stimuli.

A record is given below of an experiment with stovaine, which shows the course of events and the relation between giant fiber and locomotor fibers.

Experiment 188—Effect of Stovaine on Transmission

May 18, 1915, 4:45 p.m.—The worm (*Helodrilus caliginosa*), doubly pinned to a cork plate on a glass, was injected with a small quantity of stovaine in the body cavity of the middle region.

Almost immediately giant fiber action is lost and locomotor transmission not normal.

5:00 p.m.—Locomotor impulses pass through block, but do not run full length of posterior part.

Locomotor co-ordination between anterior and posterior parts.

As time goes on locomotor movements run further down the posterior part.

5:10 p.m.—Any stimulus to the anterior end results in locomotor movements in posterior end. Wave contractions run to posterior tip more frequently. No giant fiber action.

5:35 p.m.—Stimulation of anterior end gives increased activity of posterior end. No giant fiber action. Animal apparently normal except no end to end contractions.

5:48 p.m.—Giant fiber action returned. Animal fully recovered.

SUMMARY

1. After transverse section of nerve cord, locomotor transmission fibers regenerate before giant fibers.

2. The period of regeneration after a simple transection is very short, from three to four days.

3. Removal of short pieces of the cord gives the same results as simple transverse section, except that the period of regeneration is prolonged.

4. The effect of drugs, such as stovaine, on the cord shows that the transmission fibers may be active, while the giant fibers are still under the anesthetic. Recovery is in the same order as is shown in regeneration.

5. The general result of this study shows that the giant fibers are concerned with other functions than locomotion, and that locomotor transmission fibers lie deep in the cord.

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BY
WILLIAM C. BOECK

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Cropper and Row (1917) have recently given an account of a rapid method of concentrating the cysts of *Entamoeba* in human stools. This method has since been applied also to the concentration of the cysts of flagellates, principally those of *Giardia intestinalis,* by Carter and Matthews (1917). The method is based upon the principle that if ether is stirred into an emulsion of faecal material and normal saline solution and the mixture then placed in a separating funnel, the debris, having absorbed the ether, will float in the layer of ether which soon rises above the layer of normal saline solution, while the cysts will remain below. These cysts may then be procured by drawing off the saline solution at the bottom of the separatory funnel and concentrating them subsequently by centrifuging.

In a paper by Carter and Matthews (1917) an account is given of a fair trial of this method of concentrating cysts from stools. They conclude that the method "is more severe than the ordinary method of examination of a faecal emulsion; that when the method is used at the time the third ordinary examination is made a result is given which would probably be obtained by five ordinary examinations. The method is impracticable, however, when a large number of stools have to be examined each day, for the time required to make these concentrated examinations is not commensurate with the results obtained."

It is more important, however, to realize that the efficacy of the method is not in the least impaired by these conclusions, and that the method would be more practicable if the time involved in making the test could be shortened.

In my work on the detection of the cysts of *Giardia microti*, a species found in rodents and similar in structure and size to *Giardia intestinalis* of man, I have used certain modifications of the Cropper and Row method, which I believe are improvements not only by saving considerable time in making the examination but also of enhancing the accuracy of detection of the cysts of *Giardia* and of other Protozoa in the stools. This method has been tested with success on human stools in the Biological Laboratory of the California State Board of Health.

The first change in the method, and one that saves considerable time, is the employment of the Hamilton-Beach "Cyclone" electric mixer for emulsifying the stools. This device may be seen in use in mixing drinks at most soda fountains. It commends itself very favorably because of its rotary action and its speed in beating up an emulsion. This action favors the mingling of all parts of the stool into a condition in which the cysts are uniformly distributed. The instrument shortens the time of thirty minutes prescribed by Cropper and Row (1917) as necessary when the stools are to be shaken into an emulsion to not more than ten minutes. Naturally the time element here is dependent upon the firm or the liquid consistency of the stools. The action of emulsification may be accelerated by fastening a wire, looped back and forth in a single plane, to the rim of the glass containing the sample of the stool in the normal saline solution so that it projects down into the mixture. This simple device is of great service in that it helps to break up any lumps that may occur in the faeces. I have found that this mixer beats up a fairly uniform emulsion and is entirely satisfactory in liberating the cysts from the lumps in the stools. This wire loop was devised by Mr. J. D. McDonald, Assistant in the Biological Laboratory of the California State Board of Health for use in the examination of human stools for hookworm. I am greatly indebted to him for the suggestion of using the looped wire in order to break up the lumps in the stools, and to Professor C. A. Kofoid, Director of the Biological Laboratory of the California State Board of Health, for the permission to publish this note regarding the method of examination of stools in use in that laboratory.

Another change in the method is in the use of neutral red to stain partially and to differentiate the cysts from the debris and from the intestinal yeasts. The use of this stain in making diagnosis of faecal material was first suggested by Stitt (1911). I have used two methods

in the application of this stain. In the first, one gram of faecal material in thirty cubic centimeters of normal saline solution is emulsified by means of the electric mixer for about eight minutes. About five cubic centimeters of neutral red solution N/10,000 are then put into the emulsion, which is stirred until it is of a uniform reddish color. Five centimeters of ether are then stirred into the emulsion. The remaining steps of the process of concentration follow at once.

In the second method of application of this stain, a drop of the neutral red solution may be applied to a very small amount of residue containing the cysts and placed on a slide, preparatory to microscopic examination. The residue is obtained by centrifuging the saline solution which had been drawn off at the bottom of the separatory funnel. In the latter method of application of the solution of neutral red there results a greater intensification of the stain in the debris, affording a sharper contrast between debris, yeasts, and the cysts. The cysts may take at the most only a light pink stain, due to their wall, which prevents penetration of the reagent. In many cases the cysts are not colored at all, even by this intensive method of treatment.

The use of this stain, however, helps to cut short the time necessary for making the examination, since one is able to detect the cysts with great celerity and accuracy because of the sharp contrast that is presented between the cysts, the yeasts, and the debris. The yeasts, on the other hand, are usually entirely stained, but if not, the stain can be seen in the central vacuole, which at once differentiates the yeasts from protozoan cysts of the same size in which the structure of the contained organism may be indistinct. Since, however, only a slight amount of stain is wont to differentiate the internal structures of protozoan cysts, one is able by the use of the neutral red to distinguish the nuclei, axostyle, and the remains of the intracytoplasmic flagella in the cysts of *Giardia* more quickly than without the use of the stain. It is this feature which adds to accuracy in the detection of these cysts.

The method in full as I have been using it is as follows: Take at least one gram of the stool to be examined, place it with thirty cubic centimeters of normal saline solution in the mixing glass and stir for at least ten minutes, pouring in five cubic centimeters of neutral red solution N/10,000 at the end of eight minutes, if one desires to use the stain at this time in the method. At the end of ten minutes, while still stirring, add five cubic centimeters of ether and stir two or three minutes longer.

A general rule may be laid down here at this time. The ether tends at first to settle the emulsion temporarily, but at the end of about two minutes the emulsion begins to rise up and foam again because the ether becomes localized by absorption in the debris. In order then to get the best results and to be assured of the greatest possible flotation of ether-soaked debris, one should cease stirring at the very moment the emulsion commences to foam again. Then the emulsion should be hurried into a separatory funnel and allowed to stand for at least five to seven minutes, during which the cysts will settle to the bottom in the saline solution and debris will float in the ether above. The funnel used for this separation has a funnel-shaped bowl with steep sides contracting to a narrow neck above the turn-cock.

At the end of this period of standing, the saline solution, about fifteen cubic centimeters, is drawn off at the bottom of the separatory funnel into a centrifuge tube of a capacity of fifteen cubic centimeters, and is centrifuged for three minutes at 1600 revolutions per minute. The supernatant fluid is then drawn off and the residue is examined microscopically for the cysts. At this time a drop of neutral red is applied to a small amount of this residue preparatory to microscopic examination if the stain has not been used previously. It is preferable to use it at this time in order to procure a sharper contrast between the cysts and the surrounding debris.

By this method a faecal examination can be completed in twenty-five to thirty minutes, which is considerably less than the time required by the method which Cropper and Row (1917) described. Although I have been especially interested in the application of this modification of their method to the detection of the cysts of *Giardia,* I have noticed at the same time that it is equally applicable to the detection of cysts of *Entamoeba,* of other flagellates, and of the eggs of nematodes, which I have found in the faeces of the rat.

The great value of this method of concentrating cysts of protozoan parasites is realized when one desires the most accurate diagnosis of a suspected case.

A high degree of infection by both amoeba and flagellates is reported by Dobell (1917) from both dysenteric and non-dysenteric convalescents from the Mediterranean area in British hospitals. Each infected individual might become the source through unsanitary conditions for further distribution of the disease among the troops should he return to the front, or possibly to civilians on his return to private

life. All devices, therefore, which can assist in the certain and rapid detection of such carriers, not only of those under military conditions but of all persons returning from regions of dysenteric infections, have a preventive value, especially in view of the enhancement of the risks of contagion due to the present conditions in Europe.

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THE MUSCULATURE OF *HEPTANCHUS MACULATUS*

BY
PIRIE DAVIDSON

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CONTENTS

PAGE

Introduction 151
Material 151
Historical 152
The musculature 152
Pharyngeal musculature 152
Superficial circular muscles 153
Interarcuales 158
Subspinalis 159
Adductors 159
Hypobranchials 161
Musculature associated with the organs of special sense 162
Appendicular musculature 163
Musculature of the trunk 167
Literature cited 170

INTRODUCTION

For several years past work has been in progress on the various systems of the elasmobranch fishes in the Zoological Laboratory of the University of California and at the Scripps Institution for Biological Research at La Jolla. Material is easily obtained and many types have been studied, both of the sharks and of the rays. The seven-gilled form has been of particular interest because of its supposed generalization.

Material

The seven-gilled form of the Pacific coast is *Heptanchus* (*Notorhynchus*) *maculatus*. It is dark gray dorsally with black spots, and light colored ventrally, and may readily be recognized by the presence of

seven large gill-slits which decrease in size posteriorly. It is a large form, some of the specimens taken having reached nine feet in length. For the greater part of this study small specimens of about two to three feet in length were used. This work was suggested by Professor J. Frank Daniel, to whom the author is indebted for assistance and criticism.

Historical

The literature on the pharyngeal musculature of elasmobranchs is scanty. Vetter (1874) described the pharyngeal musculature of *Heptanchus cinereus, Acanthias vulgaris,* and *Scymnus lichia.* Tiesing (1896) published a paper on the musculature of the rays. Marion (1905) wrote a paper on *Acanthias vulgaris* and the skate, *Raia erinacea,* in which he drew comparisons between the musculature of sharks and rays. Tiesing classified muscles on the basis of ennervation and this is perhaps the most reliable single criterion although it has its disadvantages. Vetter and Marion used position and function, which plan is followed in this paper.

This work agrees as a whole with previous publications although slightly different interpretations are offered in a few instances. The various organs of *Heptanchus* seem to agree remarkably well with those of *Hexanchus griseus* as described by Ruge (1897) in an article on the facial nerve in vertebrates. There are many articles on the paired fins of selachians, but these deal mainly with their origin and relation to the paired limbs of the higher vertebrates. The papers of Krall (1908), Goodrich (1906), and Erik Müller (1909) have been particularly helpful. The bibliography on the body musculature is large, but several of the more important articles, including those of Johannes Müller and A. Schneider, have not been available.

THE MUSCULATURE

The musculature may be divided as follows:

Pharyngeal musculature.
Musculature associated with the organs of special sense.
Appendicular musculature.
Musculature of the trunk.

Pharyngeal Musculature

This group includes the muscles anterior to the pectoral girdle. These muscles are very much specialized, but still retain some of their

primitive characteristics. They are concerned chiefly with respiration and food getting, and include the following groups:

I. Superficial circular muscles.
II. Interarcuales.
III. Subspinalis.
IV. Adductors.
V. Hypobranchials.

I. The Superficial Circular Muscles (fig. 1). The superficial circular muscles form an almost complete muscular covering of the pharyngeal region. In general they are thin and flat with fibers running around the pharynx. The function of this group of muscles is to constrict the pharynx and close the gill-clefts. Several series of muscles are included in this division, some of which are very closely connected in origin, insertion, and function.

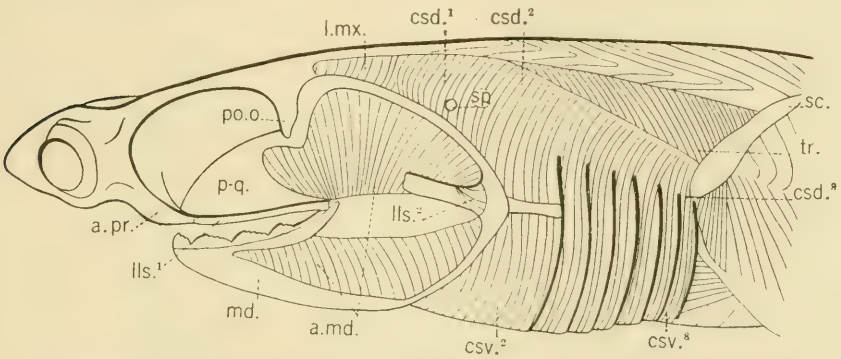

Fig. 1. Head of *Heptanchus maculatus*, lateral view (× ⅔). *a. md.*, adductor mandibulae; *a. pr.*, antorbital process; *csd.*¹⁻⁸, first to eighth dorsal constrictors; *lls.*¹,² first and second parts of levator labialis superioris; *l.mx.*, levator maxillae superioris; *md.*, mandible; *po. o.*, postorbital process; *p-q.*, palatoquadrate cartilage; *sc.*, scapula; *sp.*, spiracle; *tr.*, trapezius.

1. *Levator maxillae superioris* (*l. mx.*, fig. 1). The levator maxillae superioris is described first in this group as it seems to be an anterior continuation of the dorsal constrictors, and to share their function. It consists of a group of short fibers having its origin under the supraotic crest just posterior to the postorbital process. Its direction is ventral and anterior and it is inserted on the anterior and dorsal edge of the enlarged quadrate region of the upper jaw just anterior and continuous with the insertion of the first dorsal constrictor. Its function is to raise the upper jaw.

2. *Superficial constrictors.* The superficial constrictors form a thin muscular layer almost completely covering the branchial region. This group is divided for convenience of description into a dorsal

and ventral part. This division, however, is not a natural one for the fibers, except in the case of the first and second divisions, are continuous from the dorsal to the ventral part.

Dorsal constrictors (*csd.* $^{1\text{-}8}$). The dorsal constrictors have a continuous origin extending from the cranium, just back of the postorbital process, to the pectoral girdle. The anterior part of the origin is from the cranium, but the main part is from the sheath of connective tissue which covers the trapezius and dorsal longitudinal muscles of the pharyngeal region.

The *first dorsal constrictor* (*csd.* ^{1}, fig. 1) is continuous with the levator maxillae superioris, but the fibers of the two have a different direction. Its anterior extent is diffcult to determine in *Heptanchus maculatus,* but it is limited posteriorly by the spiracle. Its origin is on the cranium posterior to the origin of the levator maxillae superioris, and in the connective tissue described above. The fibers of the first dorsal constrictor are slightly shorter than those of the levator. It is inserted along the dorsal edge of the quadrate posterior to, and continuous with the insertion of the levator maxillae superioris. The two muscles function together in raising the jaw and constricting the spiracle.

The *second dorsal constrictor* (*csd.* ^{2}) is the largest of the dorsal series. It lies between the spiracle and the first gill-slit. Its origin is continuous with that of the first dorsal constrictor. The anterior deeper part is inserted on the middle of the dorsal segment of the hyoid arch. The main part of the muscle is inserted dorsally on the palatoquadrate from the insertion of the first of this series to the angle of the jaws. The fibers between the angle and the gill-slit are continuous with those of the corresponding part of the ventral series. In passing over the median cartilaginous rays the fibers become tendinous.

Dorsal constrictors$^{3\text{-}8}$ have a similar origin and extent. They decrease in size posteriorly corresponding to the decrease in size of the branchial apertures. Their origin is continuous in the connective tissue sheath of the trapezius. Their fibres run ventrally and are continuous with those of the corresponding ventral constrictors.

Ventral constrictors (*csv.* $^{2\text{-}8}$, fig. 1). There is a difference of opinion concerning the naming of the ventral constrictors. Vetter (1874, pp. 409–416) describes them for both *Acanthias* and *Heptanchus* and does not recognize a first ventral constrictor in either form. Marion (1905, pp. 7–8), although saying nothing of *Heptan-*

chus, divides the ventral constrictor group in *Acanthias* into six parts corresponding to those of the dorsal group. The part which he calls the first, is known as part of the second ventral constrictor by Vetter. Marion names the part inserting on the first visceral or mandibular arch the first, and that on the hyoid arch the second. There seems to be some doubt that these are separate muscles. Insertion is not an absolute criterion, as the second dorsal constrictor is inserted

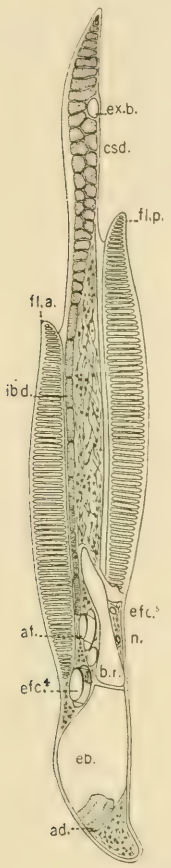

Fig. 2. Horizontal section through gill, *Heptanchus maculatus* (× ½). *ad.*, adductor of the branchial arch; *af.*, afferent artery; *br.*, branchial ray; *csd.*, dorsal constrictor muscle; *eb.*, epibranchial cartilage; *efc.*[4], fourth efferent collector artery; *efc.*[5], fifth efferent collector artery; *ex. b.*, extrabranchial cartilage; *fl. a.*, anterior gill-filament; *fl. p.*, posterior gill-filament; *ibd.*, dorsal interbranchial muscle; *n.* nerve.

both on the first and the second arches. In *Heptanchus maculatus* it is not possible to demonstrate a division of the first and second ventral constrictors as clearly as is shown for *Acanthias* by Marion (p. 9, fig. 5). The following condition is found in *Heptanchus maculatus*.

The first and second ventral constrictors appear to be united. The second ventral constrictor (*csv.*[2]) extends from the mandibular symphysis to the anterior border of the first gill-slit. The fibers of both

sides have their origin from a band of connective tissue extending from the pectoral girdle to the mandibular symphysis. It is broad near the girdle but narrows rapidly forming a triangular ventral covering for the coaracoarcuales communes. From this it continues forward as a narrow strip from which the anterior part of the second ventral constrictor takes its origin. Anteriorly this muscle is covered by the first ventral constrictor, a thin layer of fibers lying directly under the skin and being continuous from one ramus of the mandible to the other. This, the first ventral constrictor, cannot be clearly separated from the second. It is inserted on the inner side of the ramus of the mandible. The anterior part of the second dorsal constrictor is inserted along the middle third of the ceratohyoid cartilage; the posterior part is continuous with the corresponding dorsal constrictor. In passing over the median cartilaginous branchial rays the muscle forms a tendinous aponeurosis.

Ventral constrictors$^{3-8}$ (*csv.*$^{3-8}$) have their origins continuously along the edge of the triangular piece of connective tissue which covers the coracoarcuales communes. They pass between the gill-slits and continue as the fibers of the corresponding dorsal parts.

3. *Interbranchials.* The interbranchial muscles are so intimately connected with the dorsal and ventral constrictors that they are in fact parts of the same muscles. The fibers (*ibd.*, fig. 2) are parallel with and anteriorly continuous with the constrictors (*csd.*), and lie just in front of and against the cartilaginous branchial rays. They are present in the six holobranchs, but an interbranchial is absent from the hyoidean demibranch. Their function is to draw the branchial rays together and constrict the gill-pockets.

For convenience of description they may be divided into dorsal and ventral parts, corresponding to the constrictors which have been similarly grouped. The origin of the dorsal parts is in the connective tissue of the trapezius and dorsal longitudinal muscles anteriorly continuous with the origin of the corresponding dorsal constrictors. They are attached to the dorsal extrabranchial cartilages which serve to hold the muscles in place. The anterior fibers are inserted along the entire dorsal edge of the epibranchial cartilage from the insertion of the lateral interarcuales to the angle between the epibranchial and ceratobranchial segments of the branchial arches. The outer or more posterior fibers continue into the corresponding ventral part. The ventral parts (*ibv.*$^{1-6}$, fig. 4) have their origin in the connective tissue dorsal and lateral to the coracoarcuales communes. The posterior

ventral fibers are continuous with the dorsal part of the corresponding muscle. They are attached to and held in place by the ventral extrabranchial cartilages. The remaining part, which is anterior, is inserted along the posterior edge of the ceratobranchial from the epibranchial to the hypobranchial segments. The first to the fifth pass through the first five of the coracobranchiales muscles as described below. The sixth interbranchial passes between the sixth and seventh coracobranchiales.

4. *Trapezius* (*tr.*, fig. 1). The trapezius lies between the dorsal longitudinal muscles and the dorsal constrictors, and is partly covered by the latter. It arises from the fascia of the dorsal longitudinal muscles, runs ventrally and posteriorly, and is inserted in two parts. The ventral part, the origin of which is anterior, is inserted on the epibranchial segment of the degenerate seventh branchial arch. The remainder of the fibers have the same direction and are inserted anteriorly on the pectoral girdle along most of the scapular part. The trapezius raises the shoulder girdle and draws it forward.

5. *Levator labialis superioris* (*lls.*, fig. 1). Vetter (1874, p. 448) classifies this muscle in *Acanthias vulgaris* with the adductors, but Marion (1905, p. 21) basing his judgment on Vetter's description places it with the constrictors. In *Heptanchus cinereus*, according to Vetter, this muscle is absent. In *Acanthias* (Marion, 1905, p. 21 and Vetter, 1874, p. 420) there is a single pair of muscles, while in the skate (Tiesing, 1896, p. 85) the muscle is differentiated into four or five parts. In *Heptanchus maculatus* the levator labialis superioris includes two distinct parts. The first corresponds to the first levator labialis of the skate or to the whole muscle as described for *Acanthias*, although the two are not the same in origin. It is a small somewhat flattened band having its origin on the inner side of the antorbital process (*a. pr.*). Its fibers run posteriorly and outward, cross the angle of the jaws, and continue as a fibrous band of tissue which separates the dorsal and ventral parts of the adductor mandibulae. The second probably corresponds to the second muscle as described for *Raia* by Marion (1905, p. 22). Its origin is on the cranium just anterior to the preorbital process, and in the region of the nasal capsule, by a wide band of rather soft tendinous tissue. This continues posteriorly below the eye where it joins similar tissue which surrounds the eye and then crosses the adductor mandibulae. At its posterior end this tendon passes inward and by a short muscular part, is inserted on the quadrate and mandible at the place of their union.

II. Interarcuales (fig. 3). The interarcuales, the muscles of the upper segments of the gill-arches, comprise two systems, of which one is dorsal, and the other more lateral. The first is made up of five, the second of six similar muscles. Their function is to draw forward the segment of the arch upon which they are inserted.

1. *Dorsal system.* The dorsal interarcuales (*ia. d.*$^{1-5}$) are similar in origin and insertion. They have their origin posteriorly on the middle half of the first to the fifth pharyngobranchial cartilages respectively and their fibers pass posteriorly and medially to be inserted on the anterior border of the succeeding pharyngobranchial segment. The muscles of this series decrease slightly in size from anterior to posterior as do also the pharyngobranchial segments of the arches.

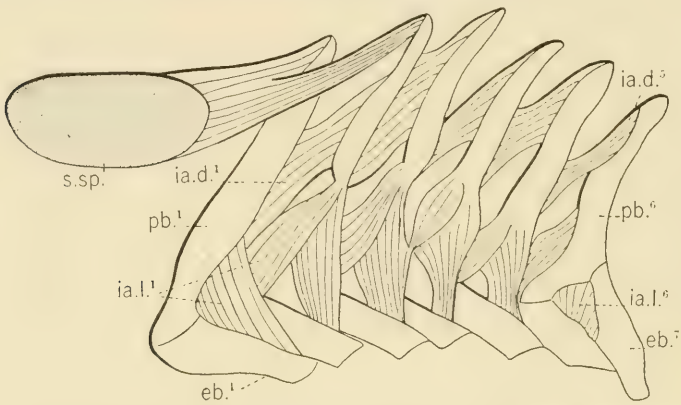

Fig. 3. Interarcuales and subspinalis muscles, *Heptanchus maculatus*, dorsal view (× 1½). *eb.*$^{1-7}$, first to seventh epibranchial cartilages; *ia. d.*$^{1-5}$, first to fifth dorsal interarcuales; *ia. l.*$^{1-6}$, first to sixth lateral interarcuales; *pb.*$^{1-6}$, first to sixth pharyngobranchial cartilages; *s. sp.*, subspinalis muscle.

2. *Lateral system.* The lateral interarcuales (*ia. l.*$^{1-6}$, fig. 3) are external to the series of muscles described above. These muscles decrease in size posteriorly and are similar except in the case of the sixth. The first may be described as typical. The greater part of its fibers arise posteriorly from the external part of the first pharyngobranchial segment. The remaining fibers have their origin anteriorly and dorsally from the middle part of the second pharyngobranchial cartilage. These unite and continue laterally to be inserted dorsally on the posterior edge of the first epibranchial cartilage. The line of insertion is continuous with that of the dorsal part of the interbranchial muscle. In the seventh arch there is no pharyngobranchial segment, and the sixth muscle of the lateral series originates by a

single head from the dorsal end of the seventh epibranchial, and from the sixth pharyngobranchial as in the case of the others of the series. The two cartilages are closely articulated by connective tissue and the origin of this muscle is continuous. The insertion is on the sixth epibranchial as in the case of the others of this series.

III. Subspinalis (*s. sp.*, fig. 3). Anterior to each series of dorsal interarcuales is a single muscle, the subspinalis (Vetter, 1874, p. 444). Marion (1905, p. 24) in disagreement with Vetter who considers this muscle as belonging to a distinct group, considers it as the most anterior dorsal interarcualis. Its origin, insertion, and occurrence, however, do not agree with the dorsal interarcual series and it seems advisable here to describe it separately as the subspinalis muscle.

It has a broad origin ventrally from the posterior part of the cranium, the vertebral column near the cranium and from the ventral fascia of the dorsal longitudinal muscles. It decreases in size abruptly and is inserted by two tendons, the larger on the median end of the first pharyngobranchial dorsally, and the smaller similarly on the second.

IV. Adductors. The adductors form a series of flexors for the dorsal and ventral parts of the visceral arches, except in case of the hyoid, on which the muscle is lacking. This is probably due to the reduction of the hyoid arch and to its dependence on the first or mandibular arch. These muscles are very small except in the case of the first which in correlation with the great use of the mandibular arch is enormously developed.

1. *Adductor mandibulae.* The adductor mandibulae (*a. md.*, fig. 1), the adductor of the first visceral arch, is very much larger and more specialized than the other members of this series. It appears as a simple muscle having its origin externally on the quadrate region of the upper jaw, and its insertion similarly on the mandible. This is the case, however, with only a small part of the muscle, the deeper posterior part which comprises less than one-third of the whole muscle. This small part corresponds closely to the adductors of the succeeding arches. The posterior superficial fibers have their origin on the quadrate, but insert on the tendinous envelope covering the ventral part of the adductor. The remainder, which is by far the greater part of the muscle, is divided into dorsal and ventral parts by the membranous posterior continuation of the first part of the levator labialis superioris. The dorsal division has its origin on the quadrate portion of the upper jaw; its direction is ventral and slightly anterior, and its insertion is

on the dorsal side of the membranous posterior continuation of the levator labialis superioris. The ventral part has its origin on the ventral side of the same membrane; its direction is the same as in the case of the dorsal fibers and it is inserted on the posterior outer surface of the mandible.

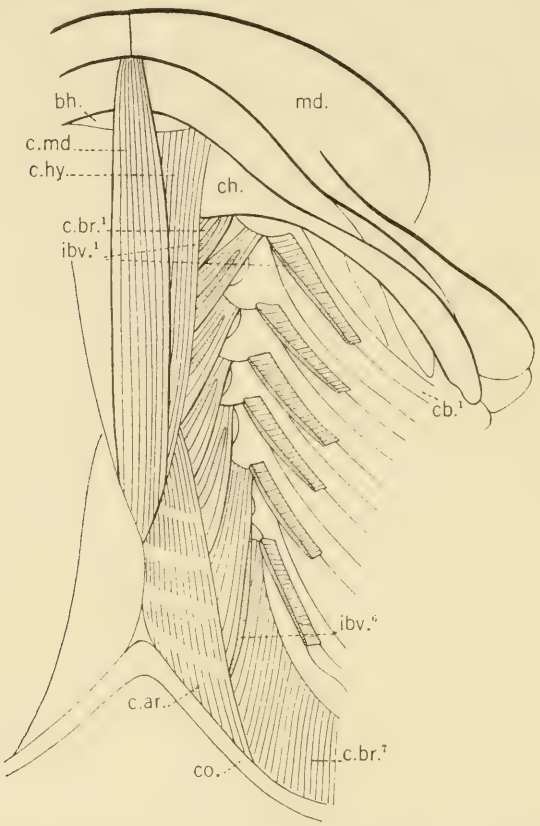

Fig. 4. Hypobranchial muscles, *Heptanchus maculatus*, ventral view (× 1). *bh.*, basihyoid cartilage; *c. ar.*, coracoarcuales muscle; *cb.*¹, first ceratobranchial cartilage; *c. br.*¹⁻⁷, first to seventh coracobranchiales muscles; *ch.*, ceratohyoid cartilage; *c. hy.*, coracohyoideus muscle; *co.*, coracoid cartilage; *c. md.*, coracomandibularis muscle; *ibv.*¹⁻⁶, first to sixth ventral interbranchial muscles; *md.*, mandibular cartilage.

2. *Adductor arcus branchialis.* An adductor, as mentioned before, is absent from the hyoid arch. The dorsal and ventral parts of each of the branchial arches (*ad.*, fig. 2) are drawn together by an adductor arcus branchialis which extends from the epibranchial to the ceratobranchial segments of each arch. The adductors are small and hinge-like and completely fill the angle between the segments. Their origin

is internally in a groove on the distal third of the epibranchial segment and they are inserted similarly on the proximal part of the ceratobranchial segment of each arch. Their contraction flattens the branchial region.

V. Hypobranchials (fig. 4). The hypobranchial or ventral longitudinal muscles lie on the ventral side anterior to the pectoral girdle. They are thick and solid and their shape is correlated with the shape of the body. They include the coracoarcuales communes, a pair of muscles extending forward from the pectoral girdle halfway to the mandibular symphysis; the coracomandibularis, a median ventral unpaired muscle; the coracohyoideus, a pair apparently continuous anteriorly with the coracoarculaes; and the coracobranchiales, including seven pairs of flat muscles extending to the gill-arches. This group of muscles has its origin on the coracoid portion of the scapula and from the connective tissue forming the floor of the pericardial cavity which fascia is attached to the coracoid.

1. *Coracoarcuales communes* (*c. ar.*). The coracoarcuales muscles lie directly under the integument just anterior to the pectoral girdle. At their origin they are quite broad but they rapidly decrease in size anteriorly. Several myosepta may be seen to cross each of these muscles and give to them the same appearance as the musculature of the body. Their origin is from the anterior surface of the coracoid. The median fibers are inserted in the strong membrane which forms the floor of the pericardial cavity, while the lateral fibers are continued forward and are inserted in the fascia in which the coracohyoideus muscles have their origin.

2. *Coracomandibularis* (*c. md.*). The coracomandibularis is an unpaired muscle lying dorsal to the first and second ventral constrictors. Its origin is in the fascia dorsal to and between the anterior part of the coracoarcuales. At its origin it is laterally compressed, but immediately becomes rounded and is inserted ventrally on the posterior edge of the mandible, extending on either side of the symphysis.

3. *Coracohyoideus* (*c. hy.*). The coracohyoideus muscles are the largest of the ventral longitudinal group. They are paired and are just dorsal to the coracomandibularis. The coracohyoideus muscles are a direct anterior continuation of the coracoarcuales. Their origin is from the fascia in which the latter insert. The more dorsal fibers take origin in the fascia between the coracohyoideus and coracobranchiales. The muscles are broad and thick and uniform in size

except for a slight decrease anteriorly. They are inserted ventrally on the anterior part of the copula of the hyoid arch. A few of the more lateral fibers are inserted by tendinous tissue, in the tissue joining the copula and ceratohyoid.

4. *Coracobranchiales* (*c. br.*$^{1-7}$, fig. 4). The coracobranchiales are the most internal or dorsal of the ventral longitudinal muscles. They include seven pairs which form an almost solid wall along the sides of the pericardial cavity. The first has its origin in the connective tissue directly over and attached to the coracohyoideus muscles. The origins of the second to the sixth coracobranchiales are in the strong connective tissue just dorsal to the coracoarcuales. The anterior part of the origin of the seventh is continuous with the origin of the sixth, while the posterior part has its origin on the pectoral girdle, just laterad of the origin of the coracoarcuales. It extends along about one-fourth of the ventral part of the pectoral girdle. Near their origin these muscles form an almost continuous sheet, but they are separated toward their insertions by the afferent arteries. The first to the fifth are also divided from their origin about two-thirds of the way to their insertions by the anterior parts of the ventral interbranchial muscles. The sixth and seventh coracobranchiales are separated by the sixth interbranchial.

The first coracobranchialis passes anteriorly and dorsally and is inserted on the posterior edge of the basihyoid. The second to the sixth are inserted posteriorly on the hypobranchial segments of the corresponding branchial arches, while the greater part of the seventh is inserted on the ceratobranchial of the last gill-arch. The insertion of the seventh extends ventrally throughout the entire length of the segment. The most anterior fibers, however, are inserted on the anterior edge of the posterior median piece. The hypobranchial segment of the seventh arch is absent or fused with the basal piece.

Musculature Associated With the Organs of Special Sense

In this division are located the muscles of the eye and of the organ located in the parietal fossa. The eyelids of *Heptanchus* are membranous and consequently musculature is not developed in them.

I. *Eye-muscles* (fig. 5). The six muscles of the eye-socket are divided into two groups. The first or oblique group is placed anteriorly and consists of two muscles, the superior (*s. o.*) and inferior oblique (*i. o.*). These two muscles extend from the anterior part of the orbit outward and backward and are inserted on the eyeball.

The second or rectus group consists of four muscles which originate from the posterior part of the orbit at the base of the optic pedicel. The dorsal member of this group is known as the superior rectus (*s. r.*), the ventral as the inferior rectus (*i. r.*), the anterior and posterior as anterior (*a. r.*) and posterior recti (*p. r.*) respectively. They pass outward and forward and are inserted on the eyeball in positions according to their naming. The function of the eye-muscles is to turn the eyeball in the orbit.

II. *Muscles of the Parietal Fossa* (fig. 6). In connection with a small shield-shaped organ present in the parietal fossa of *Heptanchus*

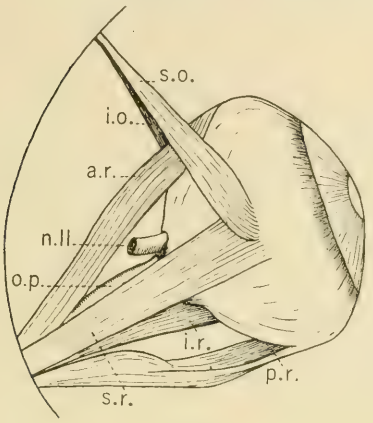

Fig. 5

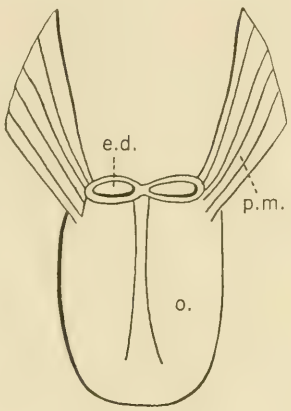

Fig. 6

Fig. 5. Eye-muscles, *Heptanchus maculatus*, dorsal view (× 1). *a. r.*, anterior rectus muscle; *i. o.*, inferior oblique muscle; *i. r.*, inferior rectus muscle; *n. II*, optic nerve; *o. p.*, optic pedicel; *p. r.*, posterior rectus muscle; *s. o.*, superior oblique muscle; *s. r.*, superior rectus muscle.

Fig. 6. Organ over parietal fossa, *Heptanchus maculatus*, dorsal view. (× 3). *e. d.*, endolymphatic duct; *o.*, organ in fossa; *p. m.*, parietal muscle.

maculatus, is a pair of small short muscles, the parietal muscles (*p. m.*). They have their origin dorsally on the cranium and the anterior part of the dorsal longitudinal muscles, just posterior to the parietal fossa. Their course is anterior and medial and they are inserted postero-laterally on the parietal organ. It seems possible that these muscles constrict this sac-like organ.

Appendicular Musculature

There are two types of fins found in the sharks, paired and unpaired. The paired fins include the pectorals and pelvics, the unpaired the dorsal, anal, and the caudal. Their musculature is similar and

quite simple except in the case of the pelvic fin of the male, where an elaborate system of muscles is developed in connection with the clasper. In all except the anal and caudal fins the muscles are differentiated into radials.

Muscles of the Paired Fins

The radials of the pectoral fin (*ra.*, fig. 7) form a dorsal and a ventral series. Dorsally they take origin posteriorly and laterally from the scapular portion of the pectoral girdle, from the pro- and mesopterygia, and from a band of tendinous connective tissue along

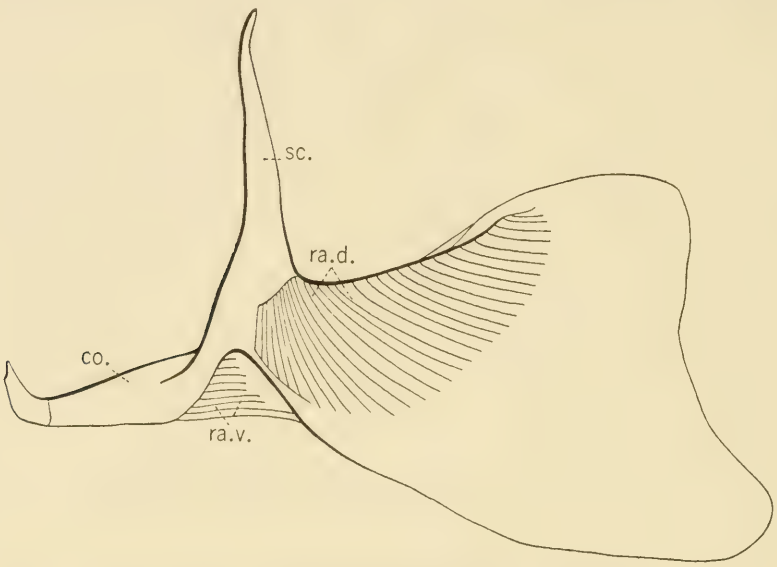

Fig. 7. Left pectoral fin, *Heptanchus maculatus*, lateral view (× ⅔). *co.*, coracoid cartilage; *sc.*, scapula; *ra. d.*, dorsal radial muscles; *ra. v.*, ventral radial muscles.

the posterior dorsal edge of the fin. Deeper fibers have their origin dorsally along the metapterygium. The origin of the fibers is not restricted to the proximal cartilages, but extends over the entire dorsal surface of the cartilaginous radials of the fin-skeleton. The muscle fibers making up the radials are short and do not extend the entire length of the muscles. Their direction is outward and distal. They insert in the connective tissue which covers each radial muscle. This tissue is tendinous and is continuous with the dermal fin rays. The radials number about thirty-two including the small posterior parts which are not very distinctly separated.

In the ventral series about twenty-six distinct radial muscles may

be counted, although the anterior part here is not clearly divided. They have their origin on the posterior side of the coracoid portion of the pectoral girdle, on the pro-, meso-, and metapterygia and on the cartilaginous fin-rays. Their direction is the same as in the dorsal series and they are inserted in the connective tissue which is continuous with the ventral dermal fin-rays.

The pelvic fins are located ventrally, one on each side of the external opening of the cloaca. In the female the musculature is quite simple, consisting of a dorsal and ventral series of radials. In the male the muscles of the clasper are quite complicated. Krall (1908) described these muscles for *Hexanchus*. The muscles are similar to those of *Heptanchus*, but the terminal cartilages described have not been found in *Heptanchus maculatus*. This may be due to the immaturity of the specimens studied. The naming of the muscles was taken from Goodey (1910) and Huber (1901).

In the female the dorsal radials of the pelvic fin number twenty-four. Their origin is double, from the connective tissue of the ventral body muscles and from the fin-skeleton. The direction of the muscles is outward and posterior. They insert in the connective tissues as do the radials of the pectoral fin. Ventrally there are twenty-six radials. Their origin is on the girdle, in the connective tissue posterior to the girdle, and on the entire cartilaginous skeleton. The insertion is the same as in the dorsals.

The radials of the pelvic fin of the male (fig. 9) are similar to those of the female. Dorsally in a large specimen they numbered twenty-one and ventrally twenty-three. Besides the usual dorsal radials there is, in the male, a posterior mass of muscle having its origin in the fascia of the ventral longitudinal muscles. This passes almost directly posterior where it spreads out and is continuous with the posterior dermal fin-rays which fold around the clasper.

The musculature of the clasper includes six muscles, an adductor, two flexors, a dilator, a compressor, and the sac muscle. In all the origin is proximal and the insertion distal.

Adductor (*ad.*, fig. 9). The adductor is a specialized part of the ventral musculature of the pelvic fin. It has its origin on the posterior border of the pelvic girdle and from the connective tissue posterior to the girdle. The direction of the fibers is posterior and the insertion is medial on the distal end of the basipterygium (see *ba. p.*, fig. 8).

Flexor externus (*f. e.*). The flexor externus has its origin along the middle third of the inner edge of the basipterygium. Its course

is posterior and medial. It is inserted along the inner side of the beta cartilage (β).

Flexor internus (*f. i.*). The flexor internus takes origin along the inner edge of the basipterygium, just under the externus and the inner side of the beta cartilage, and under the insertion of the externus. Its direction is posterior and medial and it is inserted on the inner side of the proximal end of the basal piece (*ba.*).

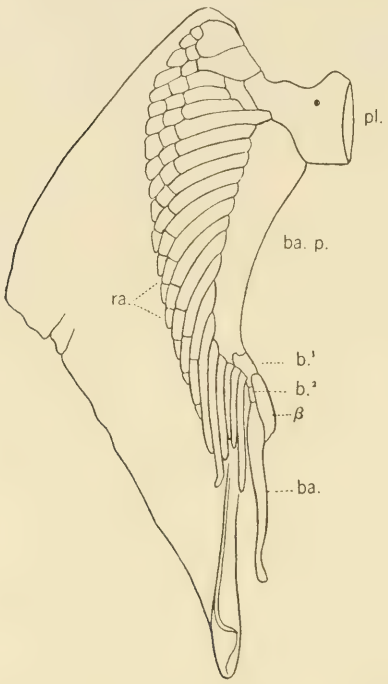

Fig. 8

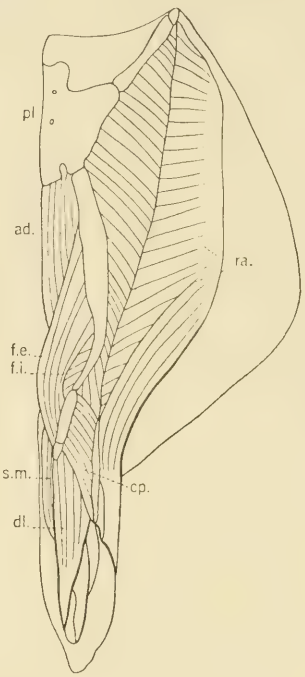

Fig. 9

Fig. 8. Skeleton of male pelvic fin, *Heptanchus maculatus*, dorsal view (× 1). β., the beta cartilage; $b.^{1-2}$, connecting segments; *ba.*, basal piece; *ba. p.*, basipterygium; *pl.*, pelvic girdle; *ra.*, radial cartilages.

Fig. 9. Musculature of male pelvic fin, *Heptanchus maculatus*, dorsal view (× 3/5). *ad.*, adductor muscle; *cp.*, compressor; *dl.*, dilator; *f. e.*, flexor externus; *f. i.*, flexor internus; *pl.*, pelvic girdle; *ra.*, radial muscles; *s. m.*, muscle of sac.

Dilator (*dl.*). The dilator has its origin on the proximal end of the basal cartilage (*ba.*) under the beta cartilage. It is inserted in the heavy connective tissue covering the basal cartilage distally, forming the inner lip of the groove.

Sac. muscle (*s. m.*). The sac muscle arises on the connecting segments (b^1 and b^2) and on the outer side of the proximal end of the basal cartilage. The dorsal fibers are inserted along the inner side of

a long curved radial which comes close to the clasper. The ventral fibers form the wall of the muscular sac. Some of these are inserted along the opposite side of the same radial, while the others continue as tendinous tissue and are inserted distally on the basal cartilage to form the outer lip of the groove.

Compressor (*cp.*). The compressor has its origin laterally from the beta cartilage (β). Its direction is posterior and lateral and it is inserted on the most posterior radial cartilage.

Muscles of the Unpaired Fins

The radials of the dorsal fin are about nineteen in number. Their origin is in the connective tissue of the dorsal longitudinal muscles and on the fin-skeleton as in the other radials described. They are inserted in the connective tissue sheaths which continue distally into the dermal fin-rays.

In the anal fin, which is on the mid-ventral line and posterior to the cloaca, the muscle is not differentiated into radials, but appears as an individual mass. The origin is from the connective tissue of the ventral longitudinal muscles and the fin-skeleton. The insertion is in the connective tissue sheath similar to that of the radials of the dorsal fin.

The spinal column continues into the upper lobe of the caudal fin, making the posterior body musculature the main part of the musculature of the caudal fin. The ventral musculature of the caudal fin is similar to that of the anal. It extends from the anterior extremity of the fin almost to the tip of the tail. Its origin is in the fascia of the ventral body muscles and from the fin-skeleton. Its fibers are inserted in the connective tissue covering, which is continuous with the dermal fin-rays.

Musculature of the Trunk

Johannes Müller in 1834 described the trunk musculature of elasmobranchs as divided by the lateral septum into a dorsal and a ventral part. A. Schneider also distinguishes a dorsal and ventral division but describes layer-formation and the presence of a rectus muscle. Humphry (1872) working on *Mustelus*, found that this division into dorsal and ventral parts separated by the lateral septum, existed in all forms. Each of these parts he again divided into two parts, the dorsal into the medio-dorsal and latero-dorsal and the ventral into the latero-ventral and medio-ventral parts. Humphry describes the

latero-ventral as having two layers. Maurer (1912) in working on the trunk musculature of a number of selachians finds that layer-formation occurs in *Mustelus,* but not in *Scyllium, Spinax, Acanthias,* and others.

In *Heptanchus maculatus* the body musculature (figs. 10, 11, 12) is divided by the lateral septum into dorsal and ventral parts. These

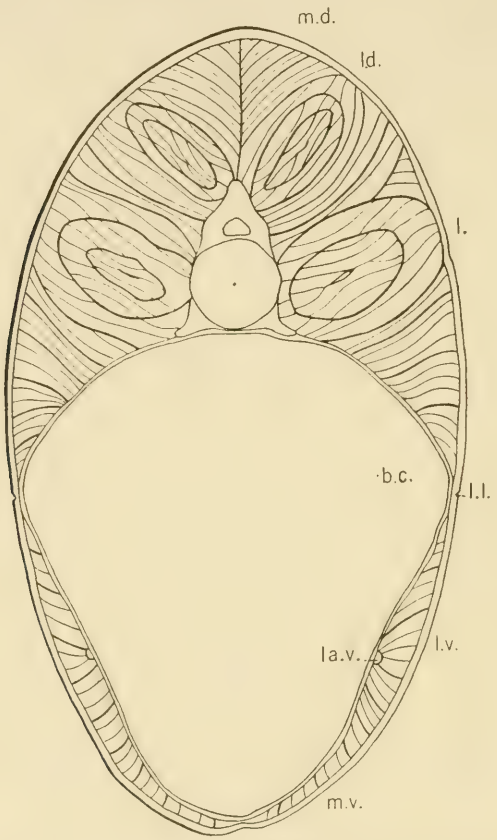

Fig. 10. Cross section in trunk region, *Heptanchus maculatus* (× ⅔). *b. c.,* body cavity; *l.,* lateral muscle bundle; *la. v.,* lateral vein; *l. d.,* latero-dorsal muscle bundle; *l. l.,* lateral line; *l. v.,* latero-ventral muscle bundle; *m. d.,* medio-dorsal muscle bundle; *m. v.,* medio-ventral muscle bundle.

longitudinal muscles extend from the cranium to the tip of the tail. Dorsal to the lateral septum there are three muscle bundles, the lateral, latero-dorsal, and medio-dorsal. Ventral to the septum are the latero- and medio-ventral parts. The dorsal part is attached anteriorly to the cranium and to the pectoral girdle, the ventral part to the pectoral girdle. The hypobranchial muscles previously described form an anterior ventral specialization of these latter muscles. The longi-

tudinal bundles are divided by connective tissue septa, the myosepta into muscle segments, which externally present a zigzag appearance. At the lateral septum there is a V which points anteriorly. The two near the median ventral and dorsal lines point posteriorly. The muscle segments do not extend directly in, as they appear to externally, but each extends far posteriorly and anteriorly in the direction of the V's, giving to each segment an irregular form. The anterior and posterior extensions of the muscle segments are in the form of

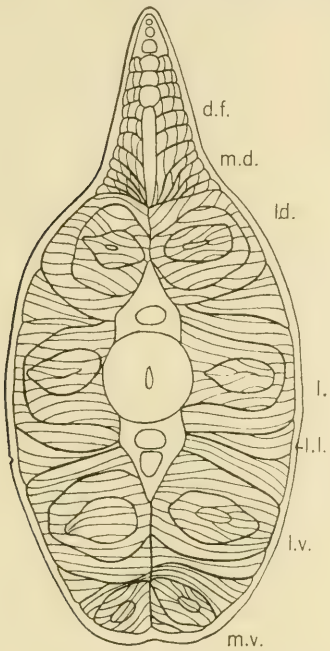

Fig. 11

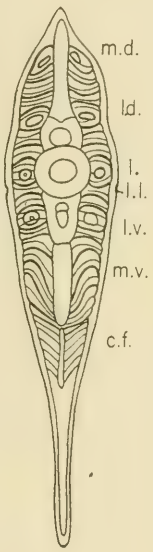

Fig. 12

Figs. 11 and 12. Cross sections through dorsal fin and caudal regions (× ⅔). *c. f.*, caudal fin; *d. f.*, dorsal fin; *l.*, lateral muscle bundle; *l. d.*, latero-dorsal bundle; *l. l.*, lateral line; *l. v.*, latero-ventral bundle; *m. d.*, medio-dorsal bundle; *m. v.*, medio-ventral bundle.

cones so that in cross section they have the appearance of concentric rings.

Dorsally the musculature is the same in the tail and in the trunk except for a difference in the sharpness of the angles of the V's. The ventral musculature shows a much more extensive change in the trunk. The voluminous organs of the body cavity greatly effect the muscles of the body wall, causing them to form a very thin layer. The V's are not sharp and the connective tissue septa pass more directly inward, forming no cones. This greatly changes the appearance of a cross section, since in it no concentric rings of muscle are formed.

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THE FACTORS CONTROLLING THE DISTRIBUTION OF THE POLYNOIDAE OF THE PACIFIC COAST OF NORTH AMERICA

BY

CHRISTINE ESSENBERG

UNIVERSITY OF CALIFORNIA PRESS
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CONTENTS

PAGE
A. Introduction 171
B. Acknowledgments 173
C. Polynoidae and their general distribution 174
I. Horizontal distribution 174
II. Bathymetrical distribution 179
1. Littoral species 182
2. Deep-water species 183
D. Factors controlling distribution 191
I. Temperature in relation to depth and latitude 191
II. Temperature as factor controlling distribution 200
III. Rôle of currents in distribution 206
IV. Winds 208
V. Chemical composition of water 209
VI. Food habits and mode of life 210
VII. Plasticity 213
E. General discussion 221
F. Summary 229
G. Literature cited 231
H. Explanation of plates 234

A. INTRODUCTION

Polychaetous annelids date back at least to the Cambrian era, fossil annelids representing several groups, some of which are similar to modern annelids, having been found in the mid-Cambrian rocks (Walcott, 1911). The geological studies of the distribution of annelids seem

to point to the conclusion that in Cambrian times the annelids had entered all the life zones of the oceanic waters except possibly the abyssal, and that the principal divisions of the annelids were clearly established in pre-Cambrian times (Walcott, 1911; Osborn, 1917).

The distribution of the annelids has received careful attention only in recent years. Michael Sars (1850), one of the first investigators of oceanic fauna, published the results of dredgings along the coasts of Norway, including in his report the annelids collected. The greatest depth to which his dredging extended, however, was only 300 fathoms. Claparède (1875) briefly described the annelids collected by the "Lightning" Expedition from depths to 650 fathoms. Ehlers' work (1875) on the distribution of Annelida, collected by the "Porcupine" Expedition, is of greater importance because that was the first expedition in which the bathymetric and horizontal distribution of the annelids was considered on a large scale. The work of Darboux (1899) on Aphroditidae along the coasts of France and in the Mediterranean Sea also adds to the knowledge of distribution of that family of annelids.

The greatest contribution to science in the studies of distribution of marine life, however, was made by the "Challenger" Expedition (1872–1876). This ship circumnavigated the globe, its dredging at various latitudes extending to depths of over 4,000 fathoms. Animals dredged were grouped and classified by a number of specialists belonging to different nationalities. The lot in annelid studies fell to McIntosh, who rendered excellent service. In this country the United States Survey Steamer "Blake" explored the Gulf of Mexico, the coasts of Florida and the Caribbean Sea. The United States Steamer "Albatross" has been engaged for a number of years in explorations of the Atlantic coast and the Pacific Ocean. Our knowledge of annelids in this country has been enlarged by the reports of E. Ehlers, J. P. Moore and A. Treadwell.

As a result of all these investigations the physical conditions of the oceans are to some extent known, and enough has been learned about the distribution of marine life so that questions as to how deep and how far north or south it extends no longer occupy the minds of biologists. It is known that life exists at all depths and in every latitude. The question that is of interest to every biologist at the present time is: What is the influence of environment on animal life in general, and why are certain kinds of animals limited to certain areas?

It has been proved by experimental methods in biological laboratories that changes in environment, such as slight variation in temperature, in chemical composition of water, etc., result in external changes of the animal and often in its death. Loeb (1915), subjecting *Fundulus* eggs to low temperature, produced abnormal and blind fish embryos, among which the mortality was very great. The eggs of the same fish when exposed to low temperature for a longer period were killed. Stockard (1909) treated the eggs of *Fundulus* with potassium cyanide, and monsters with a single cyclopean eye and with the mouth removed from the extreme anterior tip ventrally were produced. Tower (1906), subjecting the eggs of chrysomelid beetles to different temperatures, obtained beetles of different color. Beetles which developed from the eggs that had been subjected to high temperature were of dark color, while those that came from the eggs subjected to low temperature (0°–5°C) were of a light color. The mortality of the embryos varied with the period of the exposure to high or low temperatures and with the age of the eggs and embryos exposed, the more highly developed eggs and older embryos being the more resistant. Many similar cases may be cited which prove that changes in environment, either chemical or physical, have marked effects on animal life. This is especially true of animals in early stages of development. The above mentioned facts suggest the possibility that similar environmental conditions may have corresponding effects on the oceanic fauna, and may play an important rôle in their distribution.

The aim of this article is to discuss the factors controlling the distribution of the Polynoidae. Conclusions are based on the studies of the material in the Zoological Museum of the University of California collected by the U. S. S. "Albatross" and private collectors from the Pacific coast of North America, in addition to a survey of the records of other workers on this subject in this region.

B. ACKNOWLEDGMENTS

I take this opportunity to express my sincerest gratitude to Professor Charles A. Kofoid at whose suggestion this work was begun, through whose assistance I have been able to continue it and whose criticisms have been invaluable. I also wish to express my gratitude to Dr. Olive Swezy for her valuable suggestions and for the interest she has taken in my work. I further wish to express my gratitude to Dr. G. F. McEwen who kindly computed the temperatures for table 5 in this article.

C. POLYNOIDAE AND THEIR GENERAL DISTRIBUTION

The Polynoidae, one of the families of the scaly annelids, pass the first stage of their life as trochophore larvae. The eggs, after leaving the body cavity of the worm, are attached by a mucous secretion to each other and to the dorsal surface of the parent's body beneath the scales. There they develop until a preoral band of cilia is formed, when the larvae escape as the well known trochophores swimming freely near the surface of the water. The larvae finally settle to the bottom of the ocean, undergoing there further metamorphosis and assuming gradually the shape of the adult worm. Thus during its embryonal development, the stage of the greatest susceptibility, the polynoid is subjected to considerably varied environmental conditions.

Polynoidae as a group are cosmopolitan in their distribution, ranging from the arctic to the equatorial and to the antarctic regions, inhabiting the littoral as well as the abyssal zones. However, the same species may not be represented in all of these regions.

I. Horizontal Distribution

On the basis of distribution the Polynoidae may be divided into two main groups: (1) the cosmopolitan polynoids; and (2) polynoids limited to restricted areas. These groups, especially the latter, may be again separated into a number of subdivisions, according to the areas they inhabit, as will be shown in the following pages.

Of the fifty-one species of Polynoidae known up to the present time from the Pacific coast of North America, two species, or about four per cent, are cosmopolitan. These two species are *Harmothoë imbricata* and *Lepidonotus squamatus*. The former is known to occur in all European oceanic waters. Marenzeller (1902) describes it from the coasts of Japan. Other workers record its distribution from Cape Cod to the St. Lawrence, from Siberia, Greenland, Iceland and from Scandinavia. Its presence has been recorded in the Okhotsk Sea and in other parts of the Arctic Ocean. It also occurs in great abundance along the Pacific coast of North America from Alaska to San Diego, California.

Lepidonotus squamatus occurs in great abundance in the Atlantic Ocean along the shores of Great Britain and in Canadian and American waters. It has been found off the Azores at a depth of 450 fathoms (McIntosh, 1900). Although it does not occur in great abundance along the coast of California, nevertheless, specimens have

been obtained at different places along the coast from Cape Mendocino on the north to Los Angeles on the south.

Of the forty-nine species of Polynoidae restricted to the waters of the Pacific coast of North America two species, *Halosydna insignis* and *Lepidonotus cacloris,* have the widest range of distribution of all the polynoids known on this coast. The distribution of the former is recorded from Alaska and Puget Sound to Point Conception. So far as is known, however, this species has not been obtained either in the Arctic Ocean or in tropical regions south of Cape San Lucas. *Lepidonotus caeloris* occurs in great abundance along the coast of California, from Monterey to Cape Colnett. It is also recorded from the coasts of Japan and from the waters of Alaska. The remaining forty-seven non-cosmopolitan species of Polynoidae of this coast may be subdivided into definite groups on the basis of their geographical distribution. Each group belongs to a particular life zone.

The generally recognized life zones on the Pacific coast are: (1) the tropical zone, extending from the equator to Cape San Lucas; (2) the north subtropical zone, extending from Cape San Lucas to Point Conception; (3) the north temperate zone, extending from Point Conception to Cape Flattery; (4) the lower boreal zone, from Cape Flattery to the Bering Sea; and (5) the upper boreal zone, from the Bering Sea northward (Setchell, 1915).

Each zone includes a distinct group of Polynoidae. Since there are but very few strictly upper boreal or tropical species of Polynoidae represented in the annelid collection of the University of California, these two zones are of less importance in connection with this work and do not enter into the discussion on the following pages.

The following table (1) shows the geographical distribution of the Polynoidae. Certain species may be grouped as strictly subboreal, others as temperate, and still others as subtropical, although there are a few exceptions. Occasionally a species may be found in two adjacent zones, and again species may be found occupying very limited areas, not even extending throughout one entire zone included between the points given. It should be remembered that the distribution of some of the species is as yet inadequately known.

Table 1*

Horizontal Distribution of Polynoidae

Species	Localities: Lower boreal	North temperate	North subtropic	Other localities
Gattyana cirrosa	×	....	....	Greenland, shores of Norway and around the shores of England
Gattyana ciliata	×	....	....	Greenland, McCormick Bay
Gattyana amundseni	×	....	....	
Eunoë depressa	×	....	....	
Harmothoë truncata	×	....	....	
Harmothoë forcipata	×	....	....	
Hololepida magna	×	....	....	
Lagisca multisetosa	×	....	....	
Lepidonotus robustus	×	....	....	
Polynoë fragilis	×	×	....	
Polynoë lordi	×	×	....	
Harmothoë tuta	×	×	....	
Melaenis loveni	×	×?	....	
Harmothoë imbricata	×	×	×	Cosmopolitan
Lepidonotus squamatus	×	×	×	Cosmopolitan
Halosydna insignis	×	×	×	
Polynoë spicula	....	×	....	
Harmothoë bonitensis	....	×	....	
Harmothoë scriptoria	....	×	....	
Harmothoë iphionelloides	....	×	....	
Harmothoë crassicirrata	....	×	....	
Eunoë barbata	....	×	....	
Eunoë caeca	....	×	....	
Antinoë macrolepida	....	×	....	
Antinoë anoculata	....	×	....	
Nemidia microlepida	....	×	....	
Harmothoë yokohamiensis	....	×	×	
Harmothoë triannulata	....	×?	×	
Harmothoë multisetosa	....	×	×	
Polynoë californica	....	×	×	
Harmothoë lamellifera	....	....	×	
Harmothoë hirsuta	....	....	×	
Harmothoë pacifica	....	....	×	
Harmothoë fragilis	....	....	×	Eno-Sima, Japan
Harmothoë tenebricosa	....	....	×	
Harmothoë johnsoni	....	....	×	
Gattyana senta	....	....	×	
Polynoë remigata	....	....	×	
Polynoë filamentosa	....	....	×	
Polynoë aciculata	....	....	×	
Polynoë renotubulata	....	....	×	
Halosydna lagunae	....	....	×	

*Table 1 shows the horizontal distribution of Polynoidae according to the life zones as above indicated. X indicates the presence of the species in the zone.

TABLE 1—(*Continued*)

Species	Localities			
	Lower boreal	North temperate	North subtropic	Other localities
Halosydna succiniseta	....	....	×	
Halosydna macrosephala	....	....		
Halosydna interrupta	....	....	×	
Lepidosthenia gigas	....	....	×	
Lepidonotus caeloris	×	×	×	
Harmothoë complanata	×	....	×	

Considering the species with reference to distribution in the different zones we get the results shown in table 2.

As is shown in table 2 there are eleven exclusively subboreal species of Polynoidae. Four species are common to the lower boreal and north temperate zones. Of these, *Polynoë lordi* is more abundant in the lower boreal zone, occurring very rarely in the northern part of the north temperate. There are ten exclusively north temperate species, and eighteen exclusively subtropical species. *Polynoë californica* really belongs to the latter zone but occasional specimens of it have been found in the southern part of the north temperate zone. Four of the species are found in all zones. Two of these are the cosmopolitans *Harmothoë imbricata* and *Lepidonotus squamatus* and the two others are the American species *Halosydna insignis* and *Lepidonotus caeloris.*

In some cases the individuals of a species are very few in number, at least in collections, and again many species are abundantly represented. However, these species are always found in their particular zones as has been shown before and are limited to very small areas. Examples of these are *Polynoë fragilis* and *Polynoë lordi.* These have been recorded thus far only from the coastal area included between Alaska and San Francisco Bay. *Harmothoë tuta* is seemingly restricted to the northern part of the lower boreal region, its existence being known only at Puget Sound and Sitka. A great number of species of Polynoidae inhabiting this coast are limited to the southern part of the coast of California. Among these are *Lepidasthenia gigas, Polynoë californica* and *Harmothoë hirsuta.* They occupy a comparatively small area along the coast from San Pedro to San Diego. A number of other species, namely, *Harmothoë triannulata, Harmothoë fragilis, Polynoë remigata,* and *Polynoë filamentosa,* have been found thus far only around the islands west of San Diego. Some of these species are known to occur only at considerable depths. Areas of intensive collecting doubtless influence these apparent limitations to some extent.

TABLE 2

THE HORIZONTAL DISTRIBUTION OF THE POLYNOIDAE

Lower boreal exclusively	Common to lower boreal and north temperate	North temperate exclusively	Common to north temperate and subtropic	Subtropic exclusively	Common to north temperate subtropic and lower boreal
Lepidonotus robustus	Polynoë fragilis	Harmothoë crassicirrata	Polynoë californica	Polynoë pulchra	Harmothoë imbricata
Hololepida magna	Polynoë lordi	Harmothoë iphionelloides	Harmothoë multisetosa	Polynoë remigata	Lepidonotus squamatus
Eunoë depressa	Harmothoë tuta	Harmothoë scriptoria	Harmothoë yokohamiensis	Polynoë filamentosa	Lepidonotus caeloris
Harmothoë complanata	Melaenis loveni	Harmothoë bonitensis	Harmothoë triannulata	Polynoë aciculata	Halosydna insignis
Harmothoë truncata	Lepidonotus caeloris	Eunoë barbata		Polynoë renotubulata	
Harmothoë multisetosa		Eunoë caeca		Lepidasthenia gigas	
Harmothoë rarispina		Antinoë macrolepida		Halosydna interrupta	
Harmothoë forcipata		Antinoë anoculata		Halosydna lagunae	
Gattyana amundseni		Nemidia microlepida		Halosydna succiniseta	
Gattyana ciliata		Polynoë spicula		Halosydna macrocephala	
Gattyana cirrosa				Halosydna carinata	
				Harmothoë lamellifera	
				Harmothoë tenebricosa	
				Harmothoë fragilis	
				Harmothoë pacifica	
				Harmothoë hirsuta	
				Harmothoë johnsoni	
				Gattyana senta	
				Lepidonotus caelorus	
11 species	5 species	10 species	4 species	19 species	4 species

* Table 2 is merely a summary of table 1

II. Bathymetrical Distribution

An attempt is here made to group the Polynoidae according to their bathymetrical distribution. The different bathymetric groups although less strictly defined than those of horizontal distribution (tables 1, 2) are nevertheless recognizable. One difficulty with this system of bathmetric grouping is that of trying to fit Polynoidae of the entire coast into groups according to their bathymetric distribution disregarding their horizontal distribution. Consequently the results are expected to be less definite on account of the diverse environmental conditions at the different latitudes and at the different depths. As is shown in table 3, there are very few species that are strictly limited to one bathymetric zone, but they usually occur in one or more adjacent zones. On the whole it is found that certain species designated as littoral may occur in the next greater depth, but as a rule they are not found in very great depths, while on the other hand species are found in deep waters which are never found in littoral zones above one hundred fathoms. Consequently there is sufficient reason for subdividing the species on the basis of their bathymetric distribution into littoral, sublittoral and deep water species.

Table 3*

Bathymetrical Distribution of the Polynoidae

Name	Depth in fathoms					Exceptional cases
	0-30	30-100	100-500	500-1000	1000-5000	
Halosydna insignis	×	×	....	....	....	291–298 fathoms off San Nicholas Island
Halosydna succiniseta	×	....	....	....	....	
Eunoë barbata	×	....	....	....	....	
Eunoë depressa	×	....	....	....	....	
Polynoë californica	×	....	....	....	....	One specimen found in 90 fathoms deep
Polynoë fragilis	×	....	....	....	....	
Polynoë lordi	×	....	....	....	....	
Harmothoë tuta	×	....	....	....	....	
Harmothoë hirsuta	×	....	....	....	....	
Harmothoë johnsoni	×	....	....	....	....	
Harmothoë pacifica	×	....	....	....	....	
Harmothoë iphionelloides	×	....	....	....	....	

* In table 3 the bathymetrical distribution of the Polynoidae is shown. The depths are given in five columns, 0–30, 30–100, 100–500, 500–1,000, 1,000–5,000 fathoms. x signifies the presence of the species in that depth. Species found about and beyond the depth of 100 fathoms are considered in this article as deep water species. Absolute littoral species are considered those inhabiting the shallow shore waters to the depth of 30 fathoms.

Table 3—(*Continued*)

Name	Depth in fathoms					Exceptional cases
	0-30	30-100	100-500	500-1000	1000-5000	
Harmothoë complanata	×	....	....	....	....	
Harmothoë truncata	×	×	....	....	....	
Harmothoë imbricata	×	×	....	....	....	
Halosydna lagunae	×	×	....	....	....	
Polynoë pulchra	×	×	....	....	....	156–162 fathoms off Santa Catalina
Lepidonotus robustus	....	×	....	....	....	In few cases 12–51
Lepidonotus squamatus	....	×	....	....	....	fathoms
Halosydna macrocephala	....	×	....	....	....	
Harmothoë bonitensis	....	×	....	....	....	
Harmothoë crassicirrata	....	×	....	....	....	
Antinoë macrolepida	....	×	....	....	....	
Harmothoë scriptoria	....	×	×	....	....	
Harmothoë triannulata	....	×	×	....	....	
Gattyana senta	....	×	×	....	....	
Gattyana amundseni	....	×	×	....	....	Greenland at 16 fathoms depth
Halosydna interrupta	....	×	×	....	....	
Hololepida magna	....	....	×	....	....	
Lepidasthenia gigas	....	×	×	....	....	
Gattyana ciliata	....	....	×	....	....	
Nemidia microlepida	....	....	×	....	....	
Harmothoë yokohamiensis	....	....	×	....	....	One specimen in depth of 1040–1062 fathoms
Harmothoë forcipata	....	....	×	....	....	
Harmothoë fragilis	....	....	×	×	....	
Polynoë remigata	....	....	×	....	....	
Polynoë filamentosa	....	....	×	....	....	
Harmothoë tenebricosa	....	....	....	×	....	
Polynoë aciculata	....	....	....	×	....	
Eunoë caeca	....	....	....	×	....	
Antinoë anoculata	....	....	....	×	....	
Polynoë renotubulata	....	....	....	....	....	
Lepidonotus caeloris	....	....	....	....	×	One example in 1400 fathoms off Cape Colnett
Harmothoë lamellifera	×	×	×	....	×	
Harmothoë multisetosa	....	×	....	×	×	One example taken from 1400 fathoms depth off Cape Colnett
Lagisca rarispina	×	×	×	....	....	
Gattyana cirrosa	×	....	....	×	....	
Melaenis loveni	×	×	×	....	....	

Summarizing the species given in the foregoing table, we get the results shown in table 4.

TABLE 4*

BATHYMETRICAL DISTRIBUTION OF THE POLYNOIDAE

Littoral exclusively	Sublittoral exclusively	Common to littoral and sublittoral areas	Exclusively deep water	Common to sublittoral and deep water
Species	Species	Species	Species	Species
Halosydna insignis	Lepidonotus robustus	Polynoë pulchra	Eunoë caeca	Harmothoë multisetosa
Halosydna californica	Lepidonotus squamatus	Harmothoë imbricata	Antinoë anoculata	Harmothoë lamellifera
Halosydna lagunae	Lepidasthenia gigas	Harmothoë truncata	Nemidia microlepida	Harmothoë triannulata
Halosydna succiniseta	Harmothoë crassicirrata	Harmothoë scriptoria	Harmothoë yokohamiensis	Harmothoë scriptoria
Halosydna macrocephala	Harmothoë bonitensis	Melaenis loveni	Harmothoë tenebricosa	Harmothoë rarispina
Eunoë barbata	Harmothoë scriptoria		Harmothoë fragilis	Gattyana senta
Eunoë depressa	Antinoë macrolepida		Harmothoë forcipata	Gattyana amundseni
Harmothoë hirsuta	Halosydna carinata		Polynoë remigata	Gattyana cirrosa
Harmothoë johnsoni	Halosydna interrupta		Polynoë filamentosa	Lepidonotus caeloris
Harmothoë complanata	Polynoë spicula		Polynoë aciculata	
Harmothoë iphionelloides			Polynoë renotubulata	
Harmothoë pacifica			Hololepida magna	
Harmothoë tuta			Gattyana ciliata	
Polynoë fragilis				
Polynoë lordi				
15 species	10 species	5 species	13 species	9 species

* Table 4 is a short summary of table 3.

1. Littoral Species

It is a general phenomenon that oceanic animals, as far as the number of individuals is concerned, are more abundant in littoral zones than in deep water. This is true of Polynoidae, some littoral species of which are very numerous. This, however, is not true of the number of genera and species, greater numbers of groups being represented in deep waters as is shown in table 4, where fifteen species are given as exclusively littoral. The fifteen littoral species belong to four genera. There are, moreover, fourteen exclusively deep water species and seven genera, the species being equal and the genera being almost double the number of those of the littoral zones. The explanation of this may be that the littoral zone being the location of greatest abundance of individuals is the center of origin of the Polynoidae and their center of dispersal.

That the littoral zone is the center of dispersal may be assumed on the basis that the individuals are very numerous in that zone and that the species are less varied or more nearly related. On the other hand the great diversity of species in the deep waters may be attributed to the environmental change and to the sudden shock effect on the larval stages of the Polynoidae. These changes may be brought about in larvae that are driven from the shores to the deep waters undergoing there considerable change in temperature, especially when they drop to the bottom; the shock effect of the cold temperature most probably kills the majority of the larvae and the few survivors that are able to adapt themselves are physically so changed as to form new species or even new genera.

Or again, if adult polynoids are driven to depths, they possessing a greater power of resistance than the larvae, have more chance to survive but their offspring will undergo a considerable change. In the first place, the low temperature at the bottom of the ocean would naturally cause death and abnormalities among the embryonal polynoids and when rising to the surface as trochophores they are subject to a sudden temperature change. The percentage of mortality in this case would be very great, and abnormalities resulting in conspicuous variations would be great. This assumption is based on laboratory experiments in which similar results may be produced artificially by suddenly changing the temperature.

The littoral species most common on this coast occurring in less than 30 fathoms depth are not strictly confined to that bathymetric

area, but have been frequently found in depths of 100 fathoms or more. *Halosydna insignis* has been taken occasionally from a depth of 200 fathoms. A few specimens of *Halosydna californica* have been taken from depths of 90 fathoms. *Harmothoë hirsuta,* a typical littoral species, has been found occasionally in a depth of 78 fathoms. *Harmothoë imbricata* is a cosmopolitan littoral species. It is abundantly represented on this coast, being usually found between tide marks, but also occurring at various depths, even below 200 fathoms. The examples found beyond 30 fathoms, however, are comparatively few, and the species may be designated as a littoral one.

2. Deep Water Species

The converse of what has been said of littoral polynoids is also true of deep sea forms; that is, certain species of Polynoidae are exclusively inhabitants of deep waters and have seldom, if ever, been found in shallow waters. As is indicated in table 3, different deep water species occupy different bathymetric areas. As an example of such deep water species may be given *Lepidasthenia gigas.* This polynoid is restricted to a comparatively small area on the coast of southern California. It occurs there in great abundance beyond the fifty-fathom line. The greatest depth, however, from which this species has been taken is 140 fathoms. This proves it to be a species of a limited bathymetrical distribution, inhabiting the sublittoral zones.

Other species again, as *Polynoë filamentosa, Antinoë anoculata* and *Eunoë caeca,* have been reported, up to the present time, only from depths of 500 to 1,000 fathoms. Still other species, as *Halosydna interrupta, Harmothoë multisetosa, Harmothoë lamellifera, Lepidonotus caeloris,* occur in various depths between 30 and 1,400 fathoms. Those species again have never been found in the littoral zone (1–30 fathoms). A number of other species of Polynoidae of this coast appear to be restricted to definite depths and may be justly considered as deep water species (table 5). Moreover, individuals of the same deep water species occupying widely separated geographical areas occur in the same relative depths, which serves as further evidence that they, under similar conditions of temperature, are deep water species in any part of the world. As an example may be mentioned *Lepidonotus caelorus,* found off Japan between 63 and 155 fathoms depth; while on this coast examples of it have been taken from water varying in depth from 30 to 1,400 fathoms. Another

example is *Harmothoë forcipata.* This species has been found near Eno-Sima, off the coast of Japan, in depths of 100 to 250 fathoms. Individuals of the same species, however, have been found near the southern coast of California in various depths from 448 to 600 fathoms. The cosmopolitan species, *Lepidonotus squamatus,* is an exception. The species is known as a littoral form in various parts of the world. On this coast, however, the species inhabits a depth of 90 to 100 fathoms. Only in one case has that species been found at a depth of 12 to 15 fathoms.

Table 5*

Showing Vertical and Horizontal Distribution

Name	Position	Depth in fathoms	Temperature†	Other localities
Lepidonotus robustus	Shelikof Strait, Alaska (on hermit crab)	48–65	**10°.8**	Locality of one specimen unknown
Lepidonotus squamatus	Point Cavallo	12–15		Everywhere around British Isles; along the Atlantic coast; from St. Lawrence to Cape Cod, Mass.
	Black Point, San Francisco Bay, Monterey Bay and Santa Monica	90–100		
Lepidonotus squamatus	Monterey Bay, Calif.	90–100	8°–12°	
Lepidonotus squamatus	Santa Monica, Calif.		13°–20°	
Lepidonotus squamatus	Santa Monica, Calif.	450		Off Azores, 450 fathoms
Lepidonotus squamatus	Santa Monica, Calif.			Greenland, Norway, shores of Massachusetts
Lepidonotus caeloris	Vicinity of San Diego, Calif.	71–75	9°–11°	
Lepidonotus caeloris	La Jolla, Calif.	243–280	5°–7°	
Lepidonotus caeloris	Santa Catalina Island, Calif.	143–245	5°–8°	
Lepidonotus caeloris	Off Santa Barbara Island, Calif.	29	9°–14°	
Lepidonotus caeloris	San Nicolas Island, Calif.	32–33	9°–14°	
Lepidonotus caeloris	San Nicolas Island, Calif.	229–291	5°–7°	
Lepidonotus caeloris	San Nicolas Island Calif.	216–239	5°–7°	
Lepidonotus caeloris	Santa Cruz Island, Calif.	447–510	5°–7°	

* In table 5 an attempt has been made to enumerate all the species of Polynoidae known on the Pacific coast in relation to the localities, depths and temperatures in which each species is known to occur. The data regarding the temperature are not exact but in most cases an approximate estimation of the possible temperature has been made by Dr. G. McEwen and a considerable difference has been allowed for seasonal variation.

†* Temperatures printed in bold face represent actual observations. The other temperatures were computed by Dr. G. F. McEwen and are entered to give a general idea of the temperature at the corresponding depths.

TABLE 5—(*Continued*)

Name	Position	Depth in fathoms	Temperature	Other localities
Lepidonotus caeloris	Santa Cruz Island, Calif.	197–281	5°–7°	
Lepidonotus caeloris	Santa Rosa Island, Calif.	38–40	8°–13°	
Lepidonotus caeloris	Monterey Bay, Calif.	285–357	5°–8°	
Lepidonotus caeloris	Monterey Bay, Calif.	368–495	5°–10°	
Lepidonotus caeloris	Monterey Bay, Calif.	26–28	10°–12°	
Lepidonotus caeloris	At many points between Vancouver and Kadiak Islands	18–313		
Lepidonotus caeloris	Off the coast of Japan			
Lepidonotus caeloris	Stephens Passage, Alaska			
	Monterey Bay, Calif.	50–57	13°	
Lepidonotus caeloris	Off Cape Colnett, Lower California	1400	3°–4°	
Lepidonotus caeloris	San Clemente Island, Calif.	135–500	4°–10°	
Lepidonotus caeloris	San Clemente Island, Calif.	48	10°–12°	
Lepidonotus caeloris	San Pedro, Calif.	17–33	9°–16°	
Polynoë fragilis	Pleasant Beach, near Seattle, Wash.			
Polynoë fragilis	Puget Sound, Wash.			
Polynoë fragilis	Salmon Bay, Wash.			
Polynoë fragilis	Admiralty Inlet, Wash.	39	10°.4	
Polynoë fragilis	Fort Point, San Francisco Bay			
Polynoë fragilis	Sausalito Ferry, San Francisco Bay			
Polynoë lordi	Yakutat, Alaska			
Polynoë lordi	Alki Point, Puget Sound, Wash.			
Polynoë lordi	Anacortes, Wash.			
Polynoë lordi	Cape Mendocino, Calif.			
Polynoë lordi	San Pedro, Calif.			
Polynoë pulchra	Point Loma, San Diego, Calif.	71–75	9°–8°	
Polynoë pulchra	Santa Catalina Island, Calif.	156–162	8°–9°	
Polynoë pulchra	San Nicholas Island, Calif.	33	8°–9°	
Polynoë pulchra	Monterey Bay, (on Luidia), Calif.	56–62	9°.17	
Polynoë pulchra	Monterey Bay, Calif.	40–46	8°–10°	
Polynoë pulchra	San Pedro, Calif.	40–150	8°–13°	
Polynoë pulchra	Off Coronado, Calif.	8–10	12°–18°	
Polynoë pulchra	La Jolla, Calif.	40	10°–14°	

Table 5—(*Continued*)

Name	Position	Depth in fathoms	Temperature	Other localities
Polynoë pulchra	San Diego Bay, Calif.	7–9	13°–25°	
Polynoë pulchra	San Diego Bay, Calif.	40–48	13°–25°	
Polynoë californica	Off San Nicholas Island, Calif.	291–298	5°	
Polynoë californica	Monterey Bay, Calif.	10		
Polynoë californica	Off San Diego Bay, Calif.	90	8°–10°	
Polynoë californica	Off San Diego Bay, Calif.	65	9°–12°	
Polynoë californica	Off San Diego Bay, Calif.	19–31	10°–16°	
Polynoë californica	Off San Diego Bay, Calif.	8–11	12°–17°	
Polynoë californica	Off San Diego Bay, Calif.	5–9	14°–19°	
Polynoë californica	Off Coronado Islands, Calif.	15–18	12°–17°	
Polynoë californica	Off San Pedro, Calif.	4–10	12°–18°	
Polynoë californica	Off San Pedro, Calif.	35–36	9°–13°	
Polynoë californica	Avalon, Santa Catalina Island, Calif.			
Polynoë californica	Santa Barbara, Pacific Grove, Calif.			
Polynoë californica	Humboldt Bay, Calif.			
Polynoë remigata	Santa Catalina Island, Calif.	334–600	4°–6°	
Polynoë filamentosa	Santa Catalina Island, Calif.	334–600	4°–6°	
Polynoë aciculata	Vicinity of San Diego, Calif.	549–585	3°–4°	
Polynoë renotubulata	Off Santa Catalina Island, Calif.	2228	3°	
Polynoë spicula	Off Monterey Bay, Calif.	46–56	12°–15°	
Polynoë spicula	San Nicolas Island	30–32	10°–15°	Round the shores of British Isles; Siberia; Greenland; Nova Zembla; Totomi Sea, 12–13 fathoms; Spitzbergen; Iceland; Scandinavia; Adriatic and Mediterranean Seas; along all European shores
Harmothoë imbricata	Yakutat, Muir Inlet, Kakiak Islands, Alaska; Alki Point, Puget Sound, Wash.; Trinidad; Humboldt Bay, Shelter Cove, Mendocino, Point Arena, Dillon's Beach, Tomales Bay; Fort Point, San Francisco Bay, Pacific Grove, La Jolla, San Clemente Island, San Pedro, Calif.	35–36		

TABLE 5—(*Continued*)

Name	Position	Depth in fathoms	Temperature	Other localities
Harmothoë imbricata	San Diego, Calif.	8–11	12°–18°	
Harmothoë imbricata	San Diego, Calif.	19–31	10°–16°	
Harmothoë tuta	Puget Sound, Wash			Sitka, Korea
Harmothoë crassicirrata	Monterey Bay, Calif.	100		
Harmothoë iphionelloides	Pleasant Beach, Wash.			
Harmothoë scriptoria	Monterey Bay, Calif.	49–50	8°.7	
Harmothoë tenebricosa	San Diego Bay, Calif.	500–507		
Harmothoë tenebricosa	Monterey Bay, Calif.	540–800	3°–5°	
Harmothoë tenebricosa	Monterey Bay, Calif.	545–800	2°–4°	
Harmothoë tenebricosa	San Diego Bay, Calif.	500–507	2°–4°	
Harmothoë multisetosa	San Clemente Island, Calif.	654–704	4°.1	
Harmothoë multisetosa	Santa Cruz Island, Calif.	447–510	3°–5°	
Harmothoë multisetosa	Monterey Bay, Calif.	49–51	7°10°	
Harmothoë multisetosa	Monterey Bay, Calif.	759–766		
Harmothoë multisetosa	Cape Colnett, Lower California	1400	2°–3°	
Harmothoë multisetosa	Gulf of Georgia, Alaska	18–23	10°.7	
Harmothoë multisetosa	Boca de Quadra, Alaska	48–57	7°.7	
Harmothoë multisetosa	Vancouver Island	111–170	9°.05	
Harmothoë multisetosa	Vancouver Island	31–90		
Harmothoë lamellifera	Near San Diego, Calif.	67–116	11°.1	
Harmothoë lamellifera	Near San Diego, Calif.	71–75	9°–11°	
Harmothoë lamellifera	Near San Diego, Calif.	241–369	5°–6°	
Harmothoë lamellifera	Near San Diego, Calif.	639–671	4°	
Harmothoë lamellifera	San Clemente Island, Calif.	654–704	4°.1	
Harmothoë lamellifera	San Nicolas Island, Calif.	1100	3°–4°	
Harmothoë lamellifera	Santa Cruz Island, Calif.	764–891	3°–4°	
Harmothoë yokohamiensis	Santa Catalina, Calif.	152–162	7°–9°	Yokohama, Japan, 5–50 fathoms
Harmothoë yokohamiensis	Santa Cruz Island, Calif.	447–510	7°–9°	
Harmothoë yokohamiensis	Santa Cruz Island, Calif.	197–281	7°–9°	
Harmothoë yokohamiensis	Monterey Bay, Calif.	368–495	3°–4°	
Harmothoë yokohamiensis	Monterey Bay, Calif.	1041–1062	2°–3°	
Harmothoë triannulata	San Nicolas Island, Calif.	238	3°–4°	
Harmothoë triannulata	Santa Rosa Island, Calif.	38–41	8°–13°	
Harmothoë fragilis	San Diego Bay, Calif.	423–488	3°–5°	
Harmothoë fragilis	San Diego Bay, Calif.	500–507	3°–5°	

Table 5—(*Continued*)

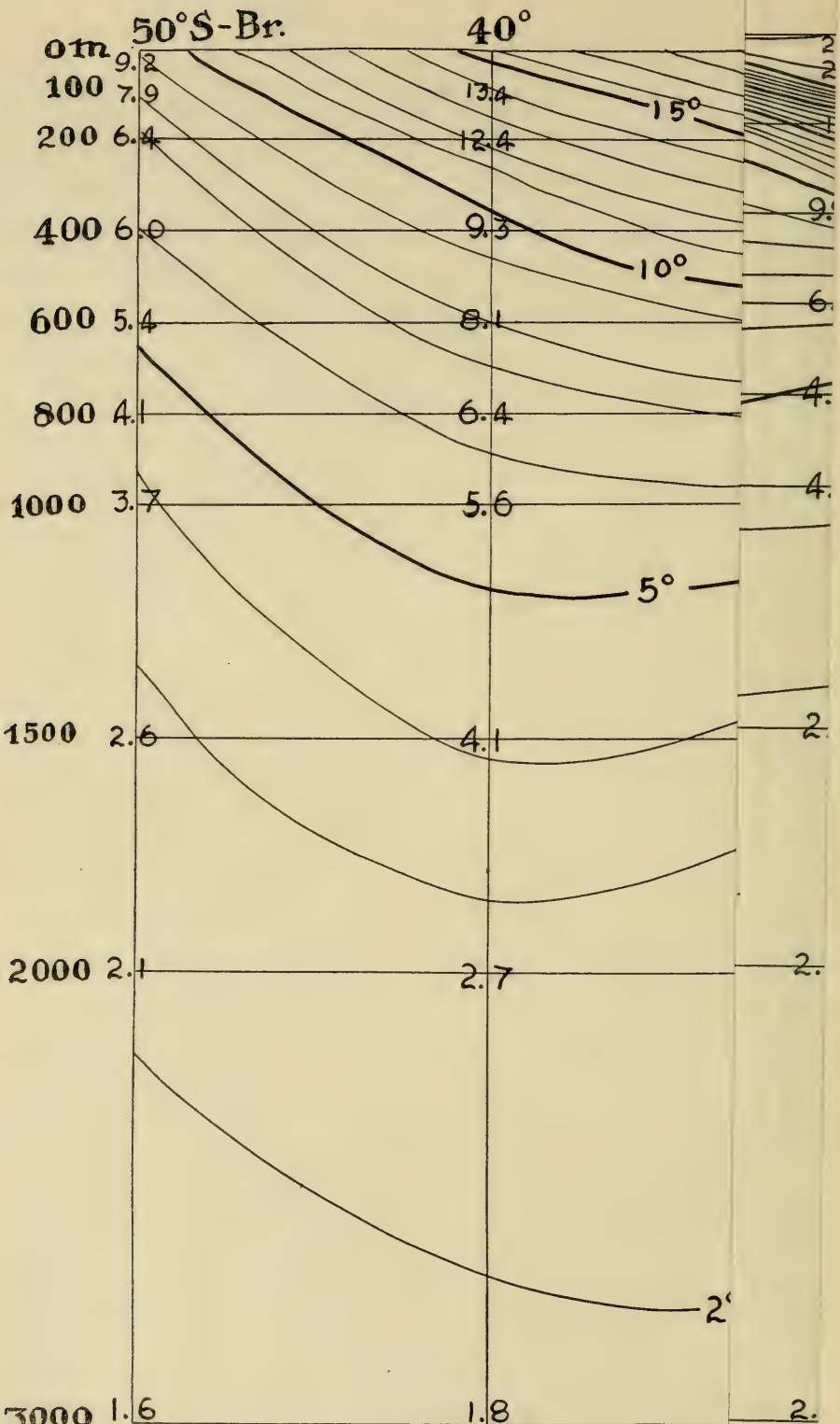
Name	Position	Depth in fathoms	Temperature	Other localities
Harmothoë fragilis	San Clemente Island, Calif.	542–600	4°.4	
Harmothoë fragilis	Santa Catalina Island, Calif.	152–162	6°–7°	
Harmothoë fragilis	Santa Barbara Island, Calif.	238–310	4°–5°	
Harmothoë fragilis	San Nicolas Island, Calif.	291–298	5°	
Harmothoë fragilis	San Nicolas Island, Calif.	216–339	5°	
Harmothoë fragilis	San Miguel Island, Calif.	264–271	4°–6°	
Harmothoë fragilis	Santa Barbara Island, Calif.	197–281	5°–7°	
Harmothoë forcipata	San Clemente Island, Calif.	448–468	4°–6°	Eno-Sima, Japan
Harmothoë forcipata	Santa Cruz Island, Calif.	447–510	5°–7°	
Harmothoë forcipata	Santa Cruz Island, Calif.	506–580	4°–5°	
Harmothoë complanata	Puget Sound, Wash.			
Harmothoë complanata	Coronado, Calif.			
Harmothoë pacifica	Locality unknown			
Harmothoë hirsuta	San Pedro, Calif.	3–4	14°–18°	
Harmothoë hirsuta	Santa Barbara, Calif.		14°–18°	
Harmothoë hirsuta	La Jolla and San Diego, Calif.		14°–20°	
Harmothoë hirsuta	Port Townsend, Wash.	15–26	10°.4	
Harmothoë hirsuta	Pacific Grove, Calif.			
Harmothoë hirsuta	Dundas Bay, Icy Strait, Alaska	21–78	7°.05	
Harmothoë hirsuta	Pillar Point, Calif.	8½–21	6°.78	
Harmothoë truncata	Halibut bank, Gulf of Georgia, Alaska	18–23	5°–10°	
Harmothoë truncata	Halibut bank, Gulf of Georgia, Alaska	31–90	5°–9°	
Harmothoë truncata	Queen Charlotte Sound, off Vancouver Island, B. C.	68–107	7°.72	
Harmothoë truncata	Admiralty Inlet, Port Townsend, Wash.	83–99	10°.28	
Harmothoë truncata	Behm Canal, Alaska	62–65	6°.56	
Harmothoë bonitensis	Point Bonita, San Francisco Bay, Calif.	45–50	12°.6	
Harmothoë johnsoni	La Jolla, Calif.	0–1	13°–22°	
Halosydna insignis	Kadiak Island, Alaska		4°.95	
Halosydna insignis	Alki Point, Puget Sound, Wash.		5°	

TABLE 5—(*Continued*)

Name	Position	Depth in fathoms	Temperature	Other localities
Halosydna insignis	Admiralty Inlet, Wash.	24–25	10°.17	
Halosydna insignis	Cape Mendocino, Calif.		11°–15°	
Halosydna insignis	Point Arena, Dillon's Bay, Tomales Bay, Calif.			
Halosydna insignis	Duxberry Reef, Bolinas, Calif.			
Halosydna insignis	San Francisco Bay, Calif.		12°–17°	
Halosydna insignis	Point San Pedro, Calif.	10–49	9°–17°	
Halosydna insignis	Pillar Point, Calif.	40–46		
Halosydna insignis	Monterey Bay, Calif.	36–51	8°.89	
Halosydna insignis	Monterey Bay, Calif.	40–46		
Halosydna insignis	Pacific Grove, Calif.			
Halosydna insignis	Avalon, Santa Catalina Island, Calif.		13°–21°	
Halosydna insignis	La Jolla, Calif.	5–18	10°–22°	
Halosydna insignis	San Pedro, Calif.	4–10	12°–18°	
Halosydna insignis	Point Firmin, Calif.	27–30	9°–14°	
Halosydna insignis	San Nicolas Island, Calif.	291–298	5°–8°	Sagami Bay, Japan, 153 fathoms
Halosydna interrupta	Off La Jolla, Calif.	55–125	8°–13°	Eno-Sima, Japan 480 meters or 250 fathoms
Halosydna interrupta	Point Firmin, Calif.	60–130	6°–13°	
Halosydna interrupta	Point Loma, near San Diego, Calif.	241–369	5°–6°	
Halosydna lagunae	Near San Diego, Calif.	14–42	9°–16°	
Halosydna lagunae	Laguna, Calif.			
Halosydna succiniseta	Laguna, Calif.	0–1	13°–18°	
Halosydna macrocephala	Off San Diego, Calif.	20–25	10°–15°	
Eunoë barbata	Blount's Reef, Calif.			
Eunoë barbata	Puget Sound, Wash.			
Eunoë barbata	Monterey Bay, Calif.	10	8°	
Eunoë barbata	Admiralty Inlet, Wash.	15–26	10°.4	
Eunoë caeca	Monterey Bay, Calif. (on holothurians)	861–1062	4°–5°	
Eunoë depressa	Dundas Bay, Alaska	8–10	9°–10°	
Antinoë macrolepida	Monterey Bay, Calif.	75–108	5°–8°	
Antinoë anoculata	Coronado Island, Calif.	618–667	3°.8	
Antinoë anoculata	Monterey Bay, Calif.	750–766	3°–4°	
Nemidia microlepida	Monterey Bay, Calif.	130–149	3°–4°	
Lepidasthenia gigas	San Pedro, Calif.	50	8°–12°	
Lepidasthenia gigas	Zuninga, Calif.			

Table 5—(*Concluded*)

Name	Position	Depth in fathoms	Temperature	Other localities
Lepidasthenia gigas	Point Loma, San Diego, Calif.	50	9°–13°	
Lepidasthenia gigas	Off Point Firmin, Calif.	60–140	6°–13°	
Gattyana senta	San Diego Bay, Calif.	91–97	4°–6°	McCormick Bay
Gattyana senta	San Diego Bay, Calif.	127–300	2°–3°	Gulf of Georgia, 18–23 fathoms
Gattyana senta	San Nicolas Island, Calif.	32–33	10°–14°	31–90; 157–230 fathoms
Gattyana senta	Monterey Bay, Calif.	48–111	10°–12°	Behm Canal, Alaska, 41–134 fathoms
Gattyana senta	Monterey Bay, Calif.	30	5°–7°	
Gattyana amundseni	Stephens Passage, Alaska	131–188	4°.9	
Gattyana amundseni	Alitak Bay, Kodiak Island, Alaska	35–36	6°.89	
Gattyana amundseni	McCormick Bay, Greenland	16	8°–9°	
Gattyana ciliata	Uyak Bay, Kodiak Island, Alaska	74–80	5°.6	
Gattyana ciliata	McCormick Bay, Greenland			St. Andrews Bay, Atlantic, 580–630 fathoms
Gattyana cirrosa	Afognak Bay, Alaska	12–17	8°–11°	Norway, Finmark, Gulf of St. Lawrence
Gattyana cirrosa	Barden Bay, Greenland	10–40	10°–12°	
Melaenis loveni	Icy Cape, Alaska			
Lagisca rarispina	Gulf of Georgia, Alaska	18–23	10°.1	
Lagisca rarispina	Gulf of Georgia, Alaska	157–230	8°.7	
Lagisca rarispina	Admiralty Inlet, Port Townsend, Wash.	16–20	10°.1	
Lagisca rarispina	Boca de Quadra, Alaska	149–181	6°.9	
Lagisca rarispina	Yes Bay, Behm Canal	130–193	7°	
Lagisca rarispina	Stephens Passage, Alaska	131–182 abundant	4°.89	
Lagisca rarispina	Lynn Canal	300–313 abundant	5°.11	
Lagisca rarispina	Dundas Bay, Icy Strait, Alaska	6½–9	6°.7	
Lagisca rarispina	Uyak Bay, Kodiak Island, Alaska	74–80	6°.78	
Hololepida magna	Gulf of Georgia on halibut bank	157–230	7°.2	
Hololepida magna	Kasan Bay, Prince of Wales Island, Alaska	95–114	4°–6°	


50°S-Br.
40°
0m 9.2
100 7.9
200 6.4
400 6.0
600 5.4
800 4.1
1000 3.7
1500 2.6
2000 2.1
3000 1.6
13.4
12.4
9.3
8.1
6.4
5.6
4.1
2.7
1.8
15°
10°
5°
2°

)°S to 60°

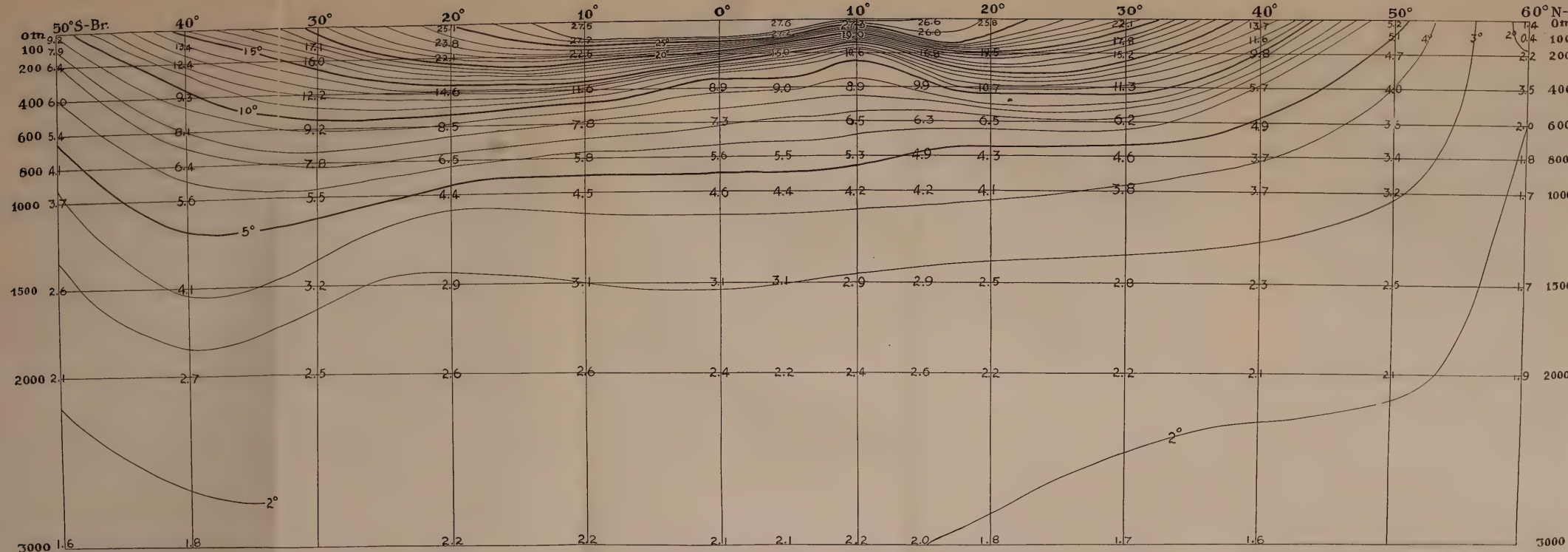
D. FACTORS CONTROLLING DISTRIBUTION

On the basis of the above examples the Polynoidae of this coast may be grouped according to their horizontal distribution into subboreal, temperate, subtropical, tropical and cosmopolitan species; and according to their vertical distribution they fall into littoral, sublittoral, and deep water groups. These facts suggest that there must be some reason for such varied distribution, or else the distribution would not occur in such a constant and definite manner. Assuming that all actions are in response to stimuli, the phenomenon of distribution may be best understood by considering the factors or stimuli which play a rôle in distribution. Many of these factors are undoubtedly so complex that they can be studied only by complicated methods of chemical and physical analyses. The most obvious factors, however, may be enumerated as follows: (1) temperature, (2) currents, (3) winds, (4) chemical composition of the water, (5) food habits and mode of life of the Polynoidae.

I. Temperature in Relation to Depth and Latitude

Before we speak of the influence of the temperature on the oceanic fauna and flora, and of the rôle it plays in distribution, it is essential to have a clear conception of the relative temperatures of the various depths and latitudes. As far as it is known from the hydrographic records of the various investigations of the oceans, the bottom temperatures of the depths of the Pacific Ocean are remarkably uniform, ranging from 1°.6 to 1°.9C (Schott and Schu, 1910; McEwen, 1915). There is a very slight variation in temperature in abyssal waters below 2,000 fathoms. The bottom waters are the coldest near the California coast. The temperature becomes gradually warmer with the increasing distance from the shore, but the variation of the temperature amounts only to a difference of 0°.45 Fahrenheit between the longitudes 120° and 160° (Clark, 1916) or from the coast of California toward the mid-Pacific. This difference in temperature is so insignificant that it is almost negligible.

This, however, is not true of the surface temperature, which is far from being uniform; in fact, considerable fluctuations in temperature due to various physical causes are found in comparatively small areas. Considering the surface temperature of the entire Pacific coast in general, one finds that it follows certain laws varying according to



The vertical distribution of temperature in the Pacific Ocean between latitudes 50°S to 60°N (at 180° longitude).

(After Schott and Sehm)

TABLE 6*

DISTRIBUTION OF TEMPERATURES IN THE PACIFIC OCEAN

(Depths in meters; depths in fathoms given in parentheses)
(After Schott and Schu)

Lat.	Long.	0 (0)	100 (55)	200 (109)	400 (219)	600 (328)	800 (437)	1,000 (547)	1,500 (820)	2,000 (1,094)	3,000 (1,640)	4,000 (2,187)	Remarks
N	W												
60°	180°	1°.4	0°.4	2°.2	3°.5	2°.5?	1°.8?	1°.7?	1°.7?	1°.9	.....	.....	Northwestern part of Bering Sea
55°	170°	3.5	3.3	2.8	3.5	3.4	3.3	3.0	2.4	2.1	1.8	.....	Eastern part of Bering Sea
	E									.....	.....	.....	The warmer part of Okhotsk Sea
50°	150°	4.0	1.6	1.8	1.8	2.2	2.4	.....	.....				
	160°	4.6	1.0	0.3	0.7	1.3	1.4	1.6	1.5	1.5	1.15	1.5	Northeastern side of the Kurile Islands
	170°	5.2	4.9	4.4	3.5	3.3	3.2	2.6	2.7	1.9	1.7	1.6	
	180°	5.2	5.1	4.7	4.0	3.6	3.4	3.2	2.5	2.1	1.7	1.6	Southwest corner of the Aleutian Islands
	W												
45°	170°	5.2	5.0	4.6	4.1	3.7	3.3	3.2	2.4	2.1	1.7	1.5	
	160°	6.2	5.0	4.7	4.3	3.8	3.2	3.2	2.3	2.2	1.8	1.4	
	150°	7.1	5.0	4.6	4.3	3.9	3.2	3.2	2.3	2.2	1.8	1.3	
	140°	8.6	6.0	5.0	4.2	3.9	3.2	3.2	23.	2.2	1.9	.....	
	130°	10.3	6.5	6.0	4.5	3.8	3.2	3.2	2.3	2.2	1.9	.....	West from Vancouver
	E												
40°	135°	12.7	4.0	2.1	0.7	0.6	0.4	.....	.....	.....	.....	.....	Japanese Sea
	145°	13.6	7.1	3.1	3.0	2.8	2.2	2.1	1.5	1.4	1.3	1.2	Southeast from Tsugar Strait

* Table 6 is after Schott and Schu, showing the distribution of temperature in the Pacific Ocean at various depths, latitudes and longitudes. Depth from 0 to 4,000 meters is given in different columns or from 0 to 2,187 fathoms given below in parentheses. The northern latitudes from 60 to 0 are considered showing the temperature at each five degrees of latitude and at each ten degrees of longitude.

TABLE 6—(*Continued*)

Lat.	Long.	0 (0)	100 (55)	200 (109)	400 (219)	600 (328)	800 (437)	1,000 (547)	1,500 (820)	2,000 (1,094)	3,000 (1,640)	4,000 (2,187)	Remarks
	160°	13.2	8.5	8.1	5.2	4.2	3.3	3.0	1.8	1.7	1.6	1.5	
	170°	13.4	11.8	10.4	5.6	4.7	3.6	3.4	2.4	1.8	1.6	1.5	
	180°	13.7	11.6	9.8	5.7	4.9	3.7	3.7	2.3	2.1	1.6	1.5	
	W												
	170°	14.8	11.5	10.0	6.5	4.8	3.8	3.6	2.2	2.2	1.6	1.5	
	160°	14.6	11.4	10.0	6.6	4.6	3.8	3.3	2.2	2.2	1.6	1.5	
	150°	15.0	11.5	9.8	6.4	4.5	3.8	3.5	2.4	2.2	1.6	1.5	
	140°	14.8	11.7	9.5	6.1	4.4	3.9	3.3	2.4	2.2	1.6	1.5	
	130°	14.0	10.0	7.7	5.6	4.2	3.9	3.2	2.4	2.2	1.6	1.5	
	125°	12.0	8.1	6.8	5.2	4.2	3.9	3.2	2.4	2.2	1.6	1.5	Near Cape Mendocino, California
	E												
30°	130°	23.0	15.0	12.5	8.0	5.5	3.0	2.8	.....	.....	.....	.....	Vicinity of Dieman Strait
	140°	23.2	17.8	16.6	13.5	9.2	5.6	3.9	2.3	2.1	1.6	1.7	Kuro Siwo Region
	E									2.2	1.7	1.7	
30°	150°	22.4	18.2	16.8	16.3	8.0	5.4	4.1	2.4	2.2	1.7	1.7	
	160°	22.2	18.3	15.9	12.7	7.0	4.7	3.8	2.4	2.3	1.7	1.7	
	170°	22.1	18.1	15.5	12.1	6.4	4.3	3.8	2.6	2.2	1.7	1.7	
	180°	22.0	17.8	15.2	11.3	6.2	4.6	3.8	2.8				
	W									2.2	1.7	1.7	
	170°	22.1	17.5	15.0	10.7	5.8	4.5	3.7	2.5	2.2	1.7	1.7	
	160°	22.0	17.5	13.5	10.1	5.5	4.4	3.6	2.4	2.2	1.8	1.7	
	150°	20.5	17.5	12.8	8.5	5.3	4.3	3.3	2.5	2.4	2.0	1.9	
	140°	19.0	17.5	12.6	7.5	4.8	4.4	3.8	2.6	2.3	2.2	2.0	
	130°	18.0	15.9	11.5	6.5	4.8	4.4	3.8	2.4	2.3	2.2	1.7	West from the shores of Lower California
	120°	17.0	12.0	8.1	6.0	4.6	4.2	3.7	2.7				

TABLE 6—(*Continued*)

Lat.	Long.	0 (0)	100 (55)	200 (109)	400 (219)	600 (328)	800 (437)	1,000 (547)	1,500 (820)	2,000 (1,094)	3,000 (1,640)	4,000 (2,187)	Remarks
	E												
20°	130°	26.4	23.0	19.4	13.2	7.8	5.7	4.2	2.6	2.2	1.8	1.7	
	140°	26.6	24.4	21.5	13.8	8.4	5.5	4.2	3.1	2.2	1.8	1.7	About 145°E Long. Marianas
	150°	26.5	25.0	21.3	13.3	8.2	5.4	4.2	2.9	2.2	1.8	1.7	
	160°	26.3	24.0	19.0	12.2	7.5	5.0	4.0	2.6	2.2	1.8	.....	
	E												
20°	170°	26.1	23.5	18.5	11.6	7.3	4.5	4.0	2.8	2.2	1.8	.....	
	180°	25.8	23.1	19.5	10.7	6.5	4.3	4.1	2.5	2.2	1.8	.....	
	W												
	170°	25.4	22.6	20.1	10.1	6.1	4.4	4.1	2.8	2.2	1.8	.....	
	160°	24.8	23.2	17.5	8.8	5.2	4.2	4.5	2.9	2.2	1.8	1.7	About 155°W long.: Honolulu
	150°	24.0	22.8	17.1	8.2	5.5	4.5	4.8	3.0	2.2	1.9	1.8	
	140°	22.8	21.5	16.1	8.1	5.5	4.6	4.2	3.3	2.2	1.8	1.8	
	130°	21.7	19.8	13.8	8.2	5.6	4.7	4.2	3.2	2.2	1.8	1.8	
	120°	22.0	17.7	11.5	8.5	6.1	5.0	4.4	3.1	2.5	1.8	1.8	
	110°	25.0	15.3	11.5	9.3	6.6	5.3	4.4	3.5	2.5	1.8	.....	South from Cape San Lucas
N	E												
15°	130°	27.4	25.3	21.1	10.2	6.8	5.7	4.7	2.7	2.2	1.8	1.8	145°E long.; Mariana
	140°	27.3	26.5	20.1	11.0	6.7	5.0	4.2	2.7	2.2	1.8	1.8	
	150°	27.3	26.2	19.0	10.9	6.7	4.9	4.3	2.9	2.2	1.8	1.8	
	160°	27.2	26.2	17.8	11.0	6.9	4.4	4.2	2.9	2.2	1.8	1.7	
	170°	27.0	26.1	17.0	10.5	7.1	4.8	4.2	2.9	2.2	1.8	1.7	
	180°	26.6	26.0	16.8	9.9	6.3	4.9	4.2	2.9	2.6	2.0	1.8	

TABLE 6—(*Continued*)

Lat.	Long.	0 (0)	100 (55)	200 (109)	400 (219)	600 (328)	800 (437)	1,000 (547)	1,500 (820)	2,000 (1,094)	3,000 (1,640)	4,000 (2,187)	Remarks
	W												
	170°	26.3	26.1	16.0	9.3	6.3	5.0	4.4	2.9	2.6	2.2	2.0	
	160°	25.9	25.8	15.7	8.4	6.5	5.2	4.8	3.2	2.6	2.4	2.1	
	150°	25.3	23.2	14.0	8.4	6.4	5.3	4.6	3.2	2.6	1.8	1.8	
	140°	24.5	22.1	13.8	8.6	6.3	5.4	4.8	3.2	2.6	1.9	1.8	
	130°	24.1	21.2	13.1	8.7	6.4	5.4	4.7	3.2	2.8	1.9	1.8	
	120°	24.3	19.5	12.4	8.7	6.2	5.3	4.8	3.2	2.8	1.9	1.8	
	110°	26.7	17.1	12.2	9.4	7.1	5.3	4.9	3.4	2.8	1.9	1.8	
	100°	28.2	19.5	13.5	10.3	7.7	5.3	4.9	3.7	2.8	1.9	1.9	South from Acapulco
	E												
10°	130°	27.9	25.0	15.0	8.1	6.5	5.6	4.5	2.9	2.2	1.9	1.8	240 miles east from North Mindanao
	140°	28.0	22.0	14.0	7.8	6.7	5.1	4.4	2.9	2.3	1.9	.....	East of Yap
	150°	27.9	16.0	10.0	8.7	6.5	5.1	4.3	2.9	2.3	1.9	1.7	Caroline region
	160°	27.9	18.5	10.5	8.7	6.5	5.2	4.2	2.9	2.3	1.9	1.7	West Marshall Island
	170°	27.6	18.0	10.5	8.7	6.6	5.5	4.2	2.9	2.2	1.9	1.7	East Marshall Island
	180°	27.3	19.0	10.6	8.8	6.5	5.3	4.2	2.9	2.4	2.2	2.0	
	W												
	170°	26.6	19.5	10.7	8.9	6.8	5.3	4.4	3.2	2.6	2.4	2.1	
	160°	26.3	19.0	10.8	8.9	7.4	5.3	4.6	3.4	2.8	2.6	2.2	
10°	150°	26.2	17.5	10.9	8.6	7.2	5.3	4.8	3.1	2.2	1.7	1.7	
	140°	26.1	17.0	10.9	8.5	7.2	5.3	4.8	3.2	.24	1.8	1.8	
	130°	26.2	16.8	11.0	8.7	7.3	5.3	4.6	3.3	2.6	1.9	1.8	
	120°	26.5	17.0	11.4	8.8	7.3	5.3	4.5	3.4	2.8	1.9	1.9	
	110°	27.5	17.4	12.0	9.5	7.7	5.3	4.7	3.5	2.8	1.9	1.9	Clipperton Island
	100°	28.1	18.0	13.0	10.2	8.0	5.6	4.9	3.6	2.8	2.1	2.0	
	90°	27.6	18.7	13.5	10.4	8.0	5.6	5.0	3.7	2.8	2.4	.....	West of Costa Rica

TABLE 6—(*Continued*)

Lat.	Long.	0 (0)	100 (55)	200 (109)	400 (219)	600 (328)	800 (437)	1,000 (547)	1,500 (820)	2,000 (1,094)	3,000 (1,640)	4,000 (2,187)	Remarks
	E												
5°	130°	28.2	22.0	17.5	8.9	7.5	5.6	4.6	3.1	2.2	1.9	1.9	West of Palau Island
	140°	28.3	25.0	18.0	8.9	7.3	5.8	4.6	3.5	2.2	1.8	.....	South Carolina
	150°	28.5	26.6	17.2	8.7	7.2	5.8	5.0	3.7	2.2	1.8	1.7	South Carolina
	160°	28.3	27.1	16.0	8.8	6.8	5.4	4.6	3.2	2.2	1.8	1.7	Jaluit
	170°	28.1	27.2	15.3	8.9	6.4	5.4	4.2	3.1	2.2	2.1	2.0	
	180°	27.6	27.2	15.0	9.0	6.7	5.5	4.4	3.1	2.2	1.8	.....	
	W												
5°	170°	27.0	27.0	14.4	9.2	7.2	5.8	4.6	3.1	2.2	2.2	2.1	
	160°	26.5	26.0	13.1	9.4	7.7	5.8	4.7	3.3	2.5	1.9	1.9	Near Fanning Island
	150°	26.3	23.0	12.3	9.0	7.5	5.8	4.8	3.4	2.7	1.9	1.8	
	140°	26.2	20.0	12.0	8.8	7.5	5.4	4.8	3.3	2.5	1.9	1.8	
	130°	26.1	18.0	11.8	8.8	7.4	5.4	4.8	3.3	2.6	2.0	1.8	
	120°	26.1	15.5	11.8	9.0	7.4	5.4	4.8	3.3	2.6	2.2	1.8	
	110°	26.1	15.6	12.1	10.0	7.7	5.4	4.8	3.3	2.6	2.0	1.9	
	100°	26.1	15.0	12.7	10.2	7.5	5.4	4.8	3.3	2.6	2.2	.....	
	90°	26.2	14.6	13.0	9.8	7.7	5.3	4.8	3.3	2.6	.....	.....	
	80°	27.1	19.9	12.8	9.5	7.6	5.5	4.6	3.3	2.6	2.2	.....	South from Gulf of Panama
	E												
0°	130°	28.5	27.3	22.0	10.5	7.5	5.7	.....	.....	.....	.....	.....	Djilolo Strait
	140°	28.5	26.5	22.2	9.0	6.0	5.5	4.4	3.0	2.2	1.6	.....	North of New Guinea
	150°	28.5	27.5	21.4	9.6	7.3	5.2	4.5	3.3	2.4	1.8	.....	North of New Hanover
	160°	28.5	27.5	20.0	8.9	7.2	5.2	4.6	3.2	2.4	1.8	.....	
	170°	28.2	27.6	17.5	8.8	7.1	5.7	4.4	3.2	2.1	1.8	.....	About 267°E long.: Nauru Islands
	180°	27.7	27.5	16.7	8.9	7.3	5.6	4.6	3.1	2.4	2.1	2.0	In vicinity Gilbert Islands

TABLE 6—(*Concluded*)

Lat.	Long.	0 (0)	100 (55)	200 (109)	400 (219)	600 (328)	800 (437)	1,000 (547)	1,500 (820)	2,000 (1,094)	3,000 (1,640)	4,000 (2,187)	Remarks
N	W												
0°	120°	23.7	20.4	13.2	9.4	7.0	5.3	4.4	3.3	2.7	1.9	1.8	
	110°	23.3	16.0	12.8	10.4	7.3	5.4	4.6	3.3	2.7	1.9	1.8	
	100°	23.0	14.6	12.7	10.6	7.4	5.4	4.6	3.3	2.7	1.9	.....	
	90°	22.9	15.4	13.5	10.0	6.8	5.3	4.8	3.3	2.7	.....	.....	Galapagos
	W												
	170°	27.2	27.0	16.0	9.0	7.5	5.6	4.8	3.1	2.5	2.2	2.1	
	160°	26.6	26.4	15.3	9.2	7.8	5.6	5.0	3.2	2.7	2.5	2.1	
	150°	25.8	25.2	14.6	9.1	7.1	5.6	4.7	3.3	2.7	1.9	1.8	
	140°	25.0	23.5	13.8	8.8	7.1	5.6	4.6	3.3	2.7	1.9	1.8	
	130°	24.3	22.0	13.5	8.8	7.0	5.4	4.4	3.3	2.7	1.9	1.8	

latitude and, to some extent, according to longitude. The highest temperature of the surface waters of the ocean, as one may naturally expect, is in the lowest latitudes on both sides of the equator, where the intensity of the solar radiation reaches its maximum. With an increase in distance from the equator toward the poles there is a gradual decrease in temperature. The difference in temperature is here about 28° to 29°C, ranging from 28°.5C near the equator to 1°.4C at latitude 60° (see table 6) or to 0° in the North Polar Basin at about 80° latitude. Again, a difference in surface temperature prevails between the surface waters of the coastal region and those of the mid-Pacific, and as a general rule the temperature of the surface water rises with the increase in distance from the Californian coast toward the mid-Pacific. But in the mid-Pacific, as well as near the coast, the temperature gradually decreases with the increase in distance from the equator toward the poles. The temperature near the shores, however, is more subject to fluctuations due to various causes. Thorade (1912) has shown in detail the variations in temperature off the coast of California with isotherms for surface temperatures for each month of the year. Certain "cold islands" surrounded by warmer waters, off Seattle and San Francisco, disappear entirely during some months but are very prominent in others, the appearance and disappearance of these "cold islands" being caused by the seasonal changes in winds with their influence upon the waters. The shifting of the isothermal lines near the shores is also conspicuously noticeable in the varying seasons. Upwelling of the cold bottom waters is the cause of cold belts along the coast of California (Holway, 1905). An instance of narrow cold water belt is found in the waters along Cape Mendocino. Some limited areas of shallow water near the coast have higher temperature than the surrounding deeper waters. All these complexities help to diversify the thermal conditions of the surface waters, but on the whole the temperature decreases with the increase of distance from the equator to the poles (table 6).

In the Arctic Ocean the surface temperature is nearly like the bottom temperature, varying from 1°.80C in April to 0°.80C in August. The temperature in the different depths in that region varies from 0°.30 to 0°.80C (Nansen, 1902) being also uniform in that region. This, however, is not true in the lower latitudes, where the temperature varies with the various depths, decreasing gradually with the increase in depth until in the greatest depth a minimum temperature is reached which is nearly identical with that of the Arctic waters.

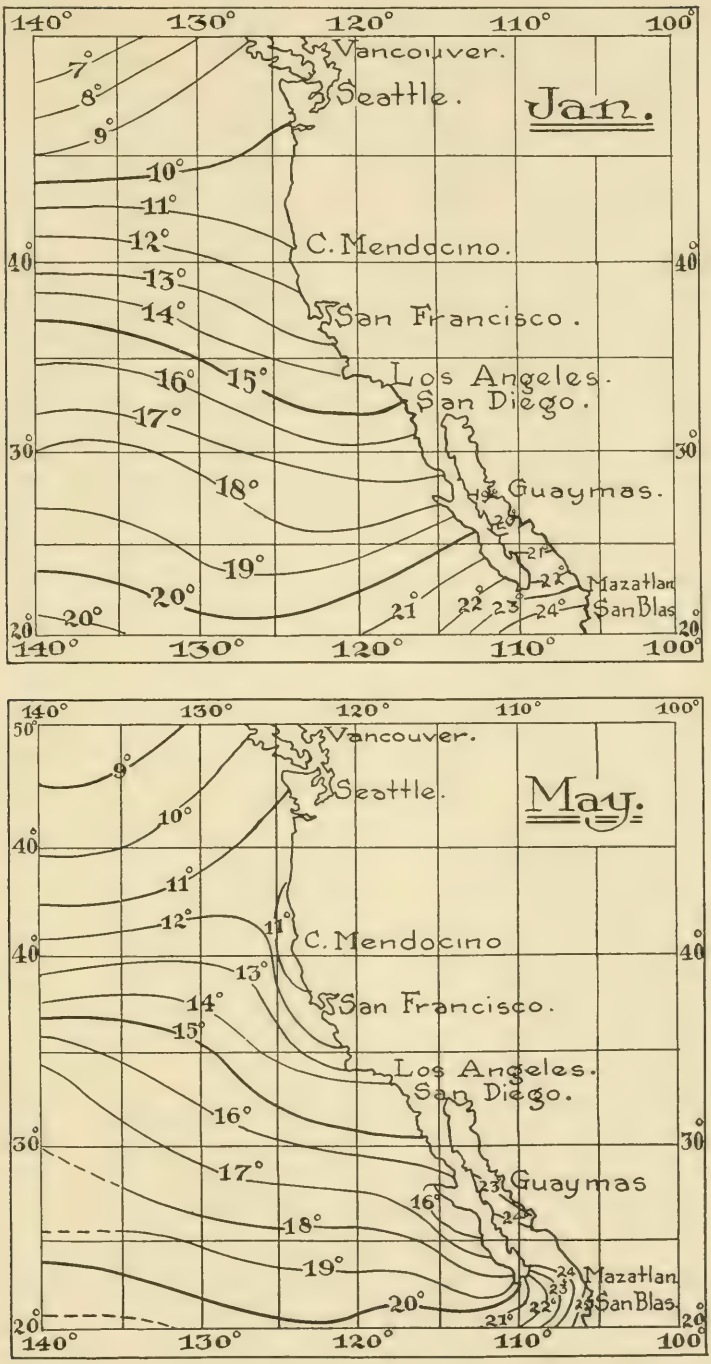


Fig. *A*. Distribution of surface temperatures off the Pacific coast of North America in January and May. After Thorade (1909).

Schott and Schu (1910) have tabulated the temperatures of the various depths and latitudes from depths of 0 meters to 4,000 meters and from 60°N latitude to 50°S latitude. Their table and the map of the Pacific coast give a very good idea of the distribution of the temperature in the different depths and latitudes (see tables 6 and 7). Comparing some of the data in this table we find that the temperatures of the various depths near the equator correspond to the temperatures of the various latitudes. The temperature at a depth of 3,000 meters near the equator corresponds to the surface temperature of 60°N latitude. The temperature of the water at a depth of 1,500 meters is identical with the surface temperature at 55° latitude. The temperature at 1,000 meters depth at 0° latitude is equal to the surface temperature of 50° latitude. The temperature in the depth of 400 meters is equal to the surface temperature at 40° latitude. The temperature at 200 meters at 0° latitude is equal to the surface temperature of 30° latitude, and the temperature in the depth of 100 meters at 0° latitude is identical with the surface temperature of 20° latitude.

II. Temperature as a Factor Controlling Distribution

The above facts show that the vertical distribution of the temperature from the surface to the bottom in the lower latitudes is comparable to the horizontal distribution from the equator to the poles. In some places along the coast the changes in temperature are so abrupt that definite geographical points serve as division lines of different isothermal areas. If the distribution of certain species of animals and plants coincide with the distribution of the temperature zones, as has been observed to be the case, it is obvious that the temperature may be regarded as one of the main factors controlling the distribution of Polynoidae.

It is a well known fact that a strong heat in summer may kill all the shallow water plants within a few days by raising the temperature beyond the maximum which those plants can stand. Many organisms of phytoplankton occur in shallow water in winter, but in deep water during summer. The phytoplankton in the Gulf of Naples was not found in surface layers but in a depth of 200 fathoms where the water is considerably cooler, while in the oceans of higher latitude, as in the North Sea, where the surface temperature is lower, the diatoms and Peridiniae are found at the surface. In these regions, again, the depth

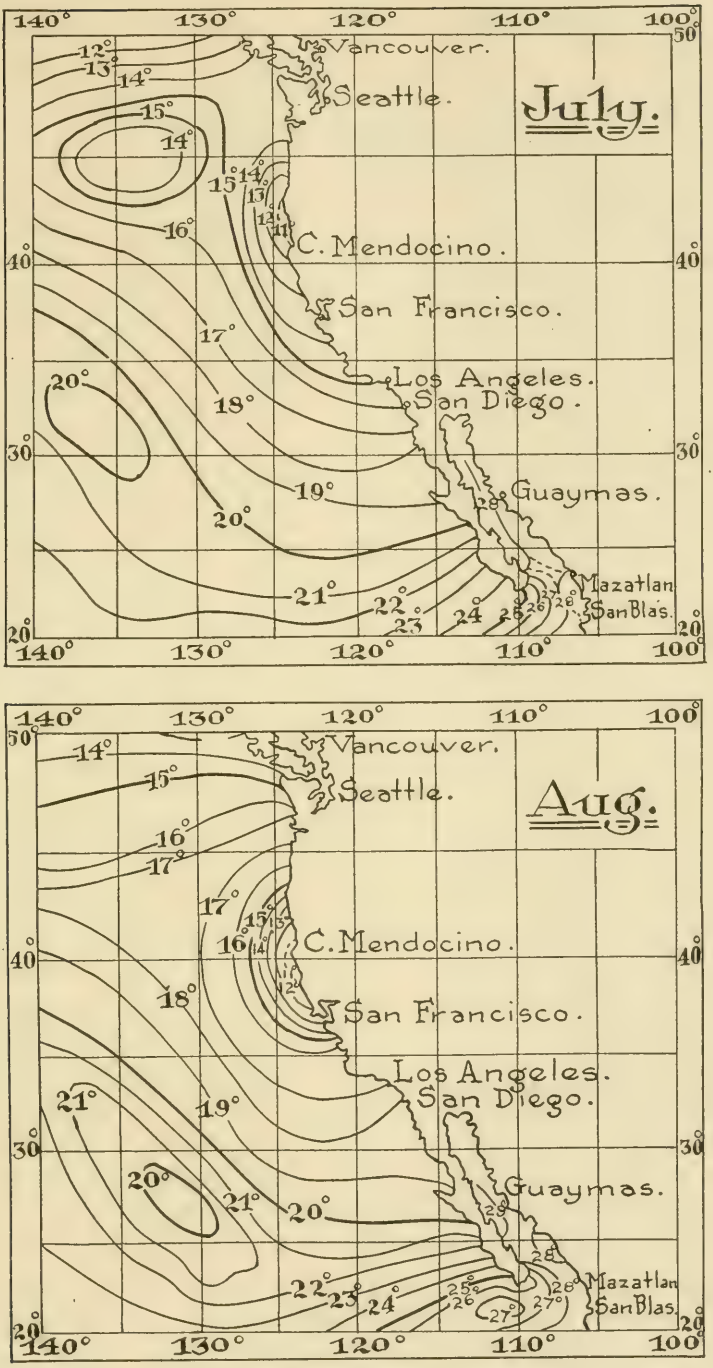


Fig. *B.* Distribution of surface temperatures off the Pacific coast of North America in July and August. After Thorade (1909).

of the habitat of the plankton varies with the seasonal changes. At the beginning of the summer the plankton generally is abundant at a depth of 20 meters. With the increasing surface temperature, however, it gradually sinks to greater depths and in late summer it is found at a depth of 60 to 80 meters (Steuer, 1911).

Observations on *Sagitta bipunctata* have revealed the fact that this species increases in abundance as the temperature increases from 9° to 14° and decreases as the temperature increases from 16° to 21° (Michael, 1916). This is a clear proof that the maximum temperature for that species lies between 14° and 16°; hence the species undergoes an oscillation downward or upward with the increase or decrease of surface temperature.

It has also been observed that some animals, such as medusae, crustaceans and pteropods, come to the surface during the night, and sink to a greater depth during the daytime. A sudden change in temperature may kill the larvae of aquatic animals. Murray and Hjort (1912) have observed that if the eggs of *Cucumaria* are shed in summer when the surface temperature of the Arctic waters is high, they are killed without hatching a single larva. Adult animals, as a rule, can stand more fluctuation of temperature, but there is a maximum and a minimum temperature above or below which the animals cannot live. The power of adaptation differs in different animals and consequently the maximum and minimum temperature cannot be the same for all animals. Hence the species will become adapted to that environment which is best fitted for its existence; while animals unable to adapt themselves perish. In whatever way temperature affects animals, it is evident that it plays an important rôle in their distribution by serving as a barrier.

One of the best illustrations of the effect of temperature is Wyville Thomson's Ridge. This ridge stretches from Iceland to Shetland, separating the Atlantic Ocean from the Norwegian Sea. The temperature in the upper strata of water, extending from 400 to 500 meters depth, is the same on both sides of the ridge, and the fauna of the upper strata is alike in both regions. But at a depth of 1,000 meters the temperature on the Norwegian side is below 0°, while on the Atlantic Ocean side it is 6° to 7°. The deep sea faunas on the opposite sides of the ridge differ greatly. Of 216 species taken from the depths of the warmer region, and the 217 species from the colder region, Murray (1898) found that only 48 species were common to both sides. Other oceanic areas where the temperature changes less

abruptly show the same corresponding gradual changes in faunal distribution.

Izuka (1912) shows that the Kyushiu Island is an important boundary line of distribution. Numerous northern species cease to exist south of Satsuma, and the southern species do not extend north beyond that point. On the Pacific side, the island Kinkwasan forms the boundary line of distribution of annelids. The cold water species rarely extend south of Kinkwasan Island, and the warm water species do not occur north of that island. Here again the chief factor, if not the only factor, controlling distribution is temperature. This difference in temperature is caused by the cold and warm currents sweeping past the Japanese Islands. The islands there form a natural division line between the warm and cold oceanic areas. Hence it is natural to find the northern species occupying the cold area on one side of the island; while on the other side of the island, in the warmer area, the warm water species only occur.

An evidence of the influence of temperature on distribution is the fact that arctic littoral species of polynoids, with a few exceptions, appear as deep water forms in warm oceans. On this coast a few species of Polynoidae are known which inhabit the littoral areas in the boreal zones, while nearer the equator, in warmer waters, they inhabit greater depths. As examples may be cited the following species: *Gattyana amundseni, Gattyana cirrosa, Harmothoë multisetosa* and *Lepidonotus caelorus.*

Gattyana amundseni has been found off Greenland, at about 77° latitude, as a littoral form at a depth of 16 fathoms, while in lower latitudes along the coasts of Alaska, it occurs in deeper waters between 50 and 100 fathoms depth (table 5). Comparing the temperatures of the corresponding latitudes we find that the temperature in waters of Greenland is about 0°, while near the Alaskan coasts, about 58° latitude, it is about 1°.4 to 2°. In a depth of 100 meters, however, about 50 fathoms, the temperature at the latter latitude is 0°.4 (see tables 6 and 7), which is about identical with the temperature of the shallow waters off Greenland.

Gattyana cirrosa occurs in the Arctic oceans off Greenland and Alaska, about 60° to 70° latitude, in depths of 10–12 fathoms, while the same species occurs off the shores of Great Britain, about 55°N latitude, at a depth of 600 fathoms. The surface temperature at the coresponding latitudes differs considerably but the temperature of 600 fathoms depth off the shores of Great Britain is nearly identical

with the surface temperature off Greenland and that of the coasts of Alaska.

Harmothoë multisetosa is found in the lower boreal zone, along the shores of Alaska, in depths of from 18 to 23 fathoms. In the temperate and subtropical zones it occurs in depths varying from 50 to 750 fathoms. It is more abundant beyond the 500 fathom line, only one case at a depth of 50 fathoms having been reported from Monterey Bay where the species occurred. Off Cape Colnett, in Lower California, however, the species occurs in 1,400 fathoms depth. Again, comparing the temperatures of the corresponding latitudes and the depths (tables 6 and 7) given in connection with the distribution, we find that the species, although occupying widely separated areas and different depths, lives in identical temperatures, and evidently for that very reason is found in deep waters in the subtropical regions, where the temperature is the same as that of the shallow waters of subboreal regions. With a farther advance toward the tropical regions, its habitat extends to greater depths, and this is true of the temperature (table 6). In order to find the temperature identical with that of the Arctic waters, one must seek it in deeper and deeper water as he approaches the equator.

Another species, *Lepidonotus caelorus,* occurs in abundance and in various depths on this coast mostly between 70 and 500 fathoms. Off Cape Colnett, Lower California, the species occurs at a depth of 1,400 fathoms. The temperatures of the various depths occupied by this species, however (table 6), are identical. These facts seem to prove that species, although they may occupy widely separated geographical areas, do live in identical temperatures. [Speaking of identical temperatures, one has to keep in mind that the temperature of an entire life zone, and not of one particular point is considered; consequently an allowance for variation in temperature of about five degrees or more should be made.] Similar observations were made by Ehlers (1875) who found that Arctic species of annelids outside of the Arctic realm always inhabited considerable depths, and were never found at the depths frequented by the same species in colder regions. This was shown remarkably well in some parts of the Norwegian Sea, where near shore the temperature is constant, ranging from 6° to 7°. Approaching the deeper basin of 600 meters the temperature is about 0°, or identical with the temperature of Arctic waters. A corresponding difference in distribution of annelids was also found there. In the warmer areas, nearer shore, were found the warm water annelids which

had migrated from southern latitudes, while in the greater depths exclusively arctic species predominated.

The observations of investigators in other fields of animal life strongly support the view that to a great extent temperature determines the distribution of oceanic fauna. The studies on Dinoflagellata prove that certain species of *Gonyaulax* (Kofoid, 1907, 1911) may be designated as distinctly warm water forms occurring in the warm waters of the tropical and subtropical zones on this coast as well as in other oceans, while the species occurring in the subboreal regions on this coast are also reported from other parts of the world from the cold waters. The ascidians of this coast (Ritter, 1913) are distinguishable as boreal, subboreal, and temperate species, each group being limited strictly to its temperature zones.

Furthermore, we find that the same temperature relations prevail in the distribution of terrestrial fauna and flora. Contrasting the valleys and mountains, where the difference in temperature is considerable, we find that many species of animals are restricted to valleys in higher latitudes which in lower latitudes in tropical areas, inhabit higher altitudes or the alpine zones; while the lowland species of a subtropical or tropical zone do not ascend to the higher altitudes of that latitude. Oregon lowland forms of insects extend southward into California where they seek a higher altitude. Some species, like *Tragosoma harrisii,* occur from Sitka to California. In the cooler regions in the higher latitudes, they are found in lowlands. They rise as they approach a more southern region until in the subtropical Californian areas they inhabit the zones above 10,000 feet altitude (Cockerell, 1893). Furthermore, some Coleoptera which occupy the lowlands in temperate zones occur as alpine species in the Andes in Ecuador and are never found in tropical lowlands. Some Coleoptera which occur as alpine and subalpine species in the tropical and subtropical areas of North America are found in Canada, Lapland and other northern countries as lowland species.

Comparing the high-alpine, mid-alpine and subalpine species of insects of tropical zones we find again that each zone has its distinct species which do not occur in the adjacent zones. The level at which certain species may be found varies with the season, the line rising up the hill during summer and receding towards the valley in winter. The valleys and the mountains on the dry land, as far as the temperature is concerned, are comparable to the shallow and deep waters in the oceans. The effect on distribution is comparable in the two cases.

These observations lead to the conclusion that the distribution of Polynoidae, which occurs in a definite manner, is not a mere accident, but that it is governed by some underlying principles or factors. One of the chief controlling factors undoubtedly is temperature.

III. Rôle of Currents in Distribution

The locomotion of Polynoidae is by means of swimming and crawling, the latter method being the more common. If a polynoid is brought to the surface of the water, it swims with undulating motions, soon returning to the bottom. The writer has never seen an adult polynoid rise to the surface under ordinary circumstances and swim, as many other polychaetous worms do. Keeping various annelids in aquarium, the writer has observed that some of them, e.g., Phyllodocidae, Nephthydidae, if disturbed rise to the surface and swim about vigorously, and very often when the aquarium overflows the worms are found outside of the aquarium. The Polynoidae, however, do not leave the aquarium even when the latter overflows. This shows that they habitually live on the bottom, crawling about slowly, searching for their food in the mud and capturing other smaller animals or attacking one another.

Since the Polynoidae are bottom dwellers and are not known to be very powerful swimmers, how then shall we account for their wide distribution? With their limited powers of locomotion they could not possibly traverse distances of thousands of miles, yet the cosmopolitan species occur in all oceans, as I have stated, from the Arctic Ocean to and south of the equator (table 5). Some Pacific coast species as *Harmothoë hirsuta* inhabit the northern subtropical zone along the shores of southern California, but one example of this species, however, has been found on the coast of Chile. *Harmothoë forcipata* also is known to occur abundantly on the coast of southern California (Moore, 1910). One specimen has been found near Eno-Sima, Japan (Ehlers, 1875), and another specimen has been found on the north coast of Korea at a depth of 1400–1600 meters (Marenzeller, 1902). *Harmothoë tuta* has been reported from Sitka (Grube, 1855) and from Puget Sound (Johnson, 1901). *Harmothoë yokohamiensis* has its habitat along the coast of California (Moore, 1910), but one example has been reported from Yokohama, Japan (McIntosh, 1885). A number of examples of *Gattyana senta* have been taken on the southern coast of California, but the same species has also been reported from McCormick Bay, Greenland (Moore, 1902). Numerous cases of this

kind are known in which Polynoidae are found occupying areas that are separated, sometimes by thousands of miles. Considering those species with relatively few individuals and found in widely separated areas, we come to the conclusion that the creatures would never have arrived there by their natural means of locomotion, but that there must be some natural factor or agent facilitating their distribution.

One of the best means of dispersal is undoubtedly the oceanic currents. These may influence the distribution indirectly or directly. First, by influencing or changing the temperature of the water. Secondly, by carrying terrigenous debris and small oceanic animals to some places, thus preparing better feeding grounds for the Polynoidae. Or the powerful currents may remove the debris from other places leaving the rocks bare and unsheltered, thus changing food conditions. Acting directly the currents may carry adult worms along the bottom of the ocean or in weeds along the surface. The latter mode of transportation is known to be true of *Nereis*. *Nereis dumerilii* was collected in the middle Atlantic Ocean (Ramsay, 1913) where it had suposedly drifted from the neighborhood of the Gulf of Mexico with the southwest drift. *Nereis mirabilis* has been recorded from the coasts of Brazil, Florida, Porto Rico, Bermuda, the Red Sea and the Persian Gulf. Since this species lives and breeds in the algae it is supposed to have been carried out with the floating weeds.

But the usual way of transportation probably is that of carrying the eggs and pelagic larvae of the worms. If the pelagic larvae happen to be caught in a current, they may drift very rapidly to great distances. This may account wholly for the wide distribution of some of the Polynoidae.

One would naturally inquire why there are not more annelids scattered in the ocean and why in so many cases only a few specimens of some particular species are found in restricted areas far away from their natural habitat. The reason, apart from imperfections of observations, that only a few individuals of a species are found far away from their original home may be due to their becoming there the prey of natural enemies. The greatest impediment, however, would be the sudden changes of temperature which would destroy the larvae. For instance, the larvae of arctic Polynoidae if carried to tropical zones, would probably be killed by the high temperature of the surface waters. Their survival would depend greatly upon the season in which the larvae were carried, and upon the character of the bottom where they happened to drop in changing from the trochophore to the adult stage.

On the other hand, assuming that the arctic larvae were carried to the lower latitudes in a favorable season, i.e., during the coldest months, the larvae, although they would have more chance to survive on their journey, would nevertheless sooner or later be killed by the temperature if they happened to be driven to warm shallow waters in the tropical zones. Those that were carried to deep waters would find a temperature identical with that of their natural habitat, and would survive and adapt themselves to the new surroundings. Considering their numerous enemies and unfavorable conditions one realizes that there is very little chance for the larvae to survive and probably for that reason we find very few individuals, and those in limited areas far away from their original habitat. Such supposition would explain why the arctic species of Polynoidae, when found on the coasts of California, are so largely deep water inhabitants. As exceptions to this are the cosmopolitan species which are found on these coasts in shallow waters. But it may be that in this species the plasticity and the power of adaptation are more highly developed, so that they would be more fit to survive the vicissitudes of such transportation. Probably for that very reason they are so widely distributed.

The most powerful oceanic current on this coast aiding in the distribution of the oceanic fauna is the extension of the Kuro Siwo, or Japan Current, flowing along the Pacific coast of North America, striking the American coast at Sitka, Alaska. At this point it broadens out, drifting slowly toward the equator and curving away from the coast. The Japan Current is joined on the west side by the southerly drifting surface waters which increase in volume and breadth until at latitude 25° the current extends more than 1,000 miles off shore (McEwen, 1915). This current undoubtedly serves as a powerful agent of transportation or distribution of species. Probably it is due to the action of this current that species from the coasts of Japan and Alaska have representatives along the coast of California and near the equator.

IV. The Winds

In addition to oceanic currents, the winds may be regarded as agents of distribution. The prevailing winds act upon the water, causing cool upwellings of the bottom layers. This has been observed to be the case along most of the Pacific coast of North America. This upwelling water is driven in an easterly direction or toward the shore, thus causing in some parts an inshore cold belt. With the moving body

of water oceanic life may be carried away. This action is especially noticeable after severe storms when deep water animals are found washed ashore and when marine algae whose habitat is far off the shores are also abundant on the beach. The same phenomenon is known to occur on other coasts. After a severe storm the beach of St. Andrews, Scotland, is known to be strewn with multitudes of *Aphrodita aculeata*. These aphrodites are driven by the currents from the offshore grounds, where they normally live in deep waters.

Many times after the retiring tides, the beach for a distance of a mile or more has been covered with aphrodites and other deep water species (McIntosh, 1900). *Gattyana cirrosa*, which normally occupies a depth of 600 fathoms in that region, has been found on the beach after storms. Similar observations on the effect of storms have been made on the coasts of Scandinavia. Since deep water species are driven to the shores it is also probable that severe storms or even the prevailing winds with their constant action on the waters may drive animals from the shores into the depths.

V. Chemical Composition of Water

As another factor controlling distribution may be mentioned the chemical composition of the water. The differences in salinity may influence the distribution of Polynoidae to some extent. Some species of Polynoidae can live in brackish waters as well as in salt. Some species have even been found in river estuaries. Others, again, are restricted to salt waters only. It is found that species most widely distributed live under more varied conditions, while very restricted species usually occur in similar environment even when they are found widely separated. Evidently some species have acquired a greater plasticity, while others may be more sensitive to changes in temperature and to chemical effects, and would either perish or undergo considerable changes. These chemical differences may also explain the greater number of genera and species in the great depths, if their environment were altered. Most probably littoral polynoids, migrating or driven to the depths of the ocean, are in a more or less pathological condition in the abnormal environment, and undergo such radical changes that they soon lose their identity with the ancestral shore species. That animals in great depths undergo pathological changes has been revealed by the studies on crinoids (Clark, 1915). These animals reach their minimum specialization between 550 and

750 fathoms, a depth which is the zone of an optimum temperature for the group. Below 750 fathoms they undergo semipathological changes, forming new genera and species. Murray (1898) suggests that the ancestors of the fauna of great depths have migrated from many shallow water areas, hence the great diversity of genera. This would hardly be necessary. If by sudden change in temperature different kinds of beetles can be produced (Tower, 1906), and if changes in temperature or treatment with potassium cyanide or magnesium sulphate can produce abnormal fish (Loeb, 1915; Stockard, 1909), it seems entirely possible that chemical and physical agents in the depths of the oceans may affect the deep water fauna in such a way as to modify their external appearance to so great an extent that in time the new generations are quite unlike their shallow water ancestors and become new species. The great number of genera and species of deep water Polynoidae may have been produced by the action of the chemical and physical influences upon migrants from the littoral zone.

A further proof that similar chemical and physical conditions may produce similar results affecting organisms equally is the fact that identical species of aquatic animals are found in corresponding life zones on both sides of the equator. Murray (1898) enumerates 150 identical species of Metazoa, and about 100 closely allied species, occurring in the extra-tropical regions of the northern and southern hemispheres, which are wholly unknown from the intervening tropical belt. This phenomenon suggests that similar chemical and physical conditions have a tendency to produce similar results. Furthermore, it is a generally known phenomenon that chitinous and calcareous animals are abundant in the tropics, while animals secreting little or no lime salts or chitin are more abundant in polar regions and in great depths. The deep water Polynoidae of the Pacific Ocean have soft, thin scales and cuticle. This condition may have been produced by chemico-physical influences which arise in the colder waters in the depths.

VI. Food Habits and Mode of Life

Polynoidae are voracious feeders, devouring any animal they can capture. Their chitinous jaws are strongly developed and well adapted for their purpose. In captivity they attack one another, severing segments and scales from the bodies of their companions; hence it is difficult to keep alive a number of Polynoidae in the same aquarium, for they inflict such serious harm to one another that they soon die.

Smaller and weaker polynoids are usually devoured by their stronger companions. They also feed on other annelids, small crustaceans, mollusks, sponges, and other small animals, as well as diatoms which are often swallowed with the debris. Some species living as commensals become ectoparasites, feeding on their messmates.

In connection with their food habits it is interesting to observe the modes of self defense or protection among the different species of Polynoidae, as well as among other annelids. The Polynoidae naturally hide beneath pebbles, empty mollusk shells or weeds in the aquarium. *Halosydna californica* when disturbed or attacked by individuals of its own kind moves away quickly but without any wriggling motions, very often leaving behind the attacked posterior segments or elytra. Some other Polynoidae act in the same manner. Harmothoë, on the other hand, when disturbed moves very swiftly with a vibrating, wriggling motion at first and then coils up, turning its ventral surface inside of the ring and spreading out its spiny, rough scales and its numerous serrated setae in such a manner as to protect the body. *Harmothoë imbricata* and *Harmothoë hirsuta* have been observed to use this mode of self defense. It seems as if the creatures knew instinctively the value of their protective organs and how to use them to the best advantage.

Other annelids that lack defensive organs such as chitinous jaws and rough elytra have other means of self protection. If Nephthydidae, Nemertidae, or Phyllodocidae are attacked by other annelids or are disturbed in some other way, they immediately protrude the proboscis, extruding a slimy substance which evidently must be disagreeable to their aggressors, for the latter immediately withdraw.

The abundance or scarcity of food undoubtedly plays an important rôle in the distribution of polynoids, so that one would naturally expect to find the worms more abundantly represented in localities where the food is at the maximum. The constitution of the bottom may determine the annelid population. It has been observed that some Polynoidae, and Annelida in general, occur in a depth of 14 fathoms in Kiel Bay, while the same species are found off the Faroes in 60 to 100 fathoms. Again, some species occur in great abundance on the shores of Greenland and Denmark at a depth of 6 to 10 fathoms, while around the Faroes they are only scantily represented at a depth of 60 fathoms. The cause of this difference in bathymetric distribution has been attributed to the differences in the constitution of the bottom. The shores of the Faroe Islands are rocky and steep, and the soft, muddy bottom

is found some distance away from the shores, while in other places the bottom nearer shore is muddy and soft (Willemoes-Suhm, 1874). The best feeding grounds of the oceanic fauna are undoubtedly the shore regions or littoral zone, where plant and animal life occurs in great abundance. Hence the Polynoidae and annelids in general are more abundant in the littoral zone. With an increase in distance from the shore and with an increase in the depth there is a decrease in individual numbers of the Polynoidae but a proportionate increase in genera and species. On this coast, although the littoral Polynoidae are very abundant so far as individual numbers are concerned, yet there are only four genera and fifteen species (table 4). Of these four genera, one, *Eunoë,* is not common in subtropical littoral zones but occurs as a littoral form in the boreal and subboreal regions, and as an abyssal form in the temperate and subtropical zones. This leaves only two strictly littoral genera in the subtropical and temperate zones. Of the exclusively deeper water polynoids we have seven genera and fourteen species. The number of deep water genera is about two times that of the littoral polynoids, and the number of species about equal. The number of individuals, however, is very small, and some deep water genera are known from but a single representative. Although we have to admit that the deep water survey is less complete than that along the shore, nevertheless the data show that there is an increase in genera with an increase in depth, and that the greatest uniformity prevails among the littoral polynoids. The species most abundantly represented on this coast, such as *Halosydna insignis, H. californica, H. carinata* and *H. interrupta,* are very much alike in their general appearance so that by superficial observation they are more likely to be taken as individuals of the same species. The same similarity may be observed among other species and genera and great diversity of species and genera found among the deep water species is not as common among the littoral species. Food conditions near the shore aid to increase and multiply the littoral polynoids. On the other hand, the scanty food supply in the depths, other things being equal, will naturally check the increase of the deep water polynoids. The deep water species of Polynoidae evidently do not inhabit the depths from choice, but many of them have been carried from the colder boreal regions and have found there identical temperature conditions although the food conditions are greatly different. Other polynoids have been driven off shore by waves or storms. Secondly, since the food supply in the great depths is insufficient only com-

paratively few animals can exist on a given area, while an area similar in size but with abundant food supply nearer shore naturally contains an abundance of animals.

Aside from the problem of food supply the mode of life of the Polynoidae deserves some consideration. The majority of the Polynoidae are free living forms and the largest numbers, as has been indicated above, are found near the shores and between tide marks where they hide in crevices and beneath rocks, pebbles and weeds or crawl about freely. Most probably they do not go very far from their dwelling place unless driven away by some physical force.

There are, however, some polynoids which depend for their distribution on the locomotion and the mode of life of other animals. These are the commensal forms. The number of strictly commensal species known up to present time is limited. Nevertheless, some species are known exclusively as commensals and depend for their distribution on their messmates; hence their distribution naturally coincides with that of the latter. These commensal polynoids are: *Lepidasthenia gigas,* commensal with a large tube dwelling annelid, *Amphitrite; Polynoë lordi,* commensal with the limpet, *Glyphis aspera* and with *Cryptochiton stelleri,* in which it occupies the branchial groove; *Polynoë fragilis,* commensal with the starfish, *Asterias ochracea.* These species are known up to the present time only as commensals, and have a very limited distribution. A few other species occur both as free living forms and occasionally as commensals. Those known on this coast are: *Halosydna insignis, Polynoë californica* and *Harmothoë imbricata.* These species do not necessarily depend on their messmates since they live both as commensals and independently. They are most widely distributed on this coast. Evidently the ability to live in a variety of environments favors the wide distribution of these polynoids. The known facts and the observations lead one to the conclusion that the food habits, food supply and the mode of life play an important rôle in determining the distribution of the Polynoidae.

VII. Plasticity

Some of the most obvious external factors controlling distribution have been enumerated. But there may be other factors of a more complex nature, which are beyond our present reach and are waiting for future investigations. There is, however, one more factor, viz., variability. Variability or plasticity may be considered both as a

factor and a result of distribution. As a factor, because species with greater plasticity and greater power of adaptation are able to live in a great variety of environments, and consequently have more chance to survive than have species with a very limited power of adaptation. Some phases of variation serve directly as a protection to the animal. Other forms of variation are usually results of environment. It is the expression of a varied mode of life, or a response to external stimuli. This has been variously proved by experimental methods, where variations are produced artificially by changing the environment. Not all living organisms, however, respond to the same external stimuli in the same way. While one form of animal life may undergo considerable changes under the influence of external stimuli, others, being unable to adapt themselves to new conditions, will perish. This is shown in Loeb's experiments with the eggs and the embryos of *Fundulus* referred to above. While a great percentage of the embryos were killed after four to seven hours exposure to low temperature, others remained alive, and among the latter 30 per cent were abnormal. This indicates that there is a difference in plasticity or in the power of adaptation even among different individuals in the same species. In sudden changes of environment the power of adaptation will determine the survival and, consequently, the distribution of a species or an individual.

Numerous instances of great adaptation are known among various organisms signifying that the animals have an innate power which enables them to resist adverse conditions. This power is designated as plasticity or adaptability. The degree of plasticity varies in different species and individuals. Hence as the distribution depends to some extent on the power of the adaptation of the animals to the changing environment, the plasticity may be justly considered as a factor determining the distribution.

From the observations made, one comes to the conclusion that the plasticity in Polynoidae, although varying in degree in the different species, is fairly great in most. Marked differences between different genera and species are found among polynoids characterizing their mode of life and the influence of the environment upon them. These differences occur in the size, the shape and the color of the body, in the size, shape, texture and color of the elytra, in the number, shape and size of the setae, in the texture of the cuticle, and in other characteristics. These variations occur not only in different species but individuals of the same species which are living in different environ-

ments show such marked differences that they appear more like different species than individuals of the same species.

It is generally known that of the cosmopolitan polynoids occupying different latitudes, the arctic examples as a rule are larger in size than are those of the temperate or subtropical zones. *Lepidonotus squamatus* exhibits a characteristic difference in size among individuals from different localities. Comparing the specimens of that species from Finmark, New England, Puget Sound and from the coast of California, great differences in size appear. The size of the specimens from the coast of California is about one-third of that of the specimens from Finmark and New England. The specimens from Puget Sound are considerably larger than are the Californian but they are inferior in size to the arctic and eastern forms. Ehlers (1875) found also that the deep water forms were considerably smaller and that they have thinner elytra. A further influence of the depth on the polynoids is seen in the lack of pigmentation and the eyeless condition of the worms. A great number of the deep water polynoids are without eyes. Moore (1910) enumerates eight blind deep water species of Polynoidae on this coast. Of all the numerous polynoids in this collection, however, not a single specimen of the *littoral* species of this coast is eyeless. Ehlers (1875) believed that it is natural for the deep water annelids to be blind since many of the deep sea species have been found in that condition. He accounts for the possibility of some deep water individuals having eyes as due to the yearly migration of littoral forms toward greater depths.

The influence of the environment on the organisms is here very marked. Considering the environmental differences in shallow and deep oceanic waters, one will naturally expect to find the corresponding physical changes in Polynoidae. Besides the minimum food conditions in the great depths and the different chemical composition of the water, the pressure in great depths is very much greater than in the shallow waters, for it is a well known fact that the pressure in the ocean increases by about one atmosphere for every ten meters in depth; consequently in a depth of about 2,000 meters (1,000 fathoms) there is a pressure of 200 atmospheres. It has also been proved by various hydrographers (e.g., Murray, 1912) that there is no light in the oceanic depths below 500 fathoms. On the brightest day and in the clearest and most transparent waters only slight traces of the blue light rays are perceptible at a depth of 1,000 meters. The green rays are absent at a depth of 500 meters, the red rays are absorbed by

the surface layers without penetrating even to a depth of 100 meters. There is an absolute darkness in the depths below 1,000 meters. Adding these combined factors to the low temperature, insufficient food supply, the small quantity of free oxygen, and carbon dioxide are sufficient causes to bring about variations and changes in abyssal Polynoidae.

The effect of the environment on the Polynoidae and the great plasticity of the latter is especially noted in commensal polynoids. The variation in size between the commensals and free-living forms of the same species is remarkable in some cases. *Halosydna insignis* is a beautiful example of this variation. This species is known as a free-living form occurring in a variety of environments; it also lives as a commensal in the tubes of *Amphitrite* and *Thelepus*. The species is widely distributed, occurring along the entire coast of North America. The commensal individuals are longer and more rounded. The elytra are thinner and, excepting the first pair, devoid of marginal cilia. They are smaller and do not cover the entire dorsum. The spinous tubercules on the elytra are very much reduced and are almost microscopic in size (pl. 8, fig. 27). The dorsalmost setae are greatly enlarged and bear an enlarged spur. The neural setae are stouter and strongly hooked. The free-living specimens are broader and shorter and usually smaller in size than the commensals. The elytra are thicker, tougher and larger, strongly overlapping and covering the entire dorsal surface (pl. 8, figs. 28–30). They are thickly covered with large, horny prickles and bulbs. The marginal cilia are longer than they are in commensals and are present on all elytra; there is also a tuft of long cilia arising a short distance from the anterior margin. The setae are more slender, less strongly hooked, and with fewer serrations. The pigmentation is stronger in commensals than in free-living examples. But the pigmentation varies considerably in both kinds. From all the characteristic differences indicated the two forms are very likely to be taken for different species rather than for members of the same species; however, these characteristic differences in the commensal and free-living *Halosydna insignis* illustrate the great plasticity in that species of polynoids and the influence of the environment upon it. Thrusting itself into a tube of a messmate the polynoid does not naturally find the tube made to fit the shape of its body, and if it were not for the great plasticity of the creature it would perish in the tube if it did not soon leave it. But here comes nature to assist the intruder in adapting itself to its

new environment. A muscular adaptation occurs. The muscles, especially those in connection with locomotion supporting the parapodia, are constantly used by the free-living worm and through this exercise they are naturally well developed. In a commensal polynoid the locomotor muscles are of no use and begin to degenerate. Secondly, the dwelling place is too narrow and the walls of the tube press upon the broad lateral surfaces. This constant pressure forces the muscles to contract laterally and to expand ventrally, dorsally and longitudinally where no pressure or resistance is met. If the commensal polynoid remains in this condition for some time, the shape of its body will naturally be changed from a compressed flat one to a rounded one. The elongation of the segments will increase the length of the worm, the parapodia become shorter and broader and we have a worm that has changed its shape so greatly that it could hardly be recognized as being an individual of the species.

That Polynoidae tend to retain the plasticity, which is common to some higher types in the very early stage of development, is proved by the great power of regeneration which they possess throughout their lives. If a polynoid loses some of its segments, elytra or appendages, it regenerates them within a few weeks. This is an indication of plasticity and adaptability to diverse conditions.

The changes of color are probably produced by some enzymes produced by the messmate of the commensal polynoid. The small size of the elytra is evidently due to the disuse and the degeneration of those structures. The absence of the chitinous bulbs and protuberances on the elytra may be accounted for in the same way. First, the free-living polynoid is under the influence of some chemicals which act as stimulants in the production of the bulbs on the elytra. Living as a commensal its environment has been changed and the secretions or enzymes of the messmate may impede the development of the rough structures on the scales of the polynoid. That this is true is proved by the fact that the first pair of elytra remain unchanged. The reason for this condition is apparent. The polynoid is hidden in the tube with its anterior end, its tentacles and head projecting. The first pair of elytra remain in the same environment in the open water as they were before the polynoid entered the tube hence they remain unchanged. The external changes in this case may be traced back to the changes of environment and to the quick response or the plasticity of the polynoid undergoing these changes.

That the environment and adaptation may lead to some extreme variations is illustrated by the shape of *Polynoë ocellata*. This species has been recorded from Japan (McIntosh, 1900; Izuka, 1912) as a commensal, living in the tubes of *Spirochaetopterus challengeria*. The worm is extremely elongated and narrow, having over one hundred segments and fifty or more pairs of elytra. The length of the worm is about 60 mm. but its breadth is only 2.5 mm., including setae. It is most vividly colored with yellow, olive, black and white markings. The elytra are exceedingly small, translucent and smooth. The first pair of elytra, however, are large, covering the prostomium completely; they are also less delicate. In a vertical section, McIntosh discovered that the cuticle and hypodermis of the worm are unusually thin. This again illustrates the great variability and the power of adaptation of this polynoid. It is remarkable that the external changes do not occur uniformly but that parts subjected to somewhat different environment, as the anterior elytra, which are naturally outside of the tube and are exposed to the free ocean water, differ in size and structure.

As far as is known it may be considered as a general rule that the commensals are usually larger in size than the free-living individuals of the same species, provided the dwelling place of the commensal is sufficiently large so as not to interfere with the expansion of its body. *Polynoë californica* is known as both commensal and as free-living. The commensal animals are noted for their large size, while the free-living individuals collected from various places are much smaller. All the largest specimens, except one from Santa Catalina, were collected near San Pedro. They range from 35 to 45 mm. in length and from 8 to 14 mm. in breadth. The specimens from other localities have a size ranging from 15 to 30 mm. in length and from 5 to 11 mm. in breadth. The average length of the worm is about 25 mm. Johnson (1897) states that the species has been found on a huge Amphitrite off San Pedro. That the commensal forms of Polynoidae are usually larger in size, relatively and absolutely, can be proved by the fact that not only individuals of the same species distinguish themselves through their larger size from the free-living specimens, but that species which are known exclusively as commensals are of relatively greater size. Thus the largest species in the family, *Lepidasthenia gigas*, is a commensal with an amphitrite. The largest specimens measure 180 mm. in length, and 7.5 mm. in width. It would be a far-reaching conclusion to assume that *Lepidasthenia gigas* has

reached its large size because of its commensalistic habits, but it is very likely that the commensalistic habit aids it in maintaining its large size. The commensal habits evidently are of some advantage to the polynoids favoring their growth and development. One advantage is that the commensals do not have to exert as much energy to obtain their food as do the free-living worms. In thickly populated places the competition among animals must be considerable, hence an animal must exert a great amount of energy in changing location and in pursuit of prey. At the same time it has to be vigilant in guarding its own safety lest it fall a victim to other animals. The free-living Polynoidae usually are found beneath rocks or weeds or in crevices. Occasionally they venture out of their hiding place, but the least disturbance causes them to disappear again. Their great activity will naturally reduce the volume of the body or check its development. On the other hand, the commensal does not have to exert any energy. It is well protected and leads a passive life. Secondly, it obtains an abundant food supply. The writer has watched some of the tube-dwelling annelids many times. They reach out their numerous tentacles in great distance forming a circle and capturing any object within their reach conveying it then to the mouth. It is surprising to see the amount of food and material they may convey to the tube. Once the writer destroyed the tube of some tube-dwelling annelids, crumbling it carefully to pieces without injuring the worms which were then put into a small glass dish where the material of their tubes had been crumbled up in fine granules. The worms immediately set to work with their tentacles rolling the small pebbles and the grains of sand toward their bodies and cementing them with some substance which was formed around the body. Within less than two hours the tubes, about two inches in length, were completed. If a terebellid worm is placed in an aquarium where the food supply is insufficient it stretches out its long tentacles covering considerable distance. The tentacles when stretched to the limit are about equal in length to the body of the worm. As soon as one of the tentacles comes in contact with some substance or food particles it immediately contracts and bends, conveying that substance to the mouth. If the polynoid is in the tube with its head at the entrance it may capture every food particle that is conveyed toward the tube, robbing thus its messmate of its food and receiving an abundance of food for itself, at the same time remaining perfectly quiet. This passive condition and the abundant food supply will naturally result in an increase in

the size of the body. Commensals that live on the surface of moving animals have the same advantage. While the food is not carried directly to their mouths, the polynoid however is carried to new feeding grounds and no energy is used in locomotion. Hence there is less chance for reduction of the size of the body. Moreover, the polynoid may become an ectoparasite, obtaining some of its food directly from its messmate. It has been found that some Polynoidae living on sponges had in their digestive tracts spicules of the sponges on which they lived. This proves that they are feeding on their hosts. They may become ectoparasites on other animals in a similar manner, consuming some of the secretions or part of the food of their hosts.

Another interesting feature is the adaptive coloration in Polynoidae. This evidently is the result of the environment. Such an example remarkable for its adaptive coloration is *Polynoë pulchra*. The worm is commensal with two animals, the sea cucumber, *Holothuria californica*, and the keyhole limpet, *Lucapina crenulata*. Living specimens from both hosts were given to me for identification. Judging from the color they look more like different species than individuals of the same species. Only microscopical examination reveals the identical specific characteristics of both. The example living on the holothurian mimics the color of the latter to perfection and can be hardly detected when it lies quietly on the surface of its host. The polynoids occupying the cavity between the mantle flap and the foot of the limpet are very conspicuously colored, with prominent black markings which show plainly against the uniformly colored, whitish yellow background of the ventral surface of the limpet.

Another example of a polynoid showing great adaptive coloration is *Polynoë fragilis*. This species lives in the ambulacral groove of the starfish, *Asterias ochracea* and *Asterias trochelii*. Johnson (1897) had an opportunity to observe the polynoid on the aboral side of the starfish where its coloration harmonized so well with that of the *Asterias* that it escaped any notice. The elytra of this polynoid also are thin and delicate, without any tubercles or prominences, and covering the dorsum only partly (pl. 8, fig. 32). A remarkable adaptation is also seen in the setae (pl. 7, fig. 14). The latter are few, slender, pointed and hooked, being thus well adapted for attachment. Moreover, the setae as they become blunt from wear are continually replaced by new pointed ones growing out from the base of the parapodia (pl. 7, fig. 15). The latter characteristic is not common to all Polynoidae but is an exception observed in a few species which are in a habit of attaching themselves to other animals.

McIntosh (1900) has observed a remarkable variation in *Polynoë scolopendrina*. This worm lives as a commensal and as a free-living form around the shores of England and off the Hebrides. Besides the remarkable differences in size between the free-living and commensal forms from the shores of Great Britain and the individuals off the Hebrides there is a difference in coloration particular to each group. The coloration is especially conspicuous in the commensals occupying the burrows of *Lysidice*. The commensal, according to McIntosh's observation, is very narrowly compressed. The pigmentation of the anterior ventral portion of the body of the worm and around the mouth has a coloration mimicking the *Lysidice*. The tube-dwelling *Polynoë scolopendrina* have the setae greatly modified; especially is this true of the dorsal setae, the tips of which are curiously wrinkled. The specimens from the Hebrides, however, prove that in the normal conditions the setae are finely tapered. The wrinkled condition has evidently been brought about through the commensal life.

E. GENERAL DISCUSSION

The fact that Polynoidae fall into different groups according to their geographical and bathymetrical distribution suggests that the phenomenon of distribution is governed by certain physical and chemical factors and that the Polynoidae, reacting in response to the external stimuli, are limited to their particular distributional areas.

One of the most important factors controlling distribution is the temperature. This is proved by the fact that certain species of Polynoidae are limited to definite temperature zones, and that boreal species, occupying the littoral zone, occur as deep water species in temperate and in subtropical zones. Since the most apparent similarity between the boreal shallow waters and the subtropical deep waters consists in the temperature, this latter may be considered as the chief factor in distribution. Other factors, as currents and winds, may act in transportation of the larval and adult forms or by influencing the temperature and the food conditions.

The food conditions may be of importance in distribution and polynoids may be naturally expected to be more abundant where food conditions are maximum. This condition is found in the littoral zones.

The greatest number of polynoids is found in the littoral zones. The number of polynoids decreases with the increase in depth. On the other hand, a greater uniformity prevails among the littoral polynoids. The number of genera and species increases with the increase in depth so that the deep water genera of this coast are almost two times the number of the littoral, and the deep water species are almost equal to the number of the littoral. This condition seems to indicate that the littoral zone is the center of origin of the Polynoidae and that they have migrated or have been driven occasionally from the littoral zones to the deep water where they have probably undergone considerable external changes, forming thus new genera and species, while the shallow water forms living in the same environment have maintained a greater uniformity. Moreover, the different environment in the greath depths, as the low temperature, the absence of light, the difference in chemical composition of the water, may produce a semipathologic condition in the polynoids affecting the germ cells, and thus bring about rapid changes and partial degeneration. This is suggested by the great degenerative changes found in the deep water polynoids. The deep water species, as compared with the littoral species, are as a rule smaller in size, and have delicate cuticle and elytra. A great number of the deep water species are without eyes. On this coast out of fourteen abyssal species eight are known to be without eyes (Moore, 1910). This shows that the deep water species have undergone certain physiological and morphological specialization in adapting themselves to their particular environment. This special adaptation or the degenerate condition, however, makes them unfit to adapt themselves to any other environment. The low temperature in the depths of the ocean undoubtedly has a great effect upon the developing annelid eggs in producing abnormalities and physical variations. This assumption is in accord with the laboratory experiments where abnormalities, such as blindness and other defects, are produced artificially by subjecting eggs in their early stages of development to a low temperature. Secondly, the embryos may be affected by the sudden environmental changes or by the shock effect of the sudden change of temperature. The annelid trochophores rising from great depths to the surface would naturally come suddenly into a very much higher temperature which would kill the majority of them or would modify them greatly. In the littoral zones where the difference between the bottom and surface temperatures is less conspicuous, the worms in their embryonal development are not

subject to the sudden environmental changes and are less likely to be killed by the temperature or to undergo any variation and abnormalities.

There is a general belief that the deep water annelids are without eyes or blind on account of the absence of the light in the great depths. Experiments in the laboratory have proved that absence of light does not produce blindness, but on the other hand by exposing eggs to 0 to 2° temperature, numerous abnormalities and blindness in embryos of the fish *Fundulus* were produced (Loeb, 1915). Since the corresponding low temperature is found in the depths of the ocean it would not be at all unlikely that the low temperature, although it may not change the adult forms which have been carried from warmer areas to the cold waters in the depth, may still affect the second generation—the eggs of the first migrants—and thus produce blindness indirectly. So that the cause of blindness and eyeless condition of the abyssal Polynoidae might be attributed to low temperature rather than to darkness.

The degree of light intensity may be a cause of modification of the eyes of deep sea animals. It has been found (Brauer, 1901) that in all fish from about 300 meters, the rods only are found in the retina of the eye, a condition which is characteristic also of the eyes of nocturnal animals; while diurnal animals have both rods and cones. The differences of the pigment of the retina in the deep sea fish signify that their eyes are adapted to nocturnal conditions. Further result of the modification and adaptation is the telescopic eyes of some fish. There are also great numbers of blind fish in the depths of the ocean; it remains an open question whether the blindness is caused by the low temperature or by the action of some chemicals in the deep sea or by a combination of both.

That the plasticity is great in Polynoidae is proved by the fact that considerable changes are produced. A remarkable difference is noticeable in the size and shape of different individuals living in different environment. Boreal species as a rule attain a larger size than individuals of the same species occurring in tropical and temperate zones. This rule of comparative size within a given species does not hold strictly true as between localized species. The largest known polynoid, *Lepidasthenia gigas,* is subtropical, inhabiting a limited area on the coast of southern California. It is quite possible, however, that its great size is an unusual development since the animal is an exclusive commensal.

The greatest variation and plasticity is seen in the commensal polynoids. As a general rule the commensals are larger in size than the free-living individuals of the same species. This fact is undoubtedly due to the greater food supply which a commensal obtains by robbing its messmate of the food which the latter has secured, or the commensal may become an ectoparasite as has been observed to be the case with some polynoids living on sponges. In examining the contents of the stomachs of polynoids (Darboux, 1899) spicules of sponges were found indicating that the commensals had been feeding on their messmates. Secondly, a commensal is protected by the messmate by living in the tube or hiding in some sheltered place of the body of the latter. Since it lives there in absolute quiescence there is less catabolism in its organism than in the free-living worm which has to exert a great deal of its energy in securing food and in watching for its own safety. Consequently almost the whole food supply of the commensal goes to build up and to increase the bulk of the body, and the natural result is the larger size of body which has been mentioned above.

Moreover, the shape of the body of the commensals may be greatly modified by an increase in length, and by reduction in breadth, thus changing from a short, compressed to a long, round form. The protective structures in commensals, as the elytra, the cuticle and the setae, are usually degenerate.

A marked adaptive variation is noticeable in the number, structure and size of the setae according to the mode of life of the commensal. In the free-living species the setae are numerous, usually from 50 to 100 on each parapodium (pl. 7, figs. 1, 19). The setae in the free-living species are also rougher, with numerous, strong serrations (pl. 7, figs. 4–6, 8–11). In commensals and ectoparasites, especially in those which are in the habit of attaching themselves to their hosts, the number of setae is greatly reduced (pl. 7, figs. 15, 17). Some species, as *Polynoë pulchra* and *Polynoë lordi,* have only 5 or 6 slender, smooth, sharply pointed setae, the blunted setae being constantly replaced by new, sharply pointed ones which arise from the base of the parapodium (pl. 7, figs. 3, 7). In some of the tube-dwelling commensals, as *Lepidasthenia gigas,* the number of the setae is small, usually 5 to 8 on each parapodium. The setae (pl. 7, fig. 13) have a few serrations and are not so sharply pointed as are those in the commensals which use their setae for attachment to their host. In *Lepidasthenia gigas,* however, there is, in addition to the ordinary

setae, a strongly developed dorsal neuro-seta (pl. 7, fig. 18) peculiar to that species only. Whether it has any significance in the commensalistic life of that polynoid is an open question. Whether the reduction of setae is a secondary characteristic developed in response to commensalistic life, or whether the polynoids chose that mode of life because of the fitness of their setae for that purpose, is another question which cannot be definitely settled at present. However, the sharply pointed and hooked setae are of special use to the polynoid as a means of attachment to the host.

One phase of plasticity in polynoids reveals itself in the variation of color in response to different environments. In the majority of cases the abyssal forms are less brightly colored. The commensals and ectoparasites, however, display a great variation in color, as is seen in some species which occur simultaneously on two or more different hosts. For example, *Polynoë pulchra,* which lives on *Lucapina crenulata* hidden between the foot and the mantle flap of the latter, is very conspicuously colored, while individuals of the same species found on holothurians, completely mimic the color of the latter.

Such changes in color may be due to various causes but in each case are evidently caused in response to some chemical or physical stimulus. The color in each animal indicates that there is some chemical reaction particular to that species. With changes in the environment the physical equilibrium is disturbed and some chemical affinities may be more stimulated to reaction than others. These changes may induce new interactions in the tissue and protoplasm of the animal, resulting in external changes, such as changes in color. Polynoidae in great depths are, as a rule, less strongly pigmented or entirely unpigmented. This fact shows that there is some inhibitory action which prevents the pigment from forming. Whether it is the absence of light, the different chemical composition of the water, or the low temperature that produces the changes in color cannot be definitely decided. It has been proved by experimental methods that no pigment was produced in the chrysomelid beetles when the embryos were kept in low temperature (0° to 5°C) while embryos kept in high temperature (43° to 45°C) developed dark pigment (Tower, 1906). Since pigmentation involves the process of oxidation or metabolism, the temperature undoubtedly is an important agent in accelerating or retarding the development of color. Furthermore, the light intensity may be of some importance in production of color. However, the light reaction seems to be of secondary importance as is shown in the

fact that some commensal worms, such as *Polynoë pulchra* living on the keyhole limpet between the foot and the mantle of the latter, and protected from the light, are conspicuously colored. The same has been observed to be true with *Polynoë ocellata,* which lives as a commensal in tubes, sheltered from light, yet is very vividly colored.

The so-called color mimicry in Polynoidae may be due to chemical responses or to stimulating enzymes. The commensals living in close contact with their messmates probably have a chemical inter-relation with the latter, and are influenced by some of the same chemical conditions which are responsible for the color production in the latter. Under a similar chemical or enzymic reaction the same color pattern is produced in the commensal polynoid. This may be a plausible explanation of how commensal polynoids adopt the color pattern of their messmates to such perfection as is shown in *Polynoë pulchra* living on the holothurian, and *Polynoë scolopendrina* living in the tube of the *Lysidice,* both mimicking the color of their messmates. These facts seem to lead to the conclusion that there must be some chemical interaction between the two commensal species stimulating the latent chemical and protoplasmic properties of the worm to color production. That animals can be stimulated to produce colors has been proved experimentally by extracting the pigment-producing enzymes from beetles and placing parts of other unpigmented beetles in the extracted enzymes, with the result that pigment was produced on the unpigmented beetle (Tower, 1906). Evidently some influence must be exerted by the enzymes of the host on the commensal worms and the chemical complexes which are present in the protoplasm of the commensal, when stimulated in the polynoid, will react in a definite manner, producing similar colors to those of the host.

The great differences in coloration between *Polynoë pulchra* living on the keyhole limpet, and the one living on the holothurian may be explained on the basis that although the former is living in the mantle fold of the limpet in an area which shows no pigmentation, yet the pigment-producing enzymes are probably present in other parts of the body of the mollusk. The cells of the lower surface of the latter may not have the base, or the color-producing properties and hence do not respond to the stimulus of the enzyme, while the protoplasm of the polynoid possesses the color producing properties which are latent. As soon as they receive the proper stimulus, they react and the dark brown or black pigment, similar to that found on the upper surface of the mollusk, is produced in certain areas of the elytra of the poly-

noid. The color producing enzyme may be obtained by the polynoid either by partly feeding on its host or the enzyme may be given off the mollusk in some kind of secretion. There may be still another possibility, viz., that both the commensal and the mollusk are obtaining the same kind of food and that this food may act as stimulant in producing the same colors. Yet food alone could not be responsible for the color production; it may be only one of the agencies concerned in color production, else the pigment would be distributed more or less equally over the entire body. Cases are known, however, as in *Polynoë scolopendrina* (McIntosh, 1900) in which dark brown pigment is produced only around the mouth and the anterior ventral region, giving that part of the body the general appearance of *Lysidice* whose tube the polynoid occupies. The rest of the body is, however, less affected by the color. Be it the similar food conditions, or the influence of some enzymes that produce the same combination of colors in the holothurian and in the polynoid, and another color pattern in the mollusk and in the polynoid, it is evident that the same forces which act on the messmates in producing a certain color pattern do act on the commensal polynoids producing the same results. The significance here lies in the fact that animals widely different in the scale of evolution possess the same properties which when aroused by similar stimuli respond in the same way producing similar results in pigmentation.

Other external changes in commensals may be caused by the various environmental influences in response to the plasticity of the animal. The close contact with the messmates, probably through the secretions and enzymes of the latter, may react variously on the commensal, weakening the external structures such as the cuticle and elytra, so that they gradually degenerate (pl. 8, figs. 27, 31) or assume a more delicate texture like that of the messmate. The abundant food supply which the commensal obtains and the lack of exercise aid in increasing the bulk of the body, while the limited space in a tube aids in shaping the body, thus entirely changing the external appearance of the commensal. This suggests the possibility that a species, if subjected to similar environmental conditions for generations may change its characteristics and become a new variety or a new species. In our well known *Halosydna insignis,* the free-living and the commensal may become two distinct varieties, if not distinct species, if kept in their corresponding environments for generations. These observations suggest the possibility that the environment and a corresponding

plasticity may result in formation of new species. They further suggest the possibility that different species occupying different geographical and bathymetrical areas are descendants from common ancestral stocks and that their differences are the results of the particular external influences and of the degree of plasticity in each species. Species with the greatest plasticity are best provided with protective structures and are more widely distributed. Being able to overcome vicissitudes and changes in environment, they are superior to species specialized for certain modes of life and for certain environments. *Lepidonotus squamatus* serves as a good illustration. It has rough spiny elytra (pl. 8, figs. 34–35) covering the entire dorsum, and numerous strongly developed setae (pl. 7, figs. 8–11). On one occasion McIntosh (1900) observed that a specimen of *Lepidonotus squamatus* which was in a tank with other animals was coiled up so as to have its scales and setae placed to the best advantage for self protection. When it was picked up by a young cod it was immediately rejected and fell to the bottom. Again it was attacked by *Cottus,* and again also immediately rejected, while *Nereis* and other annelids were devoured by the same animals. This explains partly the world wide distribution of *Lepidonotus squamatus* while the largest species of the family, *Lepidasthenia gigas,* depending entirely on a commensalistic life and being ill protected outside of the tube, has a very limited distribution. Probably young *Lepidasthenia gigas* fall victims to their enemies if they do not happen to find a vacant tube of an Amphitrite; or their adaptability is so limited that they can live only in that particular environment as commensals and perish in open ocean. Hence there are no free-living forms of that species. These facts show that, besides the external factors, the physical condition of the animal, its powers of adaptation, and its variability are equally important factors in its distribution.

F. SUMMARY

1. Polynoidae as a group have a world wide distribution, occurring in all oceanic waters. The fifty-one species of Polynoidae on this coast are divisible into two main divisions: (1) the cosmopolitan, and (2) the non-cosmopolitan species. The cosmopolitan species occur in all oceans; the non-cosmopolitan are restricted to the Pacific Ocean and many of them occur only along the shores of North America.

2. The Pacific coast polynoids, on the basis of their geographical distribution, fall into boreal, north temperate, and subtropical species, according to the life zones they occupy.

3. The polynoids are again divisible into littoral, sublittoral, and abyssal species according to their bathymetrical distribution.

4. The distribution of Polynoidae is evidently controlled by certain factors. The most important factors determining distribution are: (*a*) temperature, (*b*) currents, (*c*) winds, (*d*) chemical composition of water, (*e*) food habits and mode of life, and (*f*) plasticity or response of the animal to its environment.

5. The facts that certain species are restricted to definite life zones and to definite ranges of temperatures, that the same species occurring in widely separated areas occur in depths of similar temperature and that boreal species occur in temperate and subtropical zones as deep water species, seem to point to the conclusion that temperature is the chief factor in determining distribution.

6. Some species of Polynoidae are found in widely separated areas. Since they cannot possibly traverse such distances by their natural means of locomotion, currents may be regarded as agents in distribution, carrying the adult worms along the bottom and the pelagic larvae in the upper strata and at the surface. The currents may further influence the temperature and the food conditions of an area. Consequently they play an important rôle in determining distribution.

7. After severe storms some deep water species are usually found driven to the shores. The winds may thus serve as agents in determining distribution.

8. The chemical composition of waters differs at different depths and latitudes. Since certain species of polynoids are restricted to definite areas and to definite depths, undergoing there considerable external changes, the chemical composition of water may be of some importance in determining distribution.

9. The greatest numbers of polynoids are found in the littoral zones where food is more abundant. Hence the food conditions of a certain area may be of some importance in controlling distribution. The mode of life may also influence the distribution. This would be especially true of commensal polynoids. Their distribution would naturally depend on that of their messmates.

10. Modifications and changes in the polynoids are considerable. These changes are marked in size, shape and color of the body, in the size, shape, structure and color of the elytra, in the number, shape, size and structure of the setae, and in the texture of the cuticle. These changes are remarkable in commensal polynoids, so that commensal individuals differ greatly from the free-living forms of the same species in all the characteristics enumerated above. The deep water species differ considerably from the littoral species and certain characteristics, such as the thin cuticle, the smaller size, the delicate elytra and eyeless condition of many abyssal species, point to the conclusion that the latter have undergone a degeneration and a physical specialization which makes them fit for that particular environment only. Such changes, however, would be impossible if the polynoids did not possess a plasticity and were not able to react in response to the external stimuli. The plasticity may be therefore, regarded as one of the most important factors in controlling distribution.

11. The perfect color mimicry of the commensal polynoids suggests that there is some chemical or enzymic interaction between the messmates and the commensal, producing similar color patterns in animals widely different in kind.

12. The great uniformity of littoral species and the great diversity of abyssal genera and species lead to the conclusion that the littoral zone is the center of origin, or the center of dispersal of the polynoids, and that species migrate or are driven to abyssal areas where they undergo great specialization and partial degeneration.

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H. EXPLANATION OF PLATES

All figures drawn with camera lucida

PLATE 7

Fig. 1. Tenth parapodium of *Harmothoë hirsuta.* × 15.

Fig. 2. Dorsal cirrus of *Harmothoë hirsuta.* × 75.

Fig. 3. Twentieth parapodium of *Polynoë lordi.* × 15.

Fig. 4. Tip of upper neuropodial seta of *Harmothoë hirsuta.* × 75.

Fig. 5. Tip of a long notopodial seta of the same. × 75.

Fig. 6. Tip of a short notopodial seta of the same. × 75.

Fig. 7. Tip of supra-acicular neuroseta of *Polynoë lordi.* × 160.

Fig. 8. Tip of short notoseta of *Lepidonotus squamatus.* × 310.

Fig. 9. Tip of a long notopodial seta of the same. × 310.

Fig. 10. Tip of ventral neuropodial seta of the same. × 310.

Fig. 11. Tip of a ventral notopodial seta of the same. × 310.

Fig. 12. Tip of blunt supra-acicular seta of *Polynoë lordi.* × 160.

Fig. 13. Tip of neuroseta of *Lepidasthenia gigas.* × 160.

Fig. 14. Tip of neuropodial seta of *Polynoë fragilis.* × 160.

Fig. 15. Nineteenth parapodium of *Polynoë fragilis.* × 115.

Fig. 16. Tip of notopodial seta of *Polynoë fragilis.* × 310.

Fig. 17. Seventeenth parapodium of *Lepidasthenia gigas.* × 15.

Fig. 18. Tip of upper neuroseta of the same. × 160.

Fig. 19. Twelfth parapodium of *Lepidonotus squamatus.* × 20.

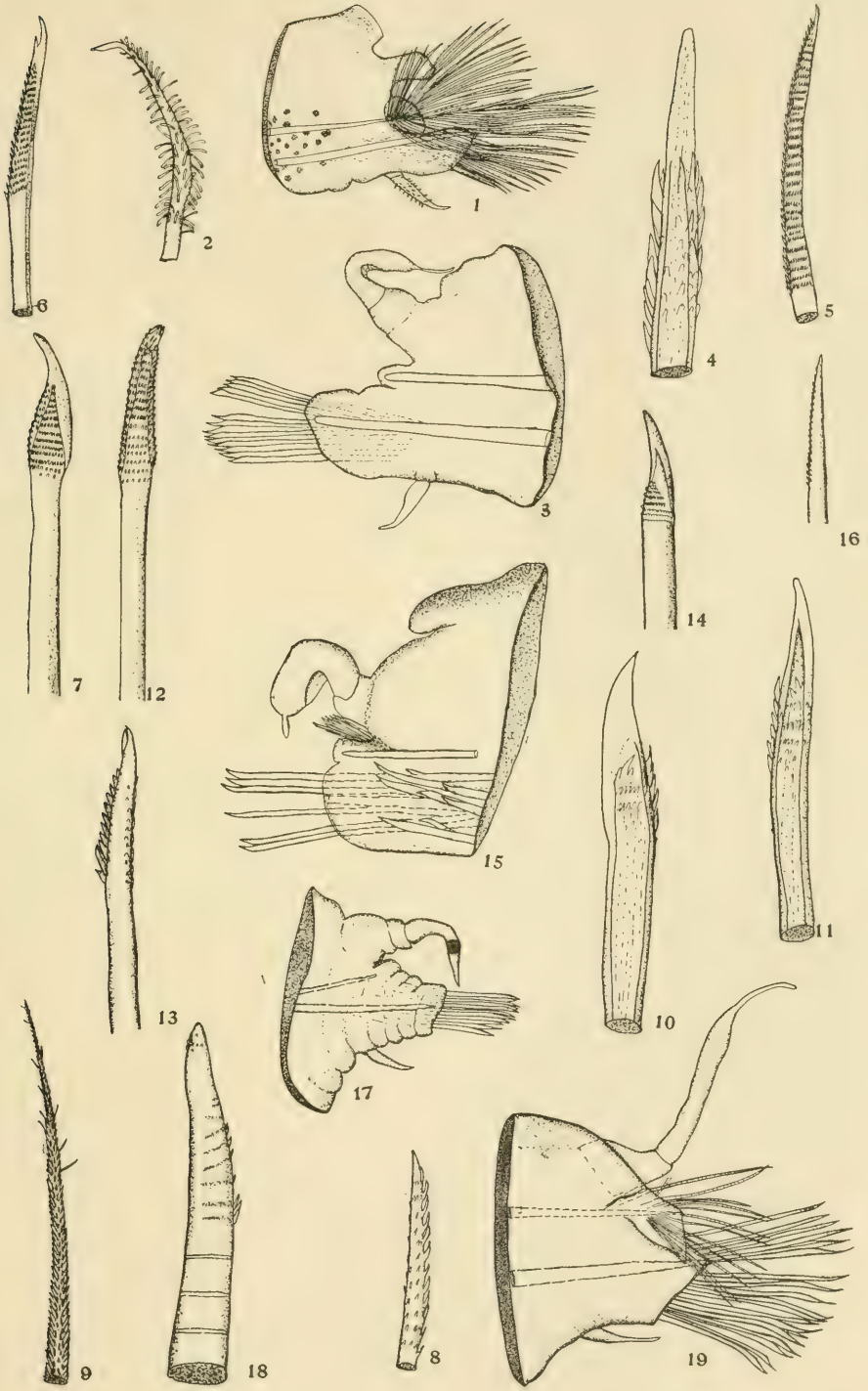
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PLATE 8

Fig. 20. Fifth elytron of *Harmothoë hirsuta*. × 15.

Fig. 21. Small section of the same elytron showing the large tubercles. × 75.

Fig. 22–24. Different kinds of tubercles of the same. × 75.

Fig. 25. Fringe of the same elytron. × 75.

Fig. 26. Tubercle of the same elytron, surface view. × 75.

Fig. 27. Tenth elytron of *Halosydna insignis* (of commensal). × 15.

Fig. 28. Tenth elytron of the same of free-living form. × 15.

Fig. 29. Fringe of the same. × 75.

Fig. 30. Tubercle of the same. × 75.

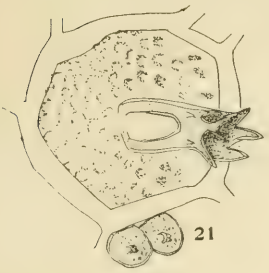
Fig. 31. Fifth elytron of *Polynoë lordi*. × 15.

Fig. 32. Second elytron of *Polynoë fragilis*. × 15.

Fig. 33. Tubercle of the first elytron of *Lepidonotus squamatus*. × 310.

Fig. 34. Highly magnified portion of the second elytron of *Lepidonotus squamatus* showing the various types of tubercles and a few fringes. × 310.

Fig. 35. First elytron of *Lepidonotus squamatus*. × 15.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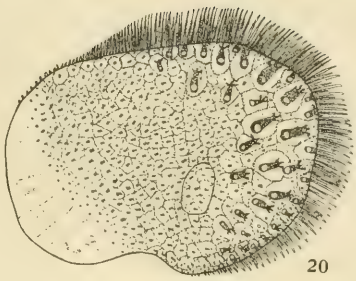
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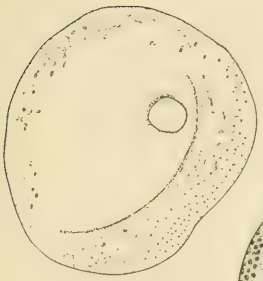
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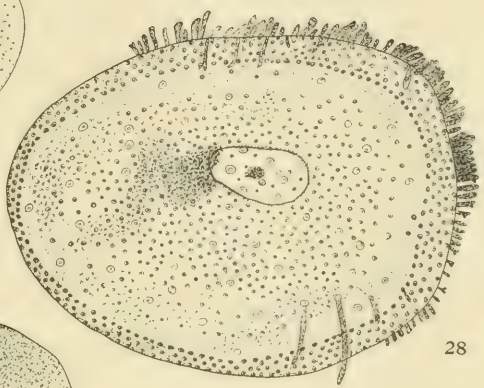
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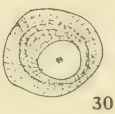
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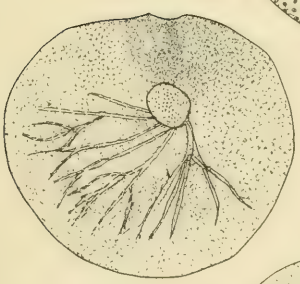
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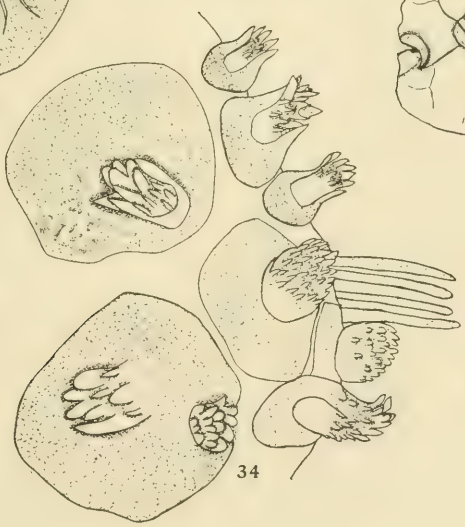
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5. Notes on the Tintinnoina. 1. On the Probable Origin of *Dictyocysta tiara* Haeckel. 2. On *Petalotricha entzi*, sp. nov., by Charles Atwood Kofoid. Pp. 63-69, 8 figures in text. December, 1915 ..... .05
6. Binary and Multiple Fission in *Hexamitus*, by Olive Swezy. Pp. 71-88, plates 9-11.
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DIFFERENTIALS IN BEHAVIOR OF THE TWO GENERATIONS OF *SALPA DEMOCRATICA* RELATIVE TO THE TEMPERATURE OF THE SEA

BY

ELLIS L. MICHAEL

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(Contribution from the Scripps Institution for Biological Research of the University of California)

CONTENTS

PAGE

Introduction 240

A. Preliminary 241
1. Description of life cycle 241
2. Crude data and method of procedure 246
3. Brief discussion of seasonal distribution 250
4. Brief discussion of vertical distribution 251

B. Temperature and surface distribution 252
1. Relations revealed by data 252
2. A morphological implication 256
3. Evidence of the existence of protruding chains 258
4. Implications regarding locomotion 261

C. Re-examination of data 262
1. Relation between season and temperature 262
2. Relation between position and temperature 265
3. Ostwald's viscocity theory 269

D. Theory of locomotion 271
1. Behavior of chains 271
2. Deduced peculiarities in temperature relations 274
3. Validity of the plankton concept 281

E. Summary and conclusions 288

F. Literature cited 291

INTRODUCTION

In working over the plankton collections made under the auspices of the Scripps Institution certain peculiarities in the occurrence of *Salpa democratica,* the smallest of the *Salpae,* led to an intensive study of its distribution within the San Diego region. Although the study is not yet complete, the relations revealed between fluctuations in surface temperature and variations in surface distribution proved so striking and so significant, especially as regards the validity of the prevailing plankton concept, as to make it advisable to publish at once the results concerning this aspect of the problem.

The way in which the morphological complexities in the life cycle are reflected in the distributional data makes it necessary to describe in some detail the successive stages in this cycle. Moreover, these morphological implications of the distributional data afford indisputable evidence of the fundamental interdependence of morphological and ecological research; they demonstrate the necessity, if we are ever rightly to interpret any biological phenomenon, of conducting our investigations, not only in a rigorous and critical manner, but also from the comprehensive *natural history* point of view so characteristic of Darwin and his immediate followers—that point of view which recognizes in all details of structure, function, behavior, and variation the unifying fact of individual and species adaptation, and which therefore holds all lines of research equally indispensable and no fact of nature negligible. Again, the data uniquely demonstrate that specificity in behavior is quite as far reaching as is specificity in structure, the two generations of this species being quite as distinguishable from the way in which they are distributed as from the way in which they are constructed.

Lastly, the distributional data afford convincing evidence in support of the conclusion that *S. democratica,* a typical plankton species, controls to a significant extent its own distribution, and that it does so, in part at least, by means of locomotion. *This is in direct contradiction to the prevailing plankton concept,* according to which plankton organisms are, as Johnstone (1908, p. 148) truly says, "particles in the physical sense and behave as such." Of course, no sane biologist actually believes this, but plankton is nevertheless defined in nearly every book dealing with such organisms, as "all floating organisms which are passively carried along by currents" (Murray and Hjort, 1912, p. 309). This matter is considered at some length at the close of this paper.

The data involved in this investigation comprise all the collections made during the months of June and July prior to 1910 with a surface net of 000XX mesh silk bolting cloth having an orifice 97.5 cm. in diameter (Michael and McEwen, 1915). The reasons for excluding later collections are first, that a net of very different "catching capacity" has been in use, and second, that the species has been captured too seldom and in too small numbers to permit satisfactory statistical treatment. The reason for excluding data relative to other months than June and July is made evident in the preliminary discussion of the seasonal distribution of the species. Lastly, while the vertical distribution of the species is briefly considered preliminary to the main discussion, too few subsurface collections were made at any one depth corresponding in time and place with the surface collections, to justify burdening this paper with a consideration of details of little aid in interpreting the facts revealed by the surface data.

It is hoped that study of the distribution of this species may be carried further in the near future. Does the species perform vertical migrations? If so, to what depth does it migrate, and how is it influenced by variations in light intensity, salinity, gas content, etc.? These are questions as yet unanswered. But sufficient attention has been given them to make it evident that a more complex statistical method than the one here employed is needed. Such a method has been devised, and is now being tested preparatory to publication.

I desire to express my obligation to Professor W. E. Ritter, director of this institution; to Dr. F. B. Sumner, biologist; and to Dr. G. F. McEwen, hydrographer, for suggestions and aid in the preparation of this paper.

A. PRELIMINARY

1. Description of the Life Cycle

Salpa democratica, like other species of the genus, is notable for its two alternating generations. One, known as the "solitary," "budding," or incorrectly as the "asexual" generation (pl. 9, fig. 2) produces offspring by budding, and the buds, when mature constitute what is known as the "aggregate" or "sexual" generation (pl. 9, fig. 3). Each individual of the aggregate generation then produces, sexually, one of the solitary generation. So the cycle repeats itself.

Although there are important structural differences between individuals of the two generations, they are superficially so nearly alike that the following description, borrowed mainly from Brooks (1893, p. 4), relates as well to an individual of one generation as to one of the other:

Each individual is transparent, ovate in form, and small, rarely exceeding eight millimeters in length. Its body may be compared to a barrel open at both ends so that water flows through it without obstruction (text fig. A). The mouth (m) occupies the anterior end of the barrel, and the lips are infolded so as to act as valves permitting the entrance of water but preventing its escape. At the

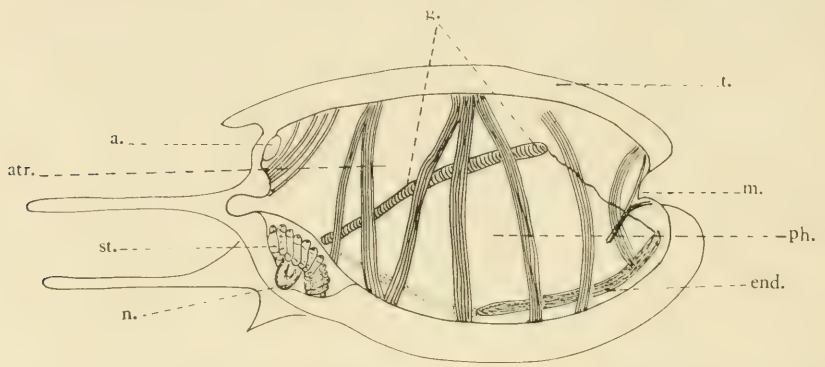

Fig. A (after Ritter). Semidiagrammatic representation of the solitary generation of *Salpa democratica:* (a) atrial aperture; (atr) atrium; (end) endostyle; (g) gill; (m) mouth; (n) nucleus or intestinal tract; (ph) pharynx; (st) portion of stolon which has been converted into individuals of the aggregate generation; (t) test or mantle cavity.

opposite end of the barrel the atrial aperture (a) affords an exit for the water but, owing to a few sphincter muscles, prevents it from entering. Essentially, the chamber of the barrel is uninterrupted from mouth to atrial aperture for, though divided by a rod-like gill (g) into the pharynx (ph) and the atrium (atr), the gill is so narrow that it offers little obstruction to the water, and there is a large free passage on all sides of it.

The body is partly encircled by six bands of muscles somewhat like barrel hoops crowded together on the upper surface midway between the two ends of the barrel, and spread apart on the lower surface. Contraction of these muscles empties the barrel, driving the water out of the atrial aperture, and propels the salpa through the water in the opposite direction. The body is encased in a thick, transparent mantle or "test" (t) which, by its elasticity, antagonizes the muscles and draws in a fresh supply of water. "The animal there-

fore moves forward by jerks along a column of water which passes through its body."

Within the body at the caudoventral extremity, lies a compact intestinal tract called the nucleus (n). Closely associated with this nucleus in the solitary salpa is an organ called the "proliferous stolon" (st), which is a complicated tubular structure joined at its proximal end to the body just anterior to the nucleus. Distally this stolon segments, thereby giving rise to the aggregate salpae. Each salpa remains attached to the preceding one in the form of a chain and as the stolon continues to segment, the salpae are crowded and pushed along a spiral path encircling the nucleus into the mantle cavity (pl. 9, fig. 2). In fact all except the proximal end of the stolon itself is coiled in the cavity of the test.

As the number of salpae in the chain increases each undergoes several changes in position. As the origin and development of the chain is so clearly described by Brooks (1893, p. 78) with reference to *Salpa pinnata* and *S. cylindrica,* I can do no better than quote from him and thereafter point out in what way *S. democratica* differs:

> The first indication of the segmentation of the stolon is a series of ectodermal folds which first appear at its sides, but soon extend up and down and completely encircle it, and, pushing inwards, mark out the body-cavities of the salpae, and also cut up the tubular structures inside the stolon into segments.
>
> The active agent in this process of segmentation is the growth of the ectodermal folds, and the other structures are actually cut by these folds. As a result of this process the nerve tube becomes cut up into a series of ganglia, one for each salpa; the perithoracic tubes become cut up into a series of perithoracic vesicles, two for each salpa; the genital string becomes cut up into a series of eggs, one for each salpa,* inclosed in a follicle; and the thickened endodermal epithelium at the sides of the endodermal tube becomes cut up into a series of vertical pouches or pockets, two for each salpa, the rudiments of the right half of the pharynx and of its left half.
>
> The structures which I have enumerated form the rudiments of a single salpa. At this stage each salpa is bilaterally symmetrical, and the plane of symmetry is the same as that of the stolon, while its long axis is at right angles to that of the stolon, which becomes converted into a single row of salpae, so placed that the dorsal surfaces of all of them are toward the base [proximal end] of the stolon, their ventral surfaces towards its tip [distal end], their right and left sides on its right and left respectively, their oral [anterior] ends at its top or neural side, and their aboral [posterior] ends at its bottom or genital side.
>
> The single row of salpae becomes converted into a double row which consists of a series of right-handed salpae and a series of left-handed ones, placed with their dorsal surfaces out, their ventral surfaces toward the ventral surfaces of those in the opposite row, and the left sides of those on the right and the right sides of those on the left towards the base of the stolon. In

* In *S. democratica* there are three eggs, but two disintegrate.

order to illustrate these secondary changes in position let us represent the series of salpae by a file of soldiers all facing the same way. Now imagine that each alternate soldier moves to the right, and the others to the left, to form two files still facing the same way. Now let them face about so that the backs of those in one row are turned toward the backs of those in the other row. They will now illustrate two rows of salpae.

To make the illustration more perfect suppose that, instead of stepping into their new places, the soldiers grow and are pushed out by mutual pressure; and suppose that their heads, growing fastest, form two rows while their feet still form one row; and suppose furthermore that, as each soldier rotates, his feet turn first, and that the twist runs slowly up his body to his head, which turns last. We must also imagine that these various changes all go on together, and that while they are taking place each soldier not only grows larger, but develops from a simple germ to his complete structure.

In *Salpa democratica* the stolon undergoes more or less regular periods of active segmentation and rest so that the aggregate salpae are developed in sets or blocks, all individuals in a single block being of approximately the same size and in the same stage of development. Leuckart (1854, p. 67) found forty in one block and sixty-five in another; while Seeliger (1886, p. 593) counted sixty-one in a single block. As there are from three to four blocks present when the distal end of the chain is ready to emerge from the mantle cavity to the exterior, the stolon carries in the neighborhood of two hundred salpae at one time. No evidence is at hand that the stolon ever exhausts its capacity for producing them, and segmentation probably continues until terminated by the death of the solitary salpa.

Again, in *S. democratica,* a later position is assumed by the salpae such that those in one row of the chain alternate with those in the other row, each salpa being connected by two processes from its body wall with the one ahead of it, by two with the one behind it, and by two to each of the two adjacent ones diagonally opposite it in the other row. To quote again from Brooks (1893, p. 88) such a chain of salpae "may be compared to two trains of cars on two parallel tracks, placed so that the middle of each car on one track is opposite the ends of the two cars on the other track, and each joined by two couplings to the car in front of it on its own track, and in the same way to the one behind it, and also to those diagonally in front of it and behind it on the other track." In this position "the long axis of the salpae are at right angles to the long axis of the stolon, as if the cars in the two trains were set on end." Now imagine the cars in each train to be pushed over until each one rests upon the one in front of it, and at the same time imagine each car to rotate so that it becomes inclined outward at an angle of about forty-five degrees.

The position of the cars will then illustrate the final positions assumed by the salpae in a chain of *S. democratica.*

The embryo which is to become an individual of the solitary generation is carried and developed within the body of the aggregate salpa. Before fertilization the egg is suspended by means of the fertilizing duct, which opens into the cloaca, into one of the blood-channels of the salpa. Quoting from Brooks (1893, p. 21): "The spermatozoa, which are drawn into the pharynx . . . with the sea water, are swept past this opening by the contractions of the muscles in swimming, and some of them enter it and one, penetrating to the egg, fertilizes it."

Without going into detail, suffice it to say that the embryo at an early stage pushes into the cloaca, carrying its wall before it, and thus becomes inclosed in an epithelial capsule. Changes soon take place by which this capsule becomes cast off and in its place, a placenta forms which, communicating with the blood-channels of the salpa, nourishes the growing embryo until birth. While the embryo projects into the cloaca, it is not at first exposed to the water but is inclosed by the epithelial capsule and after its disappearance, by an embryo sac resembling somewhat the amnion of vertebrates. Later, but still while the embryo is very young, this sac is distended and finally broken by the growing embryo, and from then until birth the embryo is directly exposed to the water in the cloaca, being fastened to the salpa only by the placenta and a narrow band of ectoderm which connects the neck of the placenta to the walls of the cloaca.

As the embryo begins its growth shortly after the aggregate salpa emerges from the mantle cavity of the solitary salpa, and as its growth is rapid, a fully grown embryo is enormous in comparison to the salpa which carries it (pl. 9, fig. 3). Leuckart (1854, p. 52) says that, at birth the embryo of *S. democratica* is fully two-fifths the size of the aggregate salpa. Before birth the stolon is completely developed in the embryo and has begun to be converted into aggregate salpae of the succeeding generation. After the embryo has made its escape a testis develops in the aggregate salpae and they become mature males.

In closing this description attention must be called to several inaccurate and misleading statements permeating the literature. One frequently reads that the solitary form is asexual, that the aggregate form is sexual (hermaphroditic), and that the developing embryo is carried within the body of its mother. Such is not the case, for Brooks has clearly demonstrated that the solitary form is, in the

strictest sense of the word, a female, while the salpa it produces by budding is a male. Virtually, the mother salpa gives rise by budding to her sons, and each son serves first as a depository for one of his mother's mature but unfertilized eggs, then as a living incubator within which his mother's daughter is housed and reared, and lastly as a father. Such, in brief, is the curious sexual situation relative to the life cycle of the salpae.

2. Crude Data and Method of Procedure

All hydrographic data corresponding to hauls herein considered, as well as description of the method of collecting, have been published elsewhere (Michael, 1911; Michael and McEwen, 1915). Accordingly, only those data directly concerned in the present inquiry are presented in table 1. But enough are included to permit anyone to check the computations. For meaning of the term, section, see page 266.

Table 1

Data relative to June and July surface hauls of the years 1908 and 1909

Haul number	Date	Period of day*	Duration in minutes	Section	Temperature in Centigrade	Number of *Salpa democratica*	
						Solitary forms	Aggregate forms
	1908						
1417	June 12	12– 2 P.M.	20	43_{10}	16°.5	7	93
1418	June 12	10–12 A.M.	20	43_{10}	16.4	11	81
1432	June 15	10–12 A.M.	20	42_8	18.9	2	10
1436	June 16	8–10 A.M.	20	43_{10}	16.5	1	25
1438	June 16	10–12 A.M.	40	42_9	18.5	0	0
1444	June 17	12– 2 P.M.	30	46_{12}	16.5	138	2860
1452	June 17	2– 4 P.M.	13	44_{12}	16.5	25	1542
1455	June 18	10–12 A.M.	35	45_{12}	16.5	23	212
1460	June 18	12– 2 P.M.	40	45_{10}	17.1	4	23
1465	June 19	8–10 A.M.	40	46_{12}	17.8	310	1980
1471	June 19	10–12 A.M.	20	40_{12}	17.5	25	311
1478	June 23	4– 6 P.M.	20	42_8	18.3	0	0
1505	June 26	12– 2 P.M.	25	42_8	20.0	775	1047
1509	June 27	6– 8 A.M.	17	40_{11}	18.6	0	0
1512	June 27	6– 8 A.M.	25	40_{11}	18.9	0	0
1530	June 30	10–12 A.M.	20	50_{13}	15.5	3	55
1535	July 8	6– 8 A.M.	20	52_{16}	18.9	0	0
1559	July 18	6– 8 A.M.	10	61_5	16.5	0	0
1560	July 18	6– 8 A.M.	40	61_5	16.5	60	4
1562	July 18	8–10 P.M.	60	61_5	19.5	0	0
1579	July 22	6– 8 P.M.	20	40_{10}	20.8	0	0

* In specifying the two-hour period it is assumed that the whole haul was made within the limits given; actually it has, in many instances, overlapped on the preceding or succeeding period. In such cases the period in which the greater amount of time was consumed is entered in this table.

TABLE 1—(*Continued*)

Haul number	Date	Period of day*	Duration in minutes	Section	Temperature in Centigrade	Number of *Salpa democratica*	
						Solitary forms	Aggregate forms
1582	July 22	8–10 P.M.	25	40_{10}	20.5	0	0
1585	July 23	4– 6 A.M.	23	40_{10}	19.8	0	0
1588	July 23	4– 6 A.M.	25	40_{10}	19.7	0	0
1594	July 23	8–10 P.M.	22	40_{10}	20.5	0	0
1597	July 24	4– 6 A.M.	20	40_{10}	20.5	0	0
1600	July 24	4– 6 A.M.	20	40_{10}	20.5	14	3
	1909						
1643	June 15	12– 2 P.M.	60	42_{10}	18.2	15	176
1650	June 16	4– 6 P.M.	45	42_{10}	18.6	6	0
1653	June 16	6– 8 P.M.	35	42_{10}	18.6	1	0
1657	June 16	6– 8 P.M.	35	42_{10}	18.4	0	0
1659	June 17	4– 6 P.M.	60	39_{10}	18.4	0	0
1660	June 17	6– 8 P.M.	45	39_{10}	18.4	0	0
1661	June 17	6– 8 P.M.	45	39_{10}	18.4	0	0
1662	June 17	6– 8 P.M.	30	39_{10}	18.4	0	0
1673	June 21	6– 8 P.M.	25	42_{10}	18.0	160	20
1680	June 21	6– 8 P.M.	35	43_{10}	15.9	13	83
1686	June 22	4– 6 A.M.	60	43_{11}	17.9	0	0
1689	June 22	4– 6 A.M.	55	43_{11}	17.9	0	0
1695	June 23	4– 6 A.M.	65	42_{10}	17.6	100	10
1698	June 23	6– 8 A.M.	40	42_{10}	17.2	132	8
1703	June 23	8–10 A.M.	115	42_{10}	17.2	31	600
1712	June 24	4– 6 P.M.	70	42_{10}	17.5	46	4
1716	June 24	6– 8 P.M.	45	42_{10}	17.5	28	154
1719	June 24	6– 8 P.M.	68	42_{10}	17.2	20	219
1728	June 25	4– 6 P.M.	60	42_{10}	17.7	91	970
1734	June 25	6– 8 P.M.	37	42_{10}	17.7	56	547
1738	June 25	8–10 P.M.	56	42_{10}	17.6	47	598
1747	June 28	6– 8 P.M.	36	42_{10}	19.0	13	387
1751	June 28	6– 8 P.M.	45	42_{10}	19.0	7	304
1754	June 28	8–10 P.M.	40	42_{10}	19.0	212	63
1759	June 29	4– 6 A.M.	20	42_{10}	18.6	500	40
1763	June 29	6– 8 A.M.	55	42_{10}	18.7	365	76
1767	June 30	4– 6 P.M.	25	49_{10}	19.1	1000	73
1772	July 1	8–10 A.M.	28	53_{10}	16.7	0	0
1779	July 1	10–12 A.M.	108	52_{10}	20.4	2	8
1784	July 2	4– 6 A.M.	21	52_{10}	18.7	28	1
1791	July 2	6– 8 A.M.	23	52_{10}	16.6	0	0
1796	July 2	8–10 A.M.	33	46_{9}	17.6	0	0
1800	July 2	12– 2 P.M.	51	42_{8}	20.5	10	2
1804	July 2	4– 6 P.M.	27	41_{8}	20.3	2	0
1810	July 2	6– 8 P.M.	50	41_{8}	20.2	1500	63
1815	July 7	4– 6 A.M.	45	42_{10}	19.0	250	72
1826	July 7	6– 8 P.M.	60	40_{11}	19.2	466	52
1836	July 7	8–10 P.M.	30	40_{11}	19.4	165	20
1850	July 9	2– 4 A.M.	45	40_{10}	18.8	2	83
1854	July 9	4– 6 A.M.	55	40_{10}	18.8	3	21
1860	July 9	4– 6 A.M.	67	40_{10}	18.6	0	21
1864	July 9	6– 8 P.M.	45	40_{10}	19.0	1	6

TABLE 1—(*Continued*)

Haul number	Date	Period of day*	Duration in minutes	Section	Temperature in Centigrade	Number of *Salpa democratica*	
						Solitary forms	Aggregate forms
1868	July 9	6– 8 P.M.	33	40_{10}	19.0	9	4
1872	July 9	6– 8 P.M.	35	40_{10}	18.8	0	12
1875	July 9	10–12 P.M.	170	40_{10}	19.0	0	89
1881	July 10	12– 2 A.M.	70	40_{10}	18.9	0	0
1883	July 10	12– 2 A.M.	213	40_{11}	19.2	53	1537
1888	July 10	4– 6 A.M.	45	40_{11}	19.1	22	220
1892	July 10	4– 6 A.M.	30	40_{11}	19.2	2	86

Several methods have been employed (Michael, 1911; Esterly, 1912) for determining the relative distribution of a marine species under different conditions. First, the direct method was used of comparing the *abundance* or average number of individuals obtained per unit volume of water filtered (= amount filtered per hour of towing). Second, as the species would in general be present in a greater proportion of those hauls made under the conditions when the species occurred in greatest numbers than of those hauls made under the conditions when it occurred in smallest numbers, the *haul frequency,* or percentage of hauls in which the species appeared under one set of conditions, was compared with that under another set. It is important that this be clearly visualized; perhaps an illustration strictly analogous in principle although not in detail will make it more intelligible. The President of the United States is elected not by popular vote but by that of states. But, as a rule, the candidate receiving the largest popular vote is elected. Suppose one wanted to compare the Democratic preference of the nation during a period of plenty with that during a period of famine. Assuming an equal population in all states, could the investigator not proceed in two ways: first, by comparing the average number of Democratic ballots cast per state under the two conditions (=the abundance method); and second, by comparing the proportion of states that went Democratic under the two conditions (= the frequency method)? If the first method indicated a greater Democratic preference during the period of plenty, the second method would, as a rule but not always, indicate the same thing.

Finally, Esterly (1912, p. 282) compared the *time frequency* of the species under one set of conditions with that under another, or to quote: "the ratio between the time occupied by hauls in which the species was taken and the total time spent in hauling." If the average time consumed per haul were the same for hauls made under all compared conditions, it is obvious that haul frequency and time frequency would be identical. However, if ten hauls consuming ten hours were

made in July, while ten hauls consuming five hours were made in December, neither the haul nor the time frequency of the July hauls would be comparable with that of the December hauls. For the probability of capture by the ten hauls consuming ten hours, would exceed that by the ten hauls consuming five hours. Therefore, it is necessary to determine what the frequency would have been had the ten December hauls consumed ten instead of five hours; otherwise both haul and time frequency might be misleading.

Since haul frequency, by definition, is unrelated to the time consumed in hauling, it can not be standardized with respect to time. Time frequency, however, is amenable to such correction; and as the method of standardization employed was developed by Dr. G. F. McEwen of the Scripps Institution, I have asked him to give, in his own language, the derivation of the formula:

Let F = time frequency,
f = standardized frequency,
a = average time per haul,
b = standard time per haul,
$m = \frac{a}{b}$,
f_n = frequency corresponding to n units of time of duration a_1,
p_1 = probability of catching no animals in a haul of duration a_1,

Then from the principle of compound probabilities of independent events:

$$\frac{f_1}{100} = 1 - p_1 \qquad \text{time} = a_1,$$

$$\frac{f_2}{100} = 1 - p_1^2 \qquad \text{time} = 2a_1$$

$$\frac{f_3}{100} = 1 - p^3_1 \qquad \text{time} = 3a_1,$$

$$\frac{f_n}{100} = 1 - p_1^n \qquad \text{time} = na_1.$$

Let

$$b = ka_1$$

then

$$a = mka_1$$

Therefore

$$\frac{f}{100} = 1 - p_1^{ka_1} \qquad \text{.....(1)}$$

and

$$\frac{F}{100} = 1 - p_1^{mka_1} \qquad \text{.....(2)}$$

From (1) and (2)

$$p_1^{ka_1} = 1 - \frac{f}{100} \qquad \text{.....(3)}$$

$$p_1^{ka_1} = \left(1 - \frac{F}{100}\right)^{\frac{1}{m}} \qquad \text{.....(4)}$$

Therefore, equating the logarithms of the second members of (3) and (4)

$$\log\left(1 - \frac{f}{100}\right) = \frac{b}{a} \log\left(1 - \frac{F}{100}\right) \qquad \text{.....Standardization formula.}$$

Since the standardized frequency given by the above formula, is that time frequency which would most probably have resulted had every haul consumed the same amount of time (= one hour), it is equivalent to what the haul frequency would have been under the same conditions. The latter is therefore of no avail and the methods employed in this investigation are two: (1) the average number of solitary forms and aggregate forms obtained per hour under the various temperature conditions are compared; and (2) their standardized frequencies under the same temperature conditions are compared. By using these two methods, the first of which is affected by variability in number of individuals collected while the latter is entirely independent of such variability, a check on interpretation is maintained.

3. Brief Discussion of Seasonal Distribution

Investigations concerning the distribution of the chaetognatha (Michael, 1911, p. 139) revealed no apparent seasonal effect. Similarly, no seasonal effect is apparent in the data discussed by Esterly (1912) relative to the copepoda. In the case of *Salpa democratica,* however, the influence of season is pronounced. As revealed by the following table, both generations of this species occur on the surface mainly during the months of June and July, solitary forms being restricted entirely to these months. No collections, however, were made during the months of January, May, October, or December.

Table 2

Seasonal surface distribution of *Salpa democratica* during 1908–09

					Number of animals			
					Solitary forms		Aggregate forms	
Month	Hauls	Hours of hauling	Average temperature	Average salinity	Total	Per hour	Total	Per hour
Feb.	5	6.3	13°6C	33.54‰	0	0	6	1
Mar.	15	12.6	15.1	33.64	0	0	0	0
Apr.	6	4.1	16.1	33.70	0	0	0	0
June	41	28.2	17.9	33.61	4,164	147	12,516	444
July	35	25.5	18.9	33.64	2,592	102	2,359	93
Aug.	15	6.5	19.9	.....	0	0	92	14
Sept.	6	2.3	18.5	33.88	0	0	14	2
Nov.	5	2.6	17.9	33.85	0	0	0	0

In addition to the almost complete restriction of both generations to the months of June and July, the table shows both to have been more abundant during June than during July. Moreover, while the aggregate forms were more abundant than the solitary forms during June, the solitary forms were the more abundant during July. This difference may have been consequent upon any or all of several influ-

ences: (1) normal sequence in the life cycle; (2) the effect of higher temperatures during July in increasing the abundance of solitary forms; and (3) a similar effect of higher salinities during July. To what extent and how each of these factors has operated in causing the difference noted it is impossible to say, but it seems probable that temperature has played an important part. This is not only made evident in the ensuing discussion but also by the fact that twenty-one surface hauls made between August 9 and 23, 1911, in the vicinity of San Diego when the temperature averaged 20°.2C failed to catch a single specimen of either generation, while on August 21, 1911, three surface hauls made with the same net in the vicinity of Santa Rosa Island when the temperature averaged 16°.4C were all successful, obtaining 115 solitary forms and 1409 aggregate forms.

In apparent contradiction to this fact, the table shows that aggregate forms occurred to some extent during August although solitary forms did not and judging from the high temperature average, this is the reverse of what might have been expected. These facts indicate the complexity of causes leading to the seasonal appearance and disappearance of *S. democratica*.

When all the hauls in all depths are examined, June and July still stand out as the months of maximum abundance, the number of specimens obtained during other months being relatively few.

4. Brief Discussion of Vertical Distribution

Considering horizontal closing net hauls from all depths, made during the months of June and July, 1908 and 1909, a total of 6,889 solitary forms and 17,091 aggregate forms were obtained. Table 3 shows how they were vertically distributed.

Table 3

Vertical distribution of *Salpa democratica* during June and July, 1908 and 1909

Depth in fathoms	Hauls	Hours of hauling	Average temperature	Number of animals			
				Solitary forms		Aggregate forms	
				Total	Per hour	Total	Per hour
0	76	53.7	18°.36C	6,756	126	14,875	276
4–6	11	3.1	17.38	59	19	1,135	366
7–12	14	4.4	16.06	56	12	505	114
15–20	11	3.2	12.92	13	4	297	93
25–35	14	4.4	10.97	3	1	253	57
40–75	14	4.1	9.73	2	1–	26	6
100–350	27	11.0	8.28	0	0	0	0

This table shows that solitary forms decrease in abundance as the depth increases, disappearing entirely below 100 fathoms, while

aggregate forms are most abundant between four and six fathoms, decreasing from that depth until they also disappear below 100 fathoms. Here again, as in table 2, the maximum abundance of solitary forms corresponds to a higher temperature than is the case with aggregate forms. Is this correspondence merely consequent upon the effects of random sampling, or does the temperature of the water play an important and differential part in the distribution of the two generations of this species?

B. TEMPERATURE AND SURFACE DISTRIBUTION

1. Relations Revealed by Data

The June and July data of the years 1908 and 1909 reveal a variation in surface temperatures taken simultaneously with surface net hauls of five degrees Centigrade, or from 15°.9C to 20°.8C. When these hauls are arranged in two groups according as the temperature was 18°.3C or less, or 18°.4C or more, it is found (table 4) that an average of 67 solitary forms per hour and an average of 529 aggregate forms per hour are associated with the lower temperatures, while an average of 156 solitary forms and an average of 124 aggregate forms are associated with the higher temperatures. In other words, solitary forms were most abundant on the surface in the warmer water, while aggregate forms were most abundant in the colder water.

Table 4

Relation between surface temperature and surface distribution of *Salpa democratica* during the months of June and July, 1908 and 1909

			Solitary forms					Aggregate forms				
				Specimens		Frequency			Specimens		Frequency	
Temperature in centigrade	Hauls	Hours of hauling	Hours of successful hauling	Total	Per hour	Time	Per hour	Hours of successful hauling	Total	Per hour	Time	Per hour
15°.9–18°.3	30	20.0	16.2	1,346	67	81	92	16.2	10,575	529	81	92
18°.4–20°.8	46	34.7	20.4	5,410	156	59	69	23.1	4,300	124	67	77

Table 4 also shows that the frequency of both solitary forms and aggregate forms was 92 when the temperature was 18°.3C or less, while that of solitary forms was 69 and that of aggregate forms 77, when the temperature was 18°.4C or more. In other words both solitary forms and aggregate forms were obtained most frequently in the colder water. To sum up, table 4 shows:

1. Solitary forms most abundant in the warmer water.
2. Solitary forms most frequent in the colder water.
3. Aggregate forms most abundant in the colder water.
4. Aggregate forms most frequent in the colder water.
5. Frequency of solitary forms very similar to that of aggregate forms.
6. Abundance of solitary forms reversed to that of aggregate forms.

With respect to aggregate forms these relations seem reasonable, for the orders of their abundance and frequency are parallel as is to be expected. Regarding solitary forms, however, the relations appear to be meaningless. Do they not signify that the solitary forms are found in greatest abundance in the places they frequent the least or, to state it differently, that they are found most often under the conditions when they occur in smallest numbers? Obviously, this is precisely what is implied if the relations revealed by table 4 are not due: (1) to systematic errors introduced by the method of collecting; (2) to the chance effect of random sampling; or (3) to what amounts to the same thing, an insufficient number of hauls.

First, as to methods used in collecting. All collections were made with surface nets of 000 mesh (Michael and McEwen, 1915, p. 201), as nearly like one another as it is possible to construct them. Furthermore, the "Agassiz" was allowed to drift during every haul, and the error introduced by variation in volume of water filtered is far within the differences in abundance noted in table 4. The ratio between the mean variability (0.172 km. per hour) and average velocity of tow (1.8 km. per hour) as determined from fifty hauls made with a current meter attached below the net, is 0.01, while the mean variability in number of organisms obtained per hour usually exceeds the average number (Michael, 1916, p. xviii). It is unlikely, therefore, that lack of standardization of nets or method of collecting could have been responsible for the relations above revealed.

It may be urged, however, that the effect of random sampling, i.e., an uneven distribution of hauls with respect to influences other than temperature, might account for the above relations. This is partly true; the hauls were unevenly distributed with respect to light, only nine night hauls (6 P.M. to 6 A.M.) having been made in the colder water, while thirty-three were made in the warmer water. The following table, however, includes only night hauls and the *same relations persist.*

Table 5

Reproduction of table 4 by excluding all except night hauls (6 P.M. to 6 A.M.)

Temperature in centigrade	Hauls	Hours of hauling	Solitary forms: Hours of successful hauling	Solitary forms: Specimens: Total	Solitary forms: Specimens: Per hour	Solitary forms: Frequency: Time	Solitary forms: Frequency: Per hour	Aggregate forms: Hours of successful hauling	Aggregate forms: Specimens: Total	Aggregate forms: Specimens: Per hour	Aggregate forms: Frequency: Time	Aggregate forms: Frequency: Per hour
15°9–18°3	9	7.4	5.5	424	58	74	81	5.5	1,631	220	74	81
18°4–20°8	33	26.0	14.5	3,248	125	56	63	18.4	3,084	118	71	79

This table shows that an average of 58 solitary forms per hour was obtained in the colder water and an average of 125 per hour in the warmer water, while an average of 220 aggregate forms per hour was obtained in the colder water and an average of 118 in the warmer water. Table 5 also shows that the frequency of both generations was 81 in the colder water, while that of solitary forms was 63 and that of aggregate forms 79 in the warmer water. Thus, table 5 corroborates table 4 in every respect, solitary forms again appearing in greatest abundance and least frequency in the warmer water, while aggregate forms appear in greatest abundance and greatest frequency in the colder water.

Even when the data are arranged in every other practicable way with respect to light, as in table 6, the same relations persist.

Table 6

Relation of surface distribution of *Salpa democratica* to temperature with respect to different periods of the day

Temperature in centigrade	Hauls	Hours of hauling	Solitary forms: Hours of successful hauling	Solitary forms: Specimens: Total	Solitary forms: Specimens: Per hour	Solitary forms: Frequency: Time	Solitary forms: Frequency: Per hour	Aggregate forms: Hours of successful hauling	Aggregate forms: Specimens: Total	Aggregate forms: Specimens: Per hour	Aggregate forms: Frequency: Time	Aggregate forms: Frequency: Per hour
A—Including only daylight hauls (6 A.M. to 6 P.M.)												
15°9–18°3	21	12.6	10.7	922	73	85	95	10.7	8,944	710	85	96
18°4–20°8	13	8.7	5.9	2,162	249	68	82	4.7	1,216	140	54	68
B—Including only intense light hauls (10 A.M to 2 P.M.)												
15°9–18°3	8	4.1	4.1	226	55	100	100	4.1	3,811	930	100	100
18°4–20°8	5	3.9	3.4	789	202	87	93	3.1	1,067	247	87	93
C—Including only early morning hauls (6 A.M. to 10 A.M.)												
15°9–18°3	9	5.8	4.2	534	92	72	86	4.2	2,617	451	72	86
18°4–20°8	4	1.95	0.9	365	187	46	71	0.9	76	39	46	71
D—Including only evening hauls (6 P.M. to 10 P.M.)												
15°9–18°3	6	4.4	4.4	324	74	100	100	4.4	1,621	368	100	100
18°4–20°8	18	11.5	6.2	2,374	206	54	70	6.2	911	79	54	70

We have now considered the data in six different ways with similar results. In table 4 data relative to all the June and July hauls are considered, while in tables 5 and 6 night hauls, day hauls, mid-day hauls, morning hauls, and evening hauls are separately considered; and in each case the following relations are shown:

1. Solitary forms most abundant in the warmer water.
2. Solitary forms most frequent in the colder water.
3. Aggregate forms most abundant in the colder water.
4. Aggregate forms most frequent in the colder water.

It must be evident that such a variety in tabulation would introduce contradictions were it not for a definite relation between fluctuations in surface temperature (or some influence closely associated with it) and the behavior of the two generations of this salpa. However, on account of the apparently paradoxical relation between the abundance and frequency of solitary forms, the probability that such a repetition of relations was due to chance, insufficient or inadequate hauling, or to anything other than an actual correspondence between temperature and distribution has been calculated and found to be less than 0.0007. The calculation is simple, as follows:

There are four possible ways in which the aggregate forms might have been related to the colder water, namely:

1. Most abundant and most frequent.
2. Most abundant and least frequent.
3. Least abundant and most frequent.
4. Least abundant and least frequent.

Whichever of these combinations might result, it is obvious that the solitary forms might have been related to the colder water in any one of the same four ways. For each tabulation, therefore, there would be sixteen possible combinations of relations, any one of which would be equally likely to occur by chance. Then, for any one of the sixteen possible combinations that appeared in the first tabulation, there would remain sixteen possible combinations that might appear in the second tabulation, whence the number of possible combinations in two tables would be 16^2. In three the number would be 16^3, in four 16^4, and in six 16^6. Hence, the probability that the same combination of relations appearing in all six tabulations was due to chance is $1/16^6$ or $1 \div 16{,}777{,}216$. If tables 4 and 5 as well as section A of table 6 be excluded on the ground that they contain part of the data in the remaining tabulations, the probability would be $1 \div 16^3$ or $1 \div 1{,}536$ which is less than 0.0007.

It may be claimed that this is an underestimate because of a natural association between maximum abundance and maximum frequency. Suppose, then, that the probability of maximum abundance and maximum frequency of the aggregate forms occurring together is large—say P. Then, since there is an equal chance of this combination being related to the colder or the warmer water, the probability of its being related to the colder water in any one tabulation would be $\frac{P}{2}$. From this it follows that the probability of minimum

abundance occurring with maximum frequency and also with the colder water in any one tabulation (as is the case with the solitary forms) would be $\frac{1-P}{2}$. Hence, the probability of maximum abundance and frequency of aggregate forms being associated with minimum abundance and maximum frequency of the solitary forms and with the colder water in any one tabluation is $\frac{P}{2}\left(\frac{1-P}{2}\right)$ or $\frac{P-P^2}{4}$, and the probability of this happening three times in succession is $\left(\frac{P-P^2}{4}\right)^3$. The value of this expression is largest when $P = \frac{1}{2}$ or when $\left(\frac{P-P^2}{4}\right)^3 = \frac{1}{16^3}$, and since this is the value P assumes if abundance be independent of frequency, it follows that the probability would be less than $\frac{1}{16^3}$ if a natural association exists between maximum abundance and maximum frequency. Furthermore, the magnitudes of the differences between maximum and minimum abundance and between maximum and minimum frequency, as well as the number of hauls, have not been considered, so that the probability 0.0007 must be regarded as a large overestimate rather than an underestimate.

It therefore follows that the odds in favor of the trustworthiness of the relations shown by tables 4, 5, and 6 are sufficiently large (more than 1,535 to 1) to justify the conclusion that temperature, or some influence intimately associated with it, must play a prominent, albeit a peculiar, part in the distribution of *Salpa democratica*.

2. A Morphological Implication

What do the foregoing facts imply? Since solitary forms accumulate on the surface in greatest numbers when the water is warm, while aggregate forms accumulate in greatest numbers when the water is cold, some definite relation must exist between them, compelling solitary forms to be taken in cold water whenever aggregate forms are captured, compelling aggregate forms to be taken in warm water whenever solitary forms are captured, and preventing any of one generation to be taken without some of the other. Were there no such relation, I can conceive of no way in which the two generations could be so nearly identical in frequency and at the same time reversed in abundance.

Upon considering the life cycle, two possible relations are suggested: (1) that individuals of the solitary generation are developed until maturity within the body of those of the aggregate generation (p. 245); and (2) that the aggregate salpae are budded off in the form of a chain by the proliferating stolon of the solitary salpa (p. 243). The first alternative might account for the capture of at least one solitary form in cold water by each haul that captured a number of

aggregate forms. For at least one individual of that generation might be captured which contained an embryo sufficiently mature to be dislodged during the processes of towing and washing the net and condensing and handling the hauls, and so be counted as a solitary form. If such were the case, the frequency of solitary forms would be identical with that of aggregate forms *in colder water*. But, even so, this could not account for the fact that those solitary forms captured in the warmer water were accompanied by aggregate forms, for the embryo does not carry the adult, and aggregate forms are shown to be most abundant in cold water, while solitary forms are most abundant in warm water. The second alternative, however, completely satisfies the conditions, providing the chain of aggregate salpae remains attached to the solitary salpa after being protruded from its mantle cavity into the water.

This will be rendered more intelligible, perhaps, if the problem is stated in symbolical language. Let a solitary form be symbolized by a cork, an aggregate form by an iron weight, warm water by the surface of a pond, and cold water by the bottom of the pond. Flotation is then analogous to accumulation in warm water, and sinking to accumulation in cold water. Our problem may now be restated as follows: Since corks float and iron weights sink, what is the relation between them that necessitates taking some corks from the bottom of the pond whenever a number of iron weights are taken therefrom, and that necessitates taking some iron weights from the surface whenever a number of corks are taken therefrom?

Stated in this symbolical language, it is evident that the only feasible answer is that at the time the corks and iron weights were removed from the pond, *they were tied together*. Now, if by experiment, we find that one cork will barely float six weights, corks with more than this number of weights attached would sink, while those with less attached would float. Moreover, if those corks with more than six weights attached *usually* outnumbered those with less attached, while *occasionally* those with less attached far outnumbered those with more attached, then both corks and weights would be so distributed with respect to surface and bottom that, while corks in the long run would be obtained in greater numbers from the surface than from the bottom, at least one would be present in a larger percentage of bottom than of surface hauls. In other words corks would be most abundant and least frequent on the surface, while iron weights would be most abundant and most frequent on the bottom.

This hypothetical distribution of corks and iron weights exactly parallels the distribution of the individuals of the two generations of *Salpa democratica* as demonstrated by tables 4 to 6. The conclusion, therefore, seems unescapable that each aggregate salpa, after being pushed to the exterior of the solitary salpa, *remains attached to its predecessor and that this chain of salpae also remains attached to the solitary salpa* as in other species of the genus.

3. Evidence of the Existence of Protruding Chains

The conclusion being reached that protruding chains of *Salpa democratica* are of normal occurrence, it is well before assuming its truth, to consider whatever other evidence there may be. To this end the literature has been searched without finding a single unequivocable statement. Brooks (1893, pl. xliii) has published a drawing of what he calls: "part of a fully grown chain of *Salpa democratica.*" It consists of six salpae attached together as described on page 244, but the magnification is not given and, while it is probable from the condition of the test that Brooks had a portion of a protruded chain before him, it is possible that by "fully grown chain" he means the final positions assumed by the salpae in the terminal portion of the stolon. Again Herdman (1889, p. 58), after refering to a cut of the posterior end of the solitary form of *S. democratica,* says: "After the solitary *Salpa* has become fully developed, the chain produced by the stolon is set free in sections, each section being composed of a number of aggregated *Salpae* at about the same stage of development." This statement sounds definite and explicit, but it is not clear that it refers to *S. democratica* in the first place nor to the freeing of the salpae from the mantle cavity of the solitary form in the second place: by "set free in sections" Herdman may refer to the periodic manner in which the stolon segments (see page 244).

But, Herdman's statement is corroborated by that of Agassiz (1866, p. 20) who, in describing *S. cabotti*—probably a large variety of *S. democratica*—says: "The young Salpae are not uniformly developed in proportion to their distance from the base of the tube [stolon]. Sections of the tube are equally advanced and we find generally, three such portions unequally developed. . . . The base of the geminiferous tube is simply slightly corrugated, next comes a section in which we find two rows of slight elevations, and finally the most advanced part of the chain where the rudimentary Salpae are

more or less advanced and resemble in every respect, long before it becomes detached, the chains which are found floating about. These sections are thus liberated in turn, new ones continually forming at the base of the geminiferous tube during the budding season. . . . These chains escape through an opening formed at the proper time through the tunic [test], near the nucleus on the ventral side, which shows afterwards no trace of the passage of the small chain.'' Agassiz repeatedly refers to these liberated chains so that, if *S. cabotti* is in reality only a variety of *S. democratica,* it is evident: (1) that the chain of aggregate forms remains intact after, as well as before, escaping from the mantle cavity of the solitary form; and (2) that the chain is liberated in blocks of from forty to sixty individuals. Obviously, this means that protruding chains must exist during the period of liberation, but what length of time this involves is not indicated.

Aside from these three instances I have failed to find a single statement applicable in any way to the question as to whether or not the salpae remain attached in the form of a protruding chain. In fact the attitude of those familiar with the group seems to be either that such chains may be assumed to exist on general principles, or that they do not exist in this species.

But negative evidence is never conclusive. Following up the implications of tables 4 to 6, examination of the crude data (table 1) shows that every haul that captured more than six solitary forms, and all but three capturing less than six, also captured aggregate forms. The three that failed (hauls 1650, 1653, and 1804) were all made in water exceeding 18°9C. Moreover, as aggregate forms accumulate in cold, and solitary forms in warm surface water, a considerable number of hauls made in the colder water ought to have captured aggregate forms, but no solitary forms, if protruding chains or salpae containing mature embryoes were not frequently encountered; but *not a single such haul was made.* Again, hauls made in the warmer water ought frequently to have captured solitary forms, without aggregate forms, if protruding chains were not generally encountered; but only three such hauls were made.

Further examination of the crude data reveals three more hauls (1860, 1872, and 1875) made in water exceeding 18°9C which captured 21, 12, and 89 aggregate forms respectively, but no solitary forms. Why? In answering this question it must be recognized that during the processes of washing the net and of condensing, separating, and examining the hauls a few specimens are nearly always lost. Con-

sequently, in hauls encountering only a very few protruding chains the chance of losing the single solitary salpa of each chain would be much greater than that of losing all the aggregate salpae. This, I believe, is why no solitary forms were found in these three hauls. Moreover, in four others (1432, 1779, 1854, and 1864) individuals of the aggregate generation alone were recognized at first, but *on reëxamination mature solitary forms were found,* which makes the above explanation more plausible. The crude data also show that out of thirty-six hauls made in water below 18°6C, each of twenty-five contained both solitary forms and aggregate forms, while each of the remaining eleven failed to obtain a single individual of either generation. This seems explicable only on the assumption that protruding chains were encountered in nearly if not all successful hauls.

It is well known that chains of even such large species as *Salpa fusiformis* and *S. zonaria* are obtained entirely intact only with the greatest difficulty. Says Herdman (1889, p. 59): "Out of the enormous number of aggregated *Salpae* collected during the Challenger expedition, none were adhering together when they reached my hands. In all cases the chains . . . had become broken up into their constituent *Salpae.*" Although this has not been the result of collections made under the auspices of the Scripps Institution, chains of no species have been obtained entirely intact except when collecting with extreme care with a dip-net. Would it be surprising, then, if the pressure and swirl of the water in a tow-net completely breaks up whatever chains of the smallest and most delicate species, *S. democratica,* may be encountered?

Granting this to be the explanation why protruding chains of this species have never been described, it follows that the effect of the swirling water in causing breakage would be less pronounced the shorter the duration of the haul. Working over the collections from this point of view, it was noticed that, while all the hauls herein considered consumed upwards of twenty minutes, a few thirteen-minute hauls had been made in the vicinity of Santa Rosa Island during August, 1911. Furthermore, while no portion of a chain was found in any of the hauls entered in table 1, *several fragments were discovered* in one of the above mentioned thirteen-minute hauls (2766). In three instances two aggregate forms were found attached together; in another, three larger ones were attached; and in still another, five were attached together so as to form a double chain as illustrated in plate 9, figure 1. There can, therefore, be no doubt that, as Agassiz

(1866) has said, each aggregate salpa remains attached to its predecessor after as well as before being pushed out of the mantle cavity of the solitary salpa into the water. Does it seem unlikely, then, that the chain also remains attached to its progenitor?

4. Implications Regarding Locomotion

If, as claimed on page 260, the general occurrence of protruding chains is the only feasible explanation of all the temperature relations, then some form of locomotion of the individuals of the two generations is implied. For, to return to the corks and iron weights, the only likely manner in which corks could be most abundant and least frequent on the surface, while the attached iron weights were most abundant and most frequent on the bottom is, as stated on page 257, for corks with less than a given number (six) of attached weights to float and for those with more attached to sink. That is, the presence of weights on the surface would be consequent upon the buoyancy of the attached cork, and the presence of corks on the bottom upon the sinking propensity of the attached weights.

Translating back into *Salpa* terminology, the inference seems clear that protruding chains of less than a given but unknown number of aggregate salpae—*short chains*—are prevented from leaving an area of warm surface water by virtue of the activity of the attached solitary form, while with chains consisting of more than this number—*long chains*—the solitary form is prevented from escaping out of an area of cold surface water by virtue of the combined activity of the attached aggregate salpae. I do not mean to stipulate that aggregate forms are negatively thermotactic and solitary forms positively thermotactic, nor that long chains move horizontally out of warm into cold areas of surface water, while short chains move horizontally out of cold into warm areas of surface water. This may or may not be the true explanation, but it seems unlikely. Further, it is not stipulated that aggregate forms are negatively geotactic and solitary forms positively geotactic in cold surface water, while the responses are reversed in warm surface water. This, again, may or may not be the true explanation; the data are inconclusive. Lastly, it is not stipulated that an internal control by aggregate forms and solitary forms over their own specific gravities leads to an accumulation of short chains in warm surface water and long chains in cold surface water; nor is it stipulated that some form of metabolic rhythm is

involved. Once, again, either of these may or may not be the true explanation, but neither seems likely. What the unescapable implications of the data are, may be listed as follows:

1. Short chains accumulate in warm surface water and long chains in cold surface water.

2. Since the only difference between short and long chains consists in the number and size of the attached salpae, a differential in the distribution of the two generations must be due to a differential in behavior of short and long chains, which obviously implies a differential in behavior of the solitary form and aggregate forms constituting the chains.

3. The only type of behavior consistent with all the facts is some form of locomotion.

However, these are implications—not facts—and it is necessary to gain some idea of their reliability by reëxamining the data.

C. REËXAMINATION OF THE DATA

1. Relation Between Season and Temperature

It has been suggested that the difference between short and long chains may actually not have been restricted to the number and size of the attached salpae. This, it is said, would be true only if all possibility of seasonal influence were eliminated. In other words, it is argued that, owing to an intimate association between increasing temperature and advancing season, even within the limits of June and July, 1908 and 1909, the relation between temperature and abundance of the two generations may have been consequent upon an increased production of solitary forms and an increased death rate of aggregate forms.

On first thought this seems reasonable, but careful consideration proves it untenable. For each individual of the aggregate generation can give birth to only one solitary form, so that an increased production of the latter requires an increased number of the former. Furthermore, as stated on page 245, the embryo is carried and developed within the body of the aggregate form and is not set free until after it has reached maturity and its stolon has begun to be converted into the salpae of the succeeding aggregate generation. Consequently, all hauls obtaining an excess of solitary forms over aggregate forms would,

according to this hypothesis, have to be restricted to that time interval between the death of many of the embryo-bearing salpae and protrusion from the mantle cavity of the solitary forms of the first salpae of the next generation—a time interval which is brief if it occurs at all. If this were not the case, either no significant temperature relations would have appeared in the data, or aggregate forms as well as solitary forms would have been most abundant in the warmer water, both of which are contrary to fact. Moreover, the hypothesis requires the death of a large number of aggregate forms prior to their maturity, for, as stated on page 245, the testis does not develop until after the embryo has matured and made its escape. Does this seem reasonable?

But to speculate gains naught. The hypothesis is therefore subjected to an empirical test. Table 7 gives the distribution of hauls involved in tables 4, 5, and 6 with respect to each of the four months concerned: June and July, 1908, and June and July, 1909.

TABLE 7

Distribution of hauls with respect to season

Temperature in centigrade	June, 1908		June, 1909		July, 1908		July, 1909	
	Hauls	Mean date	Hauls	Mean date	Hauls	Mean date	Hauls	Mean date
Section A—Hauls involved in table 4								
15°9–18°3	11	18	14	23	2	19	3	5
18°4–20°8	5	20	13	22	9	21	19	7
Section B—Hauls involved in table 5								
15°9–18°3	0	....	9	23	0	....	0	....
18°4–20°8	0	....	9	23	8	22	16	8
Section C—Hauls involved in table 6A								
15°9–18°3	11	18	5	22	2	19	3	5
18°4–20°8	5	20	4	23	1	8	3	2
Section D—Hauls involved in table 6B								
15°9–18°3	7	18	1	15	0	....	0	....
18°4–20°8	3	19	0	....	0	....	1	2
Section E—Hauls involved in table 6C								
15°9–18°3	2	17	2	23	2	18	3	5
18°4–20°8	2	27	1	29	1	8	0	....
Section F—Hauls involved in table 6D								
15°9–18°3	0	....	6	24	0	....	0	....
18°4–20°8	0	....	8	21	4	21	6	7

From these data it is difficult to understand how any seasonal effect could have been responsible for the temperature relations revealed by tables 4 to 6. In the first place section A shows that, while six more hauls were made during June, 1908, in the colder than in the warmer water, the five made in the warmer water were, as indicated by the mean date, made somewhat later in the month than were the other eleven. According to the hypothesis under consideration this might lead to an excess of solitary forms and a deficiency of aggregate forms in the warmer water. But the differentials revealed by table 4 could not have been due to the influence of this month because the same differentials are shown by table 5, and section B of the above table shows that none of the hauls involved in table 5 were made during June, 1908. Likewise, it is shown by section D that none of the hauls involved in table 6B were made during July, 1908; yet the same differentials are revealed by it as by table 4, which obviously means that the differentials could not have been due to the way in which the hauls were distributed throughout July, 1908. Similarly with respect to July, 1909: section E of the above table shows that no hauls were made in the warmer water between 6 A.M. and 10 A.M. (table 6C), while section F shows that none were made in the colder water between 6 P.M. and 10 P.M. (table 6D). Yet the differentials revealed by tables 6C and 6D, to which these data relate, are identical.

It is clear, then, that the hypothesis under consideration must justify itself, if at all, on the way in which hauls were distributed during June, 1909. But all five sections of table 8 show: (1) an almost exact equality between number of hauls made in the colder water and in the warmer water; (2) an almost identical mean date relative to hauls made in warm and cold water; and (3) that the slight differences in mean date that do exist are erratic with respect to the temperature of the water; two instances (section A, and F) indicating that the hauls made in the colder water were also made somewhat later in the month than were those made in the warmer water, while two instances (sections C and E) indicate that the reverse was true.

To demonstrate completely the inadequacy of this hypothesis, table 4 is reconstructed by eliminating therefrom all hauls except those made during June, 1909. The results are given in the following table:

TABLE 8

Reconstruction of table 4 by eliminating all hauls except those made during June, 1909

Temperature in centigrade	Hauls	Hours of hauling	Solitary forms: Hours of successful hauling	Solitary forms: Specimens: Total	Solitary forms: Specimens: Per hour	Solitary forms: Frequency: Time	Solitary forms: Frequency: Per hour	Aggregate forms: Hours of successful hauling	Aggregate forms: Specimens: Total	Aggregate forms: Specimens: Per hour	Aggregate forms: Frequency: Time	Aggregate forms: Frequency: Per hour
15°9–18°3	14	13.2	11.3	739	56	86	88	11.3	3,389	257	86	88
18°4–20°8	13	8.6	5.0	2,104	245	58	80	3.7	943	110	43	63

Table 8 not only shows the same relation as does table 4, but demonstrates that elimination of the seasonal effects due to the other three months *intensifies* the difference between the abundance of solitary forms in the colder water and their abundance in the warmer water. In the colder water their abundance is reduced from 67 per hour (table 4) to 56 per hour (table 8), while their abundance in the warmer water is increased from 160 per hour (table 4) to 245 per hour (table 8). Therefore, although advancing season and increasing temperature were associated, the salpae were so distributed during the months to which these data relate as to make it highly improbable, if not impossible, for the relations revealed by tables 4 to 6 to have been consequent upon the seasonal succession of the two generations.

2. Relation Between Position and Temperature

Another hypothesis has been raised. It is argued on the basis of certain evidence relating particularly to aphids and rotifers that high temperatures might favor production of solitary forms. Although some of the more recent investigations (Whitney, 1907; Shull, 1911) make such an effect of temperature doubtful, other causative factors, such as substances in solution, may be so associated with temperature as to lead to a greater production of solitary forms at high temperatures. It is well, therefore, to consider this hypothesis.

According to it the differentials established by tables 4 to 6 are consequent not upon locomotion of solitary forms and aggregate forms, nor upon their seasonal succession, but upon a stratification of surface water into areas of high and low temperature, in the former of which solitary forms predominate because of their greater production, while aggregate forms predominate in the latter because of their greater death rate in the warm areas. As in the case of seasonal suc-

cession, it is difficult to see how solitary forms could by this means predominate in the warm areas without also involving a predominance of aggregate forms in the same areas. For, as stated on page 245, each individual of the aggregate generation can give birth to but a single solitary form and then not until the stolon of the latter has begun to be converted into salpae of the next generation. This makes it necessary, as in the case just considered, for all hauls obtaining an excess of solitary forms over aggregate forms to have been made during that brief and improbable time interval in the life cycle between the premature death of many of the embryo-bearing salpae and protrusion of the first salpae of the next generation from the mantle cavity of the solitary form.

But, assuming the hauls to have been made in this improbable if not impossible manner, the verity of the hypothesis hinges upon whether or not stratified areas of warm and cold surface water persisted for a sufficient length of time. In other words, were the majority of warm water hauls made at one set of positions and the majority of cold water hauls at another set? If so the above hypothesis might be true; if not it is obviously inadequate.

To answer this question the following list is supplied, which gives the distribution of hauls involved in table 4 with respect to position, the unit of position being a rectangular area or *section* of five miles (or more accurately five minutes), on a side. In designating the section, the *number* denotes its distance in five-minute units west of 114°W, while the *subscript* denotes its distance in five minute units north of 32°N. For further explanation see Michael and McEwen (1915, p. 46; 1916, p. 217) and McEwen (1916, pls. 1–3).

List Showing Distribution of Hauls Involved in Table 4 by Sections

Section	Number of hauls in: Cold water 15°.9–18°.3C	Number of hauls in: Warm water 18°.4–20°.8C	Section	Number of hauls in: Cold water 15°.9–18°.3C	Number of hauls in: Warm water 18°.4–20°.8C
39_{10}	0	4	45_{10}	1	0
40_{10}	0	15	45_{12}	1	0
40_{11}	0	7	46_{9}	1	0
40_{12}	1	0	46_{12}	2	0
41_{8}	0	2	49_{10}	0	1
42_{8}	1	3	50_{13}	1	0
42_{9}	0	1	52_{10}	1	2
42_{10}	11	9	52_{16}	0	1
43_{10}	4	0	53_{10}	1	1
43_{11}	2	0	61_{5}	2	1
44_{12}	1	0			

This list shows that as the distance from the coast increased the number of hauls made in the cold water relative to those made in warm water, as a rule, also increased. According to the hypothesis under consideration, this might lead to an excess of aggregate forms in the colder water and an excess of solitary forms in the warm water and so account for the differentials.

But, as shown by table 9, the excess of warm water hauls in sections 39_{10}, 40_{10}, 41_{8}, 42_{8}, 42_{9}, and 49_{10} together with the excess of cold water hauls in sections 40_{12}, 43_{11}, 44_{12}, 45_{10}, 45_{12}, and 50_{13} can not account for the differentials in question, for the reason that the differentials are revealed by table 6C as well as by table 4, and none of the hauls involved in table 6C were made in these sections. Similarly, the excess of warm water hauls in sections 40_{11} and 52_{16} together with the excess of cold water hauls in 46_{9}, 53_{10} and 61_{5} can not account for the differentials because none of the hauls involved in table 6B were made in

TABLE 9

Distribution of hauls involved in tables 5 and 6 with respect to position

Section	Table 5		Table 6A		Table 6B		Table 6C		Table 6D	
	Cold water 15°.9–18°.3C	Warm water 18°.4–20°.8C	Cold water 15°.9–18°.3C	Warm water 18°.4–20°.8C	Cold water 15°.9–18°.3C	Warm water 18°.4–20°.8C	Cold water 15°.9–18°.3C	Warm water 18°.4–20°.8C	Cold water 15°.9–18°.3C	Warm water 18°.4–20°.8C
39_{10}	0	3	0	1	0	0	0	0	0	3
40_{10}	0	15	0	0	0	0	0	0	0	6
40_{11}	0	5	0	2	0	0	0	2	0	2
40_{12}	0	0	1	0	1	0	0	0	0	0
41_{8}	0	1	0	1	0	0	0	0	0	1
42_{8}	0	0	1	3	0	2	0	0	0	0
42_{9}	0	0	0	1	0	1	0	0	0	0
42_{10}	6	7	5	2	1	0	2	1	5	5
43_{10}	1	0	3	0	2	0	1	0	1	0
43_{11}	2	0	0	0	0	0	0	0	0	0
44_{12}	0	0	1	0	0	0	0	0	0	0
45_{10}	0	0	1	0	1	0	0	0	0	0
45_{12}	0	0	1	0	1	0	0	0	0	0
46_{9}	0	0	1	0	0	0	1	0	0	0
46_{12}	0	0	2	0	1	0	1	0	0	0
49_{10}	0	0	0	1	0	0	0	0	0	0
50_{13}	0	0	1	0	1	0	0	0	0	0
52_{10}	0	1	1	1	0	1	1	0	0	0
52_{16}	0	0	0	1	0	0	0	1	0	0
53_{10}	0	0	1	0	0	0	1	0	0	0
61_{5}	0	1	2	0	0	0	2	0	0	1

these sections, and this table as well as table 4 reveals the differentials. Again the excess of cold water hauls in section 46_{12} can not have been responsible, for none of the hauls involved in table 5 were made in this section. Finally, the excess of warm water hauls in section 52_{10} can not have caused the differentials, because none of the hauls involved in table 6D were made in this section.

All the sections except 42_{10} and 43_{10} are thus eliminated from further consideration. Relative to the latter, all the hauls were made in the colder water. According to the hypothesis in question this might account for the excess of aggregate forms in the colder water. Still, it obviously can not account for the excess of solitary forms in the warmer water. But, neither can the distribution of hauls in section 42_{10} account for it, for not only were more cold than warm water hauls made in this section, but table 9 shows that none of the warm water hauls involved in table 6B were made in it. Furthermore, every haul made in this section was made within 0°3 of 32° 52′N and all except one (1657), which failed to catch a single individual of either generation, within 0°4 of 117° 30′W. Finally, every haul save one (1815, made on July 7, 1909) was made between June 15 and June 29, 1909. This obviously means that, even if stratified areas of warm and cold water did exist within the required limits of approximately 0.64 square miles—a highly improbable occurrence—the time elapsed was insufficient to enable the excess of solitary forms and deficiency of aggregate forms in the warmer water to have arisen in consequence of an increased production of the former and death of the latter. It follows, then, that if table 4 be reconstructed by eliminating all hauls except those made in section 42_{10}, this stratification hypothesis will be put to its final test. Table 10 shows the results of such reconstruction.

Table 10

Reconstruction of table 4 by eliminating all hauls except those made in section 42_{10}

				Solitary forms				Aggregate forms				
				Specimens		Frequency			Specimens		Frequency	
Temperature in centigrade	Hauls	Hours of hauling	Hours of successful hauling	Total	Per hour	Time	Per hour	Hours of successful hauling	Total	Per hour	Time	Per hour
15°9–18°3	11	10.7	10.7	726	**68**	100	**100**	10.7	3,306	**309**	100	**100**
18°4–20°8	9	5.9	5.3	1,354	**229**	90	**98**	4.0	942	**160**	68	**80**

According to the stratification hypothesis this table ought to show an approximate equality between the abundance of solitary forms in the warmer water and their abundance in the colder water, and also between the abundance of aggregate forms in the warmer water and their abundance in the colder water. This is obviously not the case. The relations shown by table 10 are essentially the same as those shown by table 4, solitary forms again appearing as most abundant and least frequent in the warmer water, while aggregate forms appear as most abundant and most frequent in the colder water. Not only is this true, but the difference in abundance of the solitary forms in the warmer and that in the colder water has been *increased* from 93 in table 4 to 161 in table 10. Therefore, although the temperature did decrease with increasing distance from the coast, the two generations were so distributed with respect to position as to make it quite impossible for the differentials revealed by tables 4 to 6 to have been due to stratified areas of warm and cold surface water, or what amounts to the same thing, to differences in position.

3. Ostwald's Viscocity Theory

The inadequacy of this theory to explain vertical migrations has been pointed out before (Michael, 1916, p. xiv). It is not my purpose, therefore, to discuss the theory in detail. But, as someone is sure to claim that variation in viscocity of the water induced by variations in temperature is responsible for the differentials observed in the surface distribution of *Salpa democratica,* it is necessary to forestall this claim. The matter will be considered on the basis of three alternative assumptions: (a) that solitary forms or short chains have the same specific gravity as aggregate forms or long chains; (b) that solitary forms or short chains are heavier than aggregate forms or long chains; and (c) that aggregate forms or long chains are the heavier.

It needs no argument to demonstrate that if, the first case (a) were true, differentials in distribution of the two generations would be impossible if due solely to viscocity effects. For if owing to an increase in temperature, the viscocity decreases sufficiently to cause the individuals of one generation to sink, those of the other generation, being of the same specific gravity, must also sink.

In the second case (b), a decrease in viscocity might cause solitary forms or short chains to sink while aggregate forms or long chains

remained on the surface. This would, however, require a lower viscocity in cold than in warm surface water, for otherwise aggregate forms would be most abundant in warm surface water and least abundant in cold surface water, which is contrary to fact. But even so, it would be physically impossible for solitary forms or short chains to remain in maximum numbers on the surface when aggregate forms or long chains were present in minimum numbers. For, the former, being heavier than the latter, must sink if the latter do.

The third assumption (c) is, perhaps, the most probable, because since many individuals of the aggregate generation contain an embryo of the solitary generation, it may well be that their specific gravity exceeds that of the solitary forms and, for the same reason, the specific gravity of long chains may actually exceed that of short chains. Under these conditions a decrease in viscocity induced by an increase in temperature might permit the sinking of aggregate forms or long chains while solitary forms or short chains remained on the surface. This might explain why aggregate forms were most abundant and most frequent in the colder surface water and least abundant and least frequent in the warmer surface water. But, as in case (b), solitary forms could not be more abundant in warm than in cold surface water, for cold water, being denser, anything heavy enough to sink in cold water must certainly sink in warm water.

Again if it be claimed that, owing to variation in evaporation, warm surface water is at times denser than cold, while at other times cold surface water is denser than warm, what must the consequences be? Returning to the three alternative assumptions, if (a) were true, the warmer water must have been the more dense during the majority of hauls or solitary forms could not have been taken in greater numbers from the warmer water. Yet, to obtain the aggregate forms in greater numbers from the colder surface water, it would have had to be the more dense during the majority of hauls. Obviously both conditions could not have been realized, and even if they could, the frequency of solitary forms would have paralleled their abundance, which is contrary to fact.

If either (b) or (c) were true, the situation, while more complex, remains essentially unaltered. For in the first case, solitary forms or short chains, being the heavier, would of necessity sink whenever aggregate forms or long chains sank; while in the latter, aggregate forms or long chains, being the heavier, would have to sink whenever solitary forms or short chains sank.

It seems, then, that whatever the specific gravities of individuals of either generation may be, and whatever may have been the way in which viscocity of the water was related to high and low temperatures, the observed differentials could not have been caused by changes in viscocity alone. Furthermore, as any combination of physical influences could, at best, only directly affect one generation more than the other, it follows that whenever the generation least liable to be affected was affected, the other generation must of necessity have been similarly affected. This means that the observed differentials could not have thus arisen. Is it not evident then, that, although changes in viscocity, etc., have doubtless affected the magnitudes of the observed differences in abundance of the two generations, such changes alone are impotent to explain the differentials noted?

D. THEORY OF LOCOMOTION

1. Behavior of Chains

In the preceding pages it has been demonstrated that neither differences in season, differences in position, nor a combination of these, nor variations in the condition of the water are adequate to account for the facts that: (1) solitary forms are most abundant on the surface when the temperature of the water is high; (2) aggregate forms are most abundant on the surface when the temperature is low; and (3) both solitary forms and aggregate forms are most frequent on the surface when the temperature is low. Furthermore, tables 5 and 6 make it evident that influences associated with time of day could not have given rise to these relations. Is the conclusion, then, not forced upon one that, as stated on page 262, "the only type of behavior consistent with all the facts is some form of locomotion"? Since the combined effects of all surface influences directly associated with time and space, i.e., with time of day, day of the month, month of the year, and with latitude and longitude, do not materially alter the observed differentials, locomotion appears to be the only instrumentality by means of which they could have arisen.

It is characteristic of all salpae, as stated on page 242, that whenever they breathe or feed they move forward along a stream of water forced through their bodies. Concerning the movements of this species (described as *S. cabotti*) Agassiz (1866, p. 18) says: "The

chains* move along with the current, seemingly quite helpless, though the upper extremity is sometimes deflected somewhat abruptly by attempts to escape capture. The solitary individuals, on the contrary, are exceedingly active, swimming about vigorously, generally with the anterior extremity uppermost; expelling by quick and powerful jerks the water which propels them by its reaction. Their motions are very similar to *Trachynema;* they can readily change the direction of their movements, and regulate them by their powerful transverse muscular bands, though they lack in their motions the ease and grace of Jelly Fishes.'' And again, on page 21: When the individuals of a chain have become separated, ''the aggregate form is perfectly helpless, the great thickness of the tunic preventing it from regulating its motion; while, when connected as a chain, their capacity to guide the chain in any particular direction is much greater.''

Assuming, therefore, that protruding chains exist; if the oral-atrial axes of the chain salpae remain at an angle to the oral-atrial axis of the solitary form after as well as before protrusion into the water (see p. 244), the direction of locomotion of the solitary form will differ from that of the protruding salpae. Moreover, as every salpa in the left and right row respectively of the double chain, of necessity moves in the same direction, the resultant force tending to propel the chain at an angle to the direction of motion of the solitary form will increase as the number of protruding salpae increases. The mechanical result must be either to break the chain or to twist it until solitary forms and aggregate forms become headed so as to move in opposite directions. The situation is that of a ''tug of war'' in which each short chain is pulled along by the solitary form while, in each long chain, the solitary form is pulled along by virtue of the combined locomotive power of the attached aggregate forms.

As the number of salpae in the protruding chain increases, the strain upon the chain also increases, and this must sooner or later break it. Is there any clue as to how this occurs? There is. It was stated on page 244 that the stolon undergoes alternating periods of active segmentation and rest so that the salpae are formed, and, according to Agassiz (1866, p. 20), set free in blocks of from forty to sixty individuals of nearly the same size. The ''intermediate piece'' (Johnson, 1910, p. 150) connecting two blocks is composed of small, imperfect, and distorted individuals. In chains of *Salpa fusiformis,* which are

* Throughout these quotations Agassiz refers not to protruding chains but to chains completely isolated from the solitary salpa.

formed in a very similar manner to those of *S. democratica,* Johnson (1910, p. 151) says: "If one removes a large block from the chain, the separation occurs at the first zooid of the block, leaving the entire intermediate piece as the terminal remnant of the block that remains." The intermediate piece, or salpa adjacent to it, is therefore a place of weakness, or "deploying point" as Johnson (1910, p. 151) calls it, and it seems likely that, if not accidently broken sooner, the strain above mentioned will naturally break a chain of *S. democratica* at this point at about the time each block has been protruded into the water. According to Agassiz (1866, p. 20), this separation must occur some time before the entire block has been liberated, for, he says: "These chains escape through an opening formed at the proper time through the tunic . . . which shows afterwards no trace of the passage. . . ." If this be true, the load carried by the solitary form will vary periodically as budding proceeds, from zero at one extreme to the condition where the combined locomotive power of the aggregate forms greatly exceeds that of the solitary form at the other extreme.

Moreover, if as seems likely, the number of protruding salpae required to equal in locomotive power that of the attached solitary form are few, compared to the number in the protruding portion of a block at the time of separation, long chains would be encountered more frequently than short chains. Again, is it not probable that the large majority of hauls encountering a number of long chains would also encounter at least one and in some instances many liberated blocks, chain fragments, or detached aggregate salpae, while the large majority encountering a number of short chains would also encounter at least one and in some instances many solitary forms from which no salpae protruded? If this question be answered in the affirmative, and if it be granted that the preference, so to speak, of solitary forms to remain on the surface increases as the temperature of the water increases, while that of aggregate forms increases as the temperature decreases, it follows that long chains plus liberated blocks plus chain fragments plus detached aggregate forms, would be most abundant and most frequent in the colder surface water, while short chains plus detached solitary forms would be most abundant but least frequent in the warmer surface water. Finally, if each chain and liberated block and chain fragment becomes broken up into its constituent salpae by the swirl and pressure of the water during the process of towing (see p. 260), it follows that the data, when tabulated as in the foregoing tables, would reveal the solitary forms as most abundant and least

frequent on the surface when the temperature was 18°.4C or more, and the aggregate forms as most abundant and most frequent on the surface when the temperature was 18°.3C or less.

It is only by some such means of locomotion that I can conceive how the observed differentials in abundance and great similarities in frequency of the two generations could have arisen. Let it be emphasized, however, that this is theory, not fact, and can be fully established only by observations on moving protruding chains. But if correct, verification ought not to prove difficult, for the theory implies the same type of locomotion, though not the same type of behavior relative to temperature, for every species within the genus having similar double chains.

2. Deduced Peculiarities in Temperature Relations

If the foregoing theory of chain locomotion is correct, several consequences in the distribution of the two generations are implied. It is obvious that, were no solitary forms or aggregate forms ever encountered except when attached together in chains, the frequency of both generations would be identical with that of chains, and consequently parallel to the abundance of chains. Whence, if *long* chains accumulate on the surface in increasing numbers as the temperature *decreases*, while *short* chains accumulate in increasing numbers as the temperature *increases, chains*, irrespective of length, would be most abundant and frequent in the coldest and in the warmest water, and least abundant and frequent in water of medium temperature. Therefore, if as the theory stipulates, the frequency of each generation is consequent upon the characteristic occurrence of protruding chains, the frequency of both should not only be nearly identical, but should decrease as the temperature increases from its lowest to its *middle* values, i.e., from about 16°.0C to about 18°.5C, and then should increase as the temperature increases from its middle to its highest values, i.e., from about 18°.5C to about 21°.0C. Furthermore, on account of the periodic segmentation of the stolon resulting, hypothetically, in periodic breakage of the protruding chains at the "intermediate piece," it follows, as stated on page 273, that long chains would be encountered more frequently than short chains. Hence, if M represent the temperature half way between the two extremes, and x any range in temperature, the frequency of both generations relative to $M-x$ should exceed that relative to $M+x$.

Again, only *one* solitary form can be transported into cold surface water by the aggregate salpae of each long chain, while several aggregate forms must be transported into warm surface water by the solitary salpa of each short chain. In other words, a decrease in number of aggregate forms relative to an increase in temperature must be masked by an increase in number of short chains to a far greater extent than a decrease in number of solitary forms relative to a decrease in temperature would be masked by an increase in number of long chains. Therefore, aggregate forms should be more abundant in the warmest surface water than in that somewhat cooler. Indeed, their abundance should approximately parallel that of chains, so that a minimum ought to occur in water having a temperature about midway between the two extremes, i.e., about 18°.5C. Solitary forms, however, being much less affected by the distribution of long chains than aggregate forms are by that of short chains, should increase in abundance as the temperature increases from its lowest, or nearly its lowest, to its highest value.

By retabulating the data with reference to three, four, five, and more temperature groups, this locomotion theory will be subjected to an empirical test. To sum up, the relations that according to theory should be revealed are:

1. Frequency of both generations nearly identical, and decreasing with an increase in temperature to near the middle of its range, then increasing with an increase in temperature.

2. Frequency of both generations greater in the lowest than in the highest temperature group, greater in the next lowest than in the next highest, greater in the third lowest than in the third highest, and so on.

3. Abundance of aggregate forms paralleling, or nearly paralleling, frequency of both generations, appearing at its minimum relative to medium temperatures.

4. Abundance of solitary forms decreasing as the temperature decreases throughout the entire range or nearly so; if any increase in abundance accompanies a decrease in temperature, this will be evident only in the coldest water when the number of temperature groups is great enough to permit comparison of the effect of small ranges.

In table 11 the data are arranged in three groups according as the temperature varied from 15°.9C to 17°.4C, 17°.5C to 19°.0C, or 19°.1C to 20°.6C. The only haul (1579) made in water exceeding 20°.6C, and which did not capture a single individual of either generation, is excluded in order to preserve a uniform range in each group of 1°.6C.

Table 11

Surface distribution of *Salpa democratica* during June and July, 1908 and 1909, relative to three temperature groups

			Solitary forms					Aggregate forms				
				Specimens		Frequency			Specimens		Frequency	
Temperature in centigrade	Hauls	Hours of hauling	Hours of successful hauling	Total	Per hour	Time	Per hour	Hours of successful hauling	Total	Per hour	Time	Per hour
15°9–17°4	15	9.0	7.9	465	52	88	97	7.9	5,750	640	88	97
17°5–19°0	42	31.1	17.3	2,280	73	56	67	20.5	6,014	193	66	77
19°1–20°6	18	14.3	11.4	4,011	280	80	87	11.0	3,111	218	77	84

Each of the four conditions deduced from the locomotion theory is shown by this table:

1. The frequencies of the two generations are identical relative to the lowest temperature group, nearly so relative to the highest, and parallel throughout. The frequency of both is lowest in water of medium temperature (17°5C–19°0C).

2. The frequencies of both generations are greater in the coldest than in the warmest water.

3. Abundance of aggregate forms parallels frequency of both generations, being highest (640 per hour) in the coldest water, and lowest (193 per hour) in the water of medium temperature.

4. Abundance of solitary forms increases from 52 per hour in the coldest water to 73 per hour in water of medium temperature to 280 per hour in the warmest water.

In table 12 the data are retabulated again in four groups according to whether the temperature lay between 15°9C and 17°1C, 17°2C and 18°3C, 18°4C and 19°5C, or 19°6C and 20°8C. Be it noted that the two middle groups each have a range of 1°2 C, while the two extreme groups each have a range of 1°3C.

Table 12

Surface distribution of *Salpa democratica* during June and July, 1908 and 1909, relative to four temperature groups

			Solitary forms					Aggregate forms				
				Specimens		Frequency			Specimens		Frequency	
Temperature in centigrade	Hauls	Hours of hauling	Hours of successful hauling	Total	Per hour	Time	Per hour	Hours of successful hauling	Total	Per hour	Time	Per hour
15°9–17°1	12	5.2	4.2	282	54	81	98	4.2	4,923	945	81	98
17°2–18°3	18	14.8	12.0	1,064	72	81	87	12.0	5,652	382	81	87
18°4–19°5	34	27.7	15.7	3,107	112	57	65	18.9	3,177	115	68	75
19°6–20°8	12	6.9	4.7	2,303	334	68	86	4.2	1,123	163	61	81

As in table 11, each of the four conditions deduced from the locomotion theory appear in this table:

1. The frequencies of the two generations are identical in the two lowest temperature groups, nearly identical in the highest temperature group, and parallel throughout. The frequency of both generations decreases as the temperature increases from its lowest to its middle value (18°.4C–19°.5C), and then increases.

2. The frequency of both generations is greater in the coldest than in the warmest water, and also greater in the next coldest than in the next warmest water.

3. Abundance of aggregate forms parallels frequency of both generations, decreasing from a maximum (945 per hour) in the coldest water to a minimum (115 per hour) in water between 18°.4C and 19°.5C in temperature.

4. Solitary forms increase in abundance from 54 to 72 to 112 to 334 per hour as the temperature increases from its lowest to its highest value.

In table 13 the data are once more retabulated relative to five temperature groups according as the temperature lay between 15°.9C and 16°.9C, 17°.0C and 17°.9C, 18°.0C, 18°.9C, 19°.0C and 19°.9C, or 20°.0C and 20°.8C. Be it noted, that although the lowest group has a range of 1°.1C and the highest a range of 0°.9C, the range of each of the three middle groups is one degree.

TABLE 13

Surface distribution of *Salpa democratica* during June and July, 1908 and 1909, relative to five temperature groups

			Solitary forms					Aggregate forms				
				Specimens		Frequency			Specimens		Frequency	
Temperature in centigrade	Hauls	Hours of hauling	Hours of successful hauling	Total	Per hour	Time	Per hour	Hours of successful hauling	Total	Per hour	Time	Per hour
15°.9–16°.9	11	4.6	3.55	278	**60**	77	**97**	3.55	4,900	**1,065**	77	**97**
17°.0–17°.9	16	13.7	11.3	893	**65**	82	**86**	11.3	5,479	**400**	82	**86**
18°.0–18°.9	23	14.8	6.35	1,082	**73**	43	**58**	6.4	460	**31**	43	**58**
19°.0–19°.9	16	15.4	10.8	2,200	**143**	70	**71**	13.6	2,913	**189**	88	**89**
20°.0–20°.8	10	6.1	4.7	2,303	**378**	77	**91**	4.2	1,123	**184**	69	**86**

Once again are each of the four conditions deduced from theory, revealed:

1. The frequencies of the two generations are identical relative to the three lowest temperature groups, and decrease as the tempera-

ture increases from its lowest to its middle value (18°0C–18°9C) where the minimum, 58, occurs. Relative to the two remaining groups the frequency of solitary forms increases from 71 to 91 as the temperature increases, while that of aggregate forms decreases from 89 to 86. Be it noted that the former increase accords with theory, while the latter *less significant* decrease does not.

2. The frequency of both generations in the coldest water exceeds that in the warmest, and that of solitary forms in the next coldest water exceeds that in the next warmest by 15=86–71, while the corresponding frequencies of aggregate forms, 86 and 89, are reversed in order. Here again, the former excess which accords with theory, is much more significant than the latter deficiency which does not accord with theory.

3. Except for an insignificant decrease from 189 to 184 aggregate forms per hour relative to the two highest temperature groups, their abundance parallels the frequency of solitary forms exactly. Is it not striking that the abundance of 400 per hour relative to the next lowest group, exceeds *significantly* that of 189 per hour relative to the next highest group, which accords with theory, while all the relations not in accord with theory are comparatively insignificant, i.e., the decrease from 89 to 86 in frequency of aggregate forms and from 189 to 184 in their abundance instead of an increase relative to the two highest temperature groups; and the deficiency instead of an excess in frequency of aggregate forms (86) relative to the next lowest temperature group as compared to that (89) relative to the next highest group?

4. Solitary forms increase in abundance from 60 to 65 to 73 to 143 to 378 per hour as the temperature increases from its lowest to its highest value.

Attention is called to the fact that the abundance of solitary forms relative to the next lowest temperature group (as given by tables 11, 12, and 13) has *decreased* from 73 to 72 to 65 per hour as the number of groups has been increased from 3 to 4 to 5. Obviously, this accords with the fact that solitary forms decrease in abundance as the temperature of the water decreases. But, the abundance of solitary forms in the coldest water has *increased* from 52 to 54 to 60 per hour as the number of groups has been increased from 3 to 4 to 5. Apparently, this fact carries an implication directly contrary to the above. But, it accords with the theory of chain locomotion. For, does this theory not stipulate that a larger number of solitary forms should be encountered in the coldest water than would be present were they not pulled there by virtue of the combined locomotive power of the aggregate

forms in each of a number of long protruding chains? Do the facts not suggest that, if retabulated again relative to temperature groups of still smaller range, the data may reveal an excess in abundance of solitary forms in the coldest water over that in next coldest? Accordingly, table 14 is supplied, in which the data are retabulated with respect to six temperature groups each having a range of 0°.8C.

TABLE 14

Surface distribution of *Salpa democratica* during June and July, 1908 and 1909, relative to six temperature groups

			Solitary forms					Aggregate forms				
				Specimens		Frequency			Specimens		Frequency	
Temperature in centigrade	Hauls	Hours of hauling	Hours of successful hauling	Total	Per hour	Time	Per hour	Hours of successful hauling	Total	Per hour	Time	Per hour
15°.9–16°.6	10	4.1	3.55	278	68	86	99	3.55	4.900	1,195	86	99
16°.7–17°.4	5	4.9	4.4	187	38	90	91	4.4	850	174	90	91
17°.5–18°.2	14	10.8	8.3	881	81	77	85	8.3	4,825	447	77	85
18°.3–19°.0	28	20.3	9.0	1,399	69	44	55	12.2	1,189	59	60	71
19°.1–19°.8	9	8.5	6.7	1,708	205	79	81	6.7	1,988	234	79	81
19°.9–20°.6	9	5.8	4.7	2,303	398	81	93	4.2	1,123	194	72	86

Once again is each of the four conditions deduced from the locomotion theory evident, though not so strikingly, perhaps, as in the foregoing tables:

1. The frequencies of the two generations are identical relative to the lowest, second lowest, third lowest, and second highest temperature groups, and they are parallel throughout. The frequency of both decreases as the temperature increases from its lowest to its middle value (18°.3C to 19°.0C), and then increases as the temperature increases to its highest value.

2. Both generations appear more frequently in the coldest than in the warmest water, in the second coldest than in the second warmest water, and in the third coldest than in the third warmest water.

3. The abundance of aggregate forms, while more erratic than shown by the foregoing tables, parallels in general the frequency, being greatest (1195 per hour) in the coldest water and least (59 per hour) in water having a temperature between 18°.3C and 19°.0C.

4. Except that slightly less, instead of more, than 81 solitary forms per hour were obtained when the temperature was between 18°.3C and 19°.0C, they increase in abundance as the temperature increases from next to its lowest to its highest value. Is it not a significant cor-

roboration of theory that more per hour were obtained in the coldest than in the next coldest water?

Although the hauls are too few and the temperature range in each group is too small to justify retabulation relative to a still smaller range, it is found that the abundance of solitary forms relative to temperatures between 15°.9C and 16°.5C is 75 per hour, while that relative to temperatures having the same range (0°.7C) between 16°.6C and 17°.2C is 36 per hour. That the significance of this fact may be better appreciated, the abundance of solitary forms and mean temperatures relative to the two lowest temperature groups as shown by tables 11, 12, 13, and 14 are brought into relation to the fact just mentioned in the following lists:

List A (Lowest temperature group)		Groups	List B (Next lowest temperature group)	
Mean temperature	Abundance		Mean temperature	Abundance
16°.65C	52	3	18°.39C	73
16°.52	54	4	17°.55	72
16°.46	60	5	17°.53	65
16°.44	68	6	17°.08	38
16°.43	75	7	17°.00	36

Presented in this way, list A shows that solitary forms *decreased* in abundance as the mean temperature increased from 16°.43C to 16°.65C, while list B shows that they *increased* in abundance as the mean temperature increased from 17°.00C to 18°.39C. How is this apparent paradox to be explained except on the assumption that the number of solitary forms with long protruding chains exceeded the number of detached solitary forms plus the number with short protruding chains when the temperature of the water was on the average below 16°.7C, while when it was above 16°.9C, the number of detached solitary forms plus the number with short protruding chains exceeded the number with long protruding chains?

Is it not striking that the relations revealed by tables 11 to 14 verify the deductions from the theory of chain locomotion almost to the smallest detail? In order that this may be better visualized, the relation between the two generations in abundance and frequency is presented in the form of histograms by plates 10 and 11, figures 4 to 11.

5. Validity of the Plankton Concept

This is too large a subject to discuss fully, but the assumption of passivity, and consequently of uniformity, in plankton distribution so permeates the literature as to demand brief consideration in the light of the facts revealed by this investigation. The fundamental tenet of the prevailing plankton concept is, as later demonstrated, that the organism is carried about *passively* by the currents of the sea; that the organism plays a negligible part in its own distribution. Virtually, the inanimate is substituted for the animate, and the problem of plankton distribution thus becomes nothing more than a problem in mechanics; a problem resembling that of the distribution of dust in the air, or of salts in the sea; a complicated problem, perhaps, but none the less a mechanical one.

This may be better appreciated, perhaps, from an analogy. Raindrops tend to be uniformly distributed. In any particular region where the physical conditions of the air are the same, approximately the same number of raindrops fall on one square foot of the earth's surface as upon any other square foot, whence a single rain gauge is sufficient to measure quite accurately the total precipitation throughout that entire region. This is common knowledge. It is also common knowledge that the locomotive powers, say of small gnats, are too feeble to permit headway against the wind; they are carried hither and thither by the currents of the air. Let it be assumed that they are carried passively, that their own activities are negligible, and they must of necessity be distributed in a very similar manner to raindrops, or better to the dust of the air. In other words, wherever in the air the physical conditions were uniform, there also the abundance of gnats would approximate uniformity.

Of course this sounds ridiculous, but it is the unescapable consequence of an assumption of passivity. It is only necessary, therefore, to substitute plankton organisms for gnats and water for air to realize that, if the fundamental tenet of the plankton concept be true, there is no escape from the claim made by Johnstone (1908, p. 157) that "the validity of all conclusions as to the general abundance of microscopic life in the sea depends on the truth of the postulate, that wherever in the sea the physical conditions are uniform, there also the composition and abundance of the plankton is uniform." This postulate of uniformity, although rightly held by many to be absurd, either must be true or else the fundamental tenet

of the plankton concept must be false. Any given plankton species must either control its own distribution to a significant extent or it must tend to be distributed in accordance with the uniformity postulate, i.e., like the salts of the sea.

That this postulate actually does lie at the foundation of a large amount of quantitative plankton research is evident from the extent to which what might be called "rain gauge" methods of collecting are employed. Sweeping statements are not infrequently made relative to the distribution of plankton organisms over large areas of the sea which are based upon the assumption, more or less unrecognized perhaps, that owing to passivity and consequently to uniformity, one or at most a very few hauls, carefully made with a net whose "filtering capacity" is accurately determined, justifies the generalizations (Michael, 1916, pp. xvi–xix). Maps and charts are continually being published showing the distribution of various so-called types of plankton throughout large portions of the globe, the reliability of which, with few exceptions, rests upon rain gauge methods of collecting, which methods in turn, of course, depend upon the validity of the concept of passivity and uniformity.

Nothing is more natural, perhaps, than to fall into the error of supposing that, because the locomotive powers of many plankton organisms are too feeble to permit headway against a current, therefore locomotion has a negligible effect on the distribution of such organisms. In thus overlooking the fact that the ocean, being a body of three instead of two dimensions, may permit plankton organisms with feeble powers of locomotion to control their horizontal distribution by means of vertical movements, it is not surprising to find that such organisms are generally regarded, so far as concerns their horizontal distribution, as physical particles which are carried hither and thither by wave, tide, and current. In spite of the noteworthy investigations of the Port Erin Marine Biological Station, Isle of Man, as well as those of various individuals, which have established facts wholly inconsistent with this conception, it not only persists but is made apparent in almost every standard text or reference book dealing in any way with plankton organisms.

Witness, for example, the following opening statement quoted from Steur's *Planktonkunde* (1910, p. 1): "Die Planktonkunde oder Planktologie befasst sich mit der Erforschung jener im freien Wasser *schwebenden,** grössenteils mikroscopischen Lebenwesen, die wir heute

* Italics in this and two following paragraphs inserted by author.

mit dem Namen Plankton bezeichnen.'' In order that there be no doubt as to the real meaning of Steur's words, consider the following statement, also quoted from page 1: ''Die Planktonorganismen oder Planktonten sind also grösstenteils kleine Lebenwesen, die *ohne Eigenbewegung oder ungeachtet derselben hilflos im Wasser treiben* . . . und die Planktologie ist demnach die Lehre von den schwebenden Wasserorganismen.'' Compare with these statements, the following extracted from the first page of Schurig's *Plankton-Praktikum* (1910): ''Unter Plankton nun versteht man die Gesammtheit aller meist mikroscopisch kleinen im Wasser schwebenden, 'flottierenden' Lebenwesen pflanzlicher und tierischer Natur, die dem Wogen keinem Widerstand entgegenzusetzen vermögen, *die einem Spielball der Wellen repräsentieren.*''

That the extent to which this conception has guided the thinking of able investigators may be more fully appreciated, the following statements are quoted from Johnstone, *Conditions of life in the sea* (1908):

From page 56: ''There are first of all those [organisms] which by reason of their minute size and feeble powers of locomotion are carried about passively in the sea by tides and currents. These are they which are caught in the tow-nets, which Müller called the Auftrieb, and Hensen the Plankton.'' Again, from page 57: ''Then one at times finds it difficult to say whether organisms, like the medusae, which are carried about in great swarms by tides and currents, but which nevertheless are capable of some degree of locomotion, are to be included in the plankton or in the nekton.'' Or again, from page 65: ''Some worms may belong temporarily at least to the nekton, and the large medusae, though perhaps better classed with the plankton, do move about 'of their own accord.' '' Or again, from page 67: ''These [pelagic fish eggs] have absolutely no powers of locomotion and they are drifted about passively by tides and currents, the very type of planktonic organisms.'' Or again, from page 143: ''Plankton organisms . . . have little powers of locomotion, *certainly not such as will enable them to segregate themselves,* and they are drifted about in the sea quite passively.'' Or lastly, from page 148: ''Small organisms, such as those of the plankton, are *particles in the physical sense and behave as such.*'' Clearly, Johnstone (1908) has recognized the real nature of the plankton concept; similar statements might be quoted from nearly every page of his book.

This is not all. The same conception, or should it be called a misconception, is to be found, expressed more cautiously perhaps, not only in the technical writings, textbooks, and laboratory manuals, but also in most of the semipopular books and reference books that treat plankton organisms to any extent whatsoever. To cite but three instances: Hickson (1893, p. 52), in his *Fauna of the deep sea,* says: "Some animals simply float or drift about with the currents of the sea and are unable to determine for themselves, excepting, perhaps, within very small limits, the direction in which they travel. . . . This portion of the fauna has recently been called the Plankton." Again, Arnold (1903, p. 23) in her *Sea-beach at ebb-tide,* says: "Those [organisms] which float at or near the surface and are carried about by the currents . . . are *plankton.* Strong swimming animals which move about at will are *nekton.*" Finally, on page 702 of the *New International Encyclopaedia* (1916), one finds this statement: "In zoology the term [plankton] is restricted to the pelagic life which drifts, the actively swimming surface forms constituting a separate assemblage, the nekton. It consists mainly of jelly fishes, ascidians, especially salpa, and a great variety of pelagic larvae and minute crustacea with feeble powers of locomotion that are carried along almost passively by the oceanic currents."

This list of quotations might be continued almost indefinitely. All carry the implication, some more conspicuously than others, that plankton organisms, because of their feeble powers of locomotion, may be assumed to behave like corks; that the characteristic quality of such organisms is to float, to drift, to remain in suspension. It may be, perhaps, that few actually believe this; it is difficult to understand how anyone can believe it. Yet, the above list of quotations makes it certain that it is precisely this ridiculous assumption that lies at the foundation of the prevailing plankton concept; that it colors the thinking of able biologists; and that it influences the procedure of capable investigators.

There are, to be sure, a few text books, a few reference books, a few semipopular books treating of plankton that are not permeated by this dogma, but the number is remarkably small. On page 309 of Murray and Hjort's *Depths of the ocean* (1912), this statement occurs: "The term 'plankton' is now used for all floating organisms which are passively carried along by currents, while 'nekton' . . . is used to designate all pelagic animals which are able to swim against currents." Although this statement carries the same implication,

the ensuing discussion partly offsets it. Witness, for example, the following from page 773: "Hensen invented his method for the purpose of investigating the floating or suspended life in the sea, which he termed 'plankton.' This plankton is, however, very difficult to define, for among the profusion of organisms, ranging from the minutest plants . . . to the large crustaceans and fishes, there is an enormous variety in size, in activity, and consequently in the faculty of avoiding the appliances of capture. In many investigations, therefore, the word plankton may be taken to signify practically 'the catch made in the hoop-net constructed by Hensen, when new and in perfect working order.'" A further step in the same direction is taken by Fowler (1912, p. 162) in his *Science of the sea:* "To those animals and plants which float in the sea, whether at the surface or in deep water, the term 'Plankton' is applied for brevity; they are contrasted with the creatures which crawl upon, or are fixed to, the bottom. In modern usage, Plankton is generally taken to include even powerful swimmers . . . as well as helpless and minute organisms." Similarly, under the term "plankton" in the last edition of the *Encyclopaedia Britannica,* Fowler (1911, p. 720) writes: "**Plankton,** a name invented by Professor Victor Hensen for the drifting population of the sea." But, in the next column: "The fauna of the sea is divisible into the *plankton,* the swimming or drifting fauna which never rests on the bottom (generally taken now to include E. Haeckel's *nekton,* the strong swimmers such as fish and cephalopods), and the *benthos,* which is fixed to or crawls upon the bottom."

Although these statements, quoted from Fowler (1911, 1912) and from Murray and Hjort (1912), represent a decided step in advance, they still carry the implication that a large number of plankton organisms are as helpless as drifting physical particles; that they play a negligible part in their own distribution. There may be such organisms, but ought this not to be demonstrated rather than assumed?

Is it beyond question that even fish eggs are of necessity distributed in accordance with this assumption? At a depth of twenty fathoms two eggs begin development at the same time and place; the rate of growth is more rapid in one; it's specific gravity decreases and it ascends, reaching the surface by the time the second, more slowly developing, egg has ascended to the fifteen fathom level. The surface current flows southward; that at fifteen fathoms, to the west of south. At the end of two days the two eggs are ten miles apart. Has the difference in their rates of growth played a negligible part in deter-

mining their whereabouts? Does this self-induced movement—the locomotion of the egg—count for nothing in its distribution? Is the egg carried along *passively* by the current?

It would seem necessary, in the light of this investigation, to *discard completely this dogma of passivity,* and to replace it by a conception more in accordance with fact. For *Salpa democratica* is admitted by all to be a most typical plankton organism, and, if the facts revealed in the foregoing pages are trustworthy, it is evident that this plankton species, to a very large extent, does control its own distribution. It is not drifted about passively; it is not a particle in the physical sense and it does not behave as such. How explain the differentials in distribution of the two generations on any such basis? The hauls were the same; the currents were the same; the tides were the same; every conceivable condition of and in the sea was the same, during the collecting of one generation as during the collecting of the other. *Yet they were distributed differently.* Obviously, the activity of the organisms and that alone can have caused the differentials in their distribution. Further, the data strongly suggest that the main type of activity involved is locomotion. If so, it necessarily follows, not only that this plankton species influences its own distribution, but that it does so just as certainly, just as definitely, and by much the same means as does any fish or other animal included under the general term, nekton.

Salpa probably does not accomplish this by forcing its way against a current as does a fish, but the solitary forms manage to get themselves onto the surface in largest numbers when the temperature of the water is high and to avoid the surface when the temperature is low, while the reverse is true of the aggregate forms. Even granting them to be transported by surface currents, as they doubtless are, these data demonstrate that solitary forms are found for the most part in the warm currents and aggregate forms in the cold currents. Is it not, therefore, as illogical to credit the entire control of their horizontal distribution to the currents as it would be to claim that John Smith had nothing whatever to do about getting himself to New York because he was carried there on a Pennsylvania Pullman?

Fom a strictly biological point of view, it would seem necessary to disregard entirely, as Fowler (1911, 1912) has done, the distinction between plankton and nekton. There seems to be no natural line of demarcation between the two. Surely, there is far less difference in activity between sardines and jelly fishes or the larger copepods than

there is between a copepod and a fish egg or diatom. Yet sardines are excluded from the plankton, while everything from a diatom to a jelly fish is included.

Or consider the matter from another point of view; the sardine begins its career as an egg; by a gradual and continuous process of growth the successive stages in the life cycle follow: the early embryo, the late embryo, the young larva, the mature larva, the post larva, the adult. Clearly, activity characterizes the individual from egg to adult. At what stage does the sardine cease to be a constituent of the plankton and take its place with the nekton? At what stage does its activity become effective in determining its distribution? It was suggested on page 285, how activity might be effective in the egg. If so, can any differential in the type of locomotion or the degree of its effectiveness be recognized that will justify a distinction between plankton and nekton on that basis? Some say that *strong* swimmers belong to the nekton and that such animals alone are able to make headway against a current. But, how strong is a *strong* swimmer, and against a current of what velocity must headway be made? Merely to raise this question denotes the artificiality of such a distinction. With equal justification might we not distinguish between the plankton and nekton of the air, defining the latter as strong flyers capable of making headway against the wind?

However, in spite of the artificiality of distinguishing between plankton and nekton, the distinction does have a certain methodological value. Might it not be wise, therefore, to combine the statements of Fowler (1911, 1912) and of Murray and Hjort (1912) into a definition somewhat as follows? Marine and fresh water organisms are divisible into two main classes: (1) *pelagic organisms,* the fauna and flora that do not live upon, or fixed to, the bottom; and (2) *benthos,* or the fauna and flora which do live upon, or fixed to, the bottom. For practical reasons pelagic organisms are artificially subdivided into two groups: (1) *plankton,* or the sum total of all animals and plants captured by any kind of tow-net or water-bottle; and (2) *nekton,* the sum total of all animals that escape capture by such means. Does not a statement of this nature serve the purpose of distinguishing the two types of organism, insofar as there are two types, without committal as to whether or not any particular ones play an important part in controlling their own distribution?

E. SUMMARY AND CONCLUSIONS

The facts revealed by this investigation may be summarized under three heads as follows:

I. Facts relating to seasonal distribution:

1. The occurrence of *Salpa democratica* in the San Diego region at all depths during 1908 and 1909 reached its maximum in the summer, both generations being restricted almost exclusively to the months of June and July.

2. Both generations were more abundant on the surface during June than during July.

3. Aggregate forms were more abundant than solitary forms during June, while solitary forms were the more abundant during July.

II. Facts relating to vertical distribution:

1. Solitary forms are most abundant on the surface, decreasing in abundance as the depth increases.

2. Aggregate forms are most abundant in the neighborhood of five fathoms, decreasing in abundance as the depth increases below that level.

3. Aggregate forms were, on the average, more abundant than solitary forms at all levels.

4. Individuals of neither generation have been captured below seventy-five fathoms.

III. Facts concerning surface distribution during June and July, 1908 and 1909 relative to temperature of the water:

1. When the data are tabulated with respect to two temperature groups ranging in value from 15°.9C to 18°.3C and from 18°.4C to 20°.8C respectively, they show that:

a. Solitary forms are most abundant but least frequent in the warmer water.

b. Aggregate forms are most abundant and most frequent in the colder water.

c. The frequency of solitary forms in both warm and cold water is nearly identical with that of aggregate forms.

d. These same relations hold when all the June and July data are considered, when day hauls alone are considered, when night hauls alone are considered, when only hauls made

between 6 A.M. and 10 A.M. are considered, when only hauls made between 10 A.M. and 2 P.M. are considered, when only hauls made between 6 P.M. and 10 P.M. are considered, when all hauls are excluded except those made during June, 1909, and when all are excluded except those made between June 15 and June 29, 1909, and within one mile of each other.

2. When the data are tabulated with respect to three, four, five, and six temperature groups each having an equal range between 15°.9C at one extreme to 20°.8C at the other, they show that:

a. Solitary forms increase in abundance as the temperature increases from its lowest, or next lowest, value to its highest value.

b. The frequency of both solitary forms and aggregate forms decreases as the temperature increases from its lowest to its *middle* values, and then increases as the temperature increases.

c. Both solitary forms and aggregate forms are more frequent in the coldest than in the warmest water, more frequent in the next coldest than in the next warmest water, more frequent in the third coldest than in the third warmest water, and so on.

d. The abundance of aggregate forms parallels the frequency of both generations.

3. When each of the June and July surface hauls is examined on its own merits, it is found that:

a. Forty-six of the forty-nine hauls that captured solitary forms also captured some aggregate forms.

b. Twenty-four of the twenty-seven hauls that failed to capture solitary forms also failed to capture aggregate forms.

From these facts it is concluded that:

1. Differentials in distribution of solitary forms and aggregate forms are as definite and pronounced as are the differentials in their structure.

2. Seasonal succession of the two generations can not explain the observed differentials.

3. Greater production of solitary forms in stratified areas of warm surface water than in those of cold surface water, if occurring at all, can not explain the observed differentials.

4. No amount of hydrographic change or of variation in viscocity of the water can explain the observed differentials.

5. Solitary forms show an increasing preference, so to speak, for the surface, as the temperature of the surface water increases from 16°C to 20°C; while aggregate forms show a similar preference as the temperature decreases.

6. The chain of aggregate forms remains attached to the solitary salpa after having been liberated from its mantle cavity into the water.

7. One solitary form is carried into cold surface water by virtue of the combined locomotive power of the aggregate forms in each *long* protruding chain, while *short* chains are carried into warm surface water by virtue of the locomotive power of the attached solitary form.

8. Owing to the strain due to the opposite direction of locomotion of solitary form and of attached aggregate forms, the protruding chain becomes detached from the stolon periodically, i.e., at the "intermediate piece" before an entire "block" of aggregate forms has been protruded.

9. Contrary to the prevailing plankton concept, *Salpa democratica*, a typical plankton organism, controls to a significant extent its own distribution just as certainly as does any fish or other animal commonly included under the term of nekton.

It is unnecessary to state that the sixth, seventh, and eighth conclusions, while apparently unescapable, are all based upon indirect evidence and must be regarded as tentative rather than as fully established. In conclusion, if this paper serves to stimulate a closer morpho-physiological scrutiny of the life cycle of the *Salpae*, if it serves to instigate a closer study of their habits, if it serves to rectify a prevailing misconception concerning plankton distribution, and if it serves as an antitoxin against the too prevalent tendency of morphologists to ignore the ecologist's point of view and of ecologists to ignore the morphologist's point of view, its primary aim will be accomplished.

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Scripps Institution for Biological Research,
La Jolla, California.

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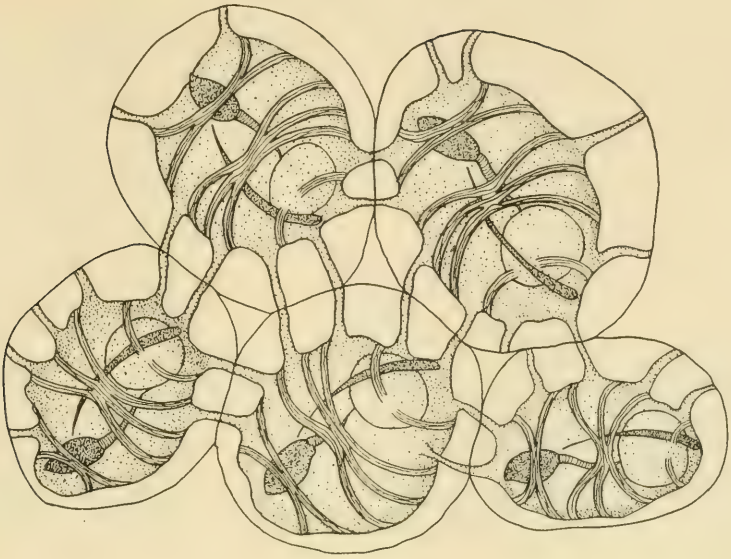
EXPLANATION OF PLATES

PLATE 9

Fig. 1. Dorsal view of a portion of a protruded chain of *Salpa democratica*. × 18.

Fig. 2. Ventral view of a mature individual of the solitary generation. × 4.5.

Fig. 3. Dorsal view of aggregate form containing a nearly mature embryo of the solitary generation. × 4.5.



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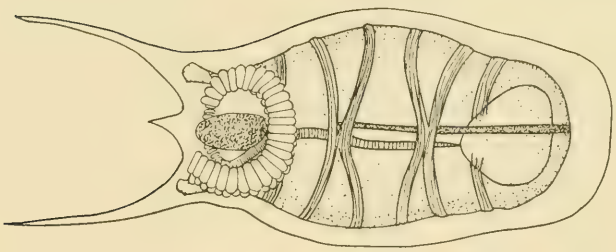

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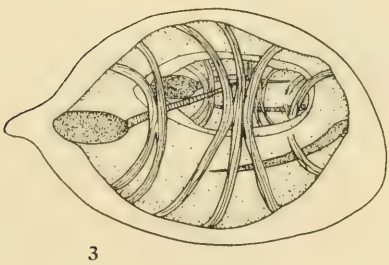

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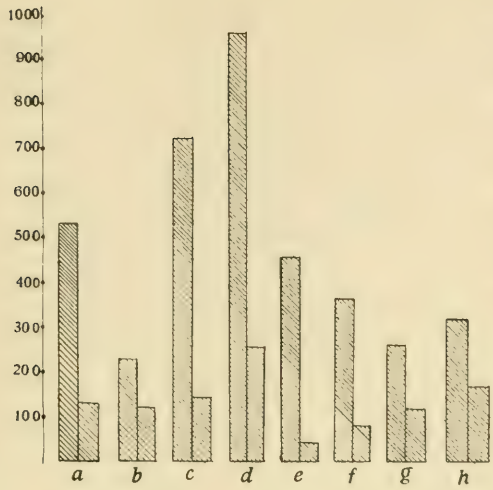
PLATE 10

Fig. 4. Histograms showing *abundance of aggregate forms,* or number obtained per hour from the surface relative to temperatures between 15°.9C and 18°.3C (left), and 18°.4C and 20°.8C (right); (*a*) based on all data pertaining to June and July, 1908 and 1909 (table 4); (*b*) based on night data (table 5); (*c*) based on day data (table 6A); (*d*) based on intense light data (table 6B); (*e*) based on early morning data (table 6C); (*f*) based on evening data (table 6D); (*g*) based on June, 1909 data (table 8); (*h*) based on data restricted to collections made within one mile of each other (table 10).

Fig. 5. Histograms showing *abundance of solitary forms* relative to the same conditions as specified in the explanation of figure 4.

Fig. 6. Histograms showing *abundance of aggregate forms* on the surface relative to temperatures between 15°.9C (left) and 20°.8C (right), divided into (*a*) three groups each having a range of 1°.6C (table 11); (*b*) four groups each having a range of 1°.2C or 1°.3C (table 12); (*c*) five groups each having a range of one degree (table 13); and (*d*) six groups each having a range of 0°.8C (table 14).

Fig. 7. Histograms showing *abundance of solitary forms* relative to the same conditions as specified in the explanation of figure 6.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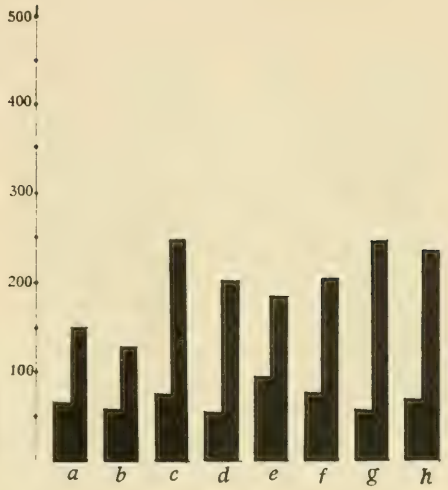
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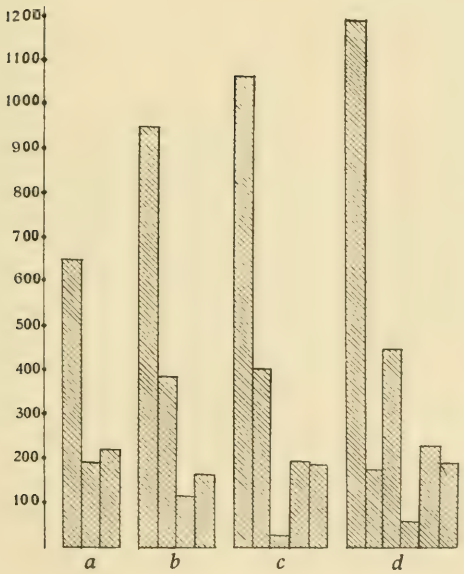
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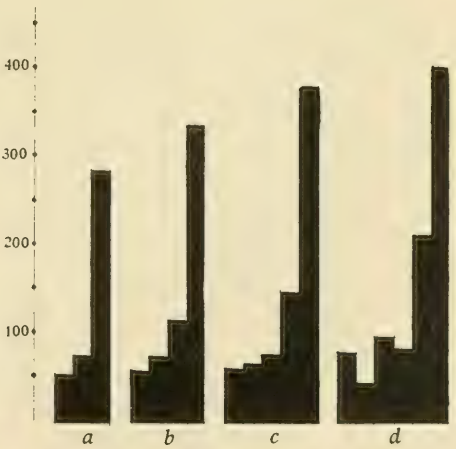
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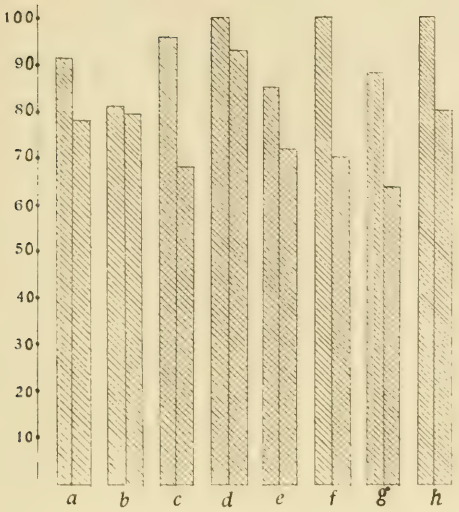
PLATE 11

Fig. 8. Histograms showing *frequency of aggregate forms;* or percentage of hour hauls in which they were captured from the surface, relative to the same conditions as specified in the explanation of figure 4.

Fig. 9. Histograms showing *frequency of solitary forms* relative to the same conditions as specified in the explanation of figure 4.

Fig. 10. Histograms showing *frequency of aggregate forms* relative to the same conditions as specified in the explanation of figure 6.

Fig. 11. Histograms showing *frequency of solitary forms* relative to the same conditions as specified in the explanation of figure 6.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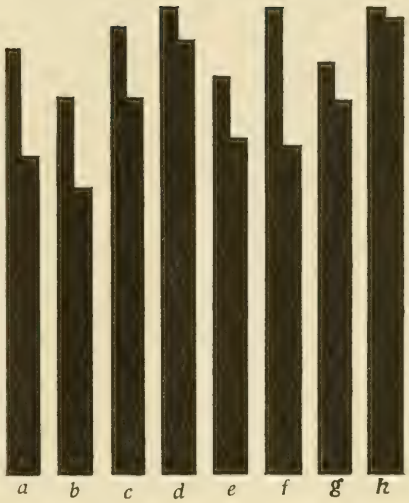
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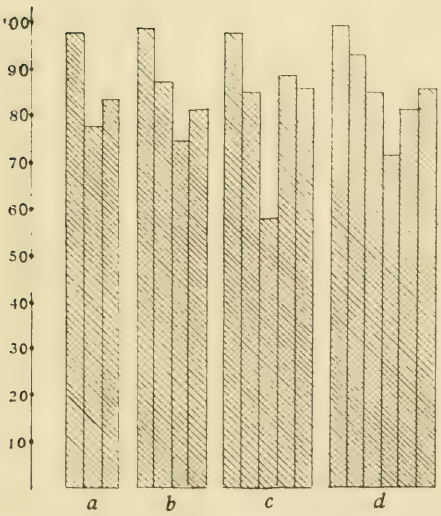
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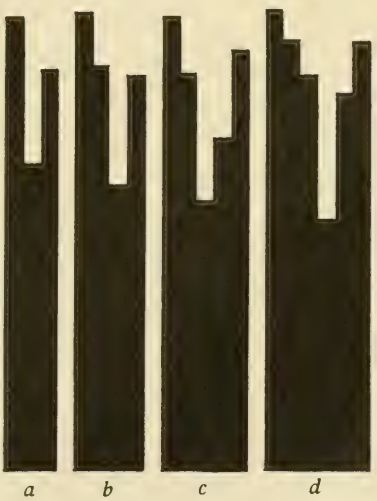
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Nos. 6 and 7 in one cover. December, 1915 ..... .25
8. On *Blepharcorys equi*, sp. nov., a New Ciliate from the Caecum of the Horse, by Irwin C. Schumacher. Pp. 95-106, plate 13. December, 1915.... .10
9. Three New Helices from California, by S. Stillman Berry. Pp. 107-111. January, 1916 ..... .05
10. On *Trypanosoma triatomae*, a New Flagellate from a Hemipteran Bug from the Nests of the Wood Rat *Neotoma fuscipes*, by Charles Atwood Kofoid and Irene McCulloch. Pp. 113-126, plates 14-15. February, 1916 ..... .15
11. The Genera *Monocercomonas* and *Polymastix*, by Olive Swezy. Pp. 127-138, plates 16-17. February, 1916 ..... .10
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A QUANTITATIVE ANALYSIS OF THE MOLLUSCAN FAUNA OF SAN FRANCISCO BAY

BY

E. L. PACKARD

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CONTENTS

PAGE
Introduction 299
General distribution of the Mollusca 301
Physical characters of San Francisco Bay 301
The molluscan fauna of San Francisco Bay 303
Economic considerations 308
Factors governing the distribution of the Mollusca 317
Relation to depth 318
Relation to type of bottom 318
Relation to salinity 322
Relation to temperature 324
Relation to the available food supply 327
Relation to the biotic environment 330
Summary 331
Appendix 332
Literature cited 333
Explanation of plates 334

INTRODUCTION

Improved methods of procedure already applied in several different regions of the world have revealed many of the actual conditions under which the marine animal lives. Increased knowledge of such matters has been made possible, locally, through the Biological Survey of San Francisco Bay made by the United States Bureau of Fisheries.

The survey was made by the U. S. S. "Albatross" under the direction of a board consisting of Dr. F. B. Sumner, naturalist, Professor Charles A. Kofoid, and Commander G. H. Burrage, U. S. N.,

succeeded by Lieutenant-Commander H. B. Soule, U. S. N., during the years of 1912 and 1913. Much assistance has been received from Dr. Sumner and from Professor Kofoid, who upon Dr. Sumner's resignation has had supervision of the work. A report by Sumner, Louderback, Schmitt, and Johnston (1914) has been published in which the physical conditions of the waters of San Francisco Bay are ably presented. The data for each dredging station in that paper have served as the basis for the discussion of the Mollusca that follows.

A portion of the general results of the studies made upon the shell-bearing Mollusca dredged by the "Albatross" in San Francisco Bay lends itself for a separate treatment preliminary to a general discussion of the molluscan fauna as a whole, and is herein presented. These results have to do with the so-called "quantitative" stations or "orange-peel bucket dredge hauls," which comprise forty-three out of a much larger total number of dredgings.

The orange-peel bucket dredge had not been previously used for biological exploration. Other devices of somewhat similar character have been employed by Petersen (1913, p. 3) whereby a definite amount of the bottom material could be obtained, thereby giving a quantitative measure of the number of organisms living within a definite area at a given locality. The orange-peel bucket dredge, described and figured by Sumner *et al.* (1914, p. 7), has proved very efficient. Regarding it, the authors state: "Its chief advantage lies in the taking of comparatively large masses of mud from a single spot, and particularly in the penetrating power of the apparatus which renders possible the capture of deeply burrowing annelids, lamellibranches, etc." Its capacity is given as 2½ cubic feet. Since its diameter is 3.16 feet, it encloses a circular area containing 7.8 square feet.

The material collected by means of this apparatus was carefully sorted and all of the macroscopic organisms preserved in formalin or in alcohol. At those stations where a considerable amount of material was obtained the following method of procedure was employed. All of the molluscan material from such hauls was first passed over a sieve of 5 millimeters mesh. The shells that remained in the sieve were identified, counted, measured, and the condition of the specimens was noted. The measurements consisted of the maximum, minimum, and modal lengths for each species in the haul. The fine material which passed through the sieve was thoroughly mixed and then quartered after the manner of taking ore samples. A convenient sample was then sorted and subjected to the same type of analysis as out-

lined above. This method of procedure when large masses of finely comminuted shells were concerned is not above criticism, yet it seemed to be the most practical method of treatment available.

Such a method gives excellent results for the larger mollusks and a fair representation for the smaller ones that are abundant, but it is slightly inaccurate for smaller shells, which are but sparsely represented in the fauna. Hence in the case of such forms as *Turbonilla, Odostomia,* or *Melanella* the figures given do not represent the actual numbers taken at a station.

The record based upon these methods shows for each species at each dredge haul the name, the number of individuals of each species (often approximate when these numbers were large), the conditions of the specimens at the time of dredging, and the maximum, minimum, and the modal lengths.

GENERAL DISTRIBUTION OF THE MOLLUSCA

Physical Characters of San Francisco Bay

Sumner *et al.* (1914, p. 22) recognized three physical and biological divisions of San Francisco Bay. The "upper" portion includes San Pablo Bay, the "middle" one extends from a line passing through the points of San Pedro and San Pablo to a line drawn from the Ferry Building to the Goat Island Light; the third or "lower" division lies south of the latter line.

The quantitative stations comprise forty-three hauls made with the orange-peel bucket dredge between the dates of December 9, 1912, and February 3, 1913. They were distributed from a point near the southern extremity of San Francisco Bay to Carquinez Strait. In the upper division of the bay twelve hauls were made at stations D 5815 to D 5820 inclusive. Twenty hauls at stations D 5821 to D 5830 inclusive were made within the middle portion; while eleven were made in the lower section of the bay at stations D 5831 to D 5841 inclusive. The position of these stations may be seen by referring to plate 12.

The physical conditions at these representative stations of San Francisco Bay are influenced largely by the surrounding topography. The Sacramento and San Joaquin rivers and several intermittent streams contribute considerable volumes of water to the bay. The total discharge of these streams affects the temperature and the salinity of the bay, besides bringing in sediment that is in part deposited within that basin.

The depth of water at the quantitative stations ranges from 4½ to 17 fathoms (8.3 to 31.3 meters). The mean tidal range for the entire bay throughout the month is given by Sumner *et al.* as 4.52 feet. The actual extremes during the course of the year are much greater, ranging from 0.4 to 7.8 at Fort Point within the Golden Gate. The rate of the tidal currents was determined for a number of localities to be about 1.4 knots per hour at a distance of a few feet below the surface. It was estimated that the mean rate of water flow over the entire bottom was between 0.67 and 0.75 of a knot per hour.

The mean annual temperature for the entire bay is 12°.91C. The highest recorded temperature is 20°.6C and the lowest is 6°.0C; the highest of the regional means for the year was obtained in the lower division and the lowest in the middle division of the bay. A regional range of 12°.65C occurs in the northern end of the bay, decreasing to 4°.92C at Golden Gate and rising to 11°.18 at the southern end. There is a considerable seasonal variation of temperature. During February the temperatures are quite uniform for the entire bay, being at that time lower than are those of the ocean outside the Golden Gate. During the latter part of April and early May the waters at either end of the bay are warmer than in February, whereas those of the middle divisions are colder than they are at the earlier period. At the next period the latter part of July a rise of temperature is noticed, the Golden Gate remaining the coolest region of the bay. During this period the temperature of the bay is higher than that of the ocean off San Francisco. In the early part of October a general decrease in the temperature is evident, and at this period, as well as in the early part of May, the ocean temperatures are nearly the same as those of the bay. In late November a general uniformity of temperature somewhat lower than that of the open ocean prevails throughout the bay. The lowest temperatures of the year occur in January, at which time the waters of the middle division are the warmest, while those of San Pablo Bay are the coldest. The waters of the bay are at this time and also in February colder than those of the ocean. The annual range of the bottom temperature for the entire bay is 8°.35C. In the winter the bottom and surface temperatures are more nearly alike than in summer.

The salinity of San Francisco Bay ranges from 3.25 to 33.27 per mille. The mean for the entire bay for the year was estimated by Sumner *et al.* to be 27.48. The regional annual mean is less than 16 per mille in Carquinez Strait, while it reaches as high as 31 within the Golden Gate. As might be expected, the annual range is greatest

in San Pablo Bay, reaching a minimum at Golden Gate and increasing but slightly toward the lower end of the bay. The minimum seasonal mean salinity for the entire bay occurs in April and May and the minimum in October. The bottom salinity for the entire bay is greater than the mean surface salinity throughout the year, the difference between the two being the greater during April and May, when the surface salinity is the lowest of the year.

A diversified bottom is encountered, the materials ranging from large stones within the Golden Gate to fine muds occurring characteristically at the extremities of the bay.

The Molluscan Fauna of San Francisco Bay

The molluscan fauna obtained by means of the orange-peel bucket dredge comprises twenty-three pelecypods and twelve gastropods. This list represents about 43 per cent of the entire molluscan fauna of the bay as obtained by the other types of dredges employed by the Survey. The species taken by means of the orange-peel bucket dredge are:

Cardium corbis (Martyn)
Gemma gemma, var. purpura Lea
Hinnites giganteus Gray
Macoma balthica (Linnaeus)
Macoma inquinata (Deshayes)
Macoma nasuta (Conrad)
Modiolus, cf. rectus Conrad
Monia macroschisma (Deshayes)
Mya arenaria (Linnaeus)
Mya california (Conrad)
Mytilus edulis Linnaeus
Ostrea lurida Carpenter
Phacoides tenuisculptus (Carpenter)
Paphia staminea (Conrad)
Pholas pacificus Stearns
Psephdia ovalis Dall
Saxidomus nuttalli (Conrad)
Schizothaerus nuttalli (Conrad)
Solen sicarius Gould
Spisula catilliformis Conrad
Tellina buttoni Dall
Tellina salmonea (Carpenter)
Zirfaea gabbi Tryon
Crepidula nivea Adams
Columbella gausapata Gould
Epitonium hindsi (Carpenter)
Epitonium sawinae (Dall)
Nassa fossata (Gould)
Nassa mendica (Gould)
Nassa perpinguis Gould
Odostomia franciscana Bartsch
Thais lamellosa (Gemelin)
Turbonilla franciscana Bartsch
Turbonilla keepi Dall and Bartsch
Turris, cf. incisa (Carpenter)

It will be noticed that nineteen genera of pelecypods and eight of gastropods are represented in this list.

Three of the genera are represented by two or more species: *Macoma* (3), *Tellina* (2), *Epitonium* (2), *Nassa* (3), and *Turbonilla* (2). The three species of *Macoma* occur quite abundantly and are of interest in as much as they are found together within the same dredge haul. Of these species, *M. balthica* was taken in 12 hauls, or at about 27 per cent of the total number of hauls; *M. inquinata* in 13, or 28 per cent of the total; while the third, *M. nasuta,* was taken

in 26, or 56 per cent of the total. *M. balthica* and *M. nasuta* were taken together alive in three hauls. Shells of these two species were associated at two additional hauls. Specimens of *M. balthica* and *M. inquinata* were found together in three dredge hauls. Shells of *M. nasuta* and *M. inquinata* were taken together at 11 hauls. Specimens of all three species were taken at two localities. It is certain, then, that the more distantly related species *M. balthica* and *M. nasuta* live together within the restricted area covered by the jaws of the orange-peel bucket dredge, and it is probable that the more closely related species *M. nasuta* and *M. inquinata* may occur together within the same restricted area. Attention should, however, be called to the different distribution pattern of these three species resulting from the plotting of all of the known local occurrences upon outline maps of San Francisco Bay. Such a procedure shows that *M. inquinata* occurs almost exclusively in the middle division of the bay, whereas *M. balthica* and *M. nasuta* have a much more general distribution.

The quantitative hauls are too few in number to serve as a basis for conclusions regarding the areal distribution of any of the species. Therefore such studies are reserved for a fuller treatment in another paper.

The most common or the prevalent species of the quantitative hauls may be defined as those that occur at one-fourth or more of the hauls (See Sumner, Osborn, Cole, and Davis, 1913, p. 69).

This list of prevalent species is as follows:

Cardium corbis	19 hauls
Macoma balthica	12 hauls
Macoma inquinata	13 hauls
Macoma nasuta	26 hauls
Mya arenaria	17 hauls
Mya californica	28 hauls
Mytilus edulis	18 hauls
Ostrea lurida	14 hauls
Zirfaea gabbi	13 hauls
Thais lamellosa	15 hauls

Of these, only *Mya californica* and *Macoma nasuta* were taken alive more than ten times.

These prevalent species include the most adaptable forms found in the local fauna. Most of them are distributed quite uniformly throughout the bay, being able to withstand easily the extremes of the diverse environments found within these waters. The hardiness of these species is attested also by their wide geographic distribution, showing a marked range of environmental conditions. It is not sur-

prising, then, that *Macoma balthica* and *Mytilus edulis* have a general distribution within San Francisco Bay, when the same species are able to endure the rigors of the littoral zone of the North Sea, north Atlantic Coast, and western coast of North America. *Thais lamellosa* and *Zirfaea gabbi* also have wide ranges on the West Coast and are closely related to if not identical to Atlantic Coast species.

TABLE 1

COMPLETE RECORD OF THE QUANTITATIVE HAULS

"Albatross" dredging stations	Number of species of Mollusca	Number of genera	Number of species represented by living specimens	Number of individuals living	Number of individuals dead	Total number of individuals	Number of species of Pelecypods	Number of species of Gastropods
D 5815 A	2	2	2	6	0	6	2	0
D 5815 B	1	1	0	0	3	3	1	0
D 5816 A	0	0	0	0	0	0	0	0
D 5816 B	2	2	2	5	2	7	2	0
D 5817 A	3	3	1	8	109	117	3	0
D 5817 B	3	3	3	4	15	19	2	1
D 5818 A	3	3	1	1	18	19	3	0
D 5818 B	4	4	1	10	39	49	4	0
D 5819 A	4	3	3	10	5	15	4	0
D 5819 B	1	1	1	3	4	7	1	0
D 5820 A	4	3	2	2	5	7	4	0
D 5820 B	1	1	0	0	9	9	1	0
D 5821 A	5	5	4	31	17	48	4	1
D 5821 B	11	11	2	3	37	40	10	1
D 5822 A	3	3	1	1	224	225	3	0
D 5822 B	6	6	2	115	83	198	5	1
D 5823 A	6	6	2	17	91	108	5	1
D 5823 B	3	3	3	13	2	15	3	0
D 5824 A	3	3	2	7	24	31	3	0
D 5824 B	11	10	3	404	2,566	2,970	8	3
D 5825 A	13	12	7	166	193	359	9	4
D 5825 B	9	8	1	1	189	190	8	1
D 5826 A	10	9	0	0	343	343	8	2
D 5826 B	10	9	2	33	126	159	8	2
D 5827 A	11	10	0	0	95	95	10	1
D 5827 B	10	9	1	2	24	26	8	2
D 5828 A	7	7	5	458	25	483	6	1
D 5828 B	13	12	6	298	527	825	9	4
D 5829 A	12	11	1	6	130	136	10	2
D 5829 B	0	0	0	0	0	0	0	0
D 5830 A	5	5	5	28	20	48	4	1
D 5830 B	2	1	2	17	2	19	2	0
D 5831	9	8	4	20	39	59	7	2
D 5832	8	7	0	0	69	69	7	1
D 5833	15	12	4	259	93	352	11	4
D 5834	8	7	2	2	80	82	6	2
D 5835	6	6	1	2	35	37	5	1
D 5836	6	6	0	0	158	158	4	2
D 5837	0	0	0	0	0	0	0	0
D 5838	0	0	0	0	0	0	0	0
D 5839	8	8	0	0	197	197	6	2
D 5840	5	5	3	24	72	96	3	2
D 5841	11	10	0	0	127	127	9	2
Average number per haul,	1.85			45.59	134.8	180.3	4.83	1.06

Table 1 shows that the average number of species of Pelecypoda per dredge haul is 4.83 as compared with 1.06 of Gastropoda. This preponderance of bivalves may be characteristic of inclosed waters, for it is considerably less, judging from the qualitative hauls alone, in the open waters just outside of the Golden Gate. The relative abundance of the forms is shown in the fourth column, where it is found that 45.59 living specimens were taken in the average quantitative haul representing the molluscan population of 7.8 square feet of bottom. These living specimens represent 1.85 species, showing that as a rule but a comparatively few forms live together at the same time within an area less than eight square feet. The largest number of living individuals dredged from a single locality is 458 at station D 5828 A, which is within the middle division of the bay just east of Angel Island (see pl. 12).

The number of dead shells, representing as they do the accumulation of a considerable period of time, have but little interest in a faunistic study. The shells, which are often heaped into veritable banks, may be transported by currents or various marine animals, of which the hermit crab is the most important. At certain localities the dredge was often completely filled with old valves of *Ostrea lurida* or *Mya arenaria*. Occasionally these hauls contained no living specimens of the species so abundantly represented by dead shells. This suggests a recent change in the physical conditions, at least in quiet waters, of such a nature as to be detrimental to that species. It is not improbable that the molluscan fauna of the bay is undergoing modifications due to the close proximity of the cities around the bay. The average number of dead shells per dredge haul is 134.8, which is far under the actual number that would be obtained if several of the above mentioned hauls of oyster shells had not been omitted.

Station D 5833 is the richest faunally of all the quantitative hauls. This most productive haul was made 0.3 of a mile west of the Oakland Harbor Light, within the lower division of the bay. The bottom was characterized by Sumner *et al.* (1914, p. 190) as being composed of 90.5 per cent of mud and 9.4 per cent of sand; the depth is 6¼ fathoms; and the haul was made January 21, 1913. The complete record of this haul is given in table 2.

TABLE 2

A Record of the Most Productive Quantitative Haul, Station D 5833

	Number of living individuals	Total number of individuals	Modal lengths in mm.
Cardium corbis	0	29	24
Macoma balthica	128	127	15
Macoma inquinata	0	7	38
Macoma nasuta	0	20	55
Mya arenaria	0	1	22
Mya california	2	7	11
Mytilus edulis	0	2	33
Ostrea lurida	0	many	....
Paphia staminea	1	3	10
Schizothaerus nuttalli	0	fragm.	....
Zirfaea gabbi	0	fragm.	....
Crepidula nivea	0	fragm.	....
Epitonium hindsi	128	128	3
Epitonium sawinae	0	1	....
Nassa fossata	0	1	22
Thais lamellosa	0	14	13

It is of interest to note the average size of a few of the prevalent species. Such data are tabulated below.

TABLE 3

The Average Size of the Living Specimens of Five Prevalent Species

Species	Number of specimens	Average length of specimens for all hauls in mm.	Maximum length of living specimens obtained in same hauls in mm.
Macoma nasuta	59	20	55
Cardium corbis	11	9	17
Mytilus edulis	4	8	17
Mya arenaria	33	25.8	80
Mya california	573	9.5	17

The averages as given above are rather low, due in part to the relatively large numbers of very young individuals. These figures, however, combined with those given elsewhere in this paper, make it possible to picture the molluscan life of a typical unit area, besides giving the approximate numbers and dimensions of the individuals living within such an area. It is also possible to estimate roughly the amount of organic matter represented by the mollusks, after once having established the average number and size of the individuals per unit area, and the ratio of the organic to that of the inorganic matter for each species.

A picture of the molluscan life of an average unit area, such as would be covered by the jaws of the orange-peel bucket dredge (7.8 square feet), may be obtained from a consideration of the data presented above.

This unit area within the upper division of the bay would yield two species, judging from the average number of species per dredge haul for that region. Similar averages for that portion of the bay indicate that such an area would support four living specimens and seventeen old shells.

The same area within the middle division would yield, according to the same line of reasoning, seven species, while the living individuals would number 80 and the old shells 235.

A similar area within the lower division would appear to yield six species, twenty-seven individuals and seventy-nine old shells.

The particular species represented within these three hypothetical areas can not be determined. It is probable that such an area depicting the average conditions would contain some of those species that have been listed as the prevalent species for the region considered. The commonest simple combination of species for the upper division, for instance, would be the two species most frequently dredged within that region, but such a combination out of a number of other possible combinations would rarely be obtained.

This difference in the abundance of the molluscan life within the different regions of the bay is shown in plate 13, where the circles of different sizes stand for the different species and the number of circles for the number of living individuals obtained in the average dredge haul for the designated divisions. No attempt has been made to show the number of old shells.

ECONOMIC CONSIDERATIONS

The molluscan fauna of San Francisco Bay and environs includes a number of edible pelecypods. The two local species most commonly found in the markets of the Bay region are *Mya arenaria,* the "soft-shelled," "mud" or "eastern clam," and *Paphia staminea,* the "hard-shell," or "butter clam." Other well known northern clams that occur in the vicinity of San Francisco include: *Saxidomus nuttalli, Schizothaerus nuttalli, Mytilus edulis, Mytilus californicus, Siliqua nuttalli, Ostrea elongata, Ostrea lurida, Panope generosa, Cardium corbis,* and *Pholadidea penita.* Two other Californian species, *Tivila crassatelloides* and *Chione undatella,* are frequently seen in the San Francisco markets, but they are southern species, the former, the Pismo clam, coming principally from San Luis Obispo County.

Mya arenaria is predominantly a mud-dwelling species, and occurs

in sheltered localities on muddy or sandy beaches. It thrives under various conditions of temperatures and salinities. The extensive mud flats of San Francisco Bay afford a very congenial habitat for this exotic form, as is attested by its phenomenal increase since 1881, when it was first reported from this region. The Survey record shows that this species now has a general distribution within the bay, being especially abundant on the extensive tidal flats of the upper and lower divisions.

An excellent account of the developmental history and economic importance of this clam may be found in the reports of the Massachusetts Commissioners on Fisheries and Game. Since no detailed work has been published regarding this particular species on our coast, Belding's conclusions will be assumed to apply in general to our local forms. The following notes are drawn freely from the papers published by the Massachusetts Commissioners on Fisheries and Game (1916).

As is well known, this mollusk burrows deeply in the soil, lying at a depth of from six to twelve inches. When the tide is out the siphon is generally partly retracted, leaving an elliptical hole in the sand, but upon the return of the tide the siphon expands and a current of water is set up through the incurrent and excurrent tubes. The clam once having established itself and having grown to a length of about one and one-half inches, seldom moves, unless crowded out of its hole by more vigorous neighbors.

Belding and Lane show that after fertilization the larva passes through the well known stages leading up to the veliger, which is characterized by a thin shell. This stage is reached in about twenty-four hours after fertilization, the organism passively floating at or near the surface of the water. A few days later it develops a prodissoconch and a ciliated foot, when it settles to the bottom and attaches itself to a suitable support by means of a byssus. It develops rapidly and soon acquires the burrowing habits of the adult.

In favorable localities on the Atlantic Coast a length of 30.5 millimeters (1¼ inches) is attained by the end of three and one-half months. Belding and Lane (1916, pl. 9) claim that a clam that has reached a length of 25 mm. at the end of six months will measure 70 mm, at 1½ years, or 81.9 mm. at 2½ years, or 90.7 mm. at 3½ years. Such a growth expressed in terms of volume is equivalent to an increase from 1 to 23 bushels at 1½ years, 36.9 at 2½ or 47 at 3½ years. This clam reproduces on the Atlantic Coast at two years of age.

On the Massachusetts coast spawning occurs from June 1 to September 1. There is considerable local difference in the spawning season due to the fact that "spawning will not take place until the water has attained a warmth suitable for the development of young larvae" (Mass. Com'rs of Fisheries and Game, 1916, p. 105). It does not necessarily follow that the spawning season of San Francisco Bay would be the same time, for the water temperature may be suitable for reproduction during other months of the year. This problem should be investigated, since it has an economic as well as a scientific significance.

It is evident that the larval stage of the clam is the most critical period of its life. During this stage it is defenseless, subject to the varying conditions of surface temperature and salinity and to the tidal currents. If the young clams drift away from a suitable bottom they are destroyed in countless numbers, or the currents may sweep many together so that many more become attached within a small area than can possibly develop.

It is highly desirable to determine the localities within San Francisco Bay where the set is heavy from year to year, for such places would supply young clams for transplanting to localities less favorably situated as regards tidal currents.

Paphia staminea occurs commonly on sandy bottom. It, too, is a hardy form, occurring within estuaries as well as along the sandy beaches of the open ocean. Apparently San Francisco Bay does not afford as suitable conditions for the development of this clam as for the preceding species, since it was more rarely taken by the "Albatross".

Saxidomus nuttalli is not abundant within San Francisco Bay, occurring, according to the Survey records, only within the Golden Gate. This species is elsewhere more frequently taken from a sandy and gravelly bottom, into which it burrows deeply. It is found along the open ocean and within inlets within which the range of salinity is not great. This large clam is quite abundant along Oregon and Washington shores, where it is taken in considerable numbers. This species, together with the following, possesses a dark epidermis around the large muscular siphon, which detracts from the appearance of the clam and which must be removed before it is canned.

Schizothaerus nuttalli burrows very deeply in the muddy sand of the open ocean or bays. It was taken alive but once within San Francisco Bay, probably because the dredge failed to sink deep enough

to capture it. This species occurs most abundantly at the low water mark and might be expected to occur sparingly along the low sandy beaches within the middle division of the Bay. It is known as the "Washington" or "horse clam" in the Puget Sound region, where it is now being utilized for clam nectar.

The mussels, represented by *Mytilus edulis* and *M. californicus,* are a sea food that has not as yet received the attention it deserves. *Mytilus edulis* occurs in varied environments wherever suitable supports abound. It is found attached to the rocks or piles mainly within the intertidal zone. These small mussels are occasionally found in local markets, where they command a good price. The large mussel, *M. californianus,* is seldom found in the markets, although it is used locally by people living near the beds. It comprised an important article in the diet of the local Indians, as is attested by the extensive shell mounds along the coast. Unlike the smaller mussels, this form lives only along the shores of the open ocean, attached to the rocks at or near low tide mark. It develops best at those places along the rocky shore where the waves are continually breaking over them. These mollusks can be easily harvested at extreme low tide by pulling them off the rock or scraping them off by means of a suitable tool. Such an industry properly regulated would add a considerable amount of sea food to the states of California, Oregon, and Washington.

Siliqua nuttalli, incorrectly named "razor clam," occurs sparingly within the middle division of San Francisco Bay. It occurs typically within the pure sands along the open ocean. No record is available of this species occurring in commercial quantities in the vicinity of San Francisco, although it might be grown on almost any gently sloping outside beach, on which but little shifting of the sand occurs.

The eastern and the native oysters occur within San Francisco Bay. The former, *Ostrea elongata,* does not reproduce within these local waters. Therefore seed oysters are brought from the Atlantic Coast to replenish the beds depleted by harvest. The principal oyster beds located within the lower division of the bay are now being investigated by the United States Bureau of Fisheries, and therefore will not be further considered. The small native or "Olympia oyster," *Ostrea lurida,* is a hardy species having a general distribution within the bay as well as in shallow waters outside of the Golden Gate. In places within the lower division of the bay these oyster shells literally pave the bottom. This small oyster is now extensively used throughout the coast.

Panope generosa is the largest of the West Coast clams. This northern form occurs only sparingly in the vicinity of San Francisco. It occurs on sandy or gravelly beaches near the low tide mark, where it burrows deeply.

Cardium corbis, the true cockle, is a hardy clam living under a variety of conditions from those of an estuary to that of the open ocean. It is perhaps predominantly a mud dweller, although it frequently occurs on sandy or gravelly bottoms. It is one of the easiest to procure, since it generally lies on the surface. Although this clam has the reputation of being tough, it is suitable for, and at present is being used, as minced clams. This species is large and lacks the thick, dark epidermis on the siphons, making it more desirable for mincing than similar sized or even larger clams, such as *Saxidomus nuttalli* or *Schizothaerus nuttalli.*

The rock-boring mollusk, *Pholadidea penita,* occurs quite abundantly in the softer rocks within the Golden Gate and along the ocean beach. It is said to be very palatable by those living near the rocks in which these, incorrectly called "rock oysters," live. As yet this clam has not been considered of economic importance, although it might well be investigated from that standpoint.

Besides these well known edible clams there are several native forms that might well serve as food if means for their cultivation were devised. One of these, the *Macoma nasuta,* occurs very abundantly on the muddy or sandy beaches along the bay. It is a very small clam, about the size of the native oyster, but it has a good flavor and is easily obtained, since it does not burrow deeply. The true "razor clam," *Solen sicarius,* is reported to be excellent. It is a deeply burrowing, sand-dwelling form that is difficult to obtain. It probably thrives best on the sandy beaches along the ocean front. *Spisula catillifornis* is represented in the Survey collections by a few specimens obtained from the Golden Gate. It is a large but rare clam that might possibly be successfully grown along the sandy beaches outside San Francisco Bay. Certain species of *Pecten* occur very abundantly in Puget Sound at depth of several fathoms. It is possible that the same or similar species may occur off the Golden Gate in quantities sufficient to have an economic significance. The dredgings of the "Albatross", however, failed to reveal any such beds at the few outside stations.

From the above discussion it is evident that the waters of San Francisco Bay and immediate vicinity offer suitable habitats for a

number of edible clams. Only a few of these, however, are extensively used for food. Unfortunately data for the production of mollusks within California are available only for the year 1916. Even these data are incomplete, since they include only the figures for those clams handled by the wholesale dealers. The following figures have been kindly furnished by the Fish and Game Commission of California.

TABLE 4

PRODUCTION OF THREE SPECIES OF MOLLUSKS FOR THE YEAR 1916

Mya arenaria		
San Francisco Bay	161,891 lbs.	$8,094.55
Tomales and San Francisco Bay	366,939	18,346.95
Bodega Bay	19,702	985.10
Total	548,532	$27,426.60
Paphia staminea		
Bodega Bay	1,034 lbs.	$103.40
Saxidomus nuttalli		
Humboldt Bay	43,488 lbs.	$2,609.28

San Francisco Bay yields more than 161,000 pounds of *Mya arenaria,* having a value of over $8000. These figures represent only a small part of the actual yield, as may be seen by referring to table 4. The present yield of the bay is thought by many local clam dealers to be much less than it was ten or more years ago. There are, however, no figures available upon which to base an estimate of a former yield. The wholesale price of this clam ranges from 5 to 8 cents per pound, the average being about 6 cents. Figures are not available for the 1916 yield of *Paphia staminea* nor *Mytilus edulis,* which are occasionally harvested within San Francisco Bay. The hard shell clam brought in from Bodega Bay and elsewhere sells for 9 or 10 cents wholesale. The mussels frequently sell for as much as 12½ cents retail, under normal conditions of the market. The other clams mentioned above are rarely on the local market, and therefore the prices are variable, depending upon the sporadic supply. The market conditions even for the mud clams are rather unstable, due in part to the uncertainties of harvesting, which under present methods depend upon a favorable tide, since dredging methods are not yet employed.

The dredging operations of the "Albatross" within San Francisco Bay have yielded data from which rough estimates of the average numbers per acre of the different clams can be calculated.

Mya arenaria was taken alive at 8 out of the 43 quantitative hauls, and is represented by 32 living specimens, making an average per haul for the entire bay of .76. This would equal approximately 1.5 bushels per acre. This figure, however, representing the average for the bay, is obviously of little significance. If those stations having a sandy bottom are segregated, it is found that this type of bottom yields on the average 1.1 living specimens per haul, or the equivalent of approximately 2.2 bushels per acre, assuming that all were of marketable size. Even such a yield has no economic significance, since under favorable conditions a yield of 500 bushels per acre is not uncommon.

The quantitative dredge hauls indicate that *Paphia staminea* and *Saxidomus nuttalli* are even less abundantly represented within the adlittoral waters of San Francisco Bay.

The intertidal zone, having an area of approximately 17,344,000 acres, yields what clams are now obtained from the bay, since dredging is not at present locally employed. It is probable that at least 50 per cent of this acreage is suitable for the production of *Mya arenaria.* If this is so, the tidal zone of San Francisco Bay would undoubtedly support 4¾ billion bushels of *Mya arenaria.* If markets could be found for such an enormous amount of sea food, an industry involving millions of dollars might be established.

This clam has been transplanted and raised experimentally on the Atlantic Coast by the Massachusetts Commissioners on Fisheries and Game and on an economic scale by many eastern growers. The labor involved is slight. The planting consists of merely scattering the young clams, obtained from localities where the set is heavy, at a rate of fifteen to twenty per square foot. Six months or a year later, depending upon the size planted or the size marketed, these may be harvested. The investment need not be great. A boat and a set of digging tools is all that is necessary. The returns are as great as from an acre of cultivated land, since in Massachusetts the average yield per acre is given by Belding and Lane as $450.

Not all of the clams that are planted reach maturity. Losses may be due to overcrowding, whereby the clam is pushed out of its hole by its more vigorous neighbors, to shifting sand, mud or sea weeds, or to enemies such as the starfish or certain predaceous gastropods. The gastropods include *Polinices lewisi* and the exotic species *Urosalpinx cinereus* and *Ilynassa obsoleta.* It is to be hoped that the eastern winkles (*Lunatia heros* and *L. duplicata*), conspicuous enemies of *Mya,* will not be inadvertently introduced in San Francisco Bay along with the young oysters brought from the east.

It is probable that the tide flats of San Francisco Bay are best adapted to *Mya arenaria,* although certain beaches are perhaps more suitable to *Paphia staminea* or other local species not as well known to the public. Those adapted to the exposed ocean beach include *Siliqua nuttalli, Mytilus californianus, Solen sicarius, Saxidomus nuttalli, Schizothaerus nuttalli,* and *Cardium corbis.*

Such an industry as clam farming would not succeed without private control of the tide flats. This has been demonstrated along the Atlantic Coast, where suitable acreage is either sold or leased to the individuals. A law giving the exclusive rights to a certain proportion of the tidal areas ought not to be enacted until an investigation of the clam beds of the state has been made. Such an investigation would include a survey of the tide lands from the standpoint of tidal bottom, naturally productive or barren beds, their present fauna, their position as regards tidal currents, and their position as regards possible contamination from sewage. From such data as these it would be possible to determine what tracts were suitable for clam farming by the individual and what tracts should be retained as public property. The clamming industry would further profit by the determination of those localities where the natural set is heavy. Such localities should perhaps remain as public property in order that the young clams might there be obtained with which to transplant the barren areas. Other problems of interest to the clam farmer that such a survey would solve are the period of spawning, the local rate of growth of the different clams, and the season of maximum growth. These would enable the clammer to determine when to transplant the young and what sizes to use. Such an investigation might well include the market conditions, and especially the possibilities of canning the product. It might also be found that the demand for such sea food could be materially increased by a well organized advertising campaign.

The possibility of locating shell deposits within San Francisco Bay which might be dredged for their lime content has led to the preparation of table 5.

Eleven out of seventy-nine tubular bottom samples examined quantitatively by Sumner *et al.* show a lime content greater than 10 per cent. These samples were obtained from four regions, from the extreme upper to the lower end of the bay. One small and economically unimportant area occurs in Carquinez Strait, at station D 5816 A. Although the bottom sample shows a high percentage of lime, the

orange-peel bucket dredge revealed only a few specimens of *Mya*. East of Point San Quentin the sample shows 12.26 per cent of lime at the surface, decreasing to about 10 per cent at a depth of 70.5 centimeters. A large number of specimens of *Ostrea lurida* were obtained at a near-by station. Again at stations D 5796 and D 5798 the lime content is fairly high, but at those stations the water is nineteen fathoms deep. The stony character of the bottom at station D 5702, which lies within the Golden Gate, would prevent dredging on a commercial scale.

TABLE 5

The Lime Content of Some of the Tubular Bottom Samples

"Albatross" stations	Nearest dredging station	Percentage of lime	Depth of sample in cm.	Depth of water in fathoms
D 5816 A	D 5816 A	20.79	.....	9
H 5301	D 5798	15.33	46–56	10
D 5796	D 5796	16.58	.....	19
H 5129 C	D 5824	10.13	50.5–70.5	2
H 5129 D	D 5824	12.26	0–20	3.5
D 5702	D 5702	27.81	.....	13
H 5306	D 5834	10.38	0–10	10
H 5309	D 5839	25.33	70–80	10
H 5310	D 5836	21.75	91–108	5
D 5783	D 5783	86.21	.....	2
D 5847 A	D 5847 A	24.86	125–136	8.5
H 5312	D 5847 A	37.27	123.5–133.5	5

Large quantities of *Ostrea lurida* were dredged off the Oakland Harbor Light at D 5832 and D 5833. They were also obtained abundantly farther south at station D 5835. Besides surface deposits, Sumner *et al.* (1914, pl. 6) show that a layer of shells from 50 to 80 centimeters thick, extending from station H 5306 to H 5312, a distance of about sixteen miles, lies buried in the mud to a depth of about 50 centimeters. It is this old layer that contributes to the lime content noted in table 5 at stations D 5847 A, H 5129 C, H 5301, H 5309, H 5310, and H 5312. At all of these stations the water is less than ten fathoms deep, and the bottom is of a type of mud that might easily be dredged and then washed, leaving the concentrated shell. It is probable that the most extensive surface and subsurface deposits occur within a radius of five miles of Hunter's Point. A resurvey of those waters need not be expensive and might lead to the discovery of even greater deposits of shell than are now known.

FACTORS GOVERNING THE DISTRIBUTION OF THE MOLLUSCA

The previous sections of this paper dealt with the general distribution of the Mollusca and with the actual numbers of individuals living within a definite area. It now remains to investigate the distribution of the mollusks from the standpoint of their environment. Some of these governing distribution are: the physical character of the bottom; the salinity, temperature and depth of the water; the distribution of the plankton which serves as food; and other biotic factors including other organisms which may not be beneficial to the animal under consideration.

The limited number of quantitative hauls offers less conclusive evidence regarding the importance of some of these factors than do the more numerous qualitative dredge hauls made during the general survey of the bay. Petersen (1913, p. 5) has shown that the common dredge gives an entirely different picture of the benthos from that obtained by means of the quantitative type of dredge. The latter brings to the surface not only the organic matter from that locality but also the bottom materials upon which or in which the animals lived, thus giving a more correct idea of certain factors of their environment.

TABLE 6

THE RELATIVE ABUNDANCE OF MOLLUSCAN SPECIES AND INDIVIDUALS FOR THE DIFFERENT SECTIONS OF SAN FRANCISCO BAY

	Average number of species per haul	Average number of genera per haul	Average number of species represented by living specimens	Average number of live individuals per haul	Average number of dead individuals per haul	Average total number of individuals per haul	Average number of species of pelecypods per haul	Average number of species of gastropods per haul	Average depth of hauls in fathoms
Entire bay	5.9	5.4	1.8	45.4	134.8	180.3	4.8	1.06	8.6
Upper bay	2.3	2.1	1.3	4.08	17.4	21.5	2.2	.08	7.8
Middle bay	7.5	7.0	2.4	80.0	235.9	315.9	6.1	2.2	9.9
Lower bay	6.9	6.2	1.2	27.9	79.0	107.0	5.2	1.6	8.3

A tabulation of data derived from table 1 shows in table 6 that the conditions within the different divisions of San Francisco Bay are not equally favorable to molluscan life. This analysis of these more restricted areas clearly shows that the middle division of the bay is a much more favorable habitat for the mollusk than either of the other two divisions. The lower section is much richer per haul than the upper in every respect, the average number of living indi-

viduals being nearly seven times as great. These differences as brought out in this table challenge investigation as to their causes.

There is such an inter-relation between the different factors that determine the distribution of animals of this class that it is difficult to determine the effect of any single one upon the molluscan life.

Reation to Depth

The effect of depth upon the distribution of the Mollusca is probably insignificant within these local waters. This conclusion is based more largely upon a study of the distribution of the entire fauna collected by the Survey than upon the results of this study. However, the following table is presented in which the averages per haul for four different bathymetric zones are given.

TABLE 7

The Relative Abundance of Species and Individuals for Different Bathymetric Zones

Depth in fathoms	Number of hauls	Average number of living individuals per haul	Average number of species per haul	
			Pelecypoda	Gastropoda
0 to 5	2	5.5	3.5	0.0
5 to 10	26	42.5	4.57	1.1
10 to 15	12	31.8	5.5	1.1
15 to 20	3	152.6	5.3	.6

This table suggests that the number of living individuals per dredge haul is greater with increase of depth. A similar correspondence is seen in the last column in table 6, where the greatest average depth for the quantitative hauls occurs in the middle division of the bay, which is there shown to be the richest faunally. This apparent bathymetric distribution may be due to other factors which are peculiar to the middle portion of the bay, in which most of the deeper hauls were made.

Relation to Type of Bottom

The character of the bottom is a recognized factor in determining the distribution of mollusks. In order to show the relative abundance of molluscan life on different types of bottoms, the following table has been prepared. Seven types of bottom have arbitrarily been recognized. This classification is based upon the physical analyses of the bottom samples, supplemented by the notes regarding the bottom

made on shipboard at the time of dredging (see Sumner *et al.*, 1914, pp. 1, 111). At a number of stations the bottom was found to be composed of two or more types of materials. These have been classified according to predominance of one type over that of the others. For instance, a bottom which might be characterized as a muddy sand is herein designated as sand and mud. Since objects for support are essential to some mollusks, groups one and seven are considered in which shells comprise a conspicuous part of the bottom material. Of course in such a case the presence of shell generally indicates that conditions have long been favorable to molluscan life, therefore the larger numbers in such a group are not necessarily entirely due to the shell element in the composition of the bottom. The figures given are derived from table 1, and represent the averages per haul within the group under consideration.

TABLE 8

THE RELATIVE ABUNDANCE OF SPECIES AND INDIVIDUALS FOR THE DIFFERENT TYPES OF BOTTOMS

Character of bottom	Number of hauls	Average number species per haul	Average number genera per haul	Average number living individuals	Average number species of pelecypods	Average number species of gastropods
1. Pure mud	11	3.2	3.2	13.9	2.6	.6
2. Mud and sand	14	4.0	3.7	41.8	3.6	.4
3. Mud and shells	4	7.0	8.7	82.5	5.5	1.5
4. Sand and mud	5	9.8	8.8	33.8	7.8	2.0
5. Pure sand	1	5.0	5.0	28.0	4.0	1.0
6. Sand and gravel	4	8.25	7.5	2.0	7.0	1.2
7. Sand and shells	4	11.5	10.0	174.0	9.2	2.7

In interpreting these figures due allowance must be made for the fact that the different types of bottoms are not represented by equal numbers of hauls. When the number of living individuals is considered, it is seen that the greatest numbers were taken on bottoms characterized as being composed of sand and shells; while the second largest numbers come from bottoms of mud and shells. The pelecypods are represented by the larger number of species per haul from bottoms characterized as sand and shells, mud and shells being the next in importance as regards the number of species per unit area.

A study of the molluscan associations peculiar to these different types of bottoms shows several interesting relationships. The list of species occurring upon various types of bottoms is given below, the asterisk indicating that the specimen was dredged alive.

Species Occurring in Group 1: Pure Mud

Cardium corbis
Macoma balthica*
Macoma nasuta*
Mya arenaria*
Mya california*
Mytilus edulis*
Ostrea lurida
Paphia staminea
Pholas pacificus
Psephidia ovalis
Zirfaea gabbi
Epitonium hindsi
Odostomia franciscana
Turbonilla franciscana

Species Occurring in Groups 2 and 4: Mud and Sand

Cardium corbis*
Gemma gemma var. purpura*
Macoma balthica*
Macoma inquinata
Macoma nasuta*
Mya arenaria
Mya california*
Mytilus edulis*
Ostrea lurida
Phacoides tenuisculptus*
Pholas pacificus
Psephidea ovalis
Schizothaerus nuttalli
Solen sicarius
Tellina buttoni*
Tellina salmonea*
Zirfaea gabbi*
Crepidula niva*
Columbella gausapata
Nassa mendica
Nassa fossata*
Nassa perpinguis
Thais lamellosa*
Turbonilla franciscana

Species Occurring in Group 3: Mud and Shells

Cardium corbis
Gemma gemma var. purpura*
Macoma inquinata
Macoma nasuta*
Mya arenaria*
Mya california*
Modiolus, cf. rectus
Mytilus edulis
Ostrea lurida
Paphia staminea
Psephidea ovalis
Zirfaea gabbi*
Columbella gausapata
Epitonium hindsi?
Nassa fossata?
Nassa mendica*
Thais lamellosa
Turbonilla keepi

Species Occurring in Group 5: Pure Sand

Mytilus edulis*
Phacoides tenuisculptus*
Psephidea ovalis*
Tellina buttoni*
Turbonilla franciscana*

Species Occurring in Group 6: Sand and Gravel

Cardium corbis
Hinnites giganteus
Macoma balthica
Macoma inquinata
Macoma nasuta
Monia macroschisma
Mya california
Ostrea lurida
Saxidomus nuttalli
Schizothaerus nuttalli
Spisula catilliformis
Tellina salmonea*
Nassa fossata
Thais lamellosa
Zirfaea gabbi

Species Occurring in Group 7: Sand and Shells

Cardium corbis
Macoma balthica
Macoma inquinata
Macoma nasuta
Mya arenaria
Mya california*
Mytilus edulis
Ostrea lurida
Psephidia ovalis*
Schizothaerus nuttalli
Tellina salmonea
Zirfaea gabbi
Epitonium hindsi*
Epitonium savinea
Nassa perpinguis
Thais lamellosa
Turbonilla keepi

Most of the species listed above occur in several groups of quite dissimilar character. This would suggest that the occurrence of a species at a certain locality does not give a true idea of its ecological relationships. The relative abundance of a species within a dredge haul gives a clue as to the optimum environment for that species, and therefore may well serve as the basis for studies in faunal associations. For this reason the average per haul for each species has been calculated. The group in which the highest average falls would appear to represent that type of bottom best suited to the mollusk in question. Such a list is given below. The number of hauls is possibly too few to more than suggest the broad outlines of such molluscan associations.

The following species are arranged according to their relative abundance on the different types of bottom:

Group 1.	Pure mud
Living:	None
Dead:	Gemma gemma var. purpura
	Mya arenaria
	Psephidia ovalis
	Columbella gausapata
	Odostomia franciscana
Group 2.	Mud and sand
Living:	Cardium corbis
	Gemma gemma var. purpura
	Crepidula nivea
Dead:	Pholas pacificus
Group 3.	Mud and shells
Living:	Macoma nasuta
	Modiolus, cf. rectus
	Zirfaea gabbi
Dead:	Cardium corbis
	Zirfaea gabbi
	Turbonilla franciscana
	Turris incisus?
Group 4.	Sand and mud
Living:	Psephidia ovalis
	Tellina buttoni
Dead:	Mytilus edulis
	Ostrea lurida
	Nassa mendica
Group 5.	Pure mud
Living:	Phacoides tenuisculptus
	Turbonilla franciscana
Group 6.	Sand and gravel
Living:	Tellina salmonea
Dead:	Hinnites giganteus
	Macoma inquinata
	Monia macroschisma
	Saxidomus nuttalli
	Tellina salmonea
	Turbonilla keepi

Group 7.	Sand and shells
Living:	Mya californica
	Macoma balthica
	Epitonium hindsi
Dead:	Mya california
	Paphia staminea
	Epitonium hindsi
	Nassa fossata
	Nassa perpinguis
	Thais lamellosa

The above list shows several different associations of species. Of the prevalent species, *Cardium corbis, Macoma nasuta, Mya arenaria,* and *Zirfaea gabbi* appear to be predominantly mud-dwelling forms; while *Mya californica, Macoma balthica, M. inquinata, Ostrea lurida,* and *Thais lamellosa* may be classed as sand dwellers. Although these conclusions are tentative, because of the paucity of the hauls upon which they are based, they suggest the broad features of the different molluscan communities.

Relation to Salinity

In order to determine the influence of salinity upon molluscan distribution, a comparison of a curve showing the number of living mollusks for most of the quantitative stations with salinity curves for the equivalent hydrographic stations as published by Sumner *et al.* (1914) may be made. In these curves the stations are arranged along the horizontal axis, at distances proportionate to their relative positions in the bay. The average number of living mollusks from the several hauls made in the immediate vicinity of the hydrographic stations is represented along the vertical axis of the specimen curve.

There is apparently little correspondence between the areal density of the mollusks and the mean annual salinity. This is evident by referring to figure B.

It appears, however, that the mean annual salinity at stations D 5815 to D 5820 inclusive (left end of curve) is unfavorable to an abundant molluscan life. The specimen curve as well as the following table indicates that the average number of individuals per haul is greatest for those stations having a mean annual salinity between 28 and 30 per mille.

TABLE 9

Mean annual salinity	Group	Number of hauls	Average number living individuals
17.16–19.37	1	8	3.1
19.38–21.57	2	2	5.5
21.58–23.79	3	0	0.0
23.80–26.07	4	6	9.0
26.02–28.23	5	8	12.3
28.24–30.45	6	15	82.0
30.46–32.67	7	4	12.7

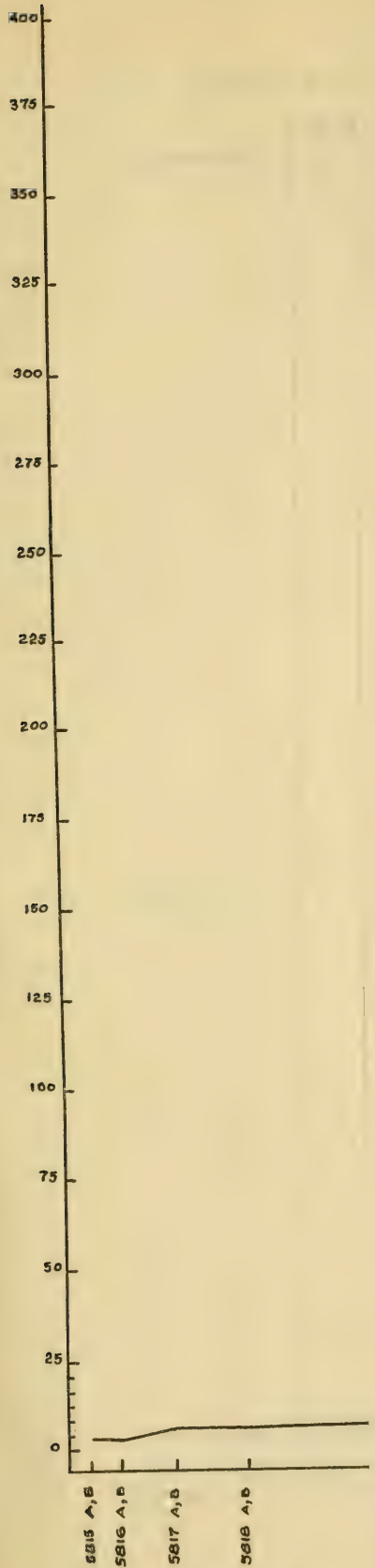
400
375
350
325
300
275
250
225
200
175
150
125
100
75
50
25
0
5815 A,B
5816 A,B
5817 A,B
5818 A,B

Fig. A—

Fig. A—Specimen curve. Average number of living mollusks obtained at each station.

Fig. B—Mean annual salinity at each of the hydrographic stations of the regular series. (After Sumner *et al.*)

It is not improbable that the annual range of salinity is even more potent in determining the abundance of mollusks than is the mean annual salinity. A comparison of the specimen curve with the published curve indicating the annual range of salinity (Sumner *et al.*, fig. N, p. 69) shows only a general increase in the number of mollusks with decrease in range of salinity, for two of the highest points of the specimen curve fall within the area of high range in salinity.

The curves showing the distribution of salinities in the bay during April 23 to May 6 corresponds more closely with the specimen curve than does any of the others representing the salinities at other periods of the year.

The highest average number of mollusks per haul is found at those stations having a mean annual salinity between 28 and 30 per mille. If this represent the optimum salinity for the bay fauna, that portion of the bay having a salinity most nearly that of these figures should yield the largest number of mollusks per unit area. No portion of the upper bay satisfies such a condition, but the middle division does fulfil such a requirement and is also the richest faunally. The lower bay is found to hold an intermediate position both faunally and from the standpoint of salinity. However, since such a salinity is the rule in the middle portion of the bay and to a lesser extent in the lower division this apparent relationship may have but little significance. If the optimum mean annual salinity is high, as seems reasonable, it might be expected that the regions where the salinity is low at any period of the year will be low in the number of mollusks per unit area. Thus the inverse relationship shown in the curves (figures A and C) might have been foretold. It appears, then, that minimum salinity is one of the factors influencing the distribution of the local mollusks. The closer correspondence between the specimen curve and the minimum seasonal salinity curve than between any of the other curves showing the salinity for the other periods of the year tends to confirm such a statement.

Relation to Temperature

It is not improbable that the molluscan larvae are more susceptible to temperature control than is the adult mollusk. An investigation of the water temperatures during the periods of reproduction is desirable from the standpoint of the oyster culture as well as from that of pure science. Unfortunately data as to the reproductive periods of the local species are not available. Therefore only the more conspicuous effects of temperature can at present be determined.

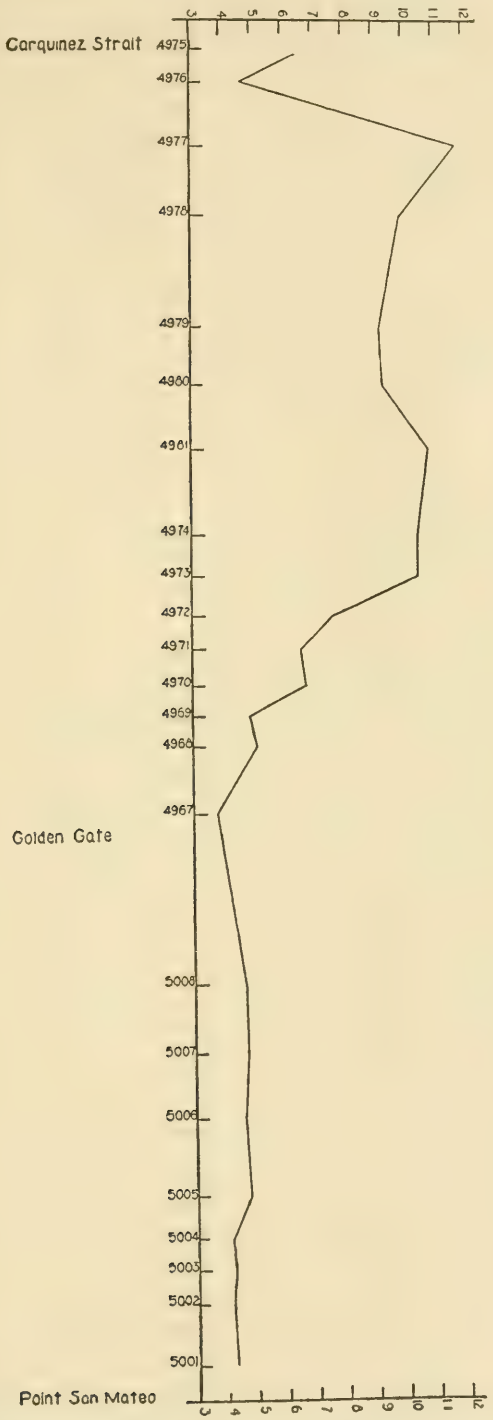

Fig. C—Seasonal range of salinity at each station. (After Sumner *et al.*)

Fig. D—Distribution of the salinities of the bay during the period of April 23 to May 6. This represents the minimum seasonal salinity. (Adapted from Sumner *et al.*)

Curves similar to those just considered suggest the importance of the temperature factor. The mean annual temperature curve as published by Sumner *et al.* appears to have little significance when compared with the specimen curve. Table 9 indicates, however, that the larger number of living individuals per haul were obtained in regions of relatively low annual temperatures.

TABLE 10

Mean annual temperature	Groups	Number of hauls	Average number living individuals
11.98–12.35	1	6	134.5
12.36–12.73	2	13	41.0
12.74–13.11	3	14	42.4
13.11–13.49	4	6	3.3
13.50–13.88	5	4	0.0

It appears from figure E that those portions of the bay where the seasonal range of temperature is high are regions in which the areal density is relatively low. It is not certain, however, that this indicates a causal relationship.

The correspondence between the October and July temperature curves and that of the specimen curve indicates that more mollusks occur within a given area where the waters are cooler during those months. In this connection it is of interest to note that the bay fauna includes a majority of predominantly northward ranging species. However, it is not evident that the warm summer temperatures of the other divisions of the bay act as a barrier to these northern forms, for the open ocean during this period is cooler than that of the bay and yet it has a fauna showing a southern facies.

If the temperature factor is important in determining the local distribution of the mollusks, the greater areal density of the middle division of the bay may be due to the low seasonal range or to the low summer temperature.

This rather indefinite relationship between molluscan distribution and temperature may indicate that this factor is effective only during the reproductive periods of a particular mollusk. If these periods do not all fall within a single season, as seems rather improbable, it is not surprising that the influence of temperature is obscure.

Relation to the Available Food Supply

The plankton probably serves as the most important food supply of the pelecypods, which in turn become the main supply for the predaceous gastropods. The distribution of the plankton within San

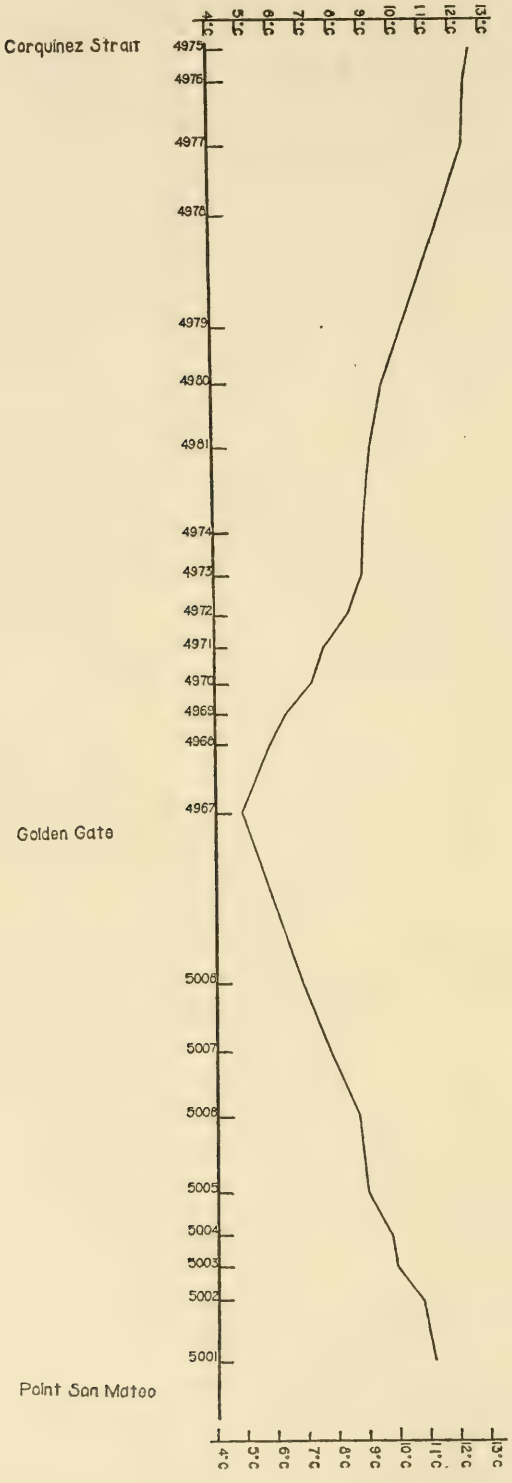

Fig. E—Seasonal range of temperature at each station. (After Sumner *et al.*)

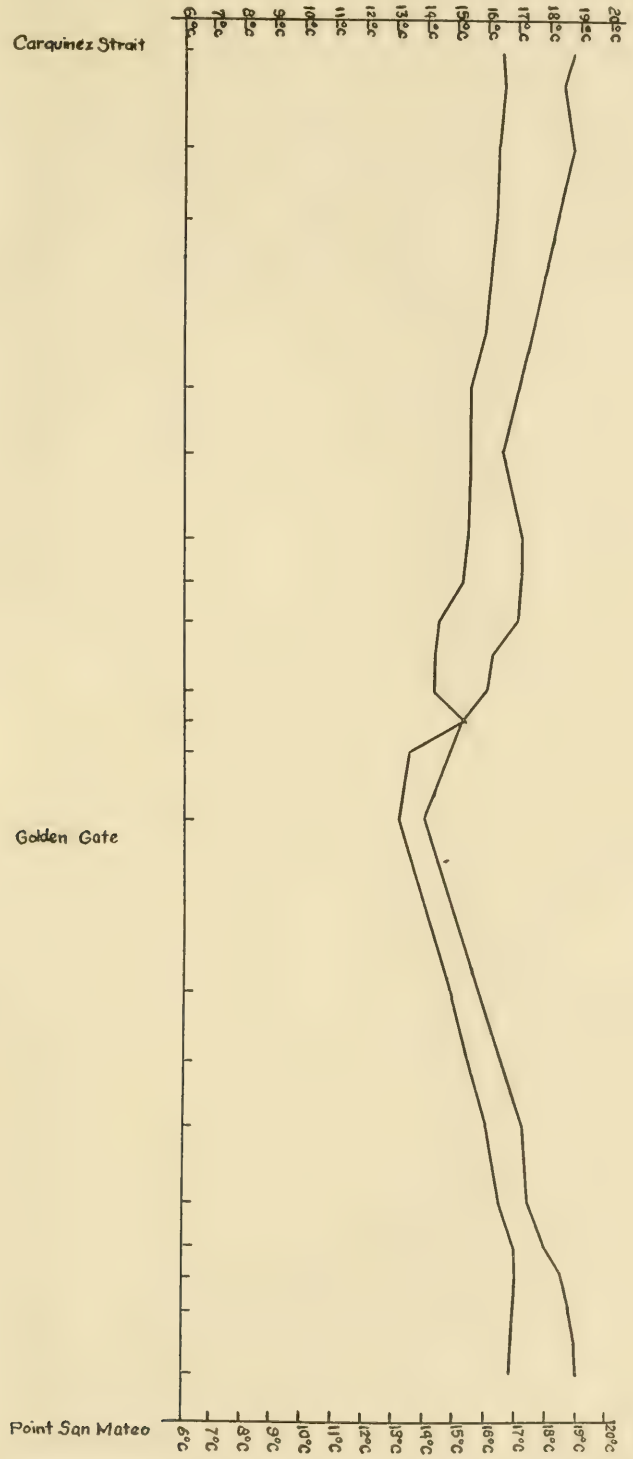

Fig. F—Distribution of bay temperatures. Upper curve, July 22–31; lower curve, October 7–12. (Adapted from Sumner *et al.*)

Francisco Bay might be a factor in determining the distribution of the mollusks if there were regions of relatively impoverished waters. That such conditions exist is suggested in the recent studies upon the diatoms made by Mr. E. P. Rankin. He shows that the number of species and individuals of these plants decreases as one passes from the middle to the upper division of the bay, and that the marine forms are not there replaced by fresh water species. The main channel through that arm of the bay is found to represent a region of impoverished water in comparison to that of the quieter and presumably more saline water near shore.

This distribution of the diatoms is paralleled in general by that of mollusks, as is shown by the relative number of species and individuals per haul for San Pablo Bay in comparison with the other regions of the bay (see p. 18). However, this apparent correlation is probably not due to the lack of food supply, for Professor Kofoid's studies show that the plankton of the bay is relatively rich; it is more probably due to the salinity, which is exceedingly variable within that region. It is thus evident that from the data at hand no definite conclusion regarding the relationship of the distribution of the plankton to that of the mollusks can be reached.

Relation to the Biotic Environment

The relation between the distribution of other forms of life and that of the Mollusca can only vaguely be suggested. From the standpoint of the food it seems that the distribution of the plankton when present in quantities above the requirements of the organism has little influence upon the occurrence of the mollusks. Until the Algae of this region are better known it is impossible to say that certain of the gastropods are not distributed according to the occurrence of certain of these plants. The distribution of some of the predaceous gastropods corresponds to that of their prey. Unfortunately no quantitative data are available regarding the distribution of the oyster drill, *Urosalpinx cinereus,* but qualitative studies show that it occurs most abundantly upon the oyster beds. The relation of the enemies of the mollusks and the distribution of several gastropods the shells of which are inhabited by hermit crabs can only be ascertained by a detailed study of the entire fauna and flora of the bay.

SUMMARY

The orange-peel bucket dredge, used for the first time for purposes of biological investigation, has been employed by U. S. S. "Albatross" at forty-three stations within San Francisco Bay.

Twenty-three species of Pelecypoda and twelve of Gastropoda were taken by means of this dredge. The ten species that were taken at more than one-fourth of the hauls represent the most adaptable forms of the molluscan fauna.

The middle division of the bay is a more favorable habitat for the Mollusca than either of the other two divisions.

Depth has little significance in determining the distribution of the local forms.

The character of the bottom is an important distributional factor. The most favorable bottom appears to be composed of sand and shells, the shells serving as supports for sessile forms.

A low salt concentration or a large annual range of salinity appear to be unfavorable to an abundant local molluscan life.

The regions in which the annual range of temperature is not great nor the maximum high during July and October support the larger number of mollusks per unit area. Nevertheless the significance of the temperature factor is obscure.

Several species of edible clams live within San Francisco Bay. Of these, *Mya arenaria* is most important. The present production of the bay is probably considerably less than it was a decade ago. The bay, under the improved methods of farming, would support an annual yield of more than four billion bushels of this clam. Such an industry should be established only after a detailed survey has been made and many of the outstanding problems solved. Laws should also be enacted which give private control to certain tracts suitable to clam farming.

APPENDIX

Table 11 is given in order to show the different groupings of the hauls that have been made in the preparation of this paper.

For further data regarding these stations and their location within San Francisco Bay the reader is referred to the often mentioned report by Sumner *et al.* (1914).

TABLE 11

Showing the Different Groupings of the Dredge Hauls

"Albatross" station numbers	Bottom groups	Temperature groups	Salinity groups	Depth groups	"Albatross" station numbers	Bottom groups	Temperature groups	Salinity groups	Depth groups
D 5815 A	2	4	1	2	D 5826 A	7	2	5	2
D 5815 B	2	4	1	3	D 5826 B	7	2	5	2
D 5816 A	1	3	1	2	D 5827 A	6	3	1	4
D 5816 B	1	3	1	3	D 5827 B	6	3	1	2
D 5817 A	2	4	1	2	D 5828 A	2	1	6	4
D 5817 B	2	4	1	2	D 5828 B	3	1	6	3
D 5818 A	1	2	2	2	D 5829 A	6	1	7	3
D 5818 B	2	2	2	1	D 5829 B	6	1	7	4
D 5819 A	2	2	4	2	D 5830 A	5	1	7	3
D 5819 B	2	2	4	2	D 5830 B	2	1	7	2
D 5820 A	2	3	5	3	D 5831	2	2	6	3
D 5820 B	2	3	5	2	D 5832	4	2	6	2
D 5821 A	2	2	5	2	D 5833	8	2	6	2
D 5821 B	2	2	5	2	D 5834	4	3	6	3
D 5822 A	1	3	4	1	D 5835	3	4	6	2
D 5822 B	1	3	4	2	D 5836	1	5	6	2
D 5823 A	3	3	5	2	D 5837	1	5	6	2
D 5823 B	3	3	5	3	D 5838	1	5	6	2
D 5824 A	1	3	4	3	D 5839	1	5	6	2
D 5824 B	7	3	4	2	D 5840	1	3	6	2
D 5825 A	4	2	6	2	D 5841	4	4	6	3
D 5825 B	4	2	6	3					

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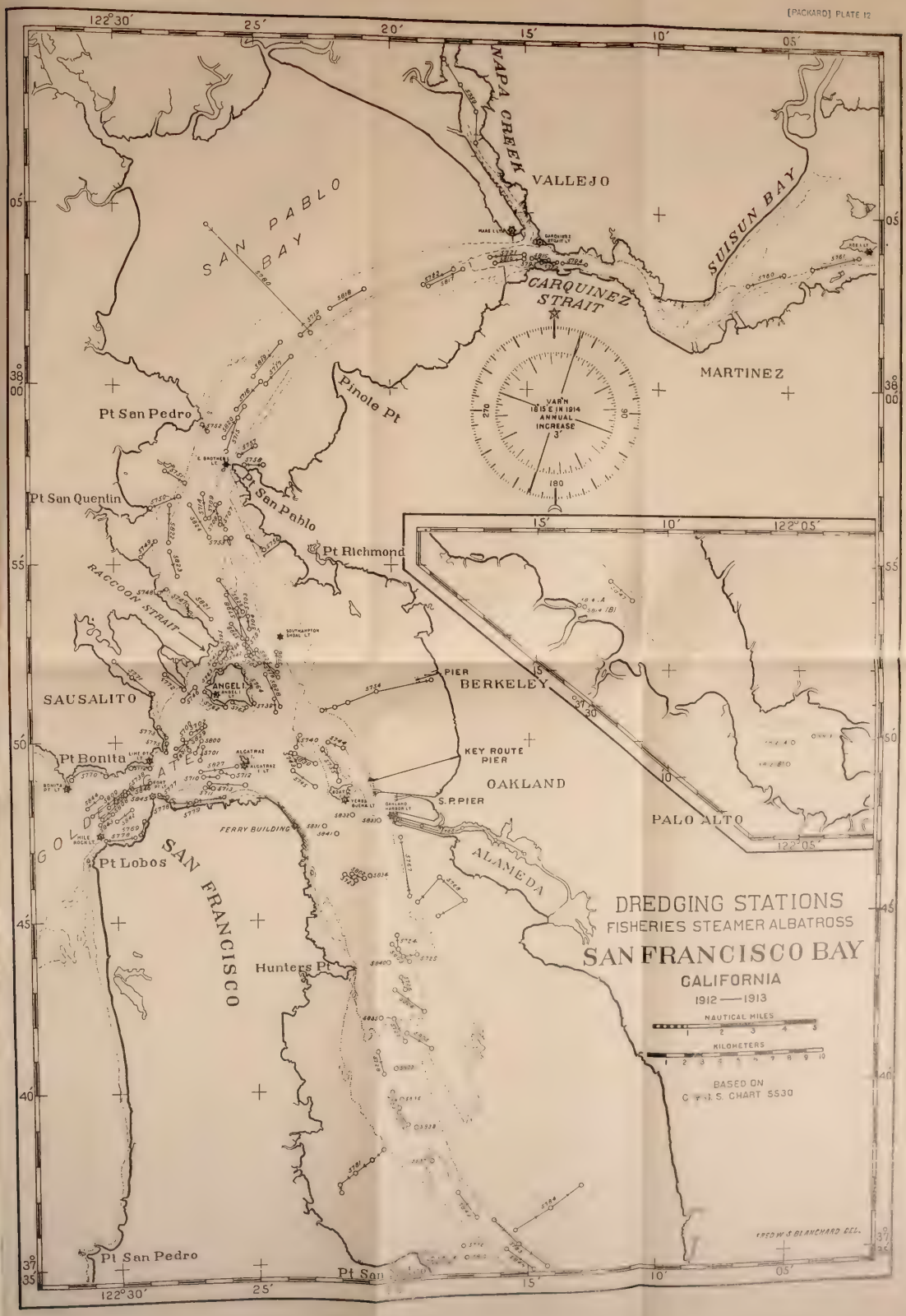
EXPLANATION OF PLATES

PLATE 12

Dredging stations of the "Albatross" in San Francisco Bay. (After Sumner *et al*).


122°30′
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NAPA CREEK
VALLEJO
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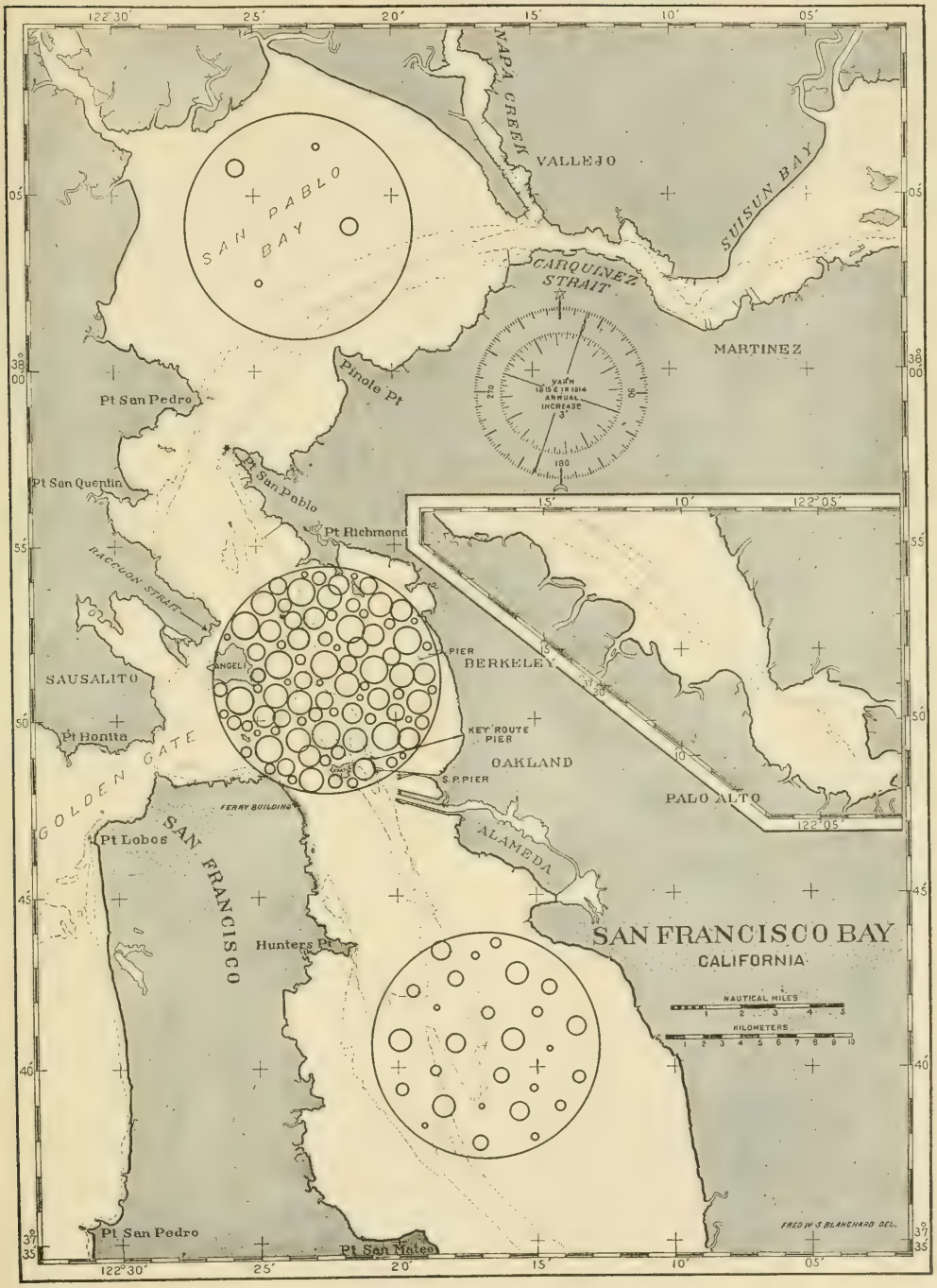
SAN PABLO BAY
CARQUINEZ STRAIT
MARTINEZ
VAR'N 1815 E IN 1914 ANNUAL INCREASE 3′
Pinole Pt
Pt San Pedro
Pt San Quentin
Pt San Pablo
Pt Richmond
RACCOON STRAIT
SAUSALITO
ANGEL
PIER
BERKELEY
KEY ROUTE PIER
OAKLAND
S.P.PIER
PALO ALTO
Pt Bonita
GOLDEN GATE
Pt Lobos
FERRY BUILDING
SAN FRANCISCO
ALAMEDA
Hunters Pt
Pt San Pedro
Pt San
DREDGING STATIONS
FISHERIES STEAMER ALBATROSS
SAN FRANCISCO BAY
CALIFORNIA
1912 — 1913
NAUTICAL MILES
KILOMETERS
BASED ON U.S.C. & G.S. CHART 5530
FRED W. S. BLANCHARD DEL.

PLATE 13

Diagram showing the relative abundance of mollusks per unit area of 7.8 square feet within the three divisions of the bay. The circles of different size stand for the different species and the number of circles for the number of living individuals obtained in the average dredge haul for the indicated region. The number of old shells is not represented.


122°30'
25'
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NAPA CREEK
VALLEJO
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SAN PABLO BAY
CARQUINEZ STRAIT
MARTINEZ
VAR'N 1915 E IN 1914 ANNUAL INCREASE 3'
Pinole Pt
Pt San Pedro
Pt San Quentin
Pt San Pablo
Pt Richmond
RACCOON STRAIT
PIER
BERKELEY
ANGEL I.
SAUSALITO
Pt Bonita
KEY ROUTE PIER
OAKLAND
S.P.PIER
PALO ALTO
GOLDEN GATE
FERRY BUILDING
Pt Lobos
SAN FRANCISCO
ALAMEDA
Hunters Pt
SAN FRANCISCO BAY
CALIFORNIA
NAUTICAL MILES
KILOMETERS
FRED'W S. BLANCHARD DEL.
Pt San Pedro
Pt San Mateo
38° 00'
05'
55'
50'
45'
40'
35'
37°

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12. A Synopsis of the Bats of California, by Hilda Wood Grinnell. Pp. 223-404, plates 14-24, 24 text figures. January 31, 1918 ..... 2.00
13. The Pacific Coast Jays of the Genus *Aphelocoma*, by H. S. Swarth. Pp. 405-422, 1 figure in text. February 23, 1918 ..... .20

Vol. 18. 1. Mitosis in *Giardia Microti*, by William C. Boeck. Pp. 1-26, plate 1. October, 1917 ..... .35
2. An Unusual Extension of the Distribution of the Shipworm in San Francisco Bay, California, by Albert L. Barrows. Pp. 27-43. December, 1917. .20
3. Description of Some New Species of *Polynoidae* from the Coast of California, by Christine Essenberg. Pp. 45-60, plates 2-3. October, 1917 ..... .20
4. New Species of *Amphinomidae* from the Pacific Coast, by Christine Essenberg. Pp. 61-74, plates 4-5. October, 1917 ..... .15
5. *Crithidia Euryophthalmi*, sp. nov., from the Hemipteran Bug, *Euryophthalmus convivus* Stål, by Irene McCulloch. Pp. 75-88, 35 text figures. December, 1917 ..... .15
6. On the Orientation of *Erythropsis*, by Charles Atwood Kofoid and Olive Swezy. Pp. 89-102, 12 figures in text. December, 1917 ..... .15
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11. The Factors Controlling the Distribution of the Polynoidae of the Pacific Coast of North America, by Christine Essenberg. Pp. 171-238, plates 6-8, 2 figures in text. March, 1918 ..... .75
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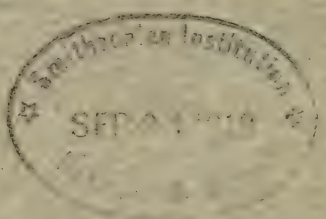

BY
HARRY B. YOCOM

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CONTENTS

PAGE

Introduction 338
Acknowledgments 340
Technique 341
Culture 341
Methods of preparation 341
Structure 344
External features 344
Internal features 348
Ectoplasm 348
Endoplasm 349
Food vacuoles 349
Contractile vacuole 350
Nuclear structure 350
Macronucleus 350
Micronucleus 351
Motor organs and neuromotor apparatus 351
Structure of cirri 352
Structure of membranelles 353
Structure of neuromotor apparatus 354
Function of neuromotor organs 359
Evidence of neural function 362
Chemical reactions 362
Morphological relationships 362
Behavior of organs at binary fission 367
Division of micronucleus 367
Division of macronucleus 368
Formation of new cirri 372
Formation of new peristome 373
Formation of new neuromotor apparatus 375

PAGE
Discussion 378
Fibrillar system in other ciliates 378
Neuromotor apparatus of flagellates 381
Homology of neuromotor apparatus in ciliates and flagellates 383
Summary 386
Literature cited 388
Explanation of plates 392

INTRODUCTION

In the year 1830 Ehrenberg gave the generic name *Euploea* to a group of hypotrichous ciliates, but since that name was already used for a group of butterflies he changed the name in 1831 to *Euplotes,* the name in use today. The same year, 1831, he gave the name *Euplotes patella* to one of the species in the genus. O. F. Müller had described this species as *Trichoda* in 1773 but in 1786 he changed it to *Kerona patella.* Later Bory (1824) called the organism *Coccudina keromina* et clausa. In the later works by Stein (1859) and Kent (1881) the generic name remains that given by Ehrenberg (1831).

The genus *Euplotes* is distinguished from the other three genera of the family Euplotidae by the presence of four marginal cirri which are entirely isolated from one another; while in *Styloplotes,* the only other genus having marginal cirri, they are arranged in two fascicles.

Besides *Euplotes patella,* the subject of this investigation, there have been described for the genus *Euplotes* five distinct species. All conform in a general way in shape of body, position of cirri and membranelles, and shape and position of nuclei as given below for *E. patella.*

Euplotes harpa Stein, the largest member of the group, has a long oval body with broad rounded anterior end. The convex dorsal surface is marked by eight longitudinal dorsal ribs. The ventral surface bears ten cirri anterior to the five anal cirri, while the anterior ventral surface carries two blunt denticulations. The posterior margin bears four unbranched cirri. The animal varies in length from 148–180 microns.

Euplotes longipes C. and L. is slightly smaller than *E. harpa,* being about 138 microns in length, while the ventral surface lacks the denticulations, the whole organism presenting a smooth contour.

Euplotes charon Ehrbg. is rounded, oval, with the right side feebly but the left side strongly convex. The anterior margin of the anterior

ventral surface is feebly denticulated. Cirri similar to the above species. Length, 78–96 microns.

Euplotes worcesteri Griffin. Body oval, anterior end rounded, posterior end bluntly pointed; dorsal surface much curved and usually characterized by eight rows of sensory bristles; ventral surface flattened, cytostome broad, containing forty-five to seventy membranelles while the pharynx contains twenty to thirty membranelles. Ten cirri anterior to the five anal cirri and from two to five marginal cirri. Length, 72–93 microns.

Euplotes vannus O. F. M. Closely resembles *E. worcesteri* in general structure. Usually the pharynx of *E. vannus* is shorter than that of *E. worcesteri.* The most important difference is that the posterior end of the macronucleus of *E. vannus* is recurved on itself and slightly enlarged.

Euplotes patella has an elliptical cuirass, somewhat truncated anteriorly with a projecting lip extending anteriorly from the cytostomal field. The dorsal side is convex, while the ventral side is concave, markedly so in the anterior part. A series of membranelles extends along the left side of the wide triangular cytostome and into the pharynx posteriorly, while anteriorly it is continued around the anterior end dorsal to the lip, to the right anterior corner of the cytostomal field. The right anterior ventral field bears nine styliform cirri, six of which according to Kent (1881) are termed frontal cirri, while the other three are the abdominal or ventral cirri. Five heavy anal cirri extend backward over the posterior margin of the body from the posterior ends of five parallel ventral grooves which begin near the middle of the body to the right of the cytostome and extend back to within twenty to twenty-five microns of the posterior end of the body. There are four caudal cirri, the two to the right being fimbricated (pl. 14, fig. 4).

The dorsal surface is marked by eleven parallel equidistant rows of granules arranged in rosettes (pl. 14, fig. 7). The macronucleus is roughly C-shaped with the open side of the C to the right (*mac.,* fig. A). The micronucleus is a small spherical body lying in an indentation on the anterior left side of the macronucleus (*mic.,* fig. A). The single contractile vacuole lies just anterior to the anal cirri (*c. v.,* fig. A).

While *Euplotes* is of widespread occurrence, little literature is found which indicates an intensive study of the animals belonging to the genus. As has been mentioned Ehrenberg (1838) gave a brief

description of the genus. Stein (1859) gave several pages to a consideration of the systematic position of the genus and described a few of the different species. Likewise Kent (1881) gave a mere synoptic account of the genus and its species. Maupas (1883) mentions seeing some fibers extending anteriorly from the anal cirri in an unnamed species of *Euplotes*. In later works (1886–1889) he considers the process of conjugation in *Euplotes patella*. Schuberg (1899) gave a short account of the process of division of this species. Wallengren (1901) contributes a rather full account of the formation and resorption of cirri in dividing individuals of *E. harpa* and also considers the origin of the new cytostome, while Prowazek (1903) describes the same species and gives special reference to a system of fibers which he finds in connection with the cirri. Griffin (1910) in two papers describes a new species, *E. worcesteri,* in which he gives a rather detailed description of certain parts including a fibrillar system in connection with the cirri, and of the division process. Other than the above mentioned works little seems to have been written about this group of highly specialized ciliates.

In this study of *Euplotes patella* it is the purpose to give a general description of the anatomy of the animal, and a detailed description of the system of fibers in connection with the cirri and membranelles. This system will be described as the neuromotor apparatus and an attempt will be made to show in what way it may be considered as having the function of a primitive nervous system. A description will also be given of the division process, with special consideration of the nuclear phenomena and the formation of the new neuromotor apparatus in each of the daughter organisms. An attempt will also be made to show that the neuromotor apparatus of flagellates is homologous with that structure found in ciliates.

Acknowledgments

This work was started in the winter of 1915 under the direction of Dr. Olive Swezy, to whom I wish to express my sincere thanks for her aid and encouragement in beginning this work. Especially do I wish to express my gratitude to Professor C. A. Kofoid for his many helpful criticisms and suggestions during the last year of the work.

TECHNIQUE

Culture

Since *Euplotes* can be found in almost any pool of standing water, it is not a very difficult matter to culture the animals in the laboratory. *Euplotes patella,* the organism which is the subject of this investigation, was kept in an old aquarium in the laboratory for over a year and seemed to thrive without the supplying of any food. However, these animals suddenly decreased in number, apparently due to the presence of great numbers of *Paramoecium bursaria,* until they finally disappeared altogether.

It was then found necessary to find some means of culturing *Euplotes.* Several culture media were tried with varying degrees of success. A weak solution of beef extract failed to give any satisfactory results. Hay infusions such as are used for obtaining *Paramoecia* for class work, seemed to be excellent for a while, as in these cultures *Euplotes* associated with *Stylonychia* were found in abundance. The ciliates in such cultures died after a week or more, probably because the infusion was too strong and became too sour.

The medium most used was a 0.25 to 0.50 per cent solution of Horlick's Malted Milk. In these cultures the animals have been kept for several weeks by adding water to overcome the loss by evaporation and occasionally a small amount of the milk. Such a medium seems best suited to supply the necessary bacteria, small flagellates and ciliates, which constitute the food of *Euplotes.* Fairly good results were also obtained by boiling dried mushrooms and diluting the infusion to a low percentage.

Small beakers of 250 cubic centimeters capacity were used as containers for the cultures, and in these the *Euplotes* associated with *Stylonychia* and *Paramoecium* often formed a light gray line on the glass just beneath the surface of the water. In case a scum of mold formed over the medium, *Euplotes* could always be found on the under side of the scum. By taking a drop of water from near the top of the culture the specimens could usually be collected in sufficient numbers for study.

Methods of Preparation

For stained preparations the cover-glass method was largely employed. If *Euplotes* was sufficiently numerous, drops of water could be taken directly from the cultures and put on the cover glasses which

had been treated with a thin coating of albumen fixative. If the animals were not numerous enough for this procedure they were centrifuged at a low speed to concentrate them. The upper part of the liquid in the tube was poured off and the few remaining drops, containing many of the animals, were put on the cover glasses as described above. The cover glasses were allowed to stand until only a thin film of the liquid remained, and then dropped film down on the killing fluid. After a little practice the right degree of dryness can be ascertained and the animals killed with little, if any, distortion.

Several killing agents were employed, depending somewhat on the stain which was to follow. If Mallory's connective-tissue stain was to be used, Zenker's or a picro-mercuric solution made up as follows was used:

Mercuric bichloride	2 gms.
Picric acid	1 gm.
Alcohol 95%	110 cc.
Ether	20 cc.
Acetic acid	20 cc.
Formol 40%	50 cc.

The latter killing agent seemed to give the best results. If haematoxylin or haematin was to be used, either Carnoy's, Schaudinn's, or the picro-mercuric solution was used with varying results. All of the killing agents except Carnoy's were used hot. The cover glasses to which the animals were attached were allowed to remain in the killing fluid for from three to five minutes, then dehydrated in the usual manner.

The same processes of staining were employed as were used by Sharp (1913) for staining *Diplodinium*. The length of time of staining with the modification of Mallory's connective-tissue stain was altered somewhat, for it was found necessary to stain longer in the acid fuchsin and less time in the anilin blue-oxalic acid-orange G solution. This stain was found suitable for both sections and *in toto* preparations. Sometimes instead of the anilin blue-orange G-oxalic acid mixture, a weak solution of Licht grün in 95 per cent alcohol was used with fairly good results. If this method is used a very few seconds should be allowed for the Licht grün, as it takes out the red very rapidly. Balsam was always used as a mounting medium. Some slides stained with the above dyes have been kept for three to four months with very little fading, but experience has proved that the stain is not permanent.

If haematoxylin or its oxidation product, haematin, was to be used, the best results were obtained by killing the animals in hot Schaudinn's sublimate-alcohol solution. Dobell's alcoholic haematin proved to be the best stain, although alcoholic iron-alum haematoxylin was quite satisfactory. These two stains were best for studying nuclear phenomena and were also very good for parts of the neuromotor apparatus, but, due to the necessity of destaining to a considerable extent in order to make the preparations usable, some of the finer fibers were completely destained and rendered indistinguishable.

If the animals were to be sectioned they were killed and dehydrated in centrifuge tubes. From xylol they were transferred into gelatine capsules of about three grains capacity containing paraffine. The method followed was that employed by Metcalf (1908) for *Opalina*. The capsules containing paraffine were held in a rack and set in a warming oven hot enough to melt the paraffine. As the paraffine melted the organisms settled to the bottom of the capsule. When cooled the gelatine could be easily soaked off and the tip of the paraffine cylinder containing the organisms cut off and put on top of another capsule of paraffine. This process was repeated until all of the xylol was removed. The animals were then imbedded in paraffine in a Lefevre watch glass. If the animals are tinged with a little eosin or erythrosin it is much easier to handle them with only a small loss.

The sections, five to seven microns thick, were treated with either haematoxylin or Mallory's connective-tissue stain. Specimens killed in the picro-mercuric solution gave the best results when treated with the latter dye.

Intravitam staining was tried but no very satisfactory results were obtained. Neutral red was the best dye tried and its value lay in its property of staining certain external ectoplasmic structures, especially the rows of granules on the dorsal side.

Silver nitrate and gold chloride were used in an attempt to demonstrate the finer fibrillar endings, but failed to give any good results.

Some animals were studied in the living condition under a cover glass. Others were killed by holding the slide with a drop of water containing them over a bottle of osmic acid or chloroform. If this was done for a very short time the animals were killed, but not distorted. Such preparations were good for a study of external features and were the only means by which the cirri could be studied in their normal condition, for when immersed in killing fluids the cirri break up into their component cilia.

STRUCTURE

External Features

Euplotes patella is, in general shape, oval with the anterior end slightly truncated. In a study of many hundreds of individuals, it has been seen that the sides are normally nearly parallel, but occasionally a culture will develop for a few days in which animals are found with wide lateral winglike outgrowths, so that at the widest part the animal is almost as wide as long. No reason can be ascribed for this phenomenon, since all of the cultures were kept under as nearly the same conditions of food, temperature, concentration, etc., as possible. The average length of *E. patella* is one hundred forty-five microns while its width is about ninety microns. The average size of individuals will vary in different cultures from animals recently divided, which are about two-thirds the average size, to animals fifteen to twenty microns in excess of the average length.

When viewed from the dorsal side, *Euplotes patella* appears almost bilaterally symmetrical, but a ventral view shows that the arrangement of the cirri and membranelles and position of the cytostome make the animal very asymmetrical (pl. 14, fig. 4).

The ventral side of *E. patella* is concave, rather strongly so anteriorly, but flattening out posteriorly. The dorsal side is strongly convex in the middle part, but flattens out toward the edges where the dorsal and ventral surfaces meet at an acute angle forming a sharp edge. The dorsal surface is marked by eleven rows of rosettes of granules (pl. 14, fig. 7). Griffin (1910) describes the rosette arrangement of granules in *E. worcesteri* and claims that at the center of the groups there are sensory bristles. Such sensory structures have never been figured for *Euplotes patella* and I have been unable to see them either on living or stained specimens.

As described above the ventral side of *Euplotes patella* is characterized by the presence of cirri and membranelles arranged in a characteristic and constant manner (pl. 14, fig. 4). These styliform cirri, the minute structure of which will be described later, fall into four groups. The six frontal cirri are grouped roughly into two rows of three each. These rows run from the right anterior corner of the cytostome to the right edge of the animal. Slightly posterior to these are three scattered ventral cirri. About two-thirds of the distance from the anterior end are five large heavy anal cirri, which extend

from the posterior ends of five longitudinal grooves over the posterior margin of the body. Along the posterior margin of the body are four small marginal cirri. The marginal cirrus to the right is always fimbricated, as is usually the one next to it.

The five furrows in which the anal cirri lie are formed by slight indentations of the pellicle along the line of the furrow and also a slight uprising of the pellicle between the furrows. These ridges are just far enough apart to permit of the insertion of the bases of the cirri. Such a close arrangement permits the anal cirri to move in only one plane, that parallel to the median plane of the body. Of the six ridges bounding the five furrows, if we number from right to left, the first, fourth, and sixth are almost twice as long as the other three, and extend from the cirri toward the anterior right corner of the cytostome for fifty to sixty microns. All stained specimens show a distinct granulation of the posterior ten to fifteen microns of the ectoplasm of the ridges. The granules of these areas are much smaller than those in the other parts of the ectoplasm and when stained give the posterior parts of the ridges a clouded appearance. Such a granulation near the bases of the cirri indicates that a possible physiological relationship exists betwen the cirri and adjacent ectoplasm.

Swezy (1916) pointed out that the parabasal body of certain simple flagellates, such as *Prowazekia lacertae,* begins as a finely granular chromidial body lying near the basal granule or blepharoplast of the flagella. The function of the parabasal body is interpreted as a kinetic reservoir or a body of reserve kinetic material. Usually this parabasal body is connected to the blepharoplast by a rhizoplast. While in *Euplotes patella* no definite threadlike connection has been found to exist between the granular portions of the ridges and the cirri between them, it seems probable that a relationship exists between them comparable to that between the parabasal body and the blepharoplast of flagellates. If this be true the granules are to be considered as indicative of reserve material which by oxidation liberates energy necessary for the vigorous movements of the cirri. While not so prominent, it is noticeable that around the bases of all of the cirri on the animal there is an area about one micron wide which retains the haematoxylin dyes to a greater degree than the main body of the cytoplasm.

At the anterior end of the animal is a crescent-shaped lip about four microns wide at its middle point. In his discussion of *Euplotes patella,* Stein (1859) describes the blunt anterior end of the animal as terminating in a three-cornered lip. In no case have I seen this lip

other than rounded along its entire anterior edge. It extends across the anterior of the animal the width of the cytostomal field and in its development it is seen that it is produced by the forward growth of the dorsal wall of the cytostome. At each end of the lip the lateral edges of the cytostome are continued forward and join the anterior edge of the lip (*l.*, fig. A). In examining the lip in either dorsal or ventral view it is seen that it contains many small vacuoles and a structure in the form of a peculiar lattice work, which will be described later as a tactile sense organ. When viewed in longitudinal section the lip is seen to be wedge shaped, the heavy cuticle of the dorsal and ventral sides joining at the margin in an acute angle in such a way as to give the lip great rigidity. In a study of the living organism its has not been possible to note any movement of this lip. Such a lack of flexibility gives no indication that the lip functions either as a locomotor organ or as a structure concerned in food getting. On the other hand its position at the anterior end and the lattice work structure which it contains, point to the fact that the lip may serve as a tactile sense organ, probably in conjunction with the series of membranelles which lie dorso-posteriorly to it.

In the anterior half of the animal is the cytostomal field, which occupies about one-fourth of the whole ventral surface (*cyt.*, fig. A). This field is approximately triangular and is formed as a deep depression of the ventral side. On the left the cytostomal field is bounded by the series of cytostomal membranelles, while on the right it is abruptly joined by a cavity which deepens dorsally and extends under the right ventral field for a distance of about fifteen microns or one-sixth the width of the body at its widest part. Anteriorly the roof of the cytostome is continuous with the projecting anterior lip. Posteriorly the cytostome narrows and leads into the ciliated pharynx, which curves rather sharply to the right and leads by a narrow tube into the endoplasm near the median line slightly posterior to the middle point of the body. By a twist of the series of membranelles the posterior left half of the cytostome is ciliated. The twist so turns the membranelles that the cilia point toward the cavity of the cytosome, instead of at right angles to the ventral surface as they do anteriorly. Posteriorly these membranelles extend into the pharynx, forming the cilia on the left side of the pharynx. Similar cilia are also found on the right hand surface of the pharynx, thus making the anterior portion of the pharynx completely ciliated. A study of the living animal shows that the cilia of the membranelles beat in such

a way that the organisms used for food are carried into the funnel-shaped pharynx and then forced into the endoplasm by the pharyngeal cilia. Often while watching *Euplotes* feeding, small ciliates have been observed struggling violently at the anterior end of the pharynx evidently striving to swim away from the cilia which were forcing them into the gullet. If the victims were large enough they often escaped, but small ciliates and flagellates were usually swept into the gullet and on into the endoplasm.

In the paragraph above, reference was made to a cavity which is abruptly joined to the cytostome. This will be named the cytostomal recess (*cyt. r.*, fig. A). It extends from the pharynx diagonally forward almost to the right anterior edge of the animal. Its shape is difficult to describe but an idea of its form may be gotten from figure A. Posteriorly this cavity lies open for nearly its whole width but anteriorly it extends under the right ventral field for as much as fifteen microns or about half of its width. At its anterior end it is bent to the right and extends under the dorsal wall of the cytostomal field. Being so directly connected with the cytostome it seemed at first that such a recess or diverticulum must be an organ concerned in feeding. However, after a careful study of this in both living animals and prepared specimens, I am unable to see any evidence which would support such a conclusion. Throughout its whole extent it is lacking in cilia, and in no case has it been seen to contain food or any other substance. As to its true function there seems to be little evidence favoring a definite conclusion. However, the following is offered as a suggestion of its possible use. If we look at the ventral surface of the animal, it is seen that a greater part of the cytoplasm lies to the left of the median longitudinal axis. This hollowing out of the body on the left would leave the right half of the body relatively heavier than the left. If now we study the diverticulum of the cytostome in its relation to the median longitudinal axis, we see that the greater part of the cavity lies to the right of the line. Such a location tends to put the center of the mass, in so far as it concerns the right and left halves nearer the median plane, thus bringing the animal more nearly to a bilateral balance of substance.

It is difficult to see how such a prominent structure as the diverticulum described above has escaped the observation of such investigators as Ehrenberg, Stein and Kent, for it can be seen in both living and prepared specimens. The fact that it never contains food and underlies a dense area of the body may account for the oversight.

As indicated above the cytostome is bounded on the left by a series of membranelles (*cyt. mem.*, fig. A). These extend forward from the pharynx to the anterior end of the animal, then around dorsal to the anterior lip to its right hand end. In shape the whole series of membranelles reminds one of the lapel and collar of a coat. For about half of the distance along the cytostome these rows of membranelles lie flat with the surface of the animal, but from about the middle of the series posteriorly the whole series twists until the membranelles are at almost right angles to the original position. In the region of the pharynx the membranelles become shorter and in its lower part they become reduced almost to the ciliated surface of the pharynx. In the anterior region the membranelles make another twist. This twist is very much like that which the lapel makes in going around the collar of the coat, and the membranelles are arranged at an angle with the dorsal side of the lip (pl. 14, fig. 7). The minute structure of the membranelles, their method of functioning and their relation to the neuromotor apparatus will be considered in detail in later paragraphs.

The pellicle (*cu.*, pl. 14, fig. 5) is a rather heavy rigid structure and appears as a distinct line covering the animal completely, thus keeping the shape of the body constant. With Mallory's stain the pellicle colors blue and in sections shows a distinct line exhibiting little differentiation in structure.

Internal Features

Ectoplasm

The ectoplasm (*ect.*, pl. 14, fig. 5) on the dorsal side of the animal is distinctly set off from the endoplasm. It is about one micron thick and is characterized by the presence of rather large granules, which when viewed in sections form a layer just beneath the pellicle. With Mallory's stain the ectoplasm on the dorsal side takes a bluish tint. Laterally the ectoplasm thins out until ventrally it is scarcely to be distinguished from the pellicle, except in regions immediately around the bases of the cirri. The ectoplasm gives rise to the cirri, membranelles, basal granules and fibers in connection with them, as will be shown in a study of the formation of new organelles. Besides these structures the ectoplasm of the dorsal side contains the eleven rows of rosettes of granules mentioned above. Each rosette is composed of from eight to ten granules. In regularly fixed and stained specimens

the granules do not show but in their places are vacuole-like structures, the granules apparently being dissolved out by the action of the killing fluids. The rosette arrangement of the granules was best shown in specimens stained with neutral red, killed by osmic acid fumes and studied in the unpreserved condition. Posteriorly the rows of granules extend to the margin of the body but anteriorly they end about ten to fifteen microns from the anterior membranelles. There is no evidence that these rosettes center around the bases of sensory bristles in *Euplotes patella* as Griffin (1910) indicated for *E. worcesteri.*

ENDOPLASM

The endoplasm (*end.*, pl. 14, fig. 5) occupies the central portion of the animal and lies just beneath the ectoplasm, but ventrally it is separated from the pellicle by only an extremely thin layer of the ectoplasm. The endoplasm is alveolar in structure and contains large granules, but these are not so numerous as in the ectoplasm. With Mallory's stain the central part of the cell stains pink. In this endoplasm are embedded the nuclei, food vacuoles and undigested food. It seems that the fibers from the cirri are also in this layer, but although this is the case it is undoubtedly true that they have arisen in the ectoplasm and have sunk into the lower layer.

FOOD VACUOLES

The food of *Euplotes* consists of bacteria, small flagellates, ciliates and diatoms, which are wafted into the pharynx by the constant action of the membranelles. Under what might be called normal feeding conditions, the ingested food lies enclosed within the area surrounded by the macronucleus and most of it lies in the space to the right of the cytostome and anterior to the anal cirri. At times when food is very abundant, *Euplotes* feeds voraciously and as a result the whole body becomes gorged with engulfed organisms. At such times the area in which the food vacuoles are normally located becomes greatly enlarged and extends forward as far as the motorium and laterally and posteriorly as far as the narrowing endoplasm permits. Under these conditions the structure of *Euplotes* is very difficult to study as the ingested food stains heavily and obscures the true body structures.

Several attempts have been made to determine the path of the food vacuoles, but neither congo red, as used by Metalnikow (1912), nor

any other of the *intravitim* stains gave satisfactory results. However, by studying animals which had become quiet under the cover glass, it has been determined that under normal feeding conditions there is a definite cyclosis of the cytoplasm in the area anterior to the anal cirri and to the right of the cytostome. This movement of the cytoplasm is in an anti-clockwise direction and may carry the food forward almost to the region of the motorium. There seems to be no evidence that the food of *Euplotes* follows the curve of the macronucleus as Greenwood (1894) has described for *Carchesium.* Powdered carmine was also put in the medium but from the very few cases in which any of it had been ingested by the *Euplotes,* it would seem that *Euplotes patella* exercises some choice in food. This is in accord with Griffin (1910) who found that *E. worcesteri* also did not ingest powdered carmine. No definite attempt has been made to determine the process of digestion in *E. patella,* but it would seem from the use of *intravitam* stains to determine the path of the food vacuoles that it would be more difficult to determine the digestive processes in the *Hypotricha* than it is in forms like *Paramoecium* and *Carchesium.*

CONTRACTILE VACUOLE

There is but one contractile vacuole. At the time of its greatest distention it is from twenty-five to thirty microns in diameter and lies anterior to the two outer anal cirri and within two or three microns of the right hand edge of the body. Its period of pulsation is relatively slow. In normal animals which are at rest the interval is seventy to seventy-five seconds, while in animals slowed down by the use of nicotine the vacuoles may pulsate only once in three to four minutes.

NUCLEAR STRUCTURE

Macronucleus.—As in the case with most ciliates, *Euplotes patella* is binucleate with large macronucleus and small micronucleus. The macronucleus is rodlike and bent in the shape of a C with the two ends on the right side of the body (*mac.,* fig. A). The macronucleus lies in the endoplasm and there is no indication that it is surrounded by ectoplasm in a manner described for *Diplodinium* by Sharp (1913). Due to its large size it is by far the most conspicuous structure in the organism. Its length is about two hundred and thirty microns, and its width, eight microns. It lies about midway dorsoventrally and with

the exception of a curve over the pharynx is almost in one frontal plane. In its finer structure the macronucleus is composed of approximately twenty-three thousand granules on a fine linin reticulum. When well stained with haematoxylin the granules, which range in size from one-fourth to one-half micron in diameter, are very distinct, well separated from one another and almost spherical. This granular condition is well brought out when stained with iron-alum haematoxylin, but in specimens stained with Mallory's stain the granules are not so distinctly separated and the whole nucleus appears cloudy and rather opaque. At the time of division a very interesting change takes place in the macronucleus, which will be described later.

Micronucleus.—The micronucleus is a small spherical body from two to three microns in diameter, lying on the anterior left hand side of the animal in an indentation in the macronucleus (*mic.*, fig. A). In specimens well stained with haematoxylin, the micronucleus appears as an almost homogeneous black body. When stained with Mallory's stain it takes the acid fuchsin quite readily and becomes a bright orange red, while the macronucleus takes only the orange color. At the time of division it migrates from its position occupied during the vegetative stage to the left of the macronucleus and there undergoes mitosis. Usually surrounding the micronucleus is an area almost devoid of granules, probably indicating an area of rapid oxidation. This is quite conspicuous at the time of division (pl. 15, fig. 15).

MOTOR ORGANS AND THE NEUROMOTOR APPARATUS

The term neuromotor apparatus was first used by Sharp (1913) in his account of *Diplodinium ecaudatum* to designate a central mass or motorium and fibers connecting it with the motor parts of the animal. To this structure he attributed a neuromotor function, due to the fact that it seemed likely that it had to do with coördinating the movements of the membranelles and operculum and with them formed a single integrated mechanism.

The neuromotor apparatus of *Euplotes patella* consists of five distinct parts, namely (1) a motorium or center of motor influences, to use the nomenclature employed by Sharp (1913), from which the fibers pass to the motor organs and sensory lip; (2) five heavy longitudinal strands connecting the anal cirri with the inner end of the motorium; (3) a fiber connecting the inner ends of the cytostomal membranelles with the outer end of the motorium; (4) a lattice-work sensory structure of the anterior lip; (5) a system of fibers, dissociated

from the above mentioned parts of the neuromotor apparatus, radiating from the nine cirri on the right ventral field and the four posterior marginal cirri.

In the following description the term neuromotor apparatus will be used in the same sense as it was used by Sharp (1913) in his account of *Diplodinium ecaudatum,* that is as a primitive nervous system over which sensory and motor impulses may pass, for coördinating the movements of the motor parts of the animal. It may be that in such forms as the Protozoa we have a condition too primitive to allow of attributing a purely nervous function to this system, and that in the evolution of the ciliates the functions of conductivity and contractility have not become entirely separated. However, in the following discussion it is our purpose to show that in *Euplotes patella* there is a system which is a primitive nervous system structurally united with the motor organs, and evidence will be brought forth to support such a contention. Nevertheless it must be understood that in considering this as a primitive nervous system we are considering it as a system in which the sensory and motor functions are not entirely separated, and that, with the exception of the structure in the anterior lip, all fibers and granules are probably endowed with the function of transmitting both sensory and motor impulses.

Structure of Cirri.—Before taking up a description of this neuromotor apparatus it is necessary to devote some space to a description of the minute structure of the motor parts of the organism. These motor organs are of two kinds, the cirri and membranelles, structures quite different in appearance but essentially alike in the structure and functioning of their elemental parts.

Little, if anything can be added to the descriptions already given of the structure of cirri as Maier (1903) has fully taken up the structure of these organs in ciliates in general and has brought together the principal facts concerning these organelles. Griffin (1910) has discussed the cirri of one species of *Euplotes.* The cirri of *E. patella* conform to the general descriptions given, but do not agree in at least one point with that for *E. worcesteri* (Griffin, 1910). This will be taken up in a discussion of the basal granules of the cirri.

The cirri of *Euplotes* may be divided into three groups according to their size. The largest cirri are the five anal cirri which extend from the ends of the five longitudinal grooves posteriorly over the margin of the body. These cirri lash back and forth in one plane. The next smaller in size are the nine cirri anterior to the anal cirri. These lash

in a spiral manner distinctly different from the back-and-forth movements of the anal cirri. The smallest cirri are the four marginal cirri, which have a movement similar to the nine cirri described in the preceding sentence. All of these cirri of the living *Euplotes* are styliform and exhibit a delicate longitudinal striation. By the action of the killing agents or by any change in density of the medium the cirri are broken up into hundreds of component cilia (pl. 14, fig. 3). Such phenomena at once show that cirri are made up of a group of cilia bound together by a thin protoplasmic membrane, very much as the hairs of a wet camel's hair brush are bound together by the film of the liquid. By a change in the medium the binding substance is broken down or dissolved and the cirri become as a dry brush with the hairs spread apart.

In a microscopic examination of the cirri it is seen that their component parts are imbedded in the ectoplasm just beneath the pellicle, for at the base of each cirrus is a dense granular plate the granules of which are the basal granules of the component cilia. Griffin (1910) claimed that the basal granules of each cirrus of *E. worcesteri* were arranged in several parallel rows indicating that in the evolution of the Hypotricha the cirri had arisen from several rows of cilia. This linear arrangement of the basal granules of the cirri I have been unable to find in *E. patella*, but rather have found that the granules are arranged in an irregular fashion in the dense, almost opaque, basal plate such as Maupas (1883) described for an unnamed species of *Euplotes* in which he saw the longitudinal fibers in connection with the anal cirri. When stained with Mallory's stain the granules of this plate color red with the acid fuchsin the same as the fibers and motorium of the neuromotor apparatus, indicating a relation at least of a chemical sort between the two structures. Connecting with each basal granule is the central contractile axis of one of the component cilia of the cirrus. These granules are imbedded in the dense plate which acts as a firm support or means of attachment for the cirrus. This is in agreement with Maier (1903), who considers the basal plate as the means of support for the cirrus, but it is to be remembered that in *Euplotes patella* the function of support is to be attributed only to the dense opaque protoplasmic plate in which the basal granules are imbedded, and that the basal granules themselves are given an entirely different function, which will be fully discussed in a later paragraph.

Structure of Membranelles.—The membranelles while of a very different shape, upon careful examination are seen to have a structure

very similar to that of the cirri. The minute structure of membranelles has been fully described by Maier (1903) while Griffin (1910) described them for *Euplotes worcesteri* and as far as I have been able to determine those on *Euplotes patella* do not vary to any noticeable extent from the descriptions already given for membranelles in other ciliates. Each membranelle is composed of two parallel rows of fused cilia which, like the component cilia of the cirri, are separated by the action of the killing fluids. However, it is, as Griffin (1910) suggested, very difficult to determine whether or not the cilia in the living animals are bound together by a protoplasmic film. The basal granules of each membranelle are arranged in two parallel rows just beneath the surface of a furrow formed between two granular ridges of ectoplasm. Such ridges are very distinct when seen in section (pl. 14, fig. 2) and their granular structure is very prominent when viewed from the ventral side. Such a granular structure probably has the same significance as that discussed in connection with the six longitudinal ridges associated with the anal cirri, namely a reserve supply of material which upon oxidation furnishes energy necessary for the continuous rapid movements of the membranelles. The granules of these ridges are not to be confused with the basal granules of the membranelles. The latter granules are definitely arranged in parallel rows and are distinctly smaller than the granules of the ridges which are irregularly arranged and are similar to the ectoplasmic granules distributed over the whole body. When stained with acid fuchsin the basal granules of the membranelles become bright red, as do those in the basal body of the cirri, indicating a similarity in composition and also in function, as will be pointed out later. Joining the inner ends of all of these rows of granules is a granular fiber which continues around the anterior end of the cytostome and joins the outer end of the motorium. A fuller description of this fiber will be given later in connection with the neuromotor apparatus. This system of membranelles, which is unified by the connecting fiber, waves in such a way that a current of water is set up in the cytostome and the heavy food is carried into the pharynx and thence on into the endoplasm.

Structure of the Neuromotor Apparatus.—We turn now to a consideration of the neuromotor apparatus, a structure to which is attributed the function of coördinating the movements of the above described motor organs. The first part of this to be described is a bilobed body lying in the right anterior part of the organism, to which certain fibers which will be described later are joined. This structure

will be called the *motorium,* a term employed by Sharp (1913) in his paper on *Diplodinium ecaudatum* to indicate a "common center of motor influences," and it is in this sense that the term will be used in this paper.

The motorium as indicated above is slightly narrower at its middle part than at the two ends, is about eight microns long and lies in a frontal plane and obliquely to the median longitudinal axis of the body (*mot.,* fig. A). It was first seen as a dark body in the animals stained with iron-alum haematin, lying close to the right anterior corner of the triangular cytostome. In specimens which are well destained this body is seen to be composed of very fine granules closely grouped together, but if too dark it has the appearance of an almost homogeneous body. When stained with Mallory's stain the motorium becomes bright red from the acid fuchsin and lacks the granular appearance characteristic of specimens colored with haematin. Plate 14, figure 5 (*mot.*) shows that this motor mass does not have a smooth contour, but rather that it has ragged edges with processes extending out into the surrounding ectoplasm.

Joining to the left end of the motorium are the five large main longitudinal fibers from the five anal cirri (*a. c. f.,* fig. A). These fibers converge to such an extent that they appear to join the motorium as a single strand. By careful examination under high magnification, these five fibers are seen to be composed of fine granules arranged so closely together that the fibers have the appearance of granular cords. This granular condition is evident only in specimens stained with haematin. After such treatment the fibers are very conspicuous, darkly stained cords lying close under the pellicle of the ventral side. When stained with Mallory's connective-tissue stain these fibers take the acid fuchsin and become bright red.

A careful study has been made to determine how these fibers join the anal cirri, but so far the results have not been entirely satisfactory. In a few cases the appearance has suggested that at the anterior edge of the cirrus the fiber begins to break up into a fan shaped structure of fine fibrils which join the basal granules of the cirrus (pl. 14, fig. 6). This point is very difficult to determine, for as was suggested in the description of the cirri, the basal plate of the cirrus is dense and opaque, and if it is sufficiently destained to become transparent enough to study, the fibers lose all of their color and become indistinguishable. Sections have failed to lend any evidence in favor of this, and the only evidence gained has been from a few well destained whole mounts.

The main longitudinal fibers were first seen and described in *Euplotes* by Maupas (1883). He briefly described them as joining the five anal cirri and extending forward, where they converge and join into a single thread which ended in the cytoplasm of the anterior end of the animal. As to their function he was unwilling to make any suggestion. Three years before this discovery by Maupas, Englemann (1880) had described a series of fibers in connection with the marginal cirri of *Stylonychia* which extended from the cirri toward the middle of the body. To these fibers Englemann gave the undoubted function of being nervous. Prowazek (1903) found fibers in *Euplotes harpa* and Griffin (1910) found them in *Euplotes worcesteri* similar to those described for *Euplotes patella*. Both of these authors ascribed to the

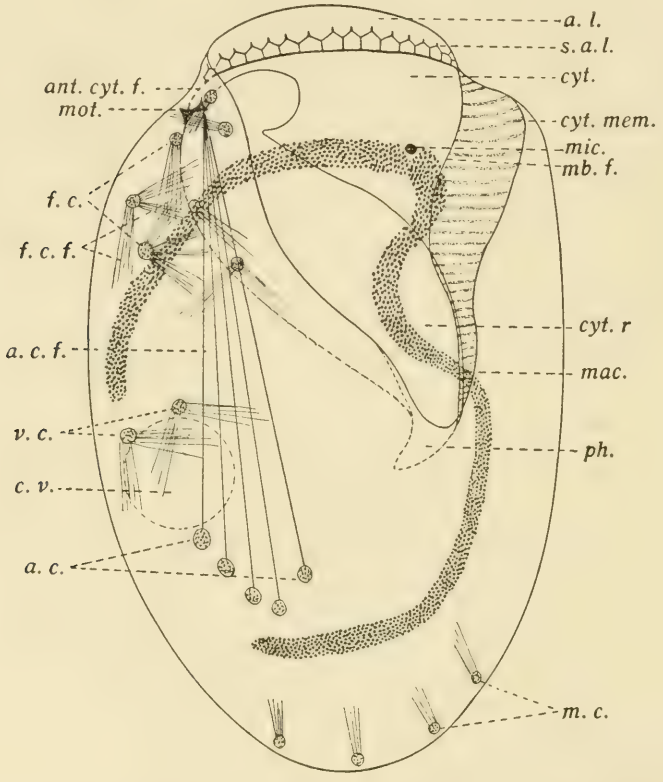

Fig. A. *Euplotes patella.* Ventral view showing principal organelles. Cirri and membranelles indicated by basal granules only. × 725. Abbreviations: *a. c.*, anal cirri; *a. c. f.*, anal cirri fibers; *a. l.*, anterior lip; *ant. cyt. f.*, anterior cytostomal fiber; *c. v.*, contractile vacuole; *cyt.*, cytostome; *cyt. mem.*, cytostomal membranelles; *cyt. r.*, cytostomal recess; *f. c.*, frontal cirri; *f. c. f.*, frontal cirri fibers; *mac.*, macronucleus; *mb. f.*, membranelle fiber; *m. c.*, marginal cirri; *mic.*, micronucleus; *mot.*, motorium; *ph.*, pharynx; *s. a. l.*, sensory structure of lip; *v. c.*, ventral cirri.

fiber the function of contractility. Maier (1903) in commenting on the fibers found in ciliates, suggests that they have a supporting function. However, none of the above mentioned investigators has described these fibers as joining to any such structure as the motorium of *Euplotes patella,* neither have they given credence to the idea that the fibers may be nervous in function.

Joining the right end of the motorium is another fiber which also connects with certain motor parts of the animal, the membranelles, thus forming an unbroken fibrillar complex between the heavy anal cirri which are chiefly used in locomotion and the membranelles of the adoral zone which function as organs of food getting, organs of locomotion and as tactile structures. This membranelle fiber (*mb. f.*, fig. A), which has the same granular structure as the motorium and fibers to the anal cirri, extends from the motorium along the base of the anterior lip around the anterior end of the cytostome where it connects with the anterior cytostomal membranelles, and the lattice-work sensory structure of the lip, along the entire left edge of the cytostome in connection with the lateral cytostomal membranelles. In the pharyngeal region this fiber is indistinct and difficult to see as it is hidden by closely massed cilia of the pharynx. When stained the membranelle fiber shows the same staining reaction as the other parts of the neuromotor apparatus, thus indicating that all parts of this structure are in some way related to one another, at least to the extent of having the same chemical composition.

In the anterior lip is another structure in connection with this associated neuromotor apparatus, which although it has not been heretofore described for any other species of *Euplotes,* is of especial interest and significance. Along the membranelle fiber in the anterior lip, at the points where the anterior cytostomal membranelles join the fiber, enlargements occur from which short rodlike projections grow out into the lip almost at right angles to the rows of basal granules of the anterior membranelle (*s. a. l.,* fig. A). Each of these processes is connected with its neighbors by bifurcating projections which meet it at an angle of about 120 degrees. These second projections meet in such a way as to form *V*s with the apices pointing anteriorly. From the apices of these *V*s, short projections extend still farther forward into the lip, forming the lattice-work structure, occupying from one-half to two-thirds of the width of the lip. Thus the lip is provided with a structure having a series of points extending well out toward its anterior edge, directly connected with the fiber of the membranelles.

When stained this structure is colored the same as the fibers and motorium with the acid fuchsin of the Mallory's stain. However, many of the specimens stained by the haematin do not show this structure so distinctly; but this is due to the fact that the lip is so thin that the stain is all removed before other parts of the organism are destained sufficiently for study. Thus it is seen that the lip contains a structure not only similar in its chemical reactions to the other parts of the neuromotor apparatus, but also in its anatomical relationships it is shown to be an integral part of the system, and a part which seems likely to furnish some very important evidence indicating the nervous function of the neuromotor apparatus, for all relations point to the conclusion that this structure lacks both motor and skeletal functions and that it functions as a tactile sense organ in connection with the anterior cytostomal membranelle.

The last part of the neuromotor apparatus to be described is the system of fibers in connection with the frontal, ventral and marginal cirri. This system of fibers will be described as a dissociated part of the neuromotor system, for in the dozens of specimens studied there has been no indication that the fibers in connection with the frontal, ventral and marginal cirri are in any way connected with the motorium or any part of the neuromotor apparatus described in the preceding paragraph.

The arrangement of the fibers of the dissociated part of the neuromotor apparatus differs greatly from that of the fibers in connection with the five anal cirri. Instead of each of the frontal, ventral and marginal cirri having a single fiber as the anal cirri, they are joined by several much finer and shorter fibers. These fibers range in number from four to six extending out in one direction from some of the cirri to two or three groups of four or six, each extending out in different directions (*f. c. f.*, fig. A). Some of these groups in connection with the frontal and ventral cirri may overlap each other, but in no case has there been any indication that the fibers from one cirrus join any other cirrus or the fibers from it. In case of the marginal cirri there is only one group of fibers connected with each cirrus and these extend anteriorly and never overlap. These fibers do not join any structure other than the cirri, but as they extend out into the cytoplasm they become finer until they are finally lost to view. Prowazek (1903) described such a system of fibers for *Euplotes harpa,* but he also pictures a system of fine fibers in connection with anal cirri in addition to the five longitudinal fibers. The latter system of fibers in

connection with the anal cirri, I have never been able to see and feel sure that such is not to be found in *Euplotes patella.* Griffin (1910) found this dissociated system of fibers in *E. worcesteri,* but pictures fewer fibers than are present in *E. patella.*

Function of Neuromotor Apparatus.—In the preceding paragraphs attention has been directed almost exclusively to a description of the anatomical relationships of the neuromotor apparatus, which has been divided into two parts, the associated or coördinating part and the dissociated part joined to certain irregularly moving cirri. In the succeeding paragraphs this neuromotor apparatus will be considered from a functional point of view and the anatomical structures will be considered in their relation to the activities of the organism.

In the above descriptions of the anatomy of the neuromotor apparatus several suggestions have been made indicating the nervous function of the system. In fact the term "neuromotor apparatus" itself predicates this meaning, namely a structure in connection with the motor parts of the organism over which neural impulses may be conveyed. With this meaning in mind it is our purpose to show how the different parts of this system function as a primitive nervous system.

The motorium which has been defined as a "common center of motor influences" lies in a position whereby it functions as a coördinating center between the constantly moving membranelles on the one hand and the heavy, vigorously lashing anal cirri on the other. Six fibers, one of which connects with the cytostomal membranelles and the sensory structure of the anterior lip and the other five heavy long fibers from the anal cirri join the bilobed motor mass, thus permitting of the coördination of the movements of locomotion with the movements of the membranelles in food getting, as well as affording a means of coördinating the movements of locomotion in response to sensations received by the anterior cytostomal membranelles and the lattice-work structure in the anterior lip, a region which first of all comes in contact with any unfavorable conditions. This function of the motorium will be better understood when we consider the function of the strands or fibers in connection with it.

By far the most conspicuous of these fibers are the five in connection with the anal cirri. These have been described in an earlier paragraph as heavy granular cords connecting the motor mass anteriorly with the large anal cirri posteriorly. In the bases of these cirri these cords break up into a fan shaped structure of fine fibrils which join to

the basal granules of the cirri. Such a relationship immediately suggests that these fibers are in some way associated with the movements of the cirri. Such an association is undoubtedly true but not in the sense that the fibers are contractile but rather that they serve as a means by which motor impulses are transmitted from the anterior coördinating center to the anal cirri, the chief organs of locomotion. There is no evidence that these fibers have the function of muscular elements, for in a study of hundreds of stained specimens I have failed to recognize any shortening or thickening of them which would indicate a contraction. It seems certain that if such a contraction did occur some specimens would show it, for the killing fluids used were such that death of the organism was undoubtedly instantaneous and so should have fixed some of the fibers in the contracted condition. A study has also been made of living animals which have been slowed down by the use of very minute quantities of a solution of nicotine. It is possible under proper conditions of light to see the fibers in animals whose cirri and membranelles are active. In no case has there been seen any evidence of a contraction of the fibers, even when the motor organs are quite active.

The criticism will probably be raised that since the fibers are granular, it would be improbable that impulses would jump from one granule to another. In answer to this it must be remembered that here we are dealing with a nervous system of a very primitive sort, merely a differentiated protoplasm. Since all protoplasm is granular to some extent and has as one of its fundamental characteristics the property of conductivity, it is perfectly logical to suppose that some of the granules have become aggregated into rows in which this fundamental characteristic of conductivity is more developed than in other parts of the surrounding protoplasm. Then, too, the granules are so close together that a careful study under high magnification is necessary to bring out the granular character of the fibers. Such granules are not lying free in space but undoubtedly are held together by a differentiated intergranular protoplasm, thus forming a complete continuous path over which impulses might pass.

Thus having established a path over which impulses may pass, it is important to see how such impulses may be transferred to the motor organs and how such motor organs may move when stimulated.

We have seen in the above descriptions that the fibers break up and come in direct contact with the basal granules of the cirri. This forms a basis for attributing to the basal granules the function of

receiving stimuli. Such impulses received cause a contraction of the central contractile axis of each component cilium of the cirrus, thus causing a lashing of the whole organ. Such an idea is very much in opposition to the view held by Maier (1903), who considers the function of the whole basal plate to be a support by which the cirrus is held firmly in the less dense ectoplasm. The fact that the granules are packed together into a dense plate might in itself be an argument that the plate serves as a support for the cirrus, but even that leaves the question of the function of the individual granules open for solution, and it seems reasonable after considering the anatomical relationship of the structure to attribute to the fibers and granules the function suggested above.

A similar function is also attributed to the single fiber connecting the motorium and membranelles. This fiber is connected to the inner ends of the rows of basal granules of the membranelles, and although I have been unable to discover a fibrous connection between the fiber and the basal granules as in the case of the anal cirri, the close juxtaposition of the granules and their surrounding protoplasm forms a continuous path for impulses which may pass over the fiber to the membranelles. Thus there is a condition not unlike that of the cirri, a granular fiber connecting the basal granules of the membranelle to motorium, the fiber to serve as a path for impulses from the motorium, while the basal granules are that part of the motor organelle especially adapted to receiving them.

Connecting with this membranelle fiber is the lattice-work structure of the anterior lip. As suggested in an earlier paragraph all evidence is lacking to suggest that this structure serves as a skeletal or muscular element. In fact its position with its many points extending out into the lip and its structural connection with the membranelles and the membranelle fiber strongly suggest a sensory function for this peculiar structure. We must undoubtedly attribute some sensory function to the anterior cytostomal membranelles, but observations show that these organs are active agents in swimming and are probably to be considered as having no greater sensory function than the membranelles along the left side of the cytostome. It is evident from watching the animals swimming about that they are very sensitive at the anterior end, and if the membranelles are considered as locomotor rather than sensory organs then the organ which is most closely associated with them is the lattice-like structure of the lip, which with its points extending well toward the anterior edge of the lip, is in position

to receive stimuli from external sources and to convey impulses to the motor organs. There is thus established a fibrillar connection between the sensory structure of the lip and the motor parts of the organism. Such a relationship strongly suggests the idea brought out in an earlier paragraph, namely, that we are dealing here with a system of such a primitive type that the motor and sensory functions are not separated but that they are both in the same fibers.

Thus it is seen that *Euplotes patella* possesses a structure well adapted for relating the organism to its environment, and to coördinate the movements of feeding and locomotion in such a way as to bring the animal under the most suitable circumstances for its existence.

Evidence of Neural Function.—The question at once arises, why attribute a nervous function to this system? Evidence favoring such a conclusion comes from a study of both living and stained specimens, so that it is not necessary to depend wholly upon one source of evidence as a basis for such ideas.

1. Chemical Reactions.—The first point favoring the idea that the neuromotor apparatus is of a truly nervous character comes from animals stained with Mallory's connective-tissue stain. In animals treated with this combination of dyes, different organs take different colors. It is characteristic in metazoan tissues treated by these colors for different tissues to stain differently, as for example nerve fibers have an affinity for acid fuchsin and are thus dyed red while nuclei stain orange red, and cytoplasm in general becomes light pink. Such a differential stain may be used to give a clue to the function of organelles in some of the more complex of the so-called unicellular organisms. At least we may assume that structures having a similar staining reaction have the same or related chemical composition and in these so-called simple organisms probably the same general function.

This is one of the reasons for basing our conclusion that the structures described as comprising a neuromotor apparatus are probably nervous in their function. All of the fibers, granules and motorium stain bright red when treated with Mallory's stain, while the other structures take other colors. The only other organ which constantly stains with acid fuchsin is the micronucleus, but in this the color is not the same as in the fibers but has more of the orange G mixed with the red.

2. Morphological relationships.—Were we to base our notion of the function of the neuromotor apparatus solely on the staining reactions our conclusions might well be subject to severe criticism. However

there are other factors which seem far more significant. Chief among these is the intimate relation between the neuromotor apparatus and the motor parts of the animal concerned in locomotion and feeding. Without exception all of the above described structures, that is the fibers, motorium and granules, are more or less closely associated and connected with every part of the animal which has to do with its locomotion or food getting, or both.

The largest cirri and those capable of the most powerful stroke are the anal cirri, and as we have seen they are connected by heavy fibers to a mass which has been termed the motorium, or as has been suggested, a coördinating center. These large cirri move in only one plane but are the chief organs of locomotion while the other cirri move in a whirling motion and are almost constantly lashing about. The fiber in connection with the cytostomal membranelles is also connected with the motorium. This likewise favors the idea that the motorium is a coördinating center and that the fibers connected with it are of nervous character, for the phenomenon of food getting must in these forms be closely associated with the phenomenon of locomotion, since the food is largely made up of free, rapid-swimming organisms and not the minute forms that serve as food for the sessile ciliates such as *Vorticella.*

In studying *Euplotes patella* that have been treated with very weak solutions of certain chemicals such as neutral red, methylene blue and especially nicotine, it has been noticed that the anal cirri and the cytostomal membranelles are the last to cease moving. The other cirri become quiet but the anal cirri and membranelles have been seen to move even after the cytoplasm has begun to break up. Such phenomena favor very strongly the idea that the motorium serves as a coördinating center between the anal cirri and cytostomal membranelles. However, other observations on living animals give even stronger evidence in favor of the neural function. It has also been noticed in specimens that have been subjected to a very weak solution of nicotine that the frontal, ventral and marginal cirri continue moving even after the animal has ceased to swim about. The membranelles also move but more slowly than in normal animals. Occasionally one or more of the anal cirri may be seen to make a feeble movement not sufficiently strong to cause the animal to move. However as the animal revives from the effects of the narcotic and begins to swim about by vigorous kicks of the anal cirri, a decided increase in the rate of movement of the membranelles may be noticed. Such an increase continues as long

as the anal cirri continue to move, but as they cease to lash back and forth and the animal comes to rest, the movements of the membranelles also slow down. No very decided change has been seen in the rate of movement of the frontal, ventral or marginal cirri. The fact that as the anal cirri move there is increased activity on the part of the membranelles, seems to be very significant, and this coupled with the fact that there is a definite anatomical connection between these motor parts, leads us to the conclusion that there is a coördination between the two structures which takes place by means of the motorium and connecting fibers.

Observations also serve as a basis for attributing to the lattice-work structure of the lip the function of being a tactile sense organ. It has been seen that animals when swimming are very sensitive at the anterior end. Their sudden reversal of movements when striking an obstacle shows that they have some means of receiving tactile stimuli. The facts that this structure in the lip is so closely connected with the organ of locomotion as well as the organs of food getting, and that it has the same chemical affinities as the other parts, show that it is a part of the neuromotor system. This structural relationship and the behavior of the organism seem to prove that this structure of the lip serves not as an organ of motility or support, but as an organ of touch for the anterior end of the body.

As shown above, the whirling irregular movements of the frontal, ventral and marginal cirri are in no way coördinated with the regular rhythmical movements of the membranelles or with the backward kick of the cirri. Such a lack of coördination may be accounted for when it is remembered that there are thirteen cirri possessing what we have called a dissociated neuromotor apparatus which is not connected with the motorium or coördinating center.

It is probable that we are dealing here with a portion of the neuromotor system, which in the evolution of the organism is not yet connected with the other central coördinating parts. Here the cytoplasm has become differentiated to a certain point—far enough for the fine fibrils to have formed, but not far enough for the fibrils to have become condensed into a single strand like the ones connected with the anal cirri. Such a system of dissociated fibers might serve to receive and convey to the cirri general impulses such as are undoubtedly carried over the whole cytoplasm of the organism. Such impulses stimulate the cirri to move but not in such a coördinated manner as is characteristic of the other motor parts of the animal.

As was suggested in an early paragraph of the description of the neuromotor apparatus, we are probably dealing with a nervous system of a very primitive sort, a nervous system formed merely by a differentiation of protoplasm having the fundamental characteristic of conductivity. Since contractility is just as fundamental a property of protoplasm as is conductivity it may be that even in this differentiated portion the two are not entirely separated and that the fibers may act as muscular elements to a slight extent. However, much as we have had this idea in mind in attacking this problem, we have so far failed to find the least evidence that the intra-cytoplasmic fibers of the neuromotor apparatus as found in *Euplotes patella* in any way serve as contractile structures.

It may be said by some critics that the fibers in *Euplotes* described above as a neuromotor apparatus are comparable to the so-called myonemes of other ciliates and that their function must be that of contractility. It seems that sufficient proof has been advanced to do away with such criticism; it might be suggested here that instead of the neuromotor apparatus being comparable to the myonemes of ciliates and the movement of cilia being due to the contraction of the fibers, the myonemes may be found by further investigation to be comparable to this neuromotor system and that the movement of cilia is due to the contractility of the central axis of each cilium, while the so-called myonemes may be found to be a fiber of a coördinating neuromotor apparatus, or it may be found to have both a neural and a muscular function combined at least in some of the less complex ciliates.

The motorium in *Euplotes patella* is quite comparable with that found in *Diplodinium* and the argument advanced against its having a motor function in the latter animal seems well set forth by Dr. Sharp:

> The shape, size, position, and absence of direct connections with surrounding structures make the possibility of the motorium functioning as an organ either of contraction or of support seem highly improbable. For in order to function as an organ of contraction it would necessarily need to have as its attachments on the one hand structures which are fixed, and on the other structures which are movable, or it would need to be located between two structures both of which were to be moved. This, however, is not the case, for the motorium seems to have no direct connections with the fixed structures of the body . . . . (1913, p. 86).

The motorium (*mot.*, pl. 14, fig. 5) of *Euplotes* lies free in the cytoplasm with no evident connection between it and the pellicle, which is the only firm structure of the body. We can add nothing to the argument quoted from Sharp for *Diplodinium* to increase its force as

an argument for *Euplotes patella*. It seems quite as adequate for the latter as it did for the organism for which it was written.

Neither can we see any way in which this neuromotor apparatus may serve as a supporting structure. Its shape is not such that it would be advantageous as a skeletal organelle; neither is it large enough to serve as a firm attachment for contractile fibers. The pellicle, which is quite thick, can serve as a means of support. In fact the pellicle is of such a character that the shape of the body is kept constant and permits of little or no bending.

The only part of the whole neuromotor apparatus which might in any way serve as a skeletal organ is the lattice-work structure in the anterior lip. However, it seems that sufficient evidence has been advanced to show that it serves as a sensory organelle, whose function it is to receive sensations caused by stimuli at the anterior end. Then too, the lip is so thin that no skeletal structure is needed aside from the rigid pellicle on both dorsal and ventral sides.

In his description of the neuromotor apparatus of *Diplodinium ecaudatum* Sharp (1913) describes a number of fibers in connection with the neuromotor apparatus which extend into the cytoplasm and end near the micronucleus. From the work on the soil amoeba, *Naegleria gruberi* (Wilson, 1916), and certain of the flagellates, such as *Polymastix* (Swezy, 1916), *Trichomonas* (Kofoid and Swezy, 1915). and *Giardia* (Kofoid and Christiansen, 1915), it has been shown that the motor organs are connected with the nucleus by a rhizoplast and are probably controlled by it. This relationship will be more fully discussed in later paragraphs in which a comparison of the neuromotor apparatus of flagellates and ciliates is taken up. However, this relation of the motor organs and nucleus in flagellates and the indication of such a relationship in *Diplodinium* suggests a possible structural relationship in other forms. In *Euplotes patella* there is no indication of a connection between the neuromotor apparatus and either the micronucleus or macronucleus. The motorium is on the opposite side of the animal from the micronucleus. At division the micronucleus migrates from its position during the vegetative stage to the left of the macronucleus, where it undergoes mitosis. The two halves separate, one remaining in the anterior end to become the micronucleus of the anterior daughter, while the other migrates posteriorly to become the micronucleus of the posterior daughter. While this is occurring there is no indication of any change in position of any part of the neuromotor apparatus. It would seem that if the neuromotor

apparatus were connected with the nucleus, changes should be noted in it comparable with those occurring in the nucleus. A consideration of the behavior of the neuromotor apparatus during cell division will be taken up later.

BEHAVIOR OF ORGANS AT BINARY FISSION

Division of the Micronucleus

The first indication of division in the micronucleus is its migration from its position in the indentation of the macronucleus to the left side of the macronucleus, where it enlarges (pl. 15, fig. 14) to two or three times its original size. In the resting condition and prophase it is very difficult to make out the arrangement of the chromatin in the micronucleus due to its compact condition. Occasionally there is some indication of a diffuse spireme formation. Griffin (1910) describes a spireme formation in *E. worcesteri* and in all probability such a change occurs in the nucleus of *E. patella*. After enlarging somewhat the nucleus assumes a spindle form with the chromatin broken into chromosomes which lie lengthwise on the spindle. The number of these chromatin bodies is small, and while I have not been able to make many conclusively satisfactory counts, it seems that there are six (pl. 15, fig. 15). This corresponds to the number given by Griffin for *E. worcesteri*. As transverse division is completed the daughter chromosomes become massed at the ends of the elongated spindle. The two poles move apart but remain connected for a time by a deeply staining thread. In such a condition it is almost impossible to make out any definite nuclear structure, for the whole drawn-out nucleus appears almost homogeneous and in haematoxylin preparations a dense black. Later the connected thread breaks (pl. 15, fig. 17) and all indications of it are lost. It is probably drawn up into the nucleus, for each daughter micronucleus becomes rounded and is to all appearances like the original micronucleus, but only about two-thirds the original diameter of the parent nucleus.

The process of division of the micronucleus is evidently quite rapid, for many cases of the beginning of migration can be found as well as of the daughter nuclei, but the cases of actual division are very rarely found.

The mitotic changes occurring in the micronucleus are accompanied by changes in the macronucleus. The reconstruction of this organelle will be described next.

Division of the Macronucleus

About the time that the micronucleus begins to migrate from its position in the indentation of the macronucleus, there appears at each end of the macronucleus a very conspicuous band. Each band is made up of two distinct areas: one a very heavily stained part, and joining to it on the side toward the end of the nucleus a non-staining portion, apparently almost, if not entirely free from chromatic material (pl. 15, fig. 14). As stated above the dark portion of the band stains very heavily and if overstained appears almost homogeneous. However, by careful destaining it can be shown that this area is in reality one in which the chromatin granules are very closely packed together. This part of the band was first noticed by Stein (1859) in *E. patella,* but from then on until Griffin (1910) described it for *E. worcesteri* no one seems to have noticed it. To this band Griffin (1910) gave the name "solution plane" and suggested that in this region the chromatin was in solution in the karyolymph. Immediately distal to this solution plane is another band which is called by Griffin (1910) the "reconstruction plane." This part of the nucleus takes no stain except for a few granules (pl. 15, fig. 16), the whole area appearing as though the chromatin material had been removed, leaving only the linin network of the nucleus. Taken together Griffin calls the two areas the "reconstruction band."

The two planes are sometimes about the same thickness but in the majority of cases the solution plane is thinner, being about two microns wide while the reconstruction plane is about three microns wide. The fine fibrils which run through the reconstruction plane seem to be connected to the ragged edge of the solution plane on one side and to the chromatin granules of the reorganized area on the other. The granules which are to be seen in the light area indicate that a reorganization process is going on in the compact area, and that the reformed granules pass along the fibers of the light area to the distal part of the nucleus, which is made up of the reconstructed granules. These two parts of the nucleus, the original nucleus and the two distal parts, are sometimes similar, that is the granules are about the same size and have a similar staining reaction, but in other specimens the granules in the reorganized area are larger and stain more heavily than those in the original unchanged part of the nucleus.

The two reorganization bands migrate toward each other until they meet at the middle of the nucleus. During about half of the period

of migration of the bands there is little change in the size of the nucleus (pl. 15, fig. 14). However, as the two bands approach each other the whole nucleus shortens and thickens, the granules are crowded close together and it seems that there is more or less of a coalescence of the granular elements, for many granules can be seen which are equal in size to three, or four or more of the original granules. As the bands come nearer together the nucleus becomes more contracted until the greatest period of concentration occurs at about the time that the body begins to constrict (pl. 16, fig. 18). At the period of greatest concentration the granular structure of the nucleus has become almost obliterated, and the nucleus has an almost homogeneous structure. In specimens which are very much destained the contracted nucleus is seen to be made up of large chromatin masses very much crowded together.

As the body begins to constrict the nucleus again elongates. The granules are very irregular in size and shape, and appear as though they were being pulled by considerable force, for many of the large granules are much elongated and look something like chromosomes (pl. 16, fig. 19). However, there is no evidence that chromosomes do form, for the macronucleus divides amitotically with no indication that the chromatin granules are divided in any way comparable to the division of chromosomes. As the constriction of the animal continues the macronucleus elongates and becomes narrow in the region of the constriction of the body until finally it is completely severed (pl. 16, fig. 21).

While it is impossible to distinguish the position of the two fused reorganization bands at the time of greatest contraction, it seems that their plane of fusion must be the plane of division of the macronucleus, for the nucleus divides into two approximately equal parts.

Before the nucleus has completely divided, it has begun to bend in what is to be the anterior daughter organism and also just posterior to the plane of constriction. When divided the nuclei are each shaped somewhat as an inverted letter L, with the base of the letter extending across the anterior end of the animal and the long arm along the left side (pl. 16, fig. 21). Associated with the daughter macronuclei are the daughter micronuclei, which lie near the angle of the L.

Such a contraction of the chromatin material at once reminds one of the contraction stages occurring in metazoan germ cells. The first contraction, that occurring in the reorganization bands, is a progressive contraction, and begins at the end of the nucleus and migrates toward

the middle of that organelle. A careful study has shown that the so-called solution band in *E. patella* at least is not homogeneous, but that it is granular, indicating a very compact massing of the granules at one region and a subsequent passing of them out over the light staining reconstruction plane to the more diffusely arranged reorganized parts of the macronucleus. This contraction reminds one of the synizesis which was designated by McClung (1905) as occurring in orthopteran germ cells. However, we are not willing to admit that this contraction in *Euplotes* is an artifact (Whiting 1917, and Hance, 1917), as some of McClung's students have recently suggested for orthopteran cells, since it appears after use of all the killing fluids and stains employed by us.

The second contraction is that of the nucleus as a whole, which follows the first contraction and immediately precedes the constriction of the organism. This was described in an earlier paragraph and its significance will be discussed later.

It seems very doubtful that the term solution plane, as used by Griffin (1910) is in any way the proper term to use in denoting the condensed band appearing across the nucleus. As was pointed out in the paragraph above, this band is not homogeneous but granular. True, a change does take place and the chromatin grains coming out of this band may not be the same as those going into it, but observational evidence fails to show that the chromatin is in solution, but rather to show that the granules in that region have become crowded into a compact mass and that they pass over the reorganization plane not as precipitated granules, but as granules which have undergone some sort of physical and possibly chemical reorganization.

For these macronuclear phenomena we would propose the terms "contraction phase" to indicate the contraction of the nucleus as a whole, while in place of the terms reconstruction bands as given by Griffin (1910) we would suggest "reorganization bands," indicating a purely physical reorganization of the nuclear material through a contraction of the chromatin, rather than a solution of the chromatin in the karyolymph.

What reason can be assigned to such a behavior of the macronucleus? This is a difficult question to answer satisfactorily. Such a phenomenon is not peculiar to *Euplotes* but has been observed in other forms. Calkins (1911) describes a distinct reorganization of the macronucleus at the time of division in *Uronychia.* Here the changes are not quite similar to those occurring in *Euplotes,* but the reorgan-

ization of the nucleus is characterized by the coalescence of its several parts into one body which divides amitotically. Anigstein (1913) finds a nuclear change in *Strombidium testaceum* quite comparable to that in *Euplotes*. In each arm of the macronucleus a diagonal uncolored area appeared. This begins at the middle and works out toward the end, leaving the granules in the central part much larger than those in the undisturbed portion. The author was unable to make any suggestion as to the reason for such changes. As will be discussed later in connection with the formation of the cirri, the whole body seems to undergo a reorganization which apparently is of two phases: (1) a period of dedifferentiation characterized by the contraction of the macronucleus and absorption of the old cirri; and (2) a period of formation of the new macronucleus from one-half of the original macronucleus and the growth of new organs. In the introductory paragraph of his well known paper, Wallengren (1901) expresses this idea concisely, "Bei diesen Infusorien (Hypotricha) ist somit auch eine mehr oder weniger durchgreifende Renovirung der Körper beider Sprösslinge mit dem Theilungsvorgang verbunden." Calkins (1911) in a study of the regeneration of *Uronychia*, operated on before, during, and after division, found that the power of regeneration was greatest in the early phases of division. He explains this power "on the supposition that substances are formed in the nucleus and transferred to the cytoplasm, where they or the products of their activity accumulate until a condition analogous to saturation is reached." After division is completed and the new organelles are formed, these substances are used up and consequently the power of regeneration is lessened or lost altogether.

In the light of recent investigations the results of which have been brought together by Child (1915) in his book entitled *Senescence and Rejuvenescence*, we perhaps are able to put a somewhat different interpretation on such phenomena as take place in ciliates at the time of division. Child has shown that in a study of *Paramoecium* and *Stentor* that the earliest indications of binary fission appear not in the nucleus but in the cytoplasm and that these are followed by the nuclear changes. Such changes are characterized by the formation of new cytostomes and contractile vacuoles. He has also proved with dividing infusorians as well as with some of the flatworms, that at the time of division the protoplasm loses its high degree of differentiation and assumes a dedifferentiated or relatively simple condition. Similarly with insects at the time of metamorphosis, some of the larval

organs are known to go through a disintegration and the whole body to undergo a reorganization. By subjecting the dividing ciliates, flatworms, and segmenting eggs to potassium cyanide, Child proved that at the time of division when the cells were in the dedifferentiated condition a period of rejuvenescence followed, which was a time when the rate of metabolism was high. This he claims was an indication that the tissue was physiologically young and most susceptible to external stimuli.

This idea of rejuvenescence following the period of dedifferentiation probably serves as a basis for explaining why regeneration in *Uronychia* occurs more readily in dividing individuals. The cytoplasm is young and so responds readily to the call to complete the organisms. Likewise, perhaps, we can explain the nuclear changes occurring in *Euplotes.* Basing our assumption on the evidence brought forth by Child for different forms, we assume that at the time of division the cytoplasm of *Euplotes* has undergone certain dedifferentiating changes and has assumed a physiological young condition with a greatly increased metabolism. Such being the case it would be necessary for the macronucleus, the important vegetative organelle of the animal, to undergo corresponding changes of dedifferentiation and rejuvenescence in order to properly control the rejuvenated cytoplasm. These changes in the nucleus are undoubtedly of two kinds, physical and chemical. The physical changes we are able to witness, while the only evidence of the chemical changes is the difference in staining reactions, which with the stains we have used tell us practically nothing of the nature of this very important phase of the whole reorganization process.

Formation of New Cirri

A detailed description of the way in which new cirri form is scarcely necessary, since Griffin (1910) gives a very accurate account of the whole process as found in *E. worcesteri,* and the description as given for that species will well serve for the process as it occurs in *E. patella:* the only noticeable point of difference being that *E. patella* has only nine ventral cirri anterior to the anal cirri, while the other species has ten.

In *Euplotes patella,* as in other species of *Euplotes,* the new cirri arise in two groups and all of the old cirri degenerate. Each group begins as five depressions in the pellicle, one group immediately anterior to the anal cirri and the other group still farther forward.

At first these depressions are quite small, but they elongate until four of them in each group are seen to have the beginnings of three new cirri in each groove. The depression to the extreme right has only two cirri forming in it. The posterior cirrus in each row becomes the anal cirrus. As the animal elongates preparatory to constriction the depressions in which the cirri form elongate, and the nine anterior cirri of each group are pulled forward to form the frontal and ventral cirri. Those which are to be on the posterior animal are carried forward nearly to the five anal cirri of the anterior daughter organism and are scattered out into something near their ultimate positions. Since in this description we are much more concerned with the anal cirri than with the others, on account of our study of the neuromotor apparatus, we shall not dwell longer on their formation since Griffin has given such an adequate account.

By the time the five new anal cirri are fairly well formed, the old anal cirri have begun to be absorbed. The innermost cirrus is the first to disappear and it is soon followed by its nearest neighbor and so on in succession, the two toward the right persisting until division is well-nigh completed. Likewise the old frontal, ventral and marginal cirri are absorbed and their functions assumed by the new ones.

At first it was thought that the new depressions form in the furrows of the original anal cirri, but this is not the case. Since the original furrows are rather wide, some of the new furrows do not form in them. For instance, the new furrow farthest to the right is quite a distance to the right of the old furrow on that side. The furrows of the anterior set, especially, bear no relation to the old furrows, but are much farther apart than the old furrows in that region. Such positions of the new cirri do not lend any evidence to the proposition that new cirri form from old cirri. Other evidence against such an idea will be suggested in a consideration of the formation of the new fibers connecting with the cirri.

Formation of New Peristome

The formation of the new peristome in *Euplotes patella* is practically the same as that described for *E. worcesteri* by Griffin (1910). At about the time that the micronucleus migrates from its resting position to the left side of the macronucleus a slight depression occurs just back and to the left of the old peristome (pl. 15, fig. 10). This depression at first seems to be only in the pellicle, but it deepens and

widens into the ectosarc. As it deepens the bottom of the depression enlarges, making a sack the bottom of which is the original depression. Very early in the enlargement of the sack a heavy staining line is seen on the left side of it, which bends to the left and forms a small almost triangular field surrounded by the dark line. Very early in the development of the new cytostome there appears in the triangular field a series of lines lying almost at right angles to the base of the triangle (pl. 15, fig. 11). These lines are the rows of the basal granules of the new membranelles. As the depression deepens it also elongates in the direction of the long axis of the body. With it the triangular field also elongates and more membranelles form. This series of membranelles increases in length until it reaches about as far forward as the micronucleus (pl. 15, fig. 12). Posteriorly it elongates some distance back past the old peristome. In some cases it seems that the anterior end of the new peristome extends under the membranelles of the old peristome, but it never comes in contact with them.

As the body of the animal elongates preparatory to constriction, the new peristome is pulled back past the posterior end of the old peristome (pl. 16, fig. 18). Both ends of the new mouth become bent, the anterior end elongating rapidly to follow the constriction which is cutting the organism in two (pl. 16, figs. 20–21). Thus by the time division of the body is complete, the new cytostome with its series of membranelles has nearly assumed its ultimate position and shape.

The opening to the peristome increases in size and by growth and curvature of the new peristome a triangular adoral field is formed. The right side of the opening to the new peristome becomes the inner edge of the anterior ventral field. The series of membranelles grows over toward the right, keeping almost in contact with the left edge of the constriction. The anterior end of the triangular adoral field grows out in a rather rounded protuberance, forming the anterior lip which comes to lie ventral to the anterior series of membranelles.

When the two daughter cells separate, the right end of the membranelles is at the point of constriction and almost if not quite in contact with the fibers from the anal cirri of the posterior daughter cell. That this may be quite significant will be brought out in later discussion. The posterior end of the newly formed peristome extends backward and dips down into the endoplasm forming the pharynx.

The above is a rather brief description of the formation of the new peristome, but it will be seen that the process differs little from that described by Griffin (1910) for *E. worcesteri*. The principal point of

difference is that *E. patelli* has the prominent anterior lip, while in *E. worcesteri* this is absent and the right anterior field overhangs the adoral field much more. Such a depression is heartily in accord with the idea that the new peristome forms quite independently of the old peristome. This is more significant than it may appear at first sight. In our consideration of the formation of the new neuromotor apparatus it will be pointed out that this structure forms from the ectoplasm. It was also seen that new cirri are of ectoplasmic origin. In the description of the formation of the new cytostome a heavy staining line was mentioned as appearing very soon after the depression has sunken into the ectoplasm. This is undoubtedly differentiated out of the ectoplasm. Very soon rows of granules form, which are the basal granules of the new membranelles. These, too, are ectoplasmic in their origin, for they form on the under side of the pellicle. It is thus quite evident that the new membranelles form not from the old membranelles but independently in an area quite set off from the old cytostome. This origin of the new cytostome in *E. patella* bears out the contention of Griffin (1910) that the new cytostome develops quite independently of the old cytostome and that the whole structure—lip, cytostomal field, membranelles and basal granules—develops *de novo* and are ectoplasmic in their origin.

Formation of the Neuromotor Apparatus

We now come to a description of the formation of the neuromotor apparatus at the time of binary fission, which must be given in its relation to the other parts which have just been described. Very soon after the formation of the new anal cirri for both daughter organisms, there can be seen extending forward from them fine but distinct fibrils having the same staining reactions as the old fibrils (pl. 16, figs. 18–21). In appearance they are the same, except that in the early stages they are much finer and nearer the surface than the old fibers. Usually the fibers from the anal cirri of the anterior daughter are to be seen before those from the posterior cirri. Early in their development the fibers are quite distinct near the cirri, but as they extend anteriorly toward the motorium they become much finer and are lost to view in the cytoplasm. This leads one to the conclusion that the fibers are ectoplasmic, rather than endoplasmic as Griffin (1910) stated, and that they grow out from the new cirri toward the anterior end. The old fibers persist until the new fibers are formed, but with

the absorption of the old cirri their fibers disappear, apparently being absorbed in the cytoplasm by dedifferentiation.

At first it was thought that the new fibers formed by a splitting of the old fibers, but it was soon seen that such an hypothesis was of no value for the following reasons: first, the new cirri do not form along the lines of the old fibers. Those for the anterior cell are as far apart as the old cirri of the posterior daughter, while the original fibers in that part of the cell were much converged. Thus the cirri are not formed in a position where it would be possible for the new fibers to form by a splitting of the old ones. In the second place, the new fibers are usually nearer the pellicle than the old ones. As the cirri become heavier they sink deeper into the ectoplasm and carry the fibers with them. Then, too, no indication has been seen that would lead to the conclusion that any splitting of the old fibers occurs. Such evidence leads one to no other conclusion than that the fibers arise independently apart from the original fibers.

As was stated in connection with the formation of the new cytostome, there is a line to which the granules of the new membranelles connect. This inner line becomes the fiber extending along the left and anterior sides of the cytostomal field. This fiber, too, is then differentiated out of the ectoplasm in the same way as the other fibers of the associated neuromotor apparatus. By the growth of the series of membranelles it is carried forward and around the anterior end of the cytostomal field. Such growth brings it around in the position of the new motorium. From this fiber the sensory apparatus of the anterior lip grows out, but its growth has not been seen before division is complete.

The formation of the new motorium is the most difficult to make out. The original motorium remains in the anterior animal and the new fibers grow forward to connect with it. Due to the unusually large amounts of food in *Euplotes* at the time of division, few cases have been clearly seen in which the formation of the new motorium could be studied. Plate 16, figure 21, shows a case in which in the anterior end of the posterior daughter *Euplotes* a number of bright red granules could be distinctly seen. These lay at the point where the fibers are drawn together when the animals were cut apart. As to the origin of these granules which are the new motorium there are three possibilities: One is that they form where the fibers are drawn together by the constriction of the animal; another is that the membranelles come in contact with the fibers from the anal cirri and the fibers form at the

point of contact; a third possibility exists that they may differentiate independently out of the ectoplasm like the other parts of the system and then become connected with the fibers from the cirri and membranelles. The second possibility seems to be the most plausible. The fibers are always connected with the motorium in a definite way, those from the anal cirri converging to the inner end of the motorium while that one from the membranelles always connects to the right hand end. This could be easily explained by supposing that the fiber from the membranelles continued its growth toward the right and carried the granules on beyond the point of convergence of the five fibers from the anal cirri. The fact that the fiber is continued on beyond the point where the membranelles and sensory structures develop is evidence in favor of such a conclusion, even though the process of growth has not been clearly seen, due to the physiological condition of the animal. By an increase in the number of granules the motorium attains its normal size.

It has thus been shown that the whole neuromotor apparatus and the motor organs are derived from the ectoplasm and that their first indication is a pitting in of the outer surface of the pellicle. This is quite significant in as much as it is always the ectoplasm that initiates the separation of two cells. We may carry our analogy still a step further and suggest the great similarity between the division process in these organisms, and the same process in all Metazoa which reproduce asexually in which the ectoderm is the most active in the separation of the organisms. Such a parallel indicates that the ectoderm is important in this regard and probably more closely related to the process of reproduction, especially asexual reproduction, than we usually think. Such an analagy may be still more closely confirmed if we say that the multinuclear condition as found in ciliates denotes a multicellular condition rather than that of unicellularity, thus making the ciliates more nearly like Metazoa with their cell divisions. Thus the analogy between ectoderm and ectoplasm is more apparent. At least we see from this study of *Euplotes* that the ectoplasm is of much more importance than a mere covering.

DISCUSSION

Fibrillar Systems in Other Ciliates

The term, neuromotor apparatus, is of late origin, being first used by Sharp (1913) to denote a new structure found in *Diplodinium ecaudatum.* This structure, from its staining reaction and its anatomical relationships, was interpreted as having a neuromotor function. Few structures like this have been described for ciliates. Engelmann (1880) was the first to call special attention to such distinct fibers. These he described in *Stylonychia,* extending from the peripheral cirri into the central part of the animal. These have been seen many times by me on slides made for a study of *Euplotes,* for *Stylonychia* and *Euplotes* are usually associated in the same cultures. To these fibers Englemann (1880) assigned a nervous function, but later writers such as Bütschli (1889), Schuberg (1891), and Maier (1903) discredited such ideas and instead gave the fibers the functions either of support or possible contraction. Maupas (1883) found fibers in *Euplotes* similar to those described in this paper as previously noted. Prowazek (1903) has described such fibers for *E. harpa* and Griffin (1910) has found them in *E. worcesteri.* In these two species of *Euplotes* the function of contractility is ascribed to the fibers. Neresheimer (1903), working on *Stentor coeruleus,* found certain fibers to which he ascribed a nervous function. However, he found two sets of fibers in the "zwischen streifen." One of these he called the myophane, indicating that it was contractile, the other he called the neurophane, indicating that it was of a nervous character. There seem certain reasons why such names are not appropriate: The first of these is that in staining with Mallory's stain those structures which have an affinity for the acid fuchsin are supposed to have a nervous function. In the work of Neresheimer structures taking this stain are called myophanes. Secondly and more significant, is the fact that the so-called myophanes are indicated as being more closely related to the basal granules of the cilia than are his neurophanes. In the later works, such as that of Sharp (1913) on *Diplodinium* and this work on *Euplotes,* the cilia, or at least the component cilia of the membranelles and cirri are shown to be associated with fibers to which are ascribed a nervous function, not to the absolute exclusion of the idea that they may possibly be contractile in their function, but with the idea that they are more nervous than muscular.

In this light it seems quite àpropos to suggest that probably a reversal of the terms would better indicate the function of these two sets of fibers in *Stentor*. Should we ascribe a nervous function to the myophanes as described by Neresheimer (1903) we might account for the rhythmical contraction of the cilia, for the contraction takes place not in the fiber but in the cilium itself, due to the central contractile axis. Likewise a contractile function might be ascribed to the so-called neurophanes. It would seem that were these contractile the contraction of the body would be explained fully as well, even though they do not extend the full length of the body. To say that they are of nervous character would seem rather improbable, since a nervous structure would naturally be expected to be found near the part of the body which is the most exposed to stimuli and most sensitive. These neurophanes are not closely associated with the large anterior cilia which in all probability are more sensitive than the small cilia covering the body. The other set of fibers is closely associated with these cilia and the undulating membrane, and it seems from their relation to these that it is far more likely that they have the nervous character rather than the so-called neurophanes.

This brings us to the more recent work of Sharp (1913). He undoubtedly found a structure in *Diplodinium ecaudatum* which is comparable to that found in *Euplotes patella* and described as the neuromotor apparatus. There is no reason to think that this structure, composed of fibers going to the motor parts and the so-called motorium to which the fibers are joined, has a function other than that given to it by Sharp, namely a neuromotor apparatus with special emphasis on the neural function. However, it seems in the light of the above criticism of the work on *Stentor* that Sharp made a wrong comparison, for instead of this system of fibers in *Diplodinium* being "probably comparable to the simple fibers of *Stentor* figured by Neresheimer (1903) and regarded by him as 'neurophanes,' " they are comparable to the myophanes. Especially is this true if we can base such a comparison on staining reactions and anatomical relationship, for the fibers of *Diplodinium* are in connection with the basal parts of the cilia composing the membranelles, a condition very similar to that of the myophanes of *Stentor*.

Besides the above mentioned examples there are many indications that a structure may be found in many ciliates comparable to the neuromotor apparatus of *Euplotes patella* and *Diplodinium*. In looking over the literature several instances are shown in which there

is a fibrillar system closely associated with the motor organs and of structures which may upon further investigation be found to be nervous in their function.

Probably the one paper which shows the most suggestive examples is that by Maier (1903). The first striking example given by him is that of *Prorodon teres* Ehrbg. In this ciliate there are to be found lying close to the rows of basal granules of the cilia, fibers which are called the myonemes. These connect with the fibrillar system around the mouth. Such a condition recalls to one's mind immediately the condition found in *Diplodinium,* where there is a definite circumesophageal nerve-fiber ring. A somewhat similar condition is suggested in *Chilodon* and *Coleps,* which also have definite fibrillar systems surrounding their gullets. In *Stentor niger* Ehrbg. there is shown by Maier (1903) in his plate 4, figure 10*b*, definite end fibers and basal fibers in connection with the basal granules of the undulating membrane. Also a system of myonemes is shown close to the basal granules of the surface cilia. Similar structures are shown in plate 4, figures 11 *a-b,* of *Spirostomum ambiguum* Ehrbg. The fibers of *Stylonychia* have been described in connection with the observations of Englemann (1880). Maier (1903) also shows in *Carchesium polypinum* Ehrbg. that the fibers are not in connection with the basal granules but are very definite in the part of the bell near the attachment of the stalk.

A later work is that by Thon (1904) on *Didinium nasutum* O.F.M. In this organism there is quite a complex system of fibrillae running from another system of fibrillae around the mouth region to a point under the nucleus. At this point of convergence Thon was unable to distinguish any definite body to which the fibers were joined, for in all well fed individuals the cytoplasm appeared undifferentiated. However, the fact that here are fibers in connection with the basal granules and the fibrillar apparatus around the mouth and that these fibers tend to converge to a point near the nucleus is very suggestive of a structure similar to that which has been described as a neuromotor apparatus in *Euplotes* and *Diplodinium.*

The most recent work which is suggestive of a neuromotor apparatus is that of Braune (1913). He describes a system of fibrillae in *Ophryoscolex purkyngei,* a form not distantly related to *Diplodinium.* This system, he suggests, is composed of elastic supporting fibers, but he seems to overlook the fact that the animal has an exoskeleton and other structures which might serve as a skeleton and that, as Sharp

(1913) has shown, such a function could scarcely be attributed to the system of fibers. Then, too, their distribution in relation to the motile parts of the organisms is like that in *Diplodinium,* so that it would seem that a function of conduction and possibly contraction to a slight degree, is more nearly correct, as Sharp (1913) has indicated for *Diplodinium.*

Of all the above works mentioned, with the exception of the works on *Stylonychia* (Englemann, 1880), *Stentor* (Neresheimer, 1903) and *Diplodinium* (Sharp, 1913), none contains any suggestion of nervous structures, but all seem to consider the function of the fibrillar systems to be that of contraction or support.

The above brief comment on forms in which there are fibrillar structures suggestive of neuromotor apparatuses shows us that in all of the orders of the Ciliata there are to be found in connection with the basal granules of the cilia, cirri, membranelles and undulating membranes, distinct fibers which lead out into the cytoplasm of the cell. In some cases, as *Didinium, Euplotes harpa,* and *Euplotes worcesteri,* there is a distinct indication that the fibers may converge to a definite body such as is found in *Euplotes patella* and *Diplodinium ecaudatum.* In others, as *Stylonychia,* the fibers have been shown to run out into the endoplasm and fade out. Whether this is the case or not further investigation alone can demonstrate. At least such suggestions open up a field which is as yet little developed, and which will perhaps yield the richest fruits when the work on prepared slides is supplemented by work of an experimental character.

The Neuromotor Apparatus of Flagellates

The term neuromotor apparatus has been used also to denote a structure found in flagellates, and there has been worked out within the last few years a series which indicates a progressive evolution of this structure in this class of Protozoa. It will be necessary to go over this series briefly in order to see whether or not the term neuromotor apparatus as applied in the study of certain flagellates indicates a structure homologous to that described in ciliates.

The first form in the series is *Naegleria gruberi,* a soil amoeba which under certain conditions temporarily changes from its rhizopod form to that of a biflagellate organism. In her work on this animal Dr. Wilson (1916) discovered a very primitive neuromotor apparatus. Flagella arises from a blepharoplast which grows out from the central

karyosome. This blepharoplast is connected with the karyosome by a rhizoplast. Exflagellation is accomplished by a shortening of the flagella and a retreating of the blepharoplast into the karyosome. Such a neuromotor apparatus consists only of a basal granule or blepharoplast from which arise two flagella, and a rhizoplast connecting the blepharoplast to the nucleus. Such a condition is very primitive and temporary.

Next on the list is *Prowazekia* or *Prowazekella,* as Alexeieff (1912) calls it, which in some phases resembles *Naegleria* in having no parabasal body, but in its development a chromidial-like cloud is extruded from the nucleus and forms a parabasal body connected to the blepharoplast by a rhizoplast. At the time of mitosis the parabasal body is depleted of its chromatin but reappears again during the vegetative phase of the daughter organism.

In *Polymastix,* Swezy (1916) found four flagella arising from a blepharoplast which is connected to the nucleus by a rhizoplast and sometimes to a parabasal body.

In *Trichomonas,* as described by Kofoid and Swezy (1915), the neuromotor apparatus consists of three equal anterior flagella, one posteriorly directed flagellum which forms an undulating membrane and one axostyle or intracellular flagellum. The parabasal body is a long chromatin-like rod running along the inner edge of the undulating membrane. Rhizoplasts connect the blepharoplast to the nucleus and parabasal body. The axostyle, which serves as the chief motor organ when the animal is on a surface, contains numerous chromatin granules which fluctuate in number, arrangement and size, denoting a kinetic function of the neuromotor apparatus.

Giardia, as described by Kofoid and Christiansen (1915), is a binucleate organism equivalent to two trichomonad flagellates, each containing one nucleus, and one blepharoplast at the end of the single axostyle, three flagella and either a half or a whole axostyle, depending on the stage of growth of the organism. Around the mouth is a heavy ring. The two blepharoplasts are connected by cross commissures and are anterior. The lateral flagella cross at a median point, the anterior chiasma. The blepharoplasts are joined to the nuclei by rhizoplasts and also to the parabasal body lying posterior along the axostyle.

Thus in *Giardia* there is a structural basis for coördinating the two individuals. In reality each half of the organism has its own complete neuromotor apparatus, but due to the crossing of the fibers at

the commissure between the blepharoplasts and in the anterior chiasma, two organisms are thus integrated into one individual.

The above series of five examples gives an idea of the progressive development of the neuromotor apparatus from the simple *Naegleria* type to the more complex coördinating type of *Giardia.* In all, the common characters are flagella, blepharoplast, and nucleus. Such a structural relationship shows that the nucleus is the kinetic center of all activity. As was shown by Kofoid and McCulloch (1916) and Swezy (1916), the parabasal body is not a kinetonucleus but rather it is a kinetic reservoir, the volume of which fluctuates according to the physiological condition of the animal.

Homology of Neuromotor Apparatus in Ciliates and Flagellates

We shall now return to a consideration of how far we can homologize the neuromotor apparatus of ciliates with that found in flagellates. An homology is rather difficult to establish, but there are at least two facts which seem to indicate that the structures are similar to a certain extent.

The first is the homology of the blepharoplast with the motorium, based upon the relation of these structures to the motor organs of their respective organisms. As we have seen in the brief review of the neuromotor apparatus of flagellates, the blepharoplast is the central structure with which the flagellar apparatus is connected. All motor organs, both intra-cellular and extra-cellular center upon this one body. Such a condition is not only true for the uninucleated forms but is equally true for the multinucleate forms such as *Stephanonympha* and *Calonympha* as described by Janicki (1915). In these forms there are many blepharoplasts, each connected with certain flagella and intra-cytoplasmic fibers, comparable to rudimentary axostyles. In all these the blepharoplasts are each connected with a nucleus.

In ciliates we have a system of structures which at first sight appear to be quite unlike any structures found in flagellates, but between which, upon careful analysis, there is a probable similarity. This similarity exists between the blepharoplast of the flagellate and the motorium as described for *Diplodinium ecaudatum* and *Euplotes patella.* As brought out above, the blepharoplast is the center around which the motor structures are built and as such may be taken as the coördinating organ serving to regulate the anterior and posterior

flagella, axostyle and undulating membrane in such forms as each or all of these structures may be found. With this idea of the character of the blepharoplast, it is easy to see how the motorium is similar to it for the motorium, too, is a structure to which part of the motor organs are connected. In this case we must consider the basal granules of the cilia, cirri, and membranelles as being secondary rather than primary structures. This is interesting in that structures may, in the process of evolution, develop from the fibrillar system in some such manner as the development of the ciliary apparatus of the spermatozoids of some plants, where a fiber grows out from the blepharoplast and becomes the band which breaking up forms the granules to which the cilia are attached (Webber, 1897; Ikeno, 1898). Such a conception does not permit of comparing the basal granules found in ciliates to the blepharoplast but makes them of secondary importance, leaving the similarity existing between the motorium and blepharoplast.

A second point of similarity upon which an homology may be based is the connection between the neuromotor apparatus and nucleus. In flagellates such a connection is very evident and consists of a rhizoplast joining the nucleus to the blepharoplast. In ciliates this connection has not been definitely established, but in his description of *Diplodinium ecaudatum* Sharp (1913) shows that certain fibers connecting with the neuromotor apparatus extend out into the cytoplasm and end in the vicinity of the micronucleus. Thon (1904) also described a system of fibers in *Didinium nasutum* which extended from the region of the esophagus to a point near the nucleus. In *Euplotes patella* there is no indication that a connection exists between the nucleus and neuromotor organs, but since other parts of the neuromotor apparatus so closely resemble the neuromotor apparatus of *Diplodinium* we may assume that in the evolution of *Euplotes* the connection between the neuromotor apparatus and nucleus has dropped out, and that this coördinating mechanism at the time of binary fission develops independently of the nuclear phenomena. However, such an idea cannot be completely verified until we know the entire life cycle of *Euplotes* and the development of its neuromotor apparatus at the time of sexual reproduction.

In the above discussion an attempt has been made to show that even in forms as diverse in structure as ciliates and flagellates there exist structures which are probably homologous. The motorium and blepharoplast may be considered homologous structures, both being centers around which the motor organs are developed in such a way

as to be controlled by the coördinating centers. In the probable parallel evolution of the two groups, the connection between the neuromotor apparatus and nucleus has been retained in flagellates but apparently lost in ciliates, with only an indication of such a connection in *Diplodinium ecaudatum,* while in *Euplotes patella* no trace remains to indicate that in this highly specialized free-living ciliate the neuromotor apparatus and nucleus are related structures.

As we look over the literature on Protozoa we are impressed with the change that has come about in the research done on this interesting group of animals. The early works had to do with little else than the classification and the study of external features upon which to base this classification. The works of Ehrenberg (1838), Stein (1859), and Kent (1881) are examples of this kind of work. However, with the improvement of microscopes and better methods of microscopical technique a more intensive study of the animals was begun from every point of view. The cytological phenomena, the minute anatomical structure, life history and economic importance of the Protozoa have occupied the attention of the investigator and many of the most common and earliest known organisms have become centers of great interest.

With all of this study we come to a realization that our old definition that the Protozoa are simple one-celled organisms is inadequate. A study of the soil amoeba as described by Wilson (1916) shows that even the amoeba which we are accustomed to give our classes in biology as an example of the simplest form of animal life, exhibits a complexity not yet understood, while a study of a form such as *Euplotes* or *Diplodinium* shows a complexity unrivalled by many of the Metazoa, and it seems that the more we learn about them the more complex they become.

SUMMARY

This study of *Euplotes patella* has brought out the following interesting and significant facts:

1. *Euplotes patella* is oval in form, concave ventrally, convex dorsally. The ventral surface is characterized by the presence of a large triangular cytostome, the dorsal part of which continues forward and forms the anteriorly projecting lip; a cytostomal diverticulum, nine ventral, five anal, and four marginal cirri; a series of membranelles extending along the left side of the cytostome and continuing forward around the anterior end dorsal to the anterior lip. The whole body is covered by a firm cuticle. The dorsal side is marked by eleven rows of granules arranged in rosettes.

2. A neuromotor apparatus is present in *Euplotes patella.* This structure is composed of a motorium, the probable center of coördination, to which are joined five fibers from the five anal cirri and a fiber which connects with the inner ends of the cytostomal membranelles, and a lattice-work structure in the anterior lip which connects with the fiber around the anterior end. This system has a probable nervous function, as is evidenced by its structural relations to the motile parts of the organism. The ventral and marginal cirri have a number of fine fibers radiating out from their bases. Their function is not clearly understood, but they probably represent a detached dissociated neuromotor apparatus.

Observations show that there is a coördination between the movements of the five anal cirri and the cytostomal membranelles. Vigorous movements of the cirri are accompanied by increased activity of the membranelles. Certain reactions to stimuli indicate that the anterior end is very sensitive to touch. Such coördinated movements and response to stimuli indicate that the neuromotor apparatus is a structure which functions as a coördinating mechanism, having the function of transmitting both motor and sensory impulses, over a system as yet undifferentiated into motor and sensory nerves.

3. The micronucleus undergoes mitosis and each daughter nucleus becomes the micronucleus for the daughter *Euplotes* resulting from binary fission. The macronucleus undergoes progressive reconstruction, beginning at the two ends and migrating toward the middle. The latter periods of this reconstruction are accompanied by a contraction of the whole macronucleus. This contraction is not unlike synizesis

as found in metazoan germ cells. After this contraction the macronucleus elongates and divides amitotically, half going to each of the daughter organisms.

4. At the time of division the new neuromotor apparatus is formed independently of the old one, by a differentiation of the ectoplasm. The old motorium persists as the motorium of the anterior daughter *Euplotes* and the cytosome in the anterior part remains. All cirri are formed anew and the old cirri and connecting fibers are absorbed. The new cytostome forms independently of the old cytostome.

5. The changes undergone by the organism at the time of binary fission indicate a dedifferentiation of the cytoplasm followed by a rejuvenescence and differentiation into new structures. The macronucleus, which is the controlling organ of the metabolic activities, undergoes a corresponding reorganization in order to govern properly the increased metabolism of the rejuvenated organism.

6. The structural relationships of the blepharoplast to the motor organs of flagellates and of the motorium to the motor organs of ciliates and the connection between the blepharoplast and nucleus in flagellates, and the indication of such a connection in some ciliates suggests that the neuromotor apparatus in flagellates and ciliates are homologous structures.

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EXPLANATION OF PLATES

PLATE 14

Fig. 1. Tangential section showing connection of fibers of anal cirri and motorium. Mallory's connective tissue stain. × 835.

Fig. 2. Cross-section of cytostomal membranelles. Mallory's connective tissue stain. × 1670.

Fig. 3. Cross-section through body. Alcoholic haematin stain. × 535.

Fig. 4. Ventral view of *Euplotes patella.* × 535.

Fig. 5. Diagonal cross-section through body. Mallory's connective tissue stain. × 835.

Fig. 6. Base of anal cirrus and connecting fiber. Alcoholic haematin stain. × 1670.

Fig. 7. Dorso-lateral view, *Euplotes patella.* × 535.

Fig. 8. Micronucleus in indentation of macronucleus. Alcoholic haematin stain. × 1670.

1 2 3 4 5 6 7 8

PLATE 15

Fig. 9. Right anterior portion of *Euplotes patella*. Mallory's connective tissue stain. × 835.

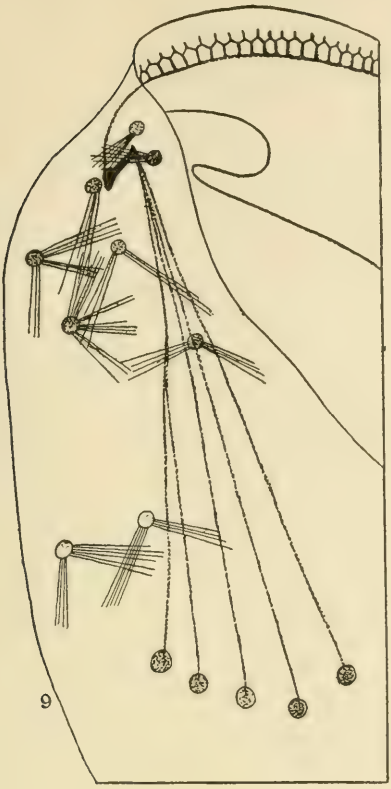
Figs. 10–13. Figures to show development of new cytostome. Alcoholic haematin stain. Figures 10, 11, and 13, × 535; figure 12, × 835.

Fig. 14. Early division stage. Alcoholic haematin stain. × 535.

Fig. 15. Mitotic figure of micronucleus. Alcoholic haematin stain. × 1670.

Fig. 16. Reorganization band of macronucleus. Alcoholic haematin stain. × 1670.

Fig. 17. Division stage showing contraction of macronucleus and division of micronucleus. Alcoholic haematin stain. × 535.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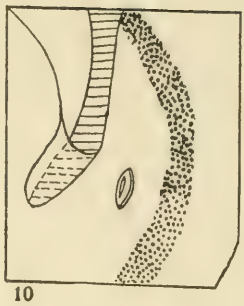
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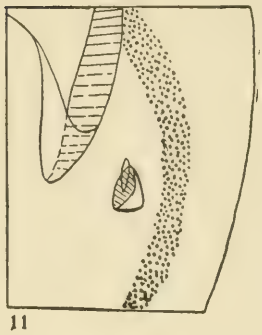
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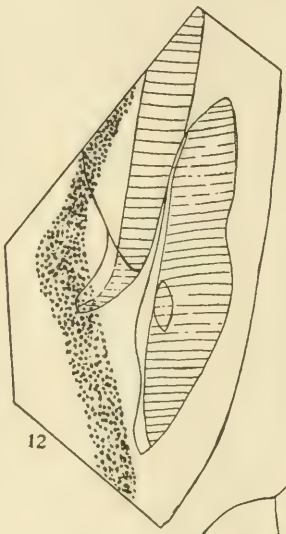
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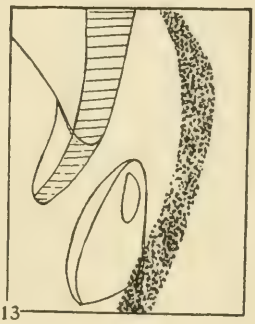
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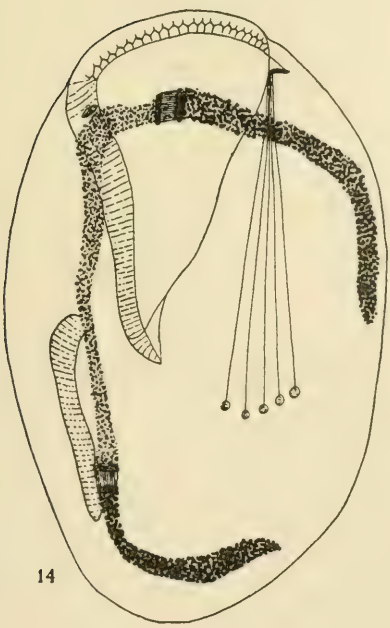

14

15

16

17

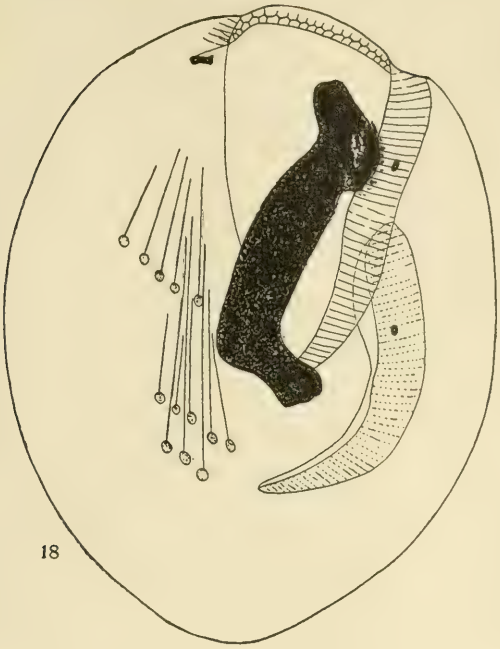
PLATE 16

Fig. 18. Division stage. Macronucleus at maximum contraction. New anal cirri fibers forming. Frontal cirri not shown. Alcoholic haematin stain. × 535.

Fig. 19. Early constriction. Mallory's connective tissue stain. × 535.

Fig. 20. Later constriction. Mallory's connective tissue stain. × 535.

Fig. 21. Division almost complete. New motorium forming in posterior daughter. Mallory's connective tissue stain. × 535.



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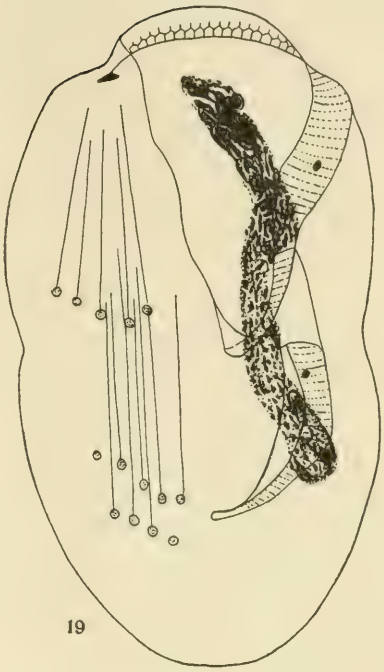

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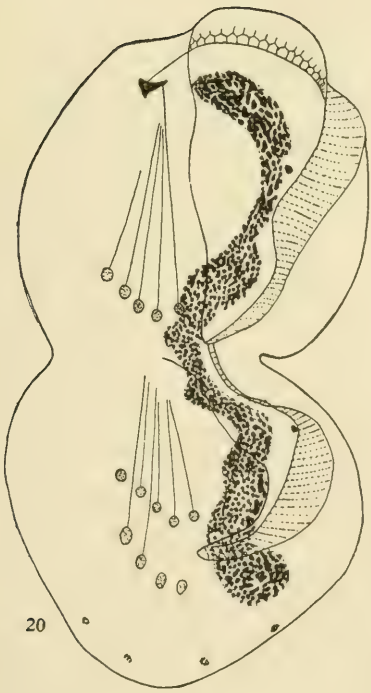

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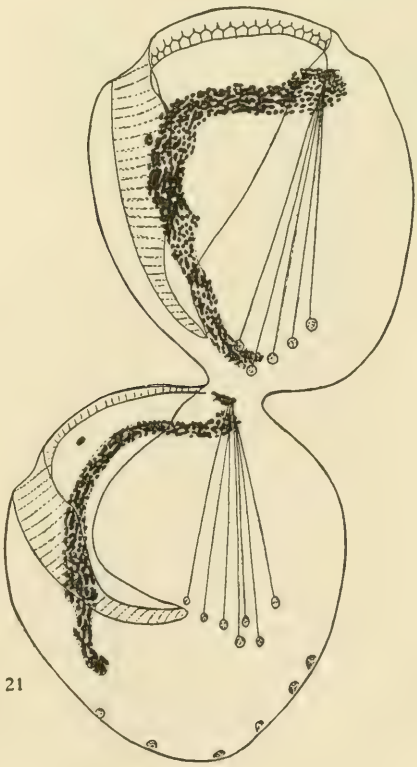

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Nos. 1 and 2 in one cover. August, 1916 ..... .10
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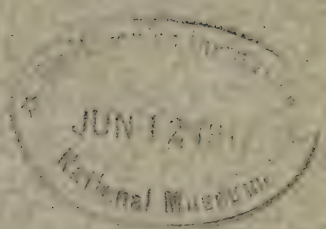
BY

A. L. BARROWS



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THE SIGNIFICANCE OF SKELETAL VARIATIONS IN THE GENUS *PERIDINIUM*

BY
A. L. BARROWS

JUN 12 1917

CONTENTS

PAGE

A. Introduction 398
Purpose and scope of this paper 398
Acknowledgments 400
Relationships and morphology of the dinoflagellates 400
Systematic position of *Peridinium* 404
Nomenclature of the plates 405
B. Main argument 408
Abstract of argument 408
Major skeletal characters of Peridinidae 408
Type of antapical horn 409
Displacement of the girdle 411
Plate patterns 412
Other skeletal characters 414
Conclusions upon the importance of plate relationships 414
Progressive plate development in genera of Peridinidae 416
Possible method for multiplication of plates 419
Regions of skeletal variation in *Peridinium* 424
Plate patterns, a basis for subdivision of the genus, *Peridinium* 426
Subdivisions of the genus, *Peridinium* 428
Subgenus, *Paraperidinium* 428
Subgenus, *Metaperidinium* 430
Subgenus, *Orthoperidinium* 431
Special considerations 433
Summary of changes of plate pattern within a species 434
Summary of skeletal relationships 435
Regions of variation in the shell of *Peridinium* 437
Variable regions 437
Origin of the accessory plates 439
Origin of the principal symmetrical dorsal plate patterns 442
Origin of the asymmetrical dorsal plate patterns 443
Summary of discussion of dorsal patterns 443

PAGE
Paired areas of change of plate patterns 444
Completeness of the series of variations 446
Geometrical patterns represented 446
Combinations of patterns 446
Variations in the length of critical sutures 448
Significance of variation in suture length 450
Mutations 456
Possible influence of the environment 457
C. Conclusions 458
D. Bibliography 466
E. Plates and explanations of plates 472

A. INTRODUCTION

Purpose and Scope of this Paper

The purpose of this paper is to describe certain structural characteristics of the theca of the genus, *Peridinium*, which have been used as a basis for the classification of these organisms, but which seem to have a much more fundamental significance, possibly portraying the basis of natural relationships and of speciation. The theca is constructed with considerable regularity and simplicity in each species of the group of dinoflagellates to which this genus belongs. The structure of the theca for different species seems to be based upon the modification of a given number of parts according to a system which may be extended to the genera of the greater part of the group. Not only in *Peridinium* but also in several other genera of the dinoflagellates the regions of comparative permanency of skeletal structure and the regions of variability are usually definitely located. These conditions give the problem of variability in this group a certain welcome discreetness.

The group, Dinoflagellata, is also a widely distributed group, usually abundant wherever found. It contains certain characteristic cold and warm water forms as well as certain species which seem to be ubiquitous. Material is thus readily accessible and may be secured from a great variety of environments.

Moreover, the medium in which these organisms live presents conditions not encountered in the environment of land organisms which have usually been employed for variational studies. In the sea, of all places on earth, life may be found under conditions which change

less rapidly and through a narrower range of fluctuation than in land environments. The physical elements into which the marine environment may be analyzed—temperature, salinity, density, viscosity, light relations, gas content of the water, ocean currents, etc.—are comparatively few, and variations in each of these may be accurately measured.

While the physical conditions of a marine environment are thus comparatively simple, the absence of concrete barriers in the sea introduces a complexity into the study of the conditions of life for marine organisms not encountered among land organisms. The continual mingling of waters of all oceans, due to surface currents and the mixing of surface waters with bottom waters as well, introduce factors of unprecedented complexity in a study of the biology of marine organisms. Hence, we have to deal with conditions which introduce at once the possibility of structural as well as functional responses to the impact of the environment.

The system of variations suggested in the dinoflagellates, especially tangible in the Peridinidae, thus offers peculiar attractions for study. It is the purpose of this paper to describe briefly the systematic position of the genus, *Peridinium*, in the group, Dinflagellata, and among the Protozoa; to discuss the morphology of the theca of the genus, *Peridinium*, and the relations on this basis of *Peridinium* to other genera of the group, Dinoflagellata, and from this discussion to bring out the peculiar relations of the patterns of the plates of the theca; to suggest the significance of variations in the relative sizes of these plates and of their arrangement into patterns which may possibly give a clue to the sequence of species in this group; and to suggest the possible existence of unit characters in the sizes of certain plates. and the coupling of these characters according to the permutations permitted by the geometrical relations of the plates themselves in the formation of species.

It will be suggested that the skeletal characters in this group apparently may vary independently of one another, or under other circumstances that they may be linked in groups; that certain characters apparently vary at random about a norm, though there seems to be a progressive advance in a general direction of specialization; that certain characters are evidently accompaniments of old age; and that of fluctuating factors of the environment the temperature of the water and its buoyancy may perhaps be the strongest stimuli for the alterations of structure.

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Relationships and Morphology of the Dinoflagellates

The Dinoflagellata form a part of that group of Protozoa, the Mastigophora, which are characterized by possessing during the greater part of their life cycle specialized organs of locomotion in the shape of one or more flagella. Except, however, for similarities in the form of the locomotor apparatus the Mastigophora present little else in common, and the several groups brought together in this class often show closer relationships in other respects to groups outside this class, such as the Bacteria, Rhizopoda, and Ciliata, than to each other. Classification according to the number of flagella is, therefore, somewhat arbitrary. The Dinoflagellata, however, which are defined not only by the possession of two flagella, but also by having a shell of material similar to cellulose in texture and in chemical composition,

and by the possession of chromatophores in some surface forms, constitute a group which is evidently bound together by intimate phylogenetic relationships.

Among this vast assemblage of parasitic as well as free living organisms included among the Mastigophora, the Dinoflagellata (Bütschli) are the largest group which is found extensively in the sea. The other free living Mastigophora are found largely in fresh water. In the sea the dinoflagellates seem, however, to have multiplied in great variety, doubtless originating there in an early geologic period. Because of the purely organic nature of the shell of these organisms dinoflagellates have been rarely found preserved as fossils, but a few figures are given by Ehrenberg of specimens from horn stone (similar to flint) from Delitzsch, Saxony (1854, pl. 37, fig. VII, 1, 3, 4); from Pottschappel, Saxony (1854, pl. 37, fig. VII, 3, 4); and from coral-crag formations of Krakow, Poland (1854, pl. 37, fig. VIII, 1), and also from blackish-brown, leaf-coal measures of Westwalde, Germany (1854, pl. 7, fig. II, 13–15). These, however, seem to have been so poorly preserved in most cases as not to permit definite descriptions or classification, though more or less of a plate pattern is discernible from some of Ehrenberg's drawings.

Only a comparatively few forms of dinoflagellates have adapted themselves to fresh water conditions, having been carried thither from the sea or from brackish water areas, most probably by water birds or in spray whipped into the air by the wind and deposited with atmospheric dust (cf. Ehrenberg, 1854, pl. 7, fig. B, 3). These fresh water forms suggest, from their close relations to the more highly developed of the dinoflagellate types rather than to the more simply organized and presumably more primitive types, a transition from the sea at a comparatively recent geologic period.

The dinoflagellates are, moreover, a fairly well known group. Extensive investigations upon them date from the time of Ehrenberg's first descriptions in 1830. Because of their abundance and importance, they have received much attention and the literature dealing with them has become very large. Hundreds of descriptions are recorded among which there must be over six hundred valid species.

The flagella in dinoflagellates commonly originate in the region of a pore, located on what is termed the ventral side. One flagellum circumscribes the body of the organism in a groove, the girdle, located according to the genus near the anterior end or about the midregion. The other flagellum trailing posteriorly lies in a more or less well

defined depression, the longitudinal groove or sulcus, which is regarded as ventral in position. In function the longitudinal flagellum imparts the forward motion and the transverse flagellum imparts a rotary motion. By means of this rotary motion spiral progression in a fairly straight line is secured, which would otherwise be impossible on account of the asymmetry of the organism. The margins of these grooves, especially of the transverse groove, carry hyaline lists, or wings, apparently supported by stiffened ridges or ribs. The purpose of these grooves with their extended hyaline margins as receptacles for the flagella is probably to serve as flanges to increase the grip of the organism upon the water, and to make more effective the beating of the flagella, thus facilitating the rotation and locomotion.

The transverse groove or girdle divides the shell into two distinct portions, the anterior of which is known as the epitheca and the posterior as the hypotheca.

The shell of the dinoflagellates has been shown by analysis to be composed of an ashless substance similar to cellulose. At certain stages of the life of an individual this shell is homogeneous and unbroken. Through a breaking down of certain parts of the shell along pattern lines peculiar to each group and species, the shell is divided into a number of plates. The cellulose substance seems to break down at the suture lines of the plates and to be replaced by a cement which yields to dissolving alkaline reagents which have little effect upon the cellulose of the plates themselves. The joint at the sutures is beveled and corrugated (Kofoid, 1909) and it seems probable that limited growth with age is permitted by the widening of this beveled edge through the addition of shell material on the margin of the plate. The great differences in the appearance of the sutures varying in different individuals from narrow, highly refractive lines to wide, striated tracts are regarded as due to the widening of the sutures to accommodate the internal pressure of growth with age. Significant in this connection is a chain of *Gonyaulax* figured by Kofoid and Rigden (1912), showing the increase in size with successive asexual divisions from a single individual, as demonstrating the possibility of increase in size in this method of reproduction, and hence the probable potentiality of dinoflagellate protoplasm for growth without actual division, provided means for alleviating the confinement of the shell can be secured, such as growth of the plates on thin edges.

The plates of the shell may be variously marked, though in many species the shell may be nearly if not quite smooth, or covered with

spines, or by a ridged reticulation with spines at the intersections of the ridges or even with papillae so large as to give a corrugated appearance to the shell (*e.g., Peridinium thorianum*). In addition to external markings, there is much evidence of the frequent if not uniform occurrence of perforations in the plates and of the existence of a thin membrane of protoplasm outside of the plates.

The protoplasm of many species carries chromatophores of yellow, brown, or green, and oil globules which may be associated with the phosphorescence of many species under certain conditions.

Nearly all members of the family, Peridinidae, are markedly asymmetrical, both laterally and dorso-ventrally. In *Triposolenia* Kofoid (1910) has shown that this asymmetry is of undoubted benefit in so orienting the organism as it falls through the water at periods of quiescence as to cause it to present as great a surface as possible in the direction of the fall, thus retarding its rate of falling. The asymmetry of many species of *Peridinium* and of other genera may be explainable upon a similar basis.

The anterior or posterior end of a dinoflagellate may be produced into hollow horns or may carry spines apparently of solid material and supported by lists in the manner of buttresses. In forms with long, hollow appendages or horns, notably in species of *Ceratium*, autotomy of these horns has been observed (Kofoid, 1908) and has been explained as an adaptation to flotation upon sudden changes in the density of the surrounding sea water.

Among the dinoflagellates a number of features fortunately combine to make the genus, *Peridinium*, a favorable subject for such an inquiry as this:

(1) The great abundance of certain species of the genus, and their wide distribution, affording a possibility for comparing representatives of the same species from regions presenting a great variety of conditions;

(2) The morphologic features of these organisms which lend themselves readily to a systematic comparison;

(3) The nature of the environment itself offering a new point of view on account of its differences from the land environment under which these problems have usually been studied;

(4) The existence in an environment which is unusually stable and free from rapid or extreme variations, and which from many aspects seems to be as simple an environment as can be found in any considerable area of the earth, and an environment which may be

supposed to approximate as nearly as possible early primitive conditions under which organic life may have existed, and under which, to judge from the fossil remains of other groups of Protista, Foraminifera, Radiolaria, and Diatomaceæ, for instance, there has been a minimum or at least a very slow evolutionary change from the forms of the Carboniferous seas to those of the present;

(5) The complications, on the other hand, introduced because of the lack of concrete barriers in the sea, making physiologic barriers of especial importance;

(6) Life in an environment without a substratum and one in which the maintenance of an organism under optimum conditions depends upon the continuance of its active functions or the rapid adjustment between surface area and volume of the organism, perhaps necessitating for the pelagic plankton further adaptation by means of resting stages during long periods of severe conditions;

(7) The vital importance of minute variations either initiated within the organism or stimulated by the stress of the environment, and the significance of small measurable variations in any of the physical factors of the environment, illustrating the delicate balance which must be maintained between these organisms and their environment if they are to continue their existence.

Systematic Position of Peridinium

Recent taxonomic arrangement recognizes two orders in the subclass, Dinoflagellata, of the Mastigophora; the Adinida containing the genera, *Exuviaella* and *Prorocentrum*, in which "the typical peculiarities of Dinoflagellate organization are not fully developed" (Minchin, 1912, p. 278), and the Dinifera, having the typical characteristics of the subclass (Minchin, 1912, p. 278; Doflein, 1911, pp. 525–531).

The order, Dinifera, is in turn regarded as composed of three comprehensive families, the Gymnodinidae, Peridinidae, and Dinophysidae. The Gymnodinidae are distinguished as being shell-less, or at least without a shell which has been divided into plates and which may be visibly distinguished as a structure set off from the main protoplasmic mass of the body. There is indeed some suggestion that some of the forms now placed in this family may be only incompletely developed forms of the next family, in which the shell characteristic of the adult stage, usually met with, has not been fully developed.

Representative genera of the Gymnodinidae as at present considered are *Pyrocystis* Murray, *Gymnodinium* Stein, *Blastodinium* Chatton (parasitic), *Oxyrrhis* Dujardin, and *Pouchetia* Schütt.

The family, Peridinidae, contains the typical members of the group and is characterized by the full development of the general characters of the group, including especially a "well developed cuirass made up of definite plates" (Minchin, 1912, p. 278) and two flagella, one lying in a transverse groove or girdle, and the other trailing posteriorly from a ventral longitudinal groove. It is with this division of the dinoflagellates that we shall be principally concerned. The representative genera of this division will be named later.

The third family, Dinophysidae, containing a number of bizarre forms, differs from the Adinida in possessing a well-defined girdle often with very large girdle lists which may extend along the margins of the longitudinal groove as well, and differs from both the Gymnodinidae and Peridinidae in having the shell divided into two lateral valves by a sagittal suture. Each valve is in turn divided into one large and one small plate by a portion of the girdle which usually lies well toward the anterior end of the organism. Representative genera are *Dinophysis* Ehrbg., *Phalacroma* Stein, and *Ornithocercus* Stein. From the fundamental skeletal character of a sagittal suture, it is possible that the Dinophysidae may be more closely related to the order, Adinida, which contains evidently the most primitive and generalized forms of the group, than to either the Gymnodinidae or the Peridinidae, and that the bizarre development of the lists, etc., is of secondary morphologic importance and perhaps acquired rather late in the phylogenetic history of this portion of the group.

Nomenclature of the Plates

In this paper the system of plate nomenclature devised by Kofoid (1909, p. 40) has been adopted as being at once the simplest, most logical, and most adaptable by extension to related genera, of several which have been proposed and which have been summarized by Kofoid (1909, p. 44). This system recognizes the girdle as a basis of reference rather than a hypothetical equatorial plane, with which the girdle rarely exactly corresponds on account of its more or less spiral course. The girdle is, moreover, the most prominent single feature of the organism and it lies in such a position relative to the plates in *Peridinium* and in related genera that it is especially convenient to use

it as a basic feature in composing a system of nomenclature. From this basis of reference the plates in *Peridinium* at once appear as arranged in circumferential rows, one row on either side of the girdle, the precingular row and the postcingular row; one group, the apicals, about the anterior pole or apex; an incomplete row interpolated between the apicals and the precingulars, the anterior accessory plates; and in this genus, a pair of plates over the posterior end, the antapicals, carrying the antapical horns, and representing an antapical row.

Each plate is designated by a composite symbol of which one factor, the superscript written as a prime point indicates the row, the rows themselves being designated by one, two, three, or four prime points as they occur in succession from the apex posteriorly. The incomplete row of anterior accessory plates is designated by the superscript a. In each row the plates are numbered from the left to the right of the organism coincidently with the direction of the course of the transverse flagellum. This direction for numbering is, as one looks at the organism from the anterior end, counter-clock-wise for the epitheca and as seen from the posterior end, clock-wise for the hypotheca. This order of numbering corresponds to the usual method for numbering serial parts distally from the proximal portion.

Thus, in *Peridinium* the apicals are numbered from 1′ to 4′, the anterior accessories from a 1^a, to 3^a, the precingulars from 1″ to 7″, the postcingulars from 1‴ to 5‴, and the antapicals 1⁗ and 2⁗. This system permits the writing of a simply expressed formula for the plate relations, the number of girdle plates being inserted without superscript or if desired for completeness with the superscript g (which, however, has not been used by Kofoid). For a typical species of *Peridinium* the plate formula would then be $4'$–3^a–$7''$–3^g–$5'''$–$2''''$.

This system presents much practical convenience. The numerals as symbols more rapidly indicate the relative position of a plate in its row than do the letters used by Bütschli (1885, p. 928), Fauré-Freimet (1908, p. 215), Stein (1883, pl. 10, figs. 1, 6), and Broch (1912, fig. 8), while the superscript indicates at once the relative position of the row antero-posteriorly. Not the least favorable feature of Kofoid's system is its elasticity and adaptability to any member of the group of dinoflagellates which has a skeleton made up of discreet plates.

This system of nomenclature, however, is based on more fundamental grounds than those of mere convenience. The fact that this system, regarding the plates as grouped in circumferential rows, holds throughout a large portion of this extensive group is in itself signifi-

cant in supporting the suggestion that the origin of the plates of the dinoflagellate skeleton is by the fragmentation of an originally homogeneous shell circumferentially rather than meridionally, and that other plates though derived from the plates of this or secondarily formed rows still preserve this arrangement.

Kofoid's system has certain points in common with that of Stein and of Bütschli in recognizing rows of plates and in enumerating these in a left-to-right direction. Broch (1912, p. 39, fig. 8) in his figure recognized the arrangement of the plates in rows, and so does Fauré-Fremiet (1912, figs. 3-14), though the figures of Fauré-Fremiet suggest that he conceived of the apical plates as lying in three meridional rows in addition to the rhomboid plate. The implication from the nomenclature of these figures is that Fauré-Fremiet regarded the accessory plates as derived by splitting off from the apicals, while the implication from the nomenclature of the accessory plates in Broch's (1912, fig. 8) figure is that these accessory plates may have been derived from the precingular plates. There are indications of shape in many of the plates, however, which make the manner of origin of the accessory plates doubtful. In view of this lack of more definite knowledge upon the origin of the accessory plates, Kofoid's system committed by implication to neither view would seem to be the more conservative. The rhomboid plate in Kofoid's nomenclature is regarded as an apical which has not divided but which has become extended to meet the girdle.

The plates of the ventral area seem never to have received a definite nomenclature, probably because of the great difficulty in determining them. On account of the considerable variability of form and extent of the ventral area in different species it is to be expected also that the plates of which it is formed will display much variation, and this has been demonstrated for shape as well as number in several forms already worked out. A system of nomenclature for the major plates of the theca in order to permit expression of the relationships of the various groups of the dinoflagellates need not include, therefore, the ventral area in its consideration, for the main relationships of the dinoflagellates seem to be sufficiently if not mainly expressed in variation in the arrangement of the major plates of the theca exclusive of those of the ventral area.

B. MAIN ARGUMENT

Abstract of Argument

The cellulose-like shell or skeleton of the genera of Peridinidae, biflagellated Protozoa of the sea, shows a progressive specialization in the increasing number of plates into which the skeleton is divided in the several genera. This process of specialization can be traced in detail in species of *Peridinium*, one of the principal genera of the family. Among the species of this genus the arrangement of the plates in four regions on the anterior part of the skeleton undergoes definite changes, producing different plate patterns limited in number by the geometric possibilities for the rearrangement of the plates. These plate patterns are not only of great convenience in classification but because of the fundamental morphologic importance of the skeleton, the arrangement of its elements may be relied upon to show the relationships of many of the species of the genus. As represented in these species, each pattern is distinct, and transitionary stages from one pattern to another are unknown. Exceptional cases, however, have been found of specimens which, while bearing many characteristic marks of a certain species still display a plate pattern different from that typical for the species.

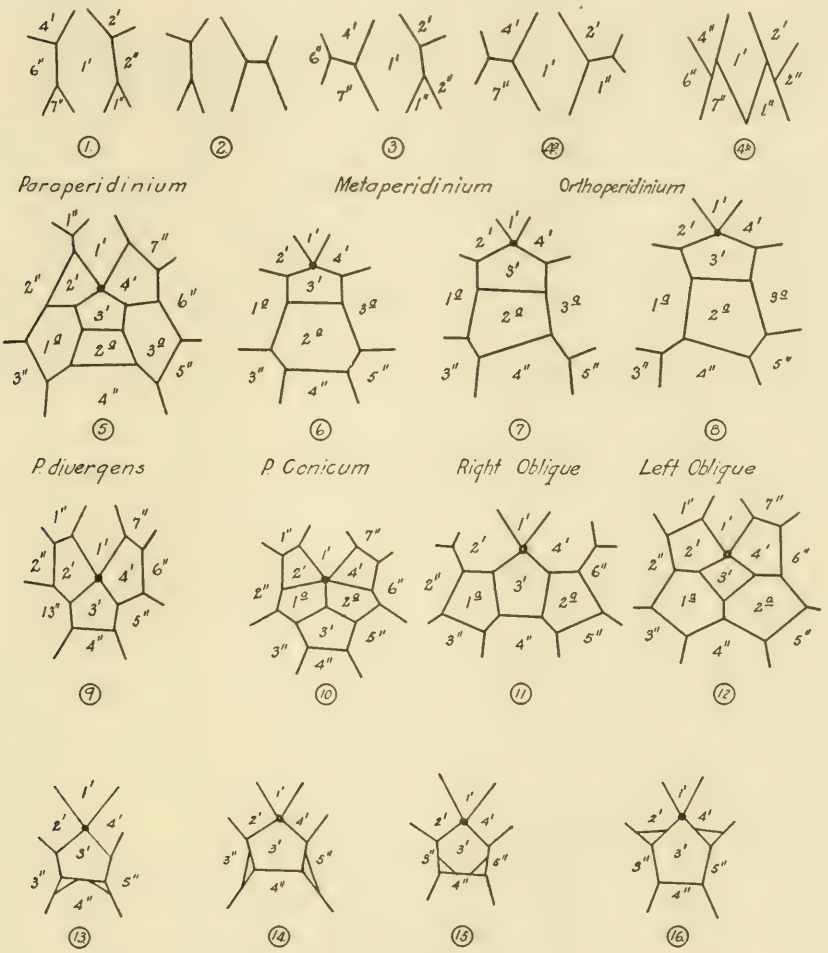
It is strongly suggested that each pattern represents a condition of skeletal equilibrium which is disturbed only by an accumulation of stress, due perhaps to some unusual environmental condition, and that when thus disturbed the plates fall into an entirely different plate pattern, much as patterns change in a kaleidoscope. The indications are, then, that in this genus species formation takes place by changes which are in the nature of saltations, rather than by means of fluctuating continuous variations.

Major Skeletal Characters of Peridinidae

Upon attempting to arrange the large number of species which come under the definition of the genus, *Peridinium*, upon a systematic basis useful for the taxonomist and expressive, so far as possible also, of the natural affinities of the members of the genus, three prominent skeletal characters present themselves for consideration. These are: (1) the type of the antapical horns; (2) the direction of the dis-

placement of the ventral ends of the girdle; and (3) the suture patterns formed by the varied arrangements assumed by the plates of the shell.

Type of Antapical Horn.—From the prominence which the antapical horns assume in many species of the genus, one is tempted to



VARIATIONS IN PLATE PATTERN OF PERIDINIUM

FIGS. 1–16.—Diagrams of the arrangement of the ventral plates of the epitheca in the three subgenera of *Peridinium* and for the several arrangements of the dorsal plates, showing in the series of figures from 9 to 12 the two probable methods for the introduction of the accessory plates and the development of the accessory row to the three-plate stage. Figures 13–16 indicate in the small triangles the regions at which the early accessory plates may have been introduced. (Figures 2, 13, 14, 15 and 16 have not been authentically reported in specimens). Figure 4*b*, is only a variation of the pattern for the subgenus *Orthoperidinium*, as given in figure 4*a*.

consider the type of horn as a primary basis in dividing the genus into its general divisions. Two different types of horns arising from the antapical plates are found in the genus, each represented in a well-developed fashion in a large number of species.

One of these types of antapical horns is formed by pushing out the center of each antapical plate ot a greater or less extent, thus forming a hollow horn which often becomes a large and prominent feature at either side of the posterior end of the longitudinal groove which terminates between the two horns. A spiny tip is often present at the end of this hollow horn. The lists of the longitudinal groove which are continuous with the posterior list of the girdle pass over the inner bases of these horns and unite around the end of the longitudinal groove. Occasionally, as in *P. cummingii* Lemm, a fresh water form having four horns, the hypotheca may be pushed out to form sharp but hollow horns on other plates than the antapicals, or a general elevation of the center of each antapical plate may terminate in two or three sharp tips, as in *P. crassipes* Kofoid.

The second type of horn seems to be quite unrelated to the former types and consists of a solid spine, buttressed by three hyaline vanes, two of which are continuous, except perhaps for a deep notch in the vanes at the base of the spine, with the lists of the longitudinal groove. The third vane lies on the opposite side of the spine from the longitudinal groove. The spines are usually located upon the antapical plates, but stand rather nearer to the longitudinal groove than do the hollow horns. This type of horn reaches its greatest development in such examples as *P. steinii Joerg.* and *P. tenuissimum* Kofoid.

It seems probable that this latter type of spine arose directly as a support for the list of the longitudinal groove and thus independently from the hollow type of horn and for a different purpose. In such a species as *P. crassipes,* in fact, the incompletely developed stages of both types of horn may be seen, the spiny type supporting the list of the longitudinal groove and the hollow type represented by two or three points arising close together from near the center of each antapical plate and producing the peculiar "flat-footed" appearance for which the species was named.

While in most species of *Peridinium* one type or the other of horn is distinctly in evidence, there are species in which not only is there no sign of elevation of the antapical plates to form the hollow type of horn nor are the lists of the longitudinal groove high enough to need support and even the spiny type of horn is indiscernible. This

character of the type of horn seems an insufficient basis, then, for the differentiation of all the species of the genus. From its variable development, moreover, throughout the genus the type of horn seems not to represent a sufficiently profound condition in the organization of the genus to merit recognition as a feature capable of dividing the genus into two morphologically correlative portions. And it is hardly to be supposed that in the presence of so many prominent variable characters as those of which *Peridinium* is possessed a single one might have been selected to direct the progress of evolution into two paths. Though perhaps a practical convenience in taxonomy as affording a basis for the ready identification of specimens, this character of the type of antapical horn can hardly be presumed to have monopolized the early differentiation of the genus.

Displacement of the Girdle.—Although the relations of the girdle are undoubtedly correlated with the function of locomotion in a very important way, it has not as yet been demonstrated that rotation of these organisms is dextrad in certain species and sinistrad in others according to the direction of deflection of the girdle, nor in which direction this rotation takes place in those species in which the girdle ends meet approximately opposite each other. Variations in the amount of deflection also occur even in the same species. We are not dealing here with the character of the presence or the position of the girdle itself but merely with the relations of the ends of the girdle. On the whole it does not seem probable that a character of such limited extent in the morphology of these forms could have assumed a dominating influence in effectually dividing the genus into two correlative parts.

As a practical aid in gaining an acquaintance with the genus, however, this character has been of considerable value. Early classifiers, Schütt, Bergh, and Gran, divided the genus abruptly into two portions on the basis of the deflection of the distal end (right end from viewpoint of the organism) of the girdle anteriorly or posteriorly with respect to the proximal end through which passes the base of the circumferential flagellum. Coupled with the character of anterior deflection in the division of the genus called *Protoperidinium* was placed the character of the solid buttressed antapical horns, and with the character of posterior deflection was coupled the character of the hollow antapical horn to define the remaining portion of the genus, *Euperidinium*. This pairing of characters, however, does not always hold throughout the genus. Moreover, in many species it is

impossible to determine any deflection of the girdle. In practical application Paulsen (1908) continued this basis of classification, subordinating to it the characters of presence or absence of antapical spines, the type of spine, shape of the body, etc.

Fauré-Fremiet (1908) divided this genus into four groups upon the basis of the total of resemblances including form, type, and development of horn, etc.

Meunier (1910) used girdle characters also in beginning the classification of the genus, but considered first the character of the girdle, whether flat and winged or impressed into the body of the organism and not winged.

The wing or hyaline list is, however, too superficial a structure to claim far-reaching significance. Meunier's system of classification may be presented as follows:

A. Planozones, girdle flat or but slightly, if at all, impressed, winged.

I. Girdle sinistro-spiral, e.g., *P. divergens.*

II. Girdle dextro-spiral (subdivided according to proportions of major axes; including the larger portion of the genus).

B. Cavozones, girdle excavated, not winged, more or less clearly sinistro-spiral, if not circular, e.g., *P. thorianum, P. conicum.*

Meunier added also a short list of small forms which he finds it difficult to insert elsewhere in his system. Examination of this system reveals many misinterpretations of structure, if not errors in description, so that it cannot be retained as a useful contribution in revealing the relationships of the genus.

Plate Patterns.—Although descriptions of species had for many years previous often been based upon the characters of plate pattern as reported in sketches, together with the features of size, shape, surface markings, etc., it was not until 1912 that a comprehensive system for the whole genus was proposed on the basis of plate relationships. Joergensen (1912) recognized on the ventral surface of the epitheca two main groupings of the plates in this genus, those given in our figures 3 and 4*a*, but he mentions also a third grouping which, however, he regards as unimportant because of its infrequent occurrence, and probably only an exceptional occurrence of the pattern of figure 1. He divides the genus primarily into two major subdivisions, giving the name, *Orthoperidinium*, to those species having the plate pattern of figure 4*a*, and *Metaperidinium* to those species having the plate pattern of figure 3. To the remaining occasionally

occurring forms having plate pattern of figure 1 he gave the group name, *Paraperidinium,* but in his later treatment he merged this group under *Metaperidinium.*

Joergensen also recognized that in both of those groups having plate patterns 3 and 4*a* and named by him *Metaperidinium* and *Orthoperidinium,* respectively, three different dorsal patterns of the plates of the epitheca also occurred. He accordingly redivided each primary subdivision of the genus on the basis of the dorsal pattern, and established under *Metaperidinium* a seventh place for the few erratic species having the pattern of *Paraperidinium* for the ventral epithecal plates. Though certain corrections and amplifications may be made in this system as given by Joergensen, its formulation was a great step in advance toward a fuller and more correct understanding of the organization of the genus than had previously existed.

Pavillard (1916) summarizes Joergensen's system as follows:

Orthoperidinium	*Metaperidinium*
Sec. I. *Tabulata*	Sect. IV. *Pyriformia*
e.g., *P. tabulatum*	e.g., *P. steinii*
Sect. II. *Conica*	Sect. V. *Paraperidinium*
e.g., *P. conicum*	e.g., *P. pallidum*
Sect. III. *Oceanica*	Sect. VI. *Humilia*
e.g., *P. depressum*	e.g., *P. ovatum*
	Sect. V. *Divergens*
	e.g., *P. crassipes*

Pavillard (1916) criticizes Joergensen's system on the basis that there is no real relation between those members of the group *Orthoperidinium* and *Metaperidinium,* which have the same dorsal pattern, nor between the species of these two subgenera differentiated by having different dorsal patterns and connected on the basis of similar ventral patterns, as members of linear series. Pavillard accordingly proposed another grouping of these seven subdivisions, accepting in the main Joergensen's definitions based upon plate patterns. Pavillard also finds a few species which cannot be included in any of these seven subdivisions which he appends as "Incertae Sedis." *P. curvipes, P. mite,* which are said to intergrade, and *P. rectum,* said to be unstable.

This historical resumé of the various bases for classification in this genus has been introduced to show the recent trend toward recognition of the importance as well as the convenience of the pattern of the plates in the organization of the genus.

Other Skeletal Characters.—This present trend to regard the skeleton of dinoflagellates as of greater and greater value seems to reflect the more and more nearly complete recognition of the morphological importance of this part of the structure of these organisms. Nor is it unreasonable to look among the dinoflagellates, as we do among almost all other groups of animals which possess skeletal structures of any sort, both internal and external, to the hard parts of the organism for the reflection of the deep-seated processes of change. Hard parts of organisms seem in all groups to be modified but slowly either by hereditary influence from generation to generation or by a possible impress of the environment. The fundamental connections of related animals seem to be impressed upon the more permanent of the structures. Particularly is this the case when the hard parts are not composed of excreted extraneous material, but are retained in a close relation to the living protoplasm of the organism.

Of the characters of the skeleton of Peridinidae there are several which may contribute more or less to an understanding of the relationships of the members of the family. The nature of the antapical horns has already been discussed and the inadequacy of this character to serve even in first instance as a common divisor for the genus, *Peridinium*.

Size is of course an important character, but is so dependent upon the extremely variable metabolic processes involved in the whole course of food assimilation and of excretion as to be hardly trustworthy to reveal far-reaching generic relationships.

Shape is an important factor, but in view of the well-known capacity for autotomy among the dinoflagellates and for individual responses to protoplasmic pressure, the shape of an organism seems to be too intimately under the control of the environment and is not to be trusted to display an all-pervading set of relationships.

Characters of the surface of the skeleton are also of a certain value, and with the shape should be taken into consideration in the confirmation of relationships proposed on any other basis, but this character again is under direct influence not only of the environment but also of age because the degree of the development of surface markings is known to vary widely not only between species but also between individuals of the same species presumably of different ages.

Conclusions upon the Importance of Plate Relationships.—The number of parts of which the skeleton is composed seems, however, to be a much more fundamental thing than any of the characters just

discussed, and to be second only in its significance to the presence of the skeleton itself. The facts that the skeleton throughout the whole group of Peridinidae is found to be divided into plates, that through-

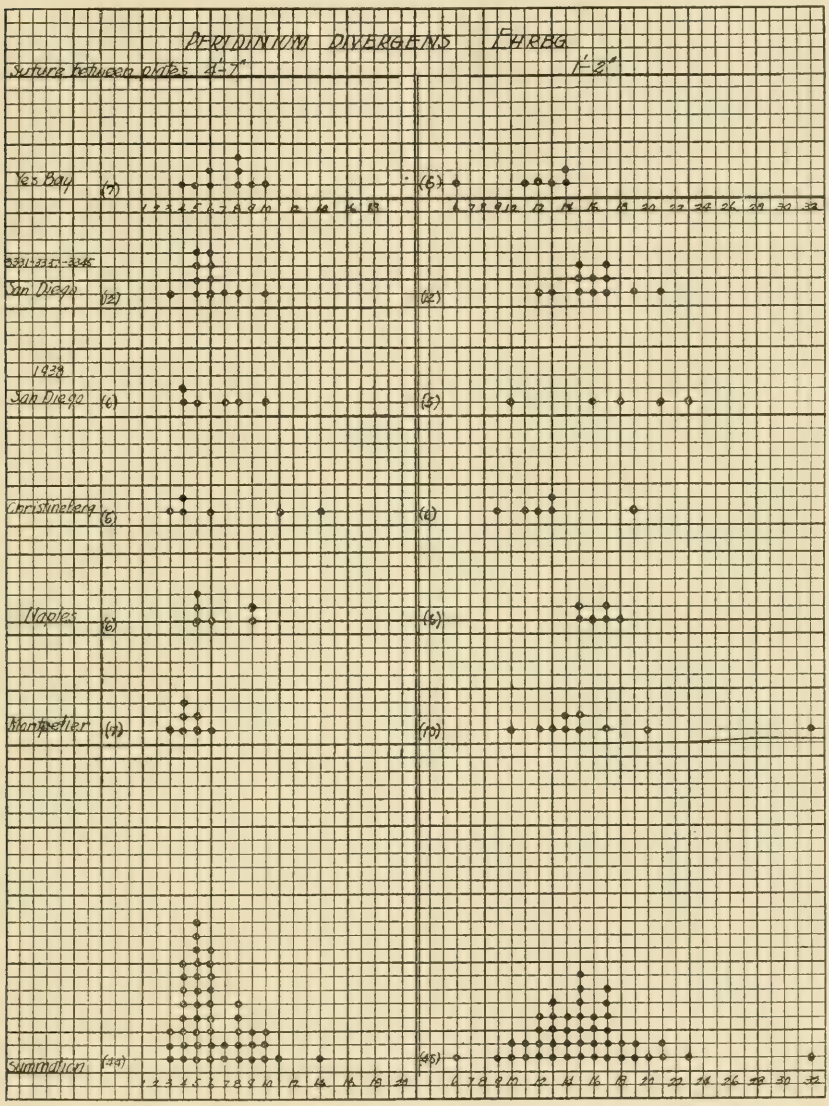


FIG. 17.—Chart of measurements of critical sutures of the ventral epithecal plate patterns for 44 and 46 specimens of *Peridinium divergens* Ehrbg., *i.e.*, the sutures between plates 1′ and 2″ on the left and between 4′ and 7″ on the right. Note that from the distribution of the specimens measured, as shown in the charts for geographic races, there is nothing to indicate a cause for the double or triple crests either in these charts or in those of figure 18. This multiplicity of the crests must, therefore, be regarded as purely accidental.

out decades of study the number and arrangement of these plates have been found to be sufficiently constant to be relied upon as bases for the descriptions of genera; and the system of rows of plates upon which the whole matter of plate arrangement seems to rest, extensible to all the genera of this large family, are other considerations which still further suggest that certain group relationships are to be revealed in a comparison of the plate formulae when taken into account together with other skeletal features which may in one part of the genus or another be of phylogenetic importance. There is indeed no other character which reveals more, not only of the detailed but also of the general relationships of the Peridinidae, than this character of the development and arrangement of the plates of the shell.

Progressive Plate Development in Genera of Peridinidae

We find ourselves confronted in viewing the family Peridinidae by a considerable assemblage of genera which can be arranged in a series according to the number of plates composing the skeleton. All of these genera have at least four circumferential rows of plates and several genera have one or more plates of a partially complete accessory row. At one end of this series stand such genera as the following:

Ceratium,–4′–0^{a}–5″4^{g}–5‴–0^{p}–2⁗
Protoceratium,–2′–0^{a}–6″(?)–6^{g}(?)‴–0^{p}–3⁗
Goniodoma,–1 (to 3)′–0^{a}–7″–(2)^{g}–5‴–0^{p}–2⁗
Heterocapsa,–4 (or 5)′–0^{a}–5 (or 6)″–?^{g}–5‴–0^{p}–2⁗
Pyrophacus,–4 (to 6)′–0^{a}–0 (to 12)′?^{g}–9 (to 12)‴–0^{p}–(3 to 5)‴

The last genus mentioned is especially noteworthy because of the large number of plates contained in each row.

In another group of genera an incomplete row of plates has been introduced on the dorsal side of the epitheca or of the hypotheca or of both, such as the following:

Heterodinium,–3′–1^{a}–6″1^{g}–7‴–0^{p}–3⁗
Gonyaulax,–1 (to 6)′–0 (to 4)^{a}–6″–6^{g}–6‴–1^{p}–1⁗
Centrodinium,–2 (to 4)′–0^{a}–6″–?^{g}–6‴–1^{p}–4⁗
Spiraulax,–4′–1^{a}–6″–6^{g}–6‴–1^{p}–1⁗
Peridinium,–4′–0 (to 3)^{a}–7″–3^{g}–5″–0^{p}–2⁗
Perindinella,–4′–0 (to 3)^{a}–7″–3^{g}–5‴–0^{p}–2⁗

It is not possible to arrange all of these and the other genera of this family in a strictly linear series because of the two ways, at least, in which the number of plates of the shell seem to differ, *i.e.*, in the number of rows and in the number of plates in each row. More-

over, the actual genetic relationships may be influenced more or less by variations in other factors than that of plate pattern, though probably on the whole not so profoundly. Suffice it to show, however, that these more or less closely related genera differ markedly in the number of plates into which the skeleton is divided. If any number of these genera arose from a common stock or if one of them is derived from another, it must be admitted that this differentiation occurred through a variation in the number of plates of the antecedent which became fixed in the succedent form.

We may now inquire whether this process of plate formation in the shell of Peridinidae may have been one of the greater and greater fragmentation of a shell originally consisting of but one or two or of a few pieces, or by the amalgamation into large plates of an originally great number of small shell particles. A clue to this is derived from the phenomenon of exuviation in the very genus, *Peridinium*, to which our especial attention will be directed. Only a vegetative method of reproduction is known in this genus. The protoplasm of the body encysts, the original shell is cast off by a process of exuviation, and directly a new shell is developed in which at first only the depressions of the girdle and longitudinal groove can be made out. The first impression of any plate formation which can be discerned shows a plate pattern which is the same as that of presumably the older, and at any rate the usual form, but differing in the prominence and width of the sutures.

Again in *Ceratium*, in which a form of reproduction by oblique fission occurs, one-half of the shell is regenerated in each daughter individual resulting from the process. Here the covering is at first homogeneous, but presently becomes divided directly into the number of plates expected for the adult individual and arranged in the specifically characteristic manner. The succession of genetically related individuals contained in chains of *Ceratium* and of *Gonyaulax* which are all of the same plate patterns demonstrates the trustworthiness of this method of reproduction in transmitting a given plate pattern. Moreover, in these chains individuals are not known which have a great number of small platelets in their shells apparently in process of merging into the larger plates of the adult shell.

Nor is it to be expected that an organism of this sort in developing a protecting covering should form first a number of small platelets on its surface which later might become fused, but rather that as in diatoms, various algae, etc., a protective film of substance will accumu-

late homogeneously on the exterior. This primitive homogeneous shell seems in the dinoflagellates to have become divided regularly into a number of plates.

In view of the great variety of stereoisomeres possible for a given number of atoms in organic substances, it is not impossible that the tendency toward fragmentation of the shell in certain of the genera of dinoflagellates and the tendency toward retaining the shell in fairly large component pieces in other genera of the group may be associated with the composition of different stereoisomeres of the same protoplasmic organic series in the shell material of these two portions of the group.

If, then, the progress of the development of shells of varying complexity on the basis of the number of plates of which they are formed is in the direction from a homogeneous shell to one of a greater and greater number of plates, those species, in general, having the smaller number of plates and particularly the smaller number of rows of plates should be regarded as the most primitive and generalized and those showing the greatest development in number of plates and in number of rows should be considered the most highly specialized in this respect.

The formation of a large number of plates in a portion of the shell in which there might have previously been a small number of plates may be considered to take place by the splitting of a previously existing single plate into two plates of equal or of unequal size or by the appearance of a new plate in a gapping area between plates which may have been pushed apart by some internal pressure, either process involving perhaps a rearrangement of the resulting elements according to quite a new pattern.

We should expect, moreover, that in the history of such a process for the development of the plates of the shell of dinoflagellates possibly to see exhibited at some stage in the ontogeny of certain individuals indications of the progressive division of the skeleton into a few plates and these into the final number of many plates. No suggestion of this has been recorded so far as we know. However, this lack of evidence on this point partakes of only a negative value.

It would seem, then, if our analysis be correct for the method by which plates of the skeleton arise, that a genus in which there are, let us say, but five precingular plates is more primitive in this respect than a genus in which the precingular row contains six or seven plates, and similarly for a comparison of the number of plates in any

other of the rows of the skeleton. Correspondingly, a genus in which a partial row of accessory plates has been interpolated on the dorsum of either the epitheca or of the hypotheca is higher in the phylogenetic series, other things being equal, than a genus in which there is no such row of accessory plates. It would seem probable, then, that a genus having, for example, seven plates in the precingular row might be derived from a form perhaps still represented in a related genus, having but six plates in this row by the division of one of these plates into two parts. We shall have need to refer to this suggestion again.

Possible Method for Multiplication of Plates

It is possible, of course, that plate multiplication takes place by the splitting of a former plate. Without saying that this may not occur in certain genera it appears from the progressive series of precingular plates, for example, which can be constructed for the genera related to *Peridinium*, that the splitting of a former plate into two equal or nearly equal plates does not occur, but rather that new plates arise at first as small skeletal elements either split off from the corner of a former plate as, perhaps, in the formation of plates 1″ and 7″ of *Peridinium* or that new plates arise to fill the gap left by a bulging of the internal protoplasm of the organism which would cause three plates to be pulled apart at their point of articulation. That is, the strain which causes the formation of a new plate seems to require the construction of a new skeletal element rather than a remolding of a formerly existing element. These elements, the plates, moreover, seem to be limited in size, and it is probably the impossibility of a shell of one piece to contain the active and growing organism which has caused the production of a shell composed of a number of plates. Physical factors of the skeletal material or of the shape of the organism may determine a limit beyond which the skeletal material cannot exist as a single plate, the actual area of each plate as well as its shape depending upon its location. In the few cases where very large plates are found, as on the dorsal side of the epitheca of *P. excentricum*, such excessively large plates are in regions where there is but little change in shape or contour. In such a region as the apex, where the contour changes sharply, there are usually found a number of plates. However, in those forms in which there is found a protracted apical horn the apical plates are narrow transversely in the direction of sharp change of contour, but elongated axially in the

direction along the horn in which the change in contour is slight and gradual.

In other genera, however, such as *Pyrophacus* and *Gonyaulax,* conditions are present which suggest the possible splitting of plates into subequal portions, due to internal strains. In both of these genera, but more especially in *Pyrophacus,* the number of apical plates varies greatly among the several species of the given genus. In the apical regions in *Pyrophacus* a cluster of as many as fourteen plates may be found irregularly arranged and not to be clearly traced in rows.

In this same connection it is also of interest to note that in different genera it is different regions of the shell which are variable, suggesting possibly a difference in the nature of the initial force influencing the change as well as a difference in the location of the point of yielding to these strains. Thus in *Pyrophacus* the yielding seems to occur in the apical region, while in *Peridinium* the alterations seem to involve a swelling of the circumference. This circumferential enlargement involves a readjustment between previously existing apical and cingular plates and the stretching apart of these two rows at some place. This separation seems to occur on the dorsal side of the epitheca rather than on the ventral side, and if the organism were oriented horizontally this might be described as a dorsal humping of the body with an anterior concavity in the hump. To meet this strain and to cover the area which would otherwise be left vacant by the stretching apart of the apical and precingular rows of plates on the dorsal side, the dorsal epithecal accessory plates are formed. Once having been established the strains seem to have been satisfied for most members of the genus by the introduction of but three such plates.

We are also interested in a peculiar manifestation of the polarity of these organisms. The hypotheca in these forms is consistently more conservative than the epitheca in regard to the multiplication of plates. The number of plates in the hypotheca is usually less than the number in the epitheca and never exceeds this number. We do not find in the genus immediately under consideration nor in related genera the evidences of reconstruction or rearrangement of plates in the hypotheca which we find in the epitheca. On the other hand there are certain modifications of the hypotheca, but these are not of the character to be caused by internal forces, but rather seem to be impressed upon the organism by the environment. Thus the development of hollow antapical horns is supposed to be due, partly at least,

to an attempt at adustment of buoyancy to density in flotation or to the imparting of a spiral method of locomotion, making rectilinear progression possible, or to such an upsetting of the body of the dinoflagellate as it falls through the water as to bring it to present as great an area as possible to the direction of falling and thus to reduce the rate of falling by increasing the amount of resistance of the water to the falling body. Solid antapical horns may also serve some of these same purposes or be coupled with the function of locomotion in somewhat the same way as the lists on the margins of transverse and longitudinal grooves are related to the activity of the flagella by confining the currents of water set up by the flagella.

Thus it seems to be the epitheca, or the anterior end of the organism, which reflects the active internal forces of the organism and the hypotheca, which possibly reflects certain superficial modifications stimulated more directly by the environment. This conclusion is somewhat in accord with the theory of gradients recently put forward by C. M. Child, according to which we should expect the rate of metabolism to be higher in the anterior than in the posterior end of organisms, and hence the initiative for profound morphologic modification more pronounced here than in the posterior region.

The number of sides of each polygonal plate of the skeleton varies in this genus from three to six, the more common number being five. Only the plates 1″ and 7″ in species of *Paraperidinium* and plate 1″ of *Metaperidinium* (dextrad) are triangular. These are presumably plates of rather recent phylogenetic origin. Hence a triangular shape is believed to be an undeveloped or primitive condition in the history of a plate.

The reticulated surface markings also enclose polygonal areas, bounded by straight or nearly straight sides, among which there are found comparatively few triangular areas, the areas being usually five- or six-sided. However, none of these plates or reticulated areas is equilateral or symmetrical. This condition is in contrast to the frequent condition in other animals of repeated hexagonal elements, in which the elements are nearly if not quite regular, such as the ommatidia of a compound arthropod eye, the comb cells of a bee hive, and the framework of the skeleton of many Radiolaria.

There is every indication that not only the formation of plates in the shell but also the size of these plates is a matter of internal regulation. This appears from the circumstance that after ecdysis the shell is reformed with plates presumably in the original pattern. While

observations have not followed every step of exuviation and regeneration of the shell under controlled conditions, it is presumed that the plate arrangements of the shell ordinarily are not changed during this ecdysis unless unusual environmental changes are encountered. The uniformity of the plate pattern in chains of individuals found for

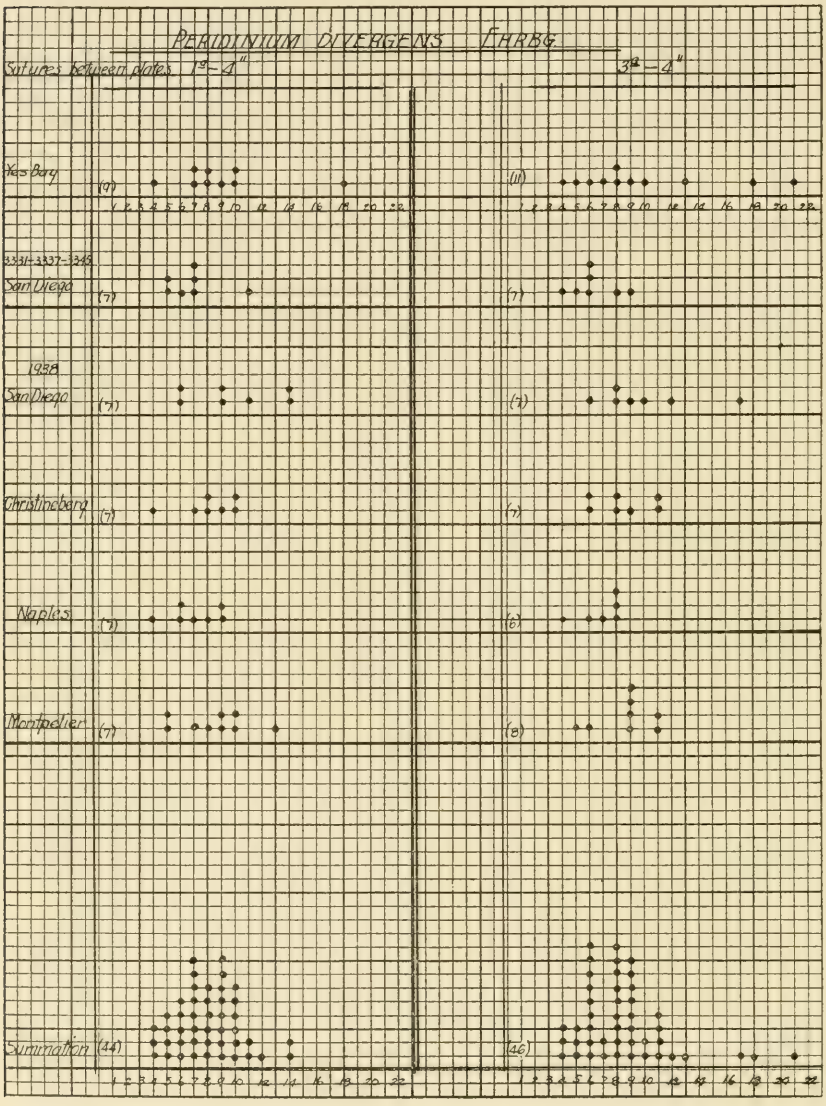


Fig. 18.—Chart of measurements of critical sutures of the dorsal epithecal plate patterns for 44 and 46 specimens of Peridinium divergens Ehrbg., *i.e.*, for the sutures between plates 1*a* and 4″ on the left and 3*a* and 4″ on the right.

certain species of *Ceratium* and *Gonyaulax* strengthens this conclusion. Further, the fact that plates rarely exceed a certain maximum size, and then only in the case of fairly flat portions of the shell, suggests the existence of some factor either within the organism itself or within the material of the shell which makes for a fragmentation of the shell into plates of a restricted size.

Regions of Skeletal Variation in *Peridinium*

We are now, perhaps, in position to apply these observations to members of the genus, *Peridinium*. Aside from variations in the plates of the ventral area which are imperfectly known because of the great difficulty in analyzing them there are no variations in plate articulations of the hypotheca within this genus. The principal morphologic variations concern the development of antapical horns, and as has been pointed out above, these cannot be regarded as of predominating significance. There is, however, variation not only in the number of plates of the epitheca but also much variation in the arrangement of the number of epithecal plates (14) which is of most frequent occurrence. These variations are found to occur in two general regions; one, on the ventral side of the epitheca on either hand of the rhomboid plate (1′), and the other on the dorsal side between the articulation of the partial row of three (in typical cases) accessory plates, presumably of recent phylogenetic origin, and the mid-dorsal precingular plate (4″). There is, however, a considerable number of species in which the partial row of accessory dorsal plates contains only two plates instead of three, the greatest number developed in this row in this genus. These species, as recorded, however, all have the same ventral plate patterns. The variations in the vicinity of the mid-dorsal precingular plate (4″) are such as might be expected to accommodate the smaller number of accessory plates present.

The regions in which these articulations change will be seen from the accompanying diagram (fig. 19) of an apical view of *Peridinium divergens* Ehrbg., showing all of the epithecal plates in this, a typical species of this genus.

It is to be noted that there are only four points of the intersection of sutures between plates at which changes in articulations occur. These four points are paired symmetrically with respect to the sagittal plane, and changes of articulation seem usually, though not always,

to occur coincidently in two dorsal regions, while the two ventral regions of change seem often to vary independently of each other. The changes occurring at the two pairs of variable regions have been diagrammed in figs. 1 to 8. Fig. 3 shows an asymmetrical ventral plate pattern, which is formed by the non-coincident variation of the pair of ventral regions of variation in the reverse order from that of fig. 2.

It is to be noted that figs. 1 and 4*a* show the only possible combinations of the plates of this part of the epitheca if the two symmetrically opposite regions of variation behave coincidently. But a stage represented by fig. 2 must have occurred in the formation of the stage given in fig. 4*a*, unless that of fig. 4*a* arose by direct symmetrical progression from the stage given in fig. 1, which, as has been explained, is presumed to represent the primitive condition for these plates in this genus. This stage shown in fig. 2, however, has not been found by the writer in any specimen, and if we may except the figure of Claparède and Lachman (1859, pl. 13, fig. 26), which may have been drawn from the inside of the shell, or from the dorsal side, instead of in correct orientation, this pattern has not been figured in literature.

The variations of the dorsal region involve the possibilities for the articulation of plates about the anterior right and left corners of the mid-dorsal precingular plate, with readjustment on the part of the adjacent accessory plates (1*a*, 2*a*, and 3*a*) and also of the abutting precingular plates (3″ and 5″).

It will be noted that in each of the regions which undergo variation there are only four plates the rearrangement of which is involved in changing from one pattern to the other; that in this quartette of plates it is the diagonally opposite pairs of plates which are either separated or brought into juxtaposition with each other; that only two patterns are possible for each quartette in a given variable region; that one of these patterns must therefore be regarded as the alternate of the other; that the patterns change by the obliteration of the suture between two plates about to be separated in forming the new pattern, and by the formation of a new suture at right angles to the one just obliterated through the newly affected contact of the alternate pair of plates.

With one exception all possible combinations for these plates in this pair of variable regions are known, and are presented in figs. 1 to 8. It may be repeated, then, that in the most fully developed presumably the most characteristic, and certainly the most abundantly

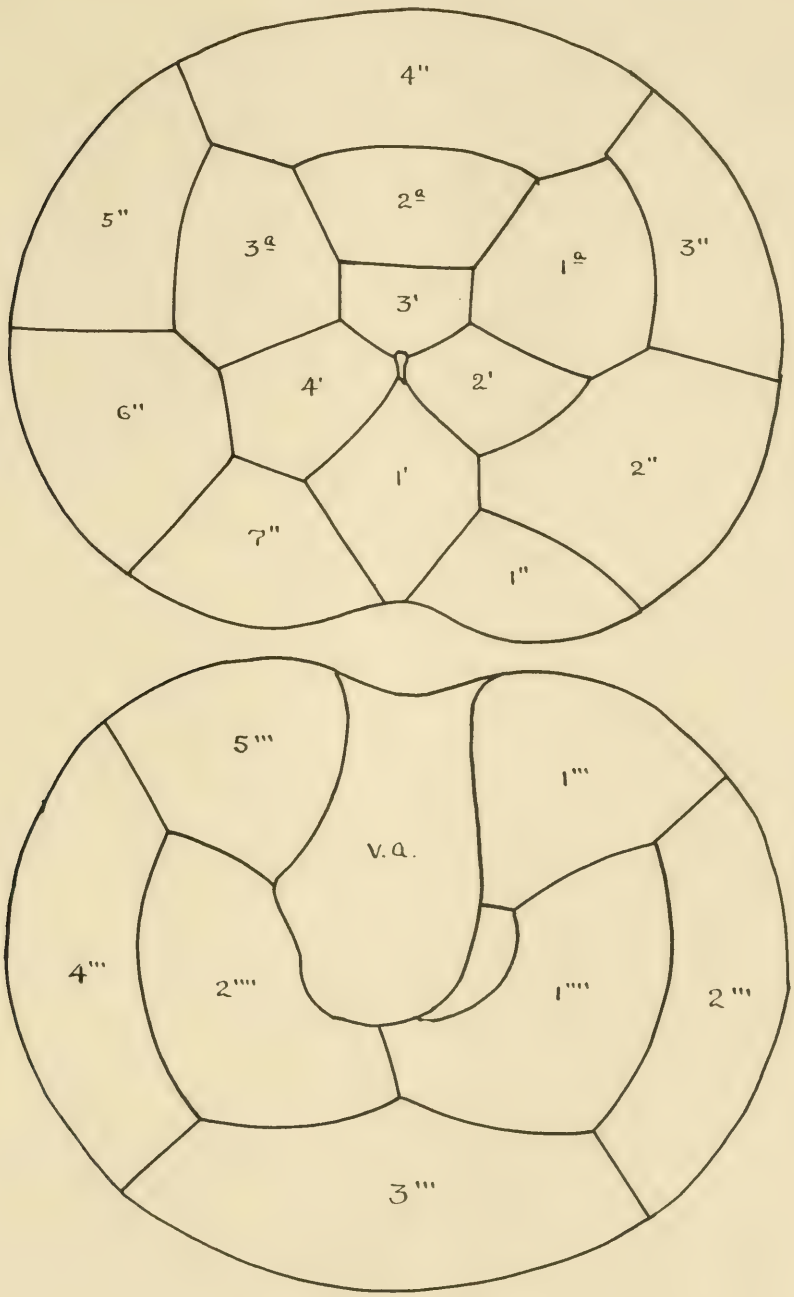


FIG. 19.—Diagrams of the arrangement of plates in a typical member of the genus *Peridinium, P. divergens* Ehrbg., for the epitheca (upper figure) and for the hypotheca (lower figure). The epithecal plate pattern is that of the subgenus *Metaperidinium,* primary division.

represented portion of this genus, both in species and in individuals, in which there are fourteen epithecal plates, variations in the pattern of articulations occur at only four points, and especially that, with the exception of one possible combination of the plates of the ventral region which is as yet unknown, cases have been found illustrating all of the combinations of the plates at each of these four regions which are geometrically possible.

Among specimens examined or among species already figured in literature, examples have been found of all of the possible combinations between figs. 1, 3, and 4 for the ventral patterns and figs. 5 and 6 for the dorsal patterns. The series of known combinations of the dorsal patterns given in figs. 7 and 8 with the three ventral patterns is incomplete, and from evidence which will be introduced later it seems that the patterns of figs. 7 and 8 may represent aberrant forms or forms in which there may have been special attempts at adjustment with unusual conditions of the environment.

Plate Patterns, a Basis for Subdivision of the Genus, *Peridinium*

The fundamental importance of the skeleton in portraying phylogenetic relationships has already been discussed. On this basis we venture to propose that the system of patterns outlined above presents a means for not only accurately describing the species of this genus but also for relating them more or less closely according to a natural order.

Superficially it might be possible to divide the genus into groups either according to the three known patterns for the ventral plates or into four groups according to the dorsal patterns represented, and to subdivide these primary divisions according to the several combinations found between these two sets of patterns. There are certain considerations, however, which make it seem reasonable to regard the variations of the ventral plates as of more fundamental significance than the variations of the dorsal plates.

In genera apparently related rather closely to *Peridinium* there are two ways in which the number of plates is increased. These genera all possess four whorls of plates—apical, precingular, postcingular, and antapical. The simplest method for increasing the number of plates—and this increase seems to be the trend of special-

ization and of evolution in this group—is by the formation of new plates in the row already represented. This method is known to have been carried to considerable development, for instance in such forms as *Pyrophacus,* in which the plate formula is 4 (to 12)′–0^{a}–9 (to 12)″–^{g}–9 (to 12)‴–0^{p}–3 (to 5)⁗. Another method for increasing the number of plates which must involve a greater readjustment of the skeleton is by the addition of what is to become either the anterior or posterior accessory row of plates. Such plates usually make their appearance on the dorsal side of either the epitheca or of the hypotheca. In other genera we do not find this method resorted to until the precingular and postcingular rows have broken up into at least five plates each, and in many genera not until six or seven plates have been formed in these rows. It would therefore seem that the increase of the number of plates to a certain point in the cingular rows is a phenomenon generally prior to occurrence to increase by the addition of an accessory partially complete row, and that increase of plates in an existing row is a simpler and less highly specialized process than the addition of a new row of plates. It seems reasonable to suppose, therefore, that the changes in the ventral plate pattern in the genus, *Peridinium,* are of more fundamental significance than changes in the dorsal pattern.

Moreover, in certain genera closely related to *Peridinium* there is a suggestion that the increase in number of precingular plates comes from the addition of a new plate at one of the ends of this row on the ventral side near the longitudinal groove. Thus in *Gonyaulax,* plate 6″ is very small. A plate introduced at the end of the precingular row of a form ancestral to the genus, *Peridinium,* with its seven precingular plates will probably be small in size in the early stages after its appearance, but as this new plate increases in size to match approximately the size of the other plates of the row it will more and more nearly approach plate 4′ of the preëxisting apical row. Thus in the early stages of the introduction of such plates at either end of the ventral row the ventral plate pattern on the side of the rhomboid plate would be represented by the pattern shown in fig. 1. A later stage representing the full growth in size of one of these plates would be represented in fig. 3, and if growth should take place to the same degree on both sides of the rhomboid plate a pattern similar to that of fig. 4*a* would result. Of the three ventral patterns known, therefore, that of fig. 1 seems to be the more primitive and that of fig. 4*a* the more highly specialized.

There seems, then, to be a broad and sound basis for the division of the genus into the two groups, *Orthoperidinium* and *Metaperidinium,* which Joergensen has defined, and quite as good ground for giving his group *Paraperidinium* correlative standing. We would, therefore, suggest that these names be preserved in common usage for these three subgenera of the genus, *Peridinium.*

Subdivisions of the Genus, *Peridinium*

It is possible, therefore, to divide the whole genus, *Peridinium,* into three subgenera upon a basis which is not only of practical convenience in diagnosis but which also has a natural significance. It might be possible in some or all of these subdivisions to carry the classification according to this system even farther on the basis of the combinations which a given plate pattern might form with the known dorsal patterns. Certainly the characters next in value after the dorsal pattern would be the characters of type of horn, general shape, surface markings, etc.

Of the four dorsal patterns figured, only the first two (figs. 5 and 6) occur extensively. Combinations are known between each of these and each of the three known ventral plate patterns. The two remaining dorsal plate patterns as shown in figs. 7 and 8, are known to be combined with one of more of the three ventral patterns.

Upon our interpretation of these ventral plate patterns and the significance of the series, the group to which Joergensen has given the name, *Paraperidinium,* becomes the first one to be considered, as probably representing the most primitive condition in which the plates 1″ and 7″ at either end of the precingular series are of relatively small size, presumably having been recently introduced. Joergensen's group, *Metaperidinium,* represents an intermediate asymmetrical stage. To distinguish this form from the possible inverse asymmetrical pattern of fig. 2, which is unknown in reality, it may be called *Metaperidinium* (dextrad), and the unknown form, *Metaperidinium* sinistrad.

Joergensen's subgenus, *Orthoperidinium,* becomes, then, the most highly specialized subdivision of the genus.

Paraperidinium.—Taking up first the known forms presenting combinations of the plate pattern of *Paraperidinium* with the symmetrical dorsal plate pattern of fig. 5 we may name the following

species as included in the primary group, *Paraperidinium*. Species presenting the dorsal plate pattern of fig. 6 might be termed as constituting a group of *Paraperidinium* secondary.

P. ovatum Pouchet
(Fauré-Fremiet, 1908, p. 219, fig. 5)
P. cerasus Pauls.
(Meunier, 1910, pl. 2, fig. 27)
P. tristylum Stein
(Stein, 1883, pl. 9, figs. 15 and 16)
(Broch, 1910, p. 187, fig. 5)

These species have not been found by the writer but two instances of what otherwise was clearly *P. divergens* Ehrbg. have been found in which the ventral pattern of *Paraperidinium* was present. Mangin (1911, pl. 7, figs. 10 and 13) has also figured *P. divergens* Ehrbg. in which this unusual pattern has occurred.

A specimen taken to have been derived from a race of *P. oceanicum* Vanh. from Sausalito, California, also shows the ventral plate pattern of *Paraperidinium* with the primary dorsal plate pattern of fig. 5. This combination in this case is explained as due to unusual physical conditions of Sausalito Bay, which have, so to speak, deformed this species characteristic of the open sea.

Species of *Paraperidinium* bearing the dorsal plate pattern of fig. 6 and which may be considered as constituting a group of *Paraperidinium* secondary, include:

P. pallidum Ost.
(Broch, 1910, p. 45, fig. 17)
P. islandicum Pauls.
(Broch, 1910, p. 46, fig. 20)
(Paulsen, 1904, p. 23, fig. 7)
P. pellucidum (Bergh) Schütt
(Paulsen, 1908, p. 49, fig. 62)
P. pellucidum (Bergh) var. *crassum* F. F.
(Fauré-Fremiet, 1908, p. 220, fig. 6)
P. pellucidum (Berg) var. *acutum* F. F.
(Fauré-Fremiet, 1908, p. 221, fig. 7)
P. spinosum, Schiller
(Schiller, 1911, p. 3, fig. 3)
P. curvipes, Ostf.
(Paulsen, 1911, p. 308, fig. 6)
P. rectum Kofoid.
(Pavillard, 1916, p. 40, fig. 17)

This combination has been confirmed in a number of specimens of *P. pellucidum* found by the writer.

The only example which we have met of a combination of the ventral pattern of *Paraperidinium* with one of the asymmetrical dorsal patterns is a figure by Paulsen (1907, p. 15, fig. 18) for *P. granii* Pauls., which agrees well enough with the general concept for *P. granii* in other respects, though specimens of this species which we have seen from Yes Bay, Alaska, carry the ventral plate pattern of *Metaperidinium* with the asymmetrical right oblique dorsal pattern.

Metaperidinium.—Under *Metaperidinium,* which may be called *Metaperidinium* (dextrad) for those species in which the growth of the girdle plates has proceeded unequally and more rapidly on the right side of the organism than on its left, we find combinations with both of the symmetrical dorsal patterns, primary and secondary, and also a combination of this ventral pattern with the asymmetrical dorsal pattern of fig. 7, which may be designated as constituting the group of *Metaperidinium* (dextrad), dorsally right oblique.

Under the group of *Metaperidinium* (dextrad) primary, we find the following species:

P. divergens Ehrbg.
(Stein, 1883, pl. 10, fig. 2; supported by numerous observations of the writer)
P. adriaticum Broch
(Broch, 1910, p. 192, fig. 8, II and III; probably a variety of *P. divergens*)
P. crassipes Kofoid forma *typica* Broch
(Broch, 1910, p. 53, fig. 27)
(Broch, 1910, p. 194, fig. 9)
P. crassipes, forma *autumnalis* Broch
(Broch, 1910, fig. 10, III)
P. quarnerense (Schröder) Broch
(Broch, 1910, p. 184, fig. 3)
P. globulus Stein
(Broch, 1910, p. 182, fig. 2, II)
P. monacanthus Broch
(Broch, 1910, p. 150, fig. 25)
P. brevipes Pauls.
(Paulsen, 1911, p. 313, fig. 13)
P. breve, Pauls.
(Broch, 1910, p. 47, fig. 21)
P. wiesneri Schiller
(Schiller, 1911, p. 2, fig. 2)
P. lenticulatum F. F.
(Fauré-Fremiet, 1908, p. 217, fig. 4)
P. curvipes Ost.
(Broch, 1910, p. 43, figs. 10, 12, and 13)
(Pavillard, 1916, p. 35, fig. 8)

Only one reliable instance of the occurrence of the secondary dorsal plate pattern in *Metaperidinium* is at hand. *P. roseum* Pauls. (Paulsen, 1904, p. 23, fig. 9).

Specimens showing an unequal development of the end plates of the precingular row but in a reverse order from that found in *Metaperidinium* (*dextrad*), and hence to be held for the group which may be known as *Metaperidinium* (sinistrad) if represented, are as yet unknown, if we may except a doubtful figure by Claparéde and Lachmann.

At least two cases are reported of the combination of the ventral plate pattern of *Metaperidinium* (dextrad) with an asymmetrical dorsal pattern, that which we have termed the dorsally right oblique pattern, shown in fig. 7. These are:

P. mite Pav.
(Pavillard, 1916, p. 37, fig. 9)
P. steinii Joerg.
(Kofoid, 1909, pl. 2, figs. 1, 5, and 7)
(Broch, 1910, p. 185, fig. 4)

Perfectly definite examples of a form attributed to *P. granii* have been found in collections in which the ventral plate pattern of *Metaperidinium* is combined with the dorsally left oblique asymmetrical pattern; and similar specimens, presumably of a form of *P. granii* also, have been taken from Union Bay, Alaska, showing the dorsally right oblique asymmetrical pattern.

Orthoperidinium.—In the subgenus, *Orthoperidinium*, the following species are found with the primary dorsal plate pattern, shown in fig. 5:

P. oceanicum Van H.
(Stein, 1883, pl. 10, fig. 1)
P. claudicans Paulsen
(pl. 3, figs. 1 and 2)
P. depressum Bail.
(Broch, 1910, p. 51, fig. 26)
P. parallelum Broch
(Broch, 1906, p. 153, fig. 4)
P. conicum (Gran) O. and S.
(Paulsen, 1908, p. 59, fig. 74)
(Gran, 1902, p. 189, fig. 14)
P. obtusum Karsten
(Fauré-Fremiet, 1908, p. 223, fig. 9)

Forms presenting the ventral plate pattern of *Orthoperidinium* and the secondary dorsal plate pattern shown in fig. 6 are:

P. tabulatum Ehrenberg
(Entz, 1904, fig. 7, a, b)
(Schilling, 1892, pl. 3, figs. 21a, b)
P. bipes Stein
(Stein, 1883, pl. 11, figs. 7 and 8)
(Schilling, 1891, pl. 3, figs. 23a, b)
P. leonis Pav.
(Pavillard, 1916, p. 33, fig. 6)
P. pentagonum Gran
(Gran, 1902, p. 191, fig. 15)
(Paulsen, 1908, p. 59, fig. 76)
P. anthonyii F. F.
(Fauré-Fremiet, 1908, p. 216, fig. 3)
P. typus Bergh
(Fauré-Fremiet, 1908, p. 222, fig. 8)
P. cinctum Ehrenberg
(Bachmann, 1911, pl. 6, fig. 7)
P. conicoides Pauls.
(Paulsen, 1905, p. 1, fig. 2)
P. faeroënse Pauls.
(Paulsen, 1905, p. 5, fig. 5)
P. obtusum Karsten
(Karsten, 1906, pl. 23, figs. 12b, c)
P. subinermis Pauls.
(Paulsen, 1907, p. 19, fig. 26)
P. willei Huitf.-Kaas., (freshwater)
(Schilling, 1913, p. 45, fig. 0)
P. westii Lemm. (freshwater)
(Schilling, 1913, p. 47, fig. 0)

Only one example has been found in literature in which the ventral plate pattern of *Orthoperidinium* has been combined with that of an asymmetrical dorsal plate pattern, in this case that termed the right oblique. This appears in *P. punctulatum* Pauls. (Paulsen, 1907, p. 19, fig. 28). This combination has also been found by the writer in a collection from Sausalito, California, in a specimen which

in all other respects except that of the dorsal plate pattern corresponds with the usual concept for *P. claudicans* (see pl. 19, figs. 1 and 2).

In addition to these examples just quoted there are a number of other species which a liberal interpretation of the definition of the genus, *Peridinium*, would include. In all of these additional species, however, the number of dorsal accessory plates is less than three, usually two. These forms also all fall into the group, *Orthoperidinium* and, strangely enough, they are, many of them, inhabitants of fresh water. In most of these forms the two accessory plates are symmetrically placed but may be grouped either as shown in figs. 10, 11, or 12. These figures represent all the possible ways in which two accessory plates could be interpolated among the preëxisting plates.

Only one species is definitely reported as having the two accessory plates arranged as in fig. 10:

P. quadridens Stein (freshwater)
(Stein, 1883, pl. 11, figs. 4, 5, and 6)
(Schilling, 1913, p. 38, fig. 41)

Among the species having the two accessory plates arranged as in fig. 11 are:

P. umbonatum Stein (freshwater)
(Stein, 1883, pl. 12, figs. 2, 4, and 6)
(Schilling, 1891, figs. 25a and b)

P. trochoideum (Stein) Lemm.
(Lemmermann, 1910, p. 336, figs. 33–36)

P. pusillum (Pen.) (freshwater)
(Schilling, 1913, p. 41, fig. 45)

P. achromaticum (Lev.) (freshwater)
(Ostenfeld, 1908, pl. 5, figs. 42–43)
(Schilling, 1913, p. 44, fig. 50)

P. marchicum Lemm. var. *javanicum* Wol. (freshwater)
(Woloszynska, 1912, p. 702, fig. 25)
(Schilling, 1913, p. 42, fig. 47)

Among the species having the arrangement of the two dorsal accessory plates as shown in fig. 12 are:

P. laeve Huitf.-Kaas (freshwater)
(Huitfeld-Kaas, 1900, pl. ? fig. 3)

P. aciculiferum Lemm. (freshwater)
(Schilling, 1913, p. 39, fig. 42)

P. multipunctatum F. F.
(Fauré-Fremiet, 1908, p. 227, fig. 12)

P. thorianum Pauls.
(Paulsen, 1905, p. 1, fig. 1)

P. monospinum Pauls.
(Paulsen, 1907, p. 12, fig. 11)

P. latum Pauls.
(Paulsen, 1908, p. 41, fig. 48)

P. minutum Kofoid
(Kofoid, 1907, pl. 30, figs. 42–43)

Beside the species just enumerated as having dorsal plate patterns of figs. 10, 11, and 12, which are fairly symmetrical, there are at least three species in which the two dorsal accessory plates are disposed of in a very asymmetrical pattern:

P. excentricum Pauls.
(Pavillard, 1916, p. 31, fig. 4)
P. paulseni Mangin
(Mangin, 1912, p. 226, fig. 12)
P. perrieri Fauré-Fremiet
(Fauré-Fremiet, 1908, p. 228, fig. 14)

A single report is extant of a species of *Peridinium* without any anterior dorsal accessory plates. This is *P. umbonatum* var. *elpatiewskyi* Ost. (Ostenfeld, 1907, pl. 9, figs. 9, 10a, and b). The plate arrangement in this case is that of fig. 9. Although attributed to the genus, *Peridinium*, it is doubtful whether, because lacking all accessory plates, this form should not be transferred to another genus. No report is known to the writer of the occurrence of a species of *Peridinium* with one accessory plate.

Special Considerations.—These lists could doubtless be enlarged by a more complete comparison of published figures and descriptions with material from dinoflagellate collections, were such always obtainable. The instances which are given here are taken from the figures which have been drawn with sufficient clearness to serve in this analysis or from the species the plate patterns of which have been confirmed or completed from observations by the writer. These species selected for mention also represent all the possible categories of plate pattern, ventral and dorsal, and the possible combinations between these patterns as completely as are known.

It is thus seen that all the six possible combinations between each of the two dorsal symmetrical plate patterns are represented by one or more, usually several species. The ventral plate pattern of the subgenus, *Paraperidinium*, is known also in combination, but probably as a sport, with one of the asymmetrical dorsal plate patterns, that termed dorsally right oblique. The group *Metaperidinium* (dextrad) is known in combination, regularly or exceptionally, with examples of both of the asymmetrical dorsal plate patterns; and the group included in *Orthoperidinium* is known, through a single report, in combination with one of the asymmetrical dorsal plate patterns, that termed dorsally right oblique.

The fact that we find the only species having but two dorsal accessory plates in the group, *Orthoperidinium*, which, it seems, must be

the most highly specialized of the three divisions of the genus, *Peridinium,* is further support for the suggestion that the modifications of the ventral plate pattern are of more fundamental significance than the interpolation of the dorsal accessory plates, because the development of the ventral plate patterns seem to have been able, at least in certain races of *Orthoperidinium,* to run through its full course before the addition of the third accessory plate.

Supporting also the view that the increase in number of the precingular plates comes from the addition of a new plate, at first small, at one end of this row near the rhomboid plate is the case of *P. minutum Kofoid* var. *tatihouensis* Fauré-Fremiet (1908, p. 227, fig. 13) in which there is at the right hand end of the precingular row a very small plate, the *eighth* in this row. In this species there are still but two dorsal accessory plates, and these are arranged as in fig. 12. The ventral plate pattern is, moreover, that of *Orthoperidinium.*

The group, *Orthoperidinium,* presents itself to us, perhaps, as a portion of the genus which because of its high specialization is in a condition of depletion in a manner "running out" and groping about in a desperate fashion for some combination of its parts which may again render it stable. It seems to be a portion of the genus which is "fraying out." This suggestion is all the more emphasized by the large number of irregular and unusually asymmetrical forms which it contains. In addition to those already mentioned in which the accessory plates are reduced to two in number, usually symmetrically placed, other forms such as *P. marsonii* Lemm. may be mentioned in which the structural system in this part of the genus seems to have broken down even more completely and all traces of symmetry in the arrangement of the epithecal plates have been lost.

Summary of Changes of Plate Pattern within a Species.—Among the figures in literature and among the observations of the writer several cases have come to light illustrating what is apparently a change in plate pattern within a given species; that is to say, the plate patterns found in two individuals are different while all the other characters agree to such an extent as to compel placing these forms in the same species.

1. *P. ovatum* Pouchet has been reported by Fauré-Fremiet (1908, p. 219, fig. 5) with an arrangement of ventral plates according to a pattern which Joergensen (1912) later termed that of *Paraperdinium,* and with the primary symmetrical dorsal plate pattern which is illustrated in fig. 5 of this paper; and again by Broch (1910, pp. 40

and 41, figs. 9 and 10) with the ventral plate pattern of Joergensen's subgenus *Metaperidinium*.

2. *P. granii* Pauls. has been figured by Paulsen (1907, p. 15, fig. 18) with the ventral plate patterns of *Paraperidinium* and the asymmetrical right oblique dorsal pattern of fig. 7. What is presumably this same species has been found in Sausalito Bay, California, with the *Metaperidinium* pattern for the ventral plates and with the asymmetrical left oblique dorsal pattern of fig. 8; and in still a third condition with the right oblique dorsal plate pattern and pattern of *Metaperidinium* for the ventral plates in forms from Union Bay, Alaska (pl. 17, figs. 1 and 2; and pl. 18, figs. 3 and 4).

3. *P. claudicans Pauls.* is usually found with the ventral plate pattern of *Orthoperidinium* and the primary symmetrical dorsal plate pattern of fig. 5. However, specimens from Sausalito, California, present a dorsal pattern of the right oblique type (fig. 7, pl. 19, figs. 5 and 6).

4. In the same Sausalito collection as that just referred to was also found a specimen of what was probably a deformed race of *P. oceanicum* Van H., which was remarkable in displaying the ventral epithecal plate pattern of the subgenus *Paraperidinium* instead of the usual pattern for *P. oceanicum* Van H., that of *Orthoperidinium* (pl. 20, figs. 7 and 8).

5. The species *P. divergens* Ehrbg. is usually found with the ventral plate pattern of *Metaperidinium* and the primary symmetrical plate pattern of fig. 5. Two specimens out of sixty-three examined by the writer have been found with a ventral plate pattern of *Paraperidinium,* and this combination has also been figured by Mangin (1910, pl. 7, figs. 10 and 13).

Summary of Skeletal Relationships.—We are dealing then with the skeleton, the most permanent of the structures of this organism, but a structure which undergoes certain modification even in the life of the individual. From genus to genus within the family, Peridinidae, we find this skeleton undergoing variations in regard to the number of its plates. We find that in this family the number of plates is increased first by additions in one or another of four fundamental rows. In this progressive increase in number of plates the antapical row usually contains the least number of plates, often not more than two. The apical row contains more plates than the antapical but usually fewer plates than either of the cingular rows. Of these cingular rows it is the precingular in which the number of

plates seems to increase most rapidly, and the latest additions to this row seem to be produced by the addition of plates, small in size at first, on the ventral side at either end of the precingular row and next to the rhomboid plate, which must be considered as belonging to the apical row but which interrupts the precingular row on account of its extent from the apex to the girdle.

At a certain stage in the progressive multiplication of the plates of this shell in this family, an accessory plate or an incomplete row of plates makes its appearance either on the dorsal side of the hypotheca between the antapical and postcingular rows or more often on the dorsal side of the epitheca between the apical and precingular rows. The number of plates in the postcingular accessory row rarely exceeds two in number and that in the anterior accessory row rarely exceeds three in number.

The genus, *Peridinium,* by definition, perhaps largely fortuitous or conventional in its formation, is made to include forms having a definite number of plates in the four main rows, no posterior accessory plate and either two or three anterior accessory plates. In the greater number of known species coming under this general definition there are three anterior accessory plates arranged continuously in a row over the dorsal part of the epitheca between the apical and precingular rows. Those species in which the number of accessory plates is less than three are readily related to the major part of the group. This reduced number of accessory plates is to be regarded as a preliminary condition introductory to the later condition of three such plates represented in the greater portion of the genus, or as of secondary acquisition due perhaps to more or less of a readjustment upon transfer to fresh-water conditions from estuarine conditions on the part of fresh-water forms, most of which present such a reduced number of accessory plates. For some reason the number of these accessory plates seems in the majority of the species of this genus to have become three in number but never to have exceeded this number. No instance is known to the writer of only one accessory plate, but at least one form has been reported with no accessory plates, which nevertheless conforms to the other characters of the definition of this genus.

Regions of Variation in the Shell of *Peridinium*

Variable Regions.—We are able to recognize in the *Peridinium* shell only four general regions in which the number of skeletal plates, so fundamental a character in this group, is undergoing change, and these regions are significant in being closely related to the phylogeny within the family to which this genus belongs.

These areas of skeletal variation are in the region of the two opposite ends of the precingular row of plates, which is interrupted by the long rhomboid plate of the apical row, and in the region of the recently acquired incomplete row of these dorsal accessory plates.

In the greater part of the genus, that characterized by having three dorsal accessory plates, there is then a constant number of plates and there are only four regions in which rearrangement of these plates seems to take place. More particularly these four places, in which the rearrangement of plates is known to occur, may be regarded as two pairs of variable regions, and both of these pairs of regions occur on the epitheca, for no plate variations are known in this genus on the hypotheca except within the longitudinal groove, and these are undoubtedly not of correlative importance with the variations of the major plates of the skeleton.

On the epitheca we are then dealing on the ventral surface with variations involving the size of plates 1″ and 7″ and with alternations in plate pattern where the anterior apices of these plates articulate with the adjacent plates, *i.e.*, for plate 1″ with plates 2″, 1′ and 2′, and for plate 7″ with plates 6″, 1′, and 4′.

In addition to the evidence of the clear progressive development of this line of variation in plate number in genera related to *Peridinium* and of the comparison of the small size of these plates 1″ and 7″ in the most closely related genera, we find that in *Peridinium* these plates vary in size and that the plate patterns or patterns of the sutures of articulation vary in this region as may be necessary according to the size of these two plates.

That these variations in plate pattern are not due to varying size of the rhomboid plate, plate 1′, is evident because of the nearly uniform proportion in size which this plate maintains in relation to adjacent plates throughout most of the species of this large genus. In no species is the rhomboid plate known to expand to the unusual

degree necessary to meet plates 2″ or 6″ without the growth, which is unknown, of these plates to meet it half way. On the other hand, it is easy to see how plates 1″ and 7″, beginning, as it were, as small plates, budded off from plates 2″ and 6″ when these latter were the end plates of the precingular row and may by increasing in size have inserted themselves between plates 1′ and 2″ on the left hand for plate 1″ and between plates 1′ and 6″ on the right hand for plate 7″ until this primary articulation is completely destroyed and plate 1″ has come to meet broadly plate 2′, and plate 7″ to meet plate 4′. We have thus before us the ventral plate patterns of the known stages for the three subdivisions of this genus proposed by Joergensen. First is that of *Paraperidinium* represented by our fig. 1 in which there is only a small precingular plate at each end of the precingular row adjacent to the rhomboid plate. A stage preliminary to this may be found in *Gonyaulax,* for example, in which but one such small plate, that of the right hand, has as yet split off. It is significant to note also that this plate first seems to split off on the right hand end at the beginning of this series of development and that later in the series it is found that the right side proceeds more rapidly in development than the left side, which seems to lag, while one stage of development on the left side seems in present faunas not to be represented at all. Secondly, the plate pattern of *Metaperidinium* is that in which the precingular end plate on the right side has increased in size until it meets plate 4′, completely separating plates 1′ and 6″. The corresponding asymmetrical stage in which the precingular plate on the left end has increased rather than that on the right end seems not to be known. Finally, we find the pattern represented in *Orthoperidinium* in which both the end plates of the precingular row have increased uniformly, or if one pleases to so regard it, in which plate 1″. on the left, has caught up with the maximum development of plate 7″ which can be permitted by the pressure of surrounding plates or by its own capacity to hold together.

Turning now to the dorsal surface of the epitheca, we find that in that portion of the genus having three accessory plates the variations in plate pattern occur in a pair of regions at or near the anterior corners of the mid-dorsal precingular plate, 4″. Among possible explanations for the variation of the suture pattern at these points, we may note that these variations may be due to the increasing size of the mid-dorsal precingular plate, 4″, so as to crowd the middle accessory plate and effect an articulation with the lateral accessory plates

which did not obtain in the primary condition. This explanation, however, seems improbable, since in all other related genera there is no suggestion that this mid-dorsal plate undergoes a great development in advance of its fellows in the precingular row.

That the mid-dorsal precingular plate does vary somewhat more than its neighboring precingular plates, however, appears from the fact that in those specimens having a small middle accessory plate with the plate pattern of fig. 5, the mid-dorsal precingular, 4″, occupies a greater arc of the equatorial circumference of the organism than in those species in which the middle accessory plate is large with the pattern of fig. 6. There seems, then, to reside in the mid-dorsal precingular plate, 4″, some capacity for variation in relative size from species to species, though there are other considerations to suggest that the major stimulus for a real change in plate pattern may take effect in the middle accessory plate just anterior to it. Moreover, since it is probable that the accessory row of plates is of the more recent introduction, phylogenetically, in the skeleton of *Peridinium*, it seems probable also that these plates are in a more plastic condition than the plates of previously existing rows.

It seems, then, that we may consider only the probability that the seat of alteration of dorsal plate patterns lies among these lately introduced plates of the accessory row. If so, is the center of expansion by which articulations are changed, seated in the middle accessory plate or symmetrically in the lateral accessory plates or in all these plates of the accessory row? Upon regarding the proportionate size of each of these three plates to the adjacent plates of the skeleton, it appears that among the species illustrating the changes in dorsal pattern the middle accessory plate varies more widely than the lateral accessory plates relatively to the size of the adjacent plates, while the lateral accessory plates undergo but comparatively slight variation in size. It seems probable, then, that in the part of this genus containing these accessory plates it is the middle one which is the more plastic or the more variable.

Origin of the Accessory Plates.—Of peculiar significance just here is the absence of any example of a single accessory plate in this genus. The accessory plates which first appear, do so as a pair, apparently in response to a stimulus applied symmetrically on the anterior dorsal region, and it is in connection with the symmetrical effect of this stimulus for the interpolation of an accessory row of plates that the significance of the absence of any form displaying a single accessory

plate lies. This pair may appear in one of two ways: either, apparently as an increase in the number of apical plates from four to six by the addition of two new plates arising at the dorsal corners of apical plates 2′ and 4′. These may have increased in size until they reached the apex (as shown in fig. 10) and come to simulate apical plates, though really of secondary origin. This arrangement of plates is illustrated by very few species. If these accessory plates, however, arose from the posterior corners of apical plate 3′, their increase in size may at first have produced the arrangement of plates given in fig. 11, and later that of fig. 12. Examples of all of these patterns have just been mentioned (see p. 410). At this stage, however, a single unpaired plate may have made its appearance just posterior to the junction of the two newly developed accessory plates shown in fig. 12, *i.e.*, at the anterior point of the mid-dorsal precingular plate of this figure, or just anterior to the junction of the two accessory plates at the posterior corner of the mid-dorsal apical plate (3′).

Here, then, are two lines of development suggested for the introduction of the accessory plates. The first, that shown in fig. 10, seems to have permitted no further progress, while the second, that illustrated in figs. 11 and 12, seems to have been that leading to such an arrangement of plates as is shown in fig. 5, and found in a large number of species of this genus. This in turn by increasing growth of the middle accessory plate probably led to the arrangement of plates shown in fig. 6, also frequently found among species of *Peridinium*.

The absence of a single unpaired accessory plate need not be regarded, however, as out of harmony with the occurrence of single accessory plates described for such genera as *Ceratocorys*, *Spiraulax*, and *Heterodinium*, since the accessory plates in these genera occur asymmetrically and in *Ceratocorys* not at all in the same region as in *Peridinium*. Moreover, the occurrence in *Peridinium* of two accessory plates together, as in the first instance, may be but the complete symmetrical progression of the same sort of development which produced but a single such plate on the right shoulder of *Spiraulax* or *Heterodinium*, and we may yet expect to find a similar asymmetrical *Peridinium* caused by some aberration or partial inhibition in its normal development, unless in fact one of these other genera may itself represent this asymmetrical stage.

It is doubtful, however, from which plate or plates these two accessory plates may have come. The fact that in many other species the mid-dorsal precingular plate, 4″ seems to possess a certain plasticity

suggests that these two accessory plates may have been budded off from the anterior corners of that plate (4″). The subsequent budding off of a third and median plate from the now single and median corner of the mid-dorsal accessory plate, 4″, or from the posterior corner of the mid-dorsal apical plate, 3′, would provide the third accessory plate, found characteristically in this genus.

On the other hand, the occurrence of such a species as *P. quadridens*, in which there are apparently six apical plates, two of which may, however, be interpreted as accessories, suggests that the two lateral accessories may have arisen from buds from the two lateral apical plates, 2′ and 4′. These plates would have forced what was originally the mid-dorsal apical plate, 3′, into the future position of the middle accessory plate, and a bud from the anterior corner of this plate may have formed another plate to take the place of the mid-dorsal apical plate just removed. The varied articulations of the mid-dorsal accessory plate, 2*a*, do not make clear, however, the manner by which these variations can be connected with this method of origin, and we are inclined, on the whole, to favor the hypothesis that the two lateral accessory plates arose in the region of the anterior lateral corners of the mid-dorsal precingular plate, 4″.

The middle accessory plate may have originated in one of at least two ways; either as a bud from the anterior corner of the mid-dorsal precingular plate, now projecting more or less between the two lateral accessory plates already formed, or the middle accessory plate may have been formed from a bud from the posterior corner of the middle apical plate, 3′. This latter suggestion seems most readily to fit in with the subsequent development of the middle accessory plate and the readjustment of the lateral accessory and other plates due to its enlargement. In the absence of definite evidence to suggest a contrary view, we are inclined to favor the origin of the middle accessory plate from a different source than that from which the lateral accessory plates may have come, and probably from the region of the anterior median corner of the mid-dorsal precingular plate secondarily after the formation of the lateral accessory plates (1*a* and 3*a*).

Evidently the forms produced in these early stages, if this hypothesis be correct, were not stable, and evolution seems to have proceeded at once to the formation of more fully specialized forms having three well-developed accessory plates. In this condition the genus seems to have settled down into approximate equilibrium and durability. Species illustrating fully all of the early stages through which this pro-

cess of evolution may have passed, by showing many different sizes of the accessory plates, seem now to be lacking, possibly having perished as unsuited for some reason to the conditions under which they would have been compelled to live. These conditions, in fact, themselves changing, may have been the stimulating cause for this series of steps in the development of this genus. Though now missing from our peridinian fauna as at present known, it is not impossible, however, that under certain conditions which might upset the equilibrium of species which find their way into bays, brackish areas, etc., reversions to or repetitions of the early stages of this development may occasionally be found.

Be the origin of the accessory plates as it may, we find the greater portion of the genus characterized by having three accessory plates, with at least four patterns for the arrangement of the constant number of plates in this general mid-dorsal region of the epitheca, two symmetrical patterns and two asymmetrical.

Origin of the Principal Symmetrical Dorsal Plate Patterns.—In this portion of the genus we may suppose, then, that at a stage shortly after the development of the third discreet accessory plate this plate became of approximately the same size as the two lateral accessory plates. At this stage the plate pattern would be that of fig. 5, the middle accessory plate having met the anterior edge of the mid-dorsal precingular plate, 4″, and flattened out against a considerable portion of the anterior margin of this plate.

By a continuation of skeletal growth in this region of the shell, which seems to be one of plasticity because of the recent introduction in this region of these additional plates, plate 2*a*, the middle accessory plate, may be presumed to have continued to increase in size. At any rate, this plate is found to vary in proportionate size as compared with adjacent plates.

When of its smallest size the middle accessory plate presents together with the adjacent plates the pattern of fig. 5, which is characteristic of such forms as *P. divergens* Ehrbg., *P. crassipes* Kofoid, and *P. oceanicum* Van H. When of a larger size it seems to have spread still farther along the anterior edge of the mid-dorsal precingular plate, 4″, and to have intruded itself between the former articulations of plates 1*a* and 4″ on the left and plates 3*a* and 4″ on the right separating these plates entirely and reaching to plate 3″ on the left and to plate 5″ on the right, presenting the plate pattern of fig. 6, one which is characteristic, for example, of *P. conicum* (Gran) O. and S.,

P. islandicum Pauls. and *P. tabulatum* Ehrbg. These are the two dorsal plate patterns most frequently found in this genus.

Origin of the Asymmetrical Dorsal Plate Pattern.—Aside from patterns caused by a reduced number of plates, there are, however, two other patterns which are occasionally represented, and, curiously enough, usually among forms taken from bays or sounds or regions in which the regularity of the physical conditions of the open sea are somewhat interfered with or altered. These two patterns are asymmetrical and are caused apparently by the greater development of one side, or of one lower or posterior corner of either plate 2*a* or 4″. We have assumed that the initiative for these readjustments lies in the region of the posterior corners of plate 2*a* as the newest skeletal member of a presumably plastic portion of the shell rather than in plate 4″. which forms part of a phylogenetically much older portion of the shell, although the shape and to some extent the size of plate 4″ seem to be more or less altered, conversely to plate 2*a*, to meet its changes.

By the development of the posterior left corner of plate 2*a* the pattern of fig. 7 is formed and this in the experience of the writer is the more common of these two asymmetrical patterns. It will be seen to be a combination of the patterns of figs. 5 and 6, and has been found by Miss Bathgate in San Francisco Bay material as well as by the writer (pl. 19, figs. 5 and 6).

By the greater development of the posterior right hand corner of plate 2*a* the pattern of fig. 8 is formed. This pattern has been figured by Joergensen (1902, p. 7).

There are, of course, other explanations which can be given for the origin of these several dorsal patterns. The two skew or asymmetrical patterns may have been formed by a sliding of the row of accessory plates over the row of precingular plates because of some force, probably internal, which may have pushed the whole row over. This suggestion, however, seems rather improbable because it attempts to account for the formation of the skew patterns on a hypothesis separate and of a different order from any upon which the original formation of these plates can be accounted for, and also because no other adjustments of surrounding plates are to be noted, as would be expected from a readjustment so great as the shifting of the position of three plates in so prominent a position as that in which the accessory plates are.

Summary of Discussion of Dorsal Patterns.—It seems, then, that the accessory plates appear first in the genus as a symmetrical pair

and that later a third plate is added between them, making the number three characterstic of the greater part of the genus. Upon the changes of articulation of this middle accessory plate, 2*a*, are rung four changes of plate pattern, depending largely upon the degree of growth and symmetry of growth of this plate. Under the symmetrical development of the plate the patterns of figs. 5 and 6 only are produced. By the unequal development of what are apparently a pair of centers of change, either pattern of figs. 7 or 8 is produced. These latter patterns appear under conditions of unusual modifications of the environment, and these changes in pattern involve the articulations of plates in the vicinity of the anterior corners of the mid-dorsal precingular plate, 4″.

The presence, however, of the two skew patterns, the reverse of each other, shows that a double center of variation or a pair of variable areas are involved, and that, whereas in the majority of cases the development in these two centers proceeds at a uniform rate, there are cases in which for some reason this balance is upset, one center developing more rapidly than that on the opposite side, producing as a result the asymmetrical dorsal plate patterns of figs. 7 and 8.

Paired Areas of Change of Plate Patterns

The fact is striking that there are on the ventral and also on the dorsal surfaces of the skeleton of the epitheca paired areas of change of plate pattern which seem to be due to some internal stresses which at first seem to have made for the production of additional plates in the history of the forerunners or early members of the genus and which later seem to have manifested themselves in modifying the arrangement of a constant number of plates.

The pair of variable ventral areas present coincident modifications in two subgenera of the genus, *Paraperidinium* and *Orthoperidinium*, but may vary independently of each other, as is shown in *Metaperidinium*. Strangely enough, a fourth group to be represented by the reverse asymmetrical pattern from that of *Metaperidinium* seems not to be found in our present fauna. Its absence, however, is to be regarded as of only negative significance.

Similarly, the variable dorsal areas usually develop coincidently, but under certain circumstances behave individually. It may be

noted that whereas the asymmetrical ventral pattern is known in a widely distributed portion of the genus represented in all seas, the asymmetrical dorsal patterns are found usually, except for such a form as *P. steinii* Joerg., in specimens which have come from a region of more or less modified environment from that of the high seas or open coast, and also that the dorsal asymmetry, among species reported, seems to be the more often produced by growth upon the left side of the middle accessory plate than upon the right side. As evidenced in *Metaperidinium*, it is on the right side, however, that development seems to proceed the more rapidly, and forms having a development of the newly acquired precingular plate, which is more rapid on the left side than on the right are unknown.

Here there are apparently four potentially independent characters, which, however, more often than not, behave in dorsal and ventral pairs.

A second important consideration is that there is apparently no particular connection between the dorsal and ventral pairs and, as will be shown later, a full set of combinations is known between both symmetrical patterns of the ventral side and the symmetrical patterns of the dorsal side, and a number of the possible combinations of these patterns with the asymmetrical patterns of both ventral and dorsal sides are also known.

It seems not impossible also that the character of a pair of horns on the hypotheca, which may or may not be developed to approximately the same degree, may be correlated with the influence making for the frequent pairing of the right and left characters of plate variation. Also, the initial occurrence of a *pair* of dorsal anterior accessory plates symmetrically placed, instead of a single accessory plate upon perhaps the left shoulder, as in *Heterodinium*, is of particular significance in connection with the occurrence of these other features in pairs by emphasizing the fundamental and natural condition of bilateral symmetry in this genus. If this be related here as elsewhere to a method of rectilinear locomotion, it is suggestive of the supersedence of a structural response to locomotion of this sort over the structural response suggested in the torsion of the shell by the addition of but a single accessory plate in other genera as a concomitant of the spiral method of locomotion and the oblique strains set up by this method.

Completeness of the Series of Variations

Geometrical Patterns Represented.—Another significant fact is that, given the constant number of plates on the ventral surface of the epitheca, all possible geometric combinations of these plates are represented among the species of this genus, except for the unknown group which should have the asymmetrical pattern, the reverse of that of *Metaperidinium*, and which we may call *Metaperidinium* (sinistrad).

Similarly, on the dorsal side, given the constant number of plates after the full development of three accessory plates, all geometric combinations possible about the pair of dorsal regions of variability are known.

This complete series of combinations makes it possible to suggest the manner by which these changes in plate pattern occurred and confirms our confidence in the hypothesis suggested for the sequence of these changes. The completeness of this series of combinations also suggests the great individuality of each region of variability as a character capable of variation independent, at times at least, of all of the other similar characters of change; and again, the great extent to which this group of organisms seems to have expanded, occupying all avenues of variation possible with a given structure.

Completeness of Combinations of Patterns.—Dealing first with the symmetrical patterns, both ventral and dorsal, we find that species are known representing combinations of the symmetrical ventral patterns of both of the subgenera, *Paraperidinium* and *Orthoperidinium*, with both of the symmetrical dorsal patterns as represented in figs. 5 and 6. The patterns of the subgenus, *Metaperidinium*, also are known in several species in combination with both of the symmetrical dorsal patterns.

It appears, therefore, that all of the combinations possible, six in number, between the two symmetrical dorsal plate patterns and the three known ventral patterns are represented more or less abundantly in the peridinian fauna. This circumstance again confirms the independence of the characters represented by the different patterns and the wide range of the trials by which nature seems to have coupled these characters of plate patterns together, and also the success which combinations of plate arrangement according to the three ventral plate patterns, two of which are symmetrical, with the symmetri-dorsal pattern.

The combinations of the asymmetrical dorsal plate patterns with the ventral plate patterns are less complete, possibly because less fully known, and it is to be expected that under certain circumstances the missing combinations may still be found occasionally, with the ever-increasing intensity of our examination of this group. At present the ventral plate pattern of the subgenus, *Metaperidinium,* is known to occur in combination with both of the dorsal symmetrical plate patterns, and at least one instance, in the case of *P. punctutatum* Pauls., is known for the combination of the ventral plate pattern of the subgenus, *Orthoperidinium,* with the right oblique asymmetrical dorsal pattern.

That portion of the genus having but two accessory plates is altogether confined to the subgenus, *Orthoperidinium.* This pair of accessory plates seems to have appeared in two methods: one, that shown in fig. 10, seems to have been able to proceed no further than this first stage; the other, shown in fig. 11, with increase in size of this pair of accessory plates, might have formed a pattern such as that of fig. 12, from which the full complement of three accessory plates as shown in figs. 5 and 6 might have developed. All of these combinations of symmetrical dorsal and ventral figures are known in *Orthoperidinium,* and also combinations with various asymmetrical patterns.

The unexpected combination of an early or primitive type of dorsal pattern, involving but two accessory plates, with a late or specialized type of ventral pattern, that of the subgenus, *Orthoperidinium,* may perhaps be explained for some of these species on the basis that many of these forms are derived from brackish water or marine progenitors, and having undergone an unusual transition upon being transferred to a body of fresh water, an intrinsic subordination of the introduction of dorsal accessory plates to the accession of ventral precingular plates may have become accentuated. The fact that nearly all freshwater species have the combination of plate patterns first described may be accounted for upon the basis that species of the subgenus, *Orthoperidinium,* are much more common than those of either of the other subgenera of *Peridinium,* and furnish the more frequent chance for accidental transfer. In such a form as *P. excentricum,* having one small and one very large accessory plate, it is not impossible that a secondary fusion may have occurred between the middle and right accessory plates.

Variations in the Length of Critical Sutures

Further light upon the manner of change of plate pattern may come from an examination of the varying length of the sutures in these variable areas, particularly of those sutures which drop out and of those new ones which are formed in the transposition from one plate pattern to the next. It will be recalled that the dorsal plate pattern of *P. divergens* Ehrbg. is that of fig. 5. The only known symmetrical change in this pattern involves the obliteration of the suture lines between plates 1*a* and 4″ and plates 3*a* and 4″ by the enlargement of plate 2*a* so as to establish articulation expressed by the sutures between plates 2*a* and 3″ and plates 2*a* and 5″. In a long series of personal observations and from an examination of published figures of *P. divergens,* the writer is not aware that this typical dorsal plate pattern for *P. divergens* is ever altered in this species. Measurements of these critical sutures, between plates 1*a* and 4″ and plates 3*a* and 4″ have been made for a total of forty-four specimens taken at random in groups of from six to eleven specimens from each of six regions: Yes Bay, Alaska; two localities in the vicinity of San Diego, California; from Christineberg in the Skagerak; from Cette on the Mediterranean; and from Naples. The results of these measurements are expressed in the accompanying chart (fig. 17), which shows that the range of variation for the length of this suture is from .0405 to .1810 of the transdiameter with a double crested norm with maxima at .07 and .09. It is to be noted that in no one of these instances measured did the length of this suture fall below .04 of the transdiameter of the specimen.

The length of the corresponding suture between plates 3*a* and 4″ passes through a somewhat similar range of variation from .0405 to .2134 of the transdiameter with a double crested norm and maxima at .06 and .08 and with no measurement less than .04 of the transdiameter.

The critical sutures of the variable areas of the ventral side of the epitheca have also been measured for most of the same specimens and for a few others, totaling again forty-four specimens, with the result that the length of the suture between plates 4′ and 7″ has been found to range in this series from .027 to .1101 and in one instance to .1397 of the transdiameter, with again a double crested norm with maxima at .05 and .08 (fig. 18).

On the opposite side of the rhomboid plate the suture between plates 1′ and 2″ was found to range from .0620 to .2389 and in one instance to .3221 of the transdiameter, the summation of the measurements of this suture giving a triple crested curve with maxima at .13, .15, and .17. The lowest maximum is so slightly separated from the rest of the curve, however, as to be probably of no significance. The occurrence of two maxima consistently in this analysis seems to be accidental and is doubtless correlated with the derivation of these specimens as geographic races from several widely separated sources, though the cause for the double crested curve is not directly apparent even upon examining suture measurements for the specimens from each region. The crests are separated in a given curve by only two units of measurement on the ordinate axis, and such a segregation may be due to the reduction of the measurements for plotting to the nearest integral number of hundredths of the length of the transdiameter of the organism.

It is to be noted that the length of the suture between plates 4′ and 7″ and plates 1′ and 2″ in no case fell below .027 of the transdiameter and that the length of the suture between plates 1′ and 2″ did not fall below .0617. In this connection a further observation is of peculiar significance. In a longer series of specimens of *P. divergens,* sixty-three in number, observed by the writer, two specimens were found which presented not the usual ventral patterns for *P. divergens* but the pattern for the subgenus *Paraperidinium.* These specimens were, however, characteristic of *P. divergens* in all other respects. Mangin (1911, pl. 7, figs. 10 and 13) also figures two specimens in which the same modification of plate pattern is found in specimens which must still be assigned to the species *P. divergens.*

We cannot but infer from these records, therefore, that occasionally the plates of the ventral side of the epitheca of *P. divergens* present a plate pattern which, upon the basis proposed for the derivation of these plates, must be regarded as more primitive than the pattern usually presented by this species in this region. It seems, therefore, that occasionally, as if inhibited by some factor, or perhaps if not stimulated as much as usual, plate 7″ in some specimens does not grow to its usual size, and does not quite reach plate 4′, nor fully separate plates 1′ and 6″. Here, then, appears to be a case of certain instability in respect to this one potentially variable region, involving not only the minor variations in lengths of sutures, which is to be expected, but involving also variations in the size of certain plates

usually contiguous—an instability of so great a moment as to produce a plate pattern very different from that characteristic for the species in this region. This instability may, moreover, be located largely in a single plate, 7″, and the inference goes to support the previous suggestion that plate 7″ in *Peridinium* is of late phylogenetic origin.

In the two specimens of *P. divergens* figured by Mangin (1911, pl. 7, figs. 10 and 13), which have an unusual pattern, the critical sutures are well developed and the pattern is unmistakable. Measurements of the unusual sutures between plates 1′ and 6″ give values of .1071 and .1587 of the transdiameter, and measurements of the corresponding suture on the left hand of the rhomboid plate, which is of the normal pattern for this species, give values of .0357 and .1270 of the transverse diameter.

The unusually short length of the suture between plates 1′ and 2″ in one of Mangin's figures is noteworthy in view of the usual great length of this suture in most of the specimens of this species measured, and is suggestive of the profound effect of any influence which would upset the normal equilibrium of the morphological elements.

These measurements were taken from drawings made to a scale of 1:1500, usually from square ventral or dorsal views. There is, however, a certain amount of foreshortening in these drawings of sutures which lie upon curved surfaces that is unavoidable. Instead of making an allowance for this foreshortening the sutures have been measured just as they have appeared in the drawings. The drawings, made with camera lucida, are thus projections of the surface of the organisms which they portray. The general effect upon these measurements is that many of the values given are less than the actual length of the sutures represented. In no case is an exaggeration of measurement possible. Any errors from this method of measuring the suture are, therefore, in favor of the general conclusions which will presently be drawn in examining the significance of the measurements.

Significance of Variation in Suture Length

The occurrence of a few specimens of *P. divergens* with an unusual ventral plate pattern is to be regarded as of very great importance. Of equal importance in this consideration is the occurrence of species answering the descriptions of *P. ovatum, P. claudicans, P. oceanicum,* and *P. granii* in every respect except that of the plate pattern, and in this one character presenting plate patterns on either dorsal or

ventral aspect, which is foreign to the usual form of the species. Applying this analysis still further to the case of *P. divergens,* this circumstance in the first place demonstrates the plasticity of this region on the right side of the ventral surface of the epitheca. However, a greater significance appears from examining the lengths of the critical sutures in this region of the shell of *P. divergens.* In no case does the value of the suture between plates 4′ and 7″ fall below .04 of the transdiameter in the pattern normal for the species. That is, these two plates always meet each other for a definite length of their periphery. The suture separating them always maintains a certain definite and considerable value. The widening of sutures in certain specimens, presumably with age, may mask this appearance, though it is possible to find that the opposed margins of these two plates always present edges of definite and considerable length and that the plates never really meet by two points bringing together the four sutures of their adjacent edges at one intersection point. Nor in any other instance have more than three sutures been found to come together at one point. Instances of the apparent meeting of four sutures at one point upon critical examination show an intervening length of suture between two intersection points of three sutures each; never do four plates actually come into contact at one point. Here, then, is the record of forty-four random instances in which this suture between plates 4′ and 7″ varying through a considerable range never falls below .03 of the transdiameter.

In contrast to this usual condition, a few instances are known in which an alternate pattern has appeared, the only other pattern possible by any rearrangement of plates at this point. This alternate pattern is caused by the failure of plate 7″ to meet plate 4′ as usual. In this alternate and unusual pattern it is, then, the suture between plates 1′ and 6″ which is of critical significance. This suture in the two exceptional cases figured by Mangin (1911, pl. 7, figs. 10 and 13) is of considerable length and is not short as though the usual pattern for the genus had barely slipped over into the alternate pattern. In two other cases observed by the writer, but unfortunately not recorded by drawings, this suture between plates 1′ and 6″ was also of considerable value.

Turning now to the varying length of the critical sutures in the three other regions of varying plate pattern in this species, *P. divergens,* there is not only no suggestion of a merging of the given pattern for *P. divergens* with the alternate pattern possible in any of these

places where changes of plate pattern seem to have occurred in the formation of other species of the genus, but the value of the critical suture in each case which must be obliterated in the formation of a new pattern never quite approaches zero.

On the left hand side of the ventral surface of the epitheca the critical suture is that between plates 1′ and 2″. In a change to the *Orthoperidinium* pattern this suture would be obliterated by the meeting of plates 2′ and 1″, which in *P. divergens* are separated. However, in *P. divergens,* there is never any suggestion of such an approximation of plates 2′ and 1″ and the suture between plates 1′ and 2″ is always of considerable length.

On the dorsal surface of the epitheca, the plate patterns at the posterior corners of the middle accessory plate usually are symmetrical in this genus. In *P. divergens,* although varying through a wide range of length, the critical sutures between plates 1*a* and 4″ and plates 3*a* and 4″, which must be obliterated in the transposition to the alternate patterns for these regions, never fall below .04 of the length of the transdiameter. In the measurement of Broch's figures these critical sutures are also found to preserve their definite and considerable value.

Here there are over 160 measured cases in which the length of the critical suture in variable regions of the shell of specimens of *P. divergens,* including the alternate unusual pattern in one of the variable regions for two of the instances, does not approach zero in value, but maintains a definite and relatively considerable length. This is maintained in spite of the fact that other species of this genus are fundamentally characterized by having a different plate pattern in these critical regions.

Now the significance of this fact seems to be this. Species in this genus are evidently formed by the rearrangement of a constant number of plates in a limited number of possible geometric patterns. There are in this genus only four regions where such adjustments occur. At each region only two different patterns are possible, one the alternate of the other. One pattern is changed into the other by the expansion of one or both of a pair of diagonally opposite plates, causing the separation of another pair of plates previously in contact and the obliteration of one suture with the establishment of a new suture.

In specimens of *P. divergens* examined, the patterns of three of the four regions of possible variation seem to be stable. The pattern

of the fourth variable region, the right hand side of the ventral surface of the epitheca, seems, however, to be unstable and to present occasionally the alternate pattern for this region, unusual in this species. This particular region seems, therefore, to be in a state of greater plasticity than any one of the other potentially variable regions.

The essential point in this portion of the discussion of plate variation in *Peridinium* is that there is no complete series of variations between the usual pattern and the exceptional pattern found in this part of the shell of this species. In such a complete series of imperceptible variations the suture between plates 4′ and 7″ would become shorter and shorter and finally disappear, after which disappearance a new suture between plates 1′ and 6″ would gradually take its place. In the series there would be a stage in which four plates and four sutures would come together.

Extremes of such a possible series are known, presenting both alternate plate patterns. Within this species this region is, therefore, known to be unusually variable and to present the full gamut of possibilities of plate arrangement possible, though the plate pattern is usually confined to one type. However, the variation of the critical suture in this usual plate pattern never approaches beyond a certain amount the point of obliteration, which must be passed before the alternate plate pattern can be produced. In a few instances found of the presence of the alternate plate pattern, the new critical suture is shown to be of definite and considerable value. No authentic instance is known of the merging of the two patterns by the meeting of four plates at one point with the obliteration of the critical sutures of both patterns. Drawings which seem to show such a condition may be rejected as not sufficiently accurate to be trusted in a matter where unprecise observation may make so great a difference as here, in view of the large number of first hand cases which have been very critically examined in this regard.

It seems probable, therefore, that when the plate pattern at a variable region changes within a species or between two different species, it does so with a jump; that each pattern is characterized by a certain suture, which varies about its own norm; that these norms do not merge into one another in each pair of alternate patterns possible at a given point, but that the two patterns are separate; and that when the plates do readjust themselves in response to internal stresses they do so with a certain amount of abruptness without passing in the process through all of the intervening stages between the normal proportions of the two patterns.

There is therefore effected a sort of limited kaleidoscopic movement of the plates upon each other in response to internal stresses with sufficient remodelling of the margins of the plates to establish contact sutures of definite and considerable length. This all goes to support the view that the plates of one pattern are in a state of equilibrium which requires a certain amount of accumulated strain before transformation into the alternate pattern can occur; that each pattern represents a state of approximate equilibrium of the skeletal elements out of which the plates may be forced only by the accumulation of an unusual stress sufficient to throw the plates over into another arrangement of equilibrium in the alternate pattern.

The equilibrium of each pattern seems usually to be characteristic and constant for each species. The abruptness of the transition from one pattern to another is illustrated in the case of *P. divergens* just described. This transition, however, is not accompanied by other morphological changes sufficient to warrant the description of a new species. As a rule it may be supposed that changes which would throw the plate patterns from one relation of equilibrium into another would also be accompanied by such other structural changes as to compel the consideration of the new form as a species.

Particularly with the pair of dorsal patterns in *P. divergens* Ehrbg. is it to be seen from the curves charted that in the groups of specimens from each locality the trend of variation of the pattern on both sides of the organism is much the same in each group, and the mode for the length of both the right hand and left hand critical sutures is about the same. This is in accord with the general observation of the dorsal symmetry of pattern in this genus, to which there are but few exceptions, some of these occurring under conditions of an unusual environment which may be presumed to have interfered with the morphological equilibrium of a species.

The ventral patterns are, however, not so closely coupled as was noted in defining the subgenera of this genus, *Paraperidinium, Metaperidinium* (dextrad), and *Orthoperidinium,* on the basis of ventral plate pattern.

It is presumed that at least one of the specimens figured by Mangin showing the *Paraperidinium* pattern does not differ otherwise from the average run of specimens of *P. divergens.* The other specimen differs somewhat in surface markings, but this may be merely an age difference. These specimens are, therefore, regarded as specimens of the species, *P. divergens,* which show an unusual form of plate pattern.

From the absence of intervening stages showing the transition from one pattern to the other; from the fact that in the exceptional patterns found in Mangin's figures, these patterns do not at all approach a transitional condition; from the fact that the critical suture of this unusual pattern is very long; and from the position of the mode of variation of length of the critical suture in the typical *divergens* pattern with a minimum extreme for the curve for the length of this suture which does not reach closer than .03 of the transdiameter to the vanishing point for this suture, we conclude that the normal shape for plate 7″ in this species carries a truncated anterior portion where it meets plate 4′; that with a truncation of its anterior border of a greater or less extent, as represented by the curve of variation given above, the plate pattern in this region is in a state of equilibrium; that any force tending to upset this equilibrium throws the arrangement of plates at once over into the only other pattern possible, with already a critical suture of considerable length; and that a condition of two opposite plates in a pattern meeting at a point without a truncated margin, and bringing together four suture lines at one point is an extremely unstable and an unknown condition.

In this connection a discussion of the suture relations of the dorsal pattern of such a species as *P. conicum* is apropos because here the critical sutures of the pattern, in this case that of fig. 6, are very short. In fact, the pattern in this region has frequently been figured as the intersection of four sutures. In a considerable number of specimens of this species which we have examined, however, it has always been possible to resolve these obscure relationships into the pattern shown in fig. 6. In no case was found the alternate pattern that is possible in this region. We regard this circumstance in *P. conicum* as no different from that observable more clearly in *P. divergens* and in other species: that a certain juxtaposition of plates in a given region effects a condition of stability in the arrangement of these plates with a certain amount of fluctuating variation in the length of the articulations of the plates of the pattern; that in a transition from one pattern to the alternate a stage of instability is encountered of which no representatives persist; and that a more or less broadly truncated juxtaposition of opposite plates of the quartette involved in a pattern is essential to the establishment of equilibrium. This juxtaposition manifests itself in presence of the so-called "critical suture," for which a mode and extreme limits of variation can be determined.

This method of analysis might be applied to all of the other cases

cited—*P. oceanicum, P. claudicans, P. granii,* and *P. ovatum*—in which two plate patterns occur in specimens which must still be regarded as belonging to the same species. These rare changes of pattern are always well isolated from the normal pattern characteristic of the given species. No series of gradations has been observed between such an unusual pattern and the normal pattern; on the contrary, the length of the critical suture for the normal pattern seems to vary between definitely recognizable extremes, the minimum limit of which is still well above the vanishing point for the suture. The genral conclusion from all of these observations is, therefore, that a certain pattern is characteristic for a given species; that this pattern may occasionally be changed; but that such changes occur abruptly as mutations and are without a connecting series of intergradations.

Mutations

We have pointed out here several definite and different arrangements of the plates of the shell of species of *Peridinium.* These arrangements presumably represent states of equilibrium between potentially variable elements. A change in pattern involves the shortening of one suture and the introduction of another suture at right angles to it and between two different plates. However, each suture maintains its own norm for the fluctuating variations which it may be expected to undergo, and transitional stages between the two possible patterns which a given group of plates may assume are unknown.

Hence, in at least this superficial character of plate pattern, these organisms undergo mutations which must be recognized as such if we are to admit any phylogentic sequence at all among these species; that is, the change from one plate pattern to another requires a certain saltation to bridge the gap. That such saltations when they have occurred have remained permanent at least for a time is shown by the presence of species exhibiting nearly all of the arrangements of a given group of plates which are geometrically possible. This character of the plate pattern seems, therefore, to undergo mutations in the generally accepted meaning of abrupt, discontinuous, morphological changes which reappear in successive generations after their first occurrence.

The pattern of the sutures is, however, not the real character, but is dependent upon the size of the plates which the sutures bound. The

size of these plates is in turn under control of whatever may be the factor making for the orderly fragmentation of the shell and the arrangement of its parts found in this group of organisms. Whether this fundamental factor for plate growth proceeds by leaps and bounds or not we cannot determine, because the very material of the shell in which this factor is expressed may by some physical quality of its own tend to retain its fragments in a given arrangement until a certain accumulation of strain may become sufficient to cast it over into another arrangement in somewhat the same way as the crystals of a kaleidoscope retain a given pattern even though the barrel of the instrument be moved through an appreciable arc of rotation before falling into another pattern which in turn retains a certain degree of permanency.

However, so far as the character of the arrangement of the plates themselves and its expression in suture pattern are concerned, these certainly behave as mutations. There is no suggestion that the patterns are connected by a series of fluctuating or continuous variations, but on the contrary, evidence is present that given patterns are not so connected at all, and that a considerable gap of unknown relations of the plates concerned remains between the alternate patterns in a given variable region. This seems to be a perfectly clear and clean cut result so far as can be judged from the mass evidence of a general population. It is to be regretted that the cultural methods of the protozoan geneticist have not been adapted as yet to this material.

The independent behavior of each of these four variable areas in certain cases, as well as the coupling of the dorsal and ventral areas in pairs in certain other cases suggests that in these characters of varying plate patterns we may be dealing with unit characters in an unusually simple and discreet form.

Possible Influence of the Environment

There is some evidence to suggest that conditions of the environment different from those of neritic or pelagic localities where given species may be "at home" may be responsible for changes in plate pattern as well as in other characters of dinoflagellates. Thus, for example, such a form as *P. granii* is found in embayments such as San Francisco Bay and Union Bay, Alaska, and particularly in the Baltic Sea where the salinity is very much lower than in the open ocean. An even more striking instance comes from the specimens from San Francisco Bay which undoubtedly are related to *P. oceanicum* Van H. but

in which the pattern of *Orthoperidinium* characteristic of *P. oceanicum* in its typical form has given way to the more primitive pattern of *Paraperidinium*. This striking reversion is accompanied also by an abortion of the antapical horns. Other characters, and particularly the relation of its position in the fauna of the collection in which it occurred to the general population of the region, leave little doubt that this particular specimen is a highly modified specimen of the species *P. oceanicum*. In San Francisco Bay were taken the specimens of *P. claudicans* which display the unusual right oblique dorsal pattern. *P. claudicans* and *P. oceanicum* are both species of the open sea, and it seems highly probable that the altered conditions of salinity, density, and temperature encountered by those specimens swept into bays by the tide may have stimulated these departures from the normal structure of these species.

C. CONCLUSIONS

From this analysis of the morphology of the skeleton of *Peridinium* the following conclusions are suggested:

1. A distinct difference is to be pointed out not only in the organization of the shell in the two principal families of the Dinifera, the Peridinidae and the Dinophysidae, but also in the manner of development followed in each family. In the Dinophysidae the number of plates remains constant. These four major plates seem to be able to conform to a great variety of forms of the body without breaking up into smaller plates. The skeletal variations in this family consist of differences in the development of such skeletal appendages as the lists of the girdle and of the longitudinal groove, and also in the degree of porulation, distribution of pores, and association of pores with other surface markings.

In the Peridinidae, on the other hand, the skeleton behaves very differently, and progressive development seems to proceed in an orderly fashion in the direction of an increase in the number of plates of which the skeleton consists, as well as in the development of various features of minor importance, including porulation, surface markings, and antapical horns. The plates become at once arranged in circumferential rows parallel to the girdle, which is of dominant importance in the activity of the organism. The family, Peridinidae, is to be characterized especially by this capacity for a peculiar and orderly fragmentation of the shell according to a progressive scheme.

2. In the classification of species of *Peridinium* skeletal characters, particularly the relationships of the fundamental skeletal elements, the plates, are of much more real value than the type of antapical

3. The size which these plates in Peridinidae attain is limited, and is apparently correlated somewhat with the degree of curvature of the shell. The dimension of the plate is usually longer in the direction of slight curvature than it is in the direction of great curvature. In certain regions, *e.g.,* the middle of the dorsal surface or of the apical horns in *Peridinium,* the expansion of a given plate seems to have become accomodated to the expansion by an extension within limits, in the direction of expansion, of the plates overlying the expanded portion of the body, rather than by a shifting of the surrounding plates to distribute the strain. The direction of expansion, however, is usually not in the form of a curve.

4. There is evidence to suggest that new plates are added to fill gaps occurring when the three plates meeting at a given point are separated by some internal pressure, rather than that new plates are split off from previously existing plates.

5. At a certain stage among the genera in the part of the family in which *Peridinium* belongs, the number of plates in the precingular row increases so that these plates can no longer reach the apical row and an accessory row of plates is interpolated on the dorsal side between the two previously existing rows.

The progress of this increase in the number of the plates in the precingular row may be traced from such genera as *Heterodinium, Spiraulax,* and *Gonyaulax* which have six precingular plates (the plate of the right hand end of this row, 6″, frequently being of small size), through the several stages of development pointed out in the three subgenera of *Peridinium* to such an exceptional form as that figured by Fauré-Fremiet (1908, p. 227, fig. 13) for *P. minutum* Kofoid var. *tatihousensis* in which there is apparent an *eighth* precingular plate at the right hand end of the row.

6. In *Peridinium* the first plates to appear in this accessory row come in as a pair of plates. It is not until a later stage that a third accessory plate makes its appearance between the original pair. Subsequent changes in the arrangement of the dorsal plates occur over the spots on the body of the organism at which the two accessory plates appeared. The addition originally of but a single accessory plate is unknown.

7. On the ventral surface of the organism additional plates added

apparently as the end plates of the precingular row are pulled away from the mid-ventral or rhomboid plate, and hence what are apparently new plates appear at the ventral median corners of the previous end plates of the precingular row which come to be plates 2″ and 6″ in the genus, *Peridinium.*

8. Four regions of variability are found in that portion of the genus, *Peridinium,* characterized by having the full complement of three accessory plates: two on the ventral surface of the epitheca on opposite sides of the rhomboid plate near the location of the appearance of the most recently added precingular plates, and two on the dorsal surface at opposite corners of the middle accessory and mid-dorsal precingular plates, near the place where the first two accessory plates appeared.

9. The two dorsal regions usually vary coincidentally, but the two ventral regions seem to have varied frequently independently of each other.

10. The variations in these four variable regions consist in the rearrangement of four plates which approach each other in each of these regions. Only two alternate patterns can be found among these four plates of each region, aside from the conjunction of four plates at one point—a condition which is unknown. Not more than three plates come together at one point.

11. There thus become possible four different combinations between the alternate patterns at the variable areas on the ventral side and four combinations between the patterns of the variable dorsal areas. Of these sets of four ventral and four dorsal pattern combinations two of each are symmetrical and two of each are asymmetrical. Altogether sixteen combinations of plate patterns are possible between all the dorsal and ventral variations in that portion of the genus having three accessory plates.

12. Joergensen has suggested a subdivision of the genus, *Peridinium,* on the basis of the one asymmetrical ventral pattern and the two symmetrical patterns which are known. The fourth possible ventral pattern, asymmetrical, is probably unknown. To these subgenera he has given the names, *Paraperidinium, Metaperidinium,* and *Orthoperidinium.* Classification on this basis is not only a convenience but is to be justified upon a natural basis since it seems that in the progress of plate development through several genera an increase in the number of plates in the precingular row up to the number of seven holds priority over the interpolation of accessory plates and hence

over modifications of the dorsal plate pattern. The absence from present authenticated records of an asymmetrical ventral plate pattern, the reverse of the pattern of the subgenus, *Metaperidinium,* can only be given negative significance.

13. Since the end plates in *Orthoperidinium* are much larger than in *Paraperidinium,* the former subdivision of the genus is supposed to represent a more highly specialized condition in respect to plate growth than that of *Paraperidinium. Metaperidinium* by reason of the lagging of the growth of the plate at the left end of the precingular row represents an intermediate stage of specialization.

As might be expected in the more highly specialized portion of the genus, there are, to judge from published records and figures, more species in the subgenus, *Orthoperidinium,* than in both of the two other subgenera combined, indicating the prolific diversity of form in highly specialized stages.

14. Over half of the sixteen possible combinations between all the dorsal and ventral plate patterns are known, including: all four of the combinations between the symmetrical ventral patterns, *Paraperidinium* and *Orthoperidinium,* and the two symmetrical dorsal patterns known; also combinations between one of the two asymmetrical ventral patterns, *Metaperidinium,* and both of the symmetrical as well as both of the asymmetrical dorsal patterns; and the combination of the ventral plate pattern of *Orthoperidinium* with the right oblique (asymmetrical) dorsal pattern, reported for at least one species. One asymmetrical ventral pattern is wholly unknown and combinations of the asymmetrical dorsal pattern with *Paraperidinium* and *Orthoperidinium* are also unknown.

15. In that portion of the genus in which there are only two accessory dorsal plates, whether symmetrical or of unequal size, the dorsal patterns thus formed are known in combination only with the symmetrical ventral pattern of *Orthoperidinium.* No instance is known of the occurrence of but a single dorsal accessory plate in this genus.

Of the species on record, many of those having but two accessory plates are fresh water forms and most of the fresh water forms have only two accessory plates. This primitive character for this genus is, however, coupled with the presence of the specialized ventral plate pattern of the subgenus, *Orthoperidinium.* Such an unexpected combination is perhaps to be explained on the hypothesis that the development of accessory plates is of secondary importance to the rearrangement of the plates developing about the rhomboid plate after the addi-

tion of plates 1″ and 7″ of this genus. Another factor in this connection may be the small size of most fresh water forms, due perhaps to the lack of buoyant power of the fresh water which, prohibiting any great disparity between surface and volume, may set a limit upon expansion.

16. There are then four variable regions which may vary either independently of each other or in dorsal or ventral couples and which may combine their variations with each other in a total of sixteen possible combinations of which at least nine are represented in the existing species of this genus.

17. The significance of this complete series of combinations of approximately symmetrical patterns shows not only the pressure of the influence for variation and the great extent to which this group of organisms seems to have expanded in all possible directions of change, but even more significantly demonstrates the progressive sequence in which these changes of pattern must have occurred.

18. Each of the symmetrical patterns seems to represent a stage of stability in this process of progressive change, a period when the skeletal elements and the forces playing upon them are in a state of approximate equilibrium. Less frequently do the asymmetrical patterns seem to be so stable, though that of *Metaperidinium* for the ventral plates is found consistently in a considerable number of species. The asymmetrical patterns of the dorsal side often seem, however, to be concomitants of extensive changes of the physical condition of the environment, and do not pervade a great portion of the genus.

19. A significant consideration with respect to the combination of symmetrical and asymmetrical patterns appears from the correlation of the asymmetrical dorsal patterns only with the asymmetrical ventral pattern. The principal of symmetry seems to be the controlling one in this genus and the species having asymmetrical patterns are apparently less able, in most cases, to persist than are those having symmetrical patterns.

The symmetry referred to in examining the various plate patterns of *Peridinium* is only an approximate and not a perfect symmetry, it being apparently a fundamental character of Dinoflagellata that the body is still more or less asymmetrical. However, in view of the extreme asymmetry displayed by related genera in the development of antapical horns and in the position for the introduction of the accessory plates, where these occur, the approximate symmetry maintained by the skeletal structures in most of the species of *Peridinium* attracts attention.

20. As might be expected in conformity with Child's law of metabolic gradients, the greatest morphologic activity and tendency for fundamental change is located in the anterior portion of the shell, while the posterior portion is conservative and carries modifications which may be due not so much to an internal stimulus as to more direct but minor responses to an outside stimulus. It seems probable that in these organisms, as well as those upon which Child worked, it is the strong unceasing impact of the environment upon the anterior end of the organism which has made it the more active and the more likely to respond with profound morphological modifications.

21. In each varying pattern the suture which marks the juxtaposition of two of the quartette of plates involved in the given pattern and which therefore becomes characteristic for that pattern varies about a mode of its own. Intervening stages of the gradual shortening of such a suture in a supposed transition to the alternate pattern beyond the established limits of variation for the suture are unknown. Each pattern is separate and distinct from its alternate and one pattern by no means grades into the other. There is, thus, a definite gap between variations of the alternate members of a pair of plate patterns at each of the four variable regions, as examined intensively for the species, *P. divergens Ehrbg.,* and a similar gap apparent between certain rare changes in plate pattern observed in four other species.

In the experience of the writer no case has been found in which four sutures actually meet at one point. Cases which at first sight appeared as such, upon closer analysis in a favorable position have been resolved into two junction points of three sutures each separated by a short suture which is one of the two critical sutures for the pair of alternate plate patterns possible by the rearrangement of plates in the given region.

22. Mutations appear in two ways in this genus: (1) by the sudden change of plate pattern within a species as found occasionally in the species just referred to above; and (2) by the introduction of new plates from time to time in the history of the family to which the genus, *Peridinium,* belongs. These new plates become new characters abruptly introduced, and each passes through a process of development, involving enlargement and various adjustments with the adjacent plates of the shell.

23. It seems probable then if the species of this genus are in verity phylogentically related: that one species arose from a previously existing species by a mutation, involving an abrupt addition of a new

plate or pair of plates, or involving a sudden rearrangement of the plates of one or another of the four variable patterns; and that each pattern with its own mode of variation for the length of its critical suture marks a settled arrangement of the plates in which they are for the time being at least in equilibrium.

24. To judge from the constancy of a given pattern in a given well recognized species, it seems to be usual that an influence sufficient to upset the plate arrangement in one or more of the variable regions is of sufficient moment to cause other changes also, the sum total of which would place the organism in quite a new species. That this is not always the case appears from a few exceptional occurrences of a change in the ventral plate pattern, without any other morphologic changes which would warrant placing these individuals in another species.

25. These exceptional cases of unusual changes in the ventral plate pattern of the species just mentioned are to be regarded as reversions from a specialized to a more generalized type; that is, these changes may be due to either an inhibitory factor suppressing the full development of the ventral plates usual for the species, or more probably to a lack of the usual stimulus for growth in plates 1″ and 7″, on account of which a more primitive plate pattern is produced. Any interference with the normal progress of a race of these organisms seems to result in an inhibition or retardation of progress and fixation at some phylogentically earlier stage of development, rather than in the stimulation of new lines of variation. The normal progress of development in this family is suggestive in certain respects of an orthogenetic mode of evolution.

26. These changes in plate pattern within a species or between species are, therefore, to be regarded as mutations, and their significance is very great in suggesting the mutationary method of species formation in this group.

27. The suture or plate pattern is, of course, only a superficial indication of a deeper seated variable factor governing the orderly skeletal fragmentation and plate growth characteristic of this family. The kaleidoscopic readjustment of the plates may be of secondary importance and may be induced by some physical quality of the skeletal material which retains its inertia until acted upon by a sufficient accumulation of strain to cast it over into another state of temporary equilibrium. Such a circumstance would, however, even if the underlying form were more regular in its action, alter the mutationary

nature of the superficial character of plate variation. There is no evidence at all that the fundamental character for plate growth does not proceed at an even pace.

28. Plate formation in this family seems, therefore, to be the external expression of an internal force which is guided in its expression by physical properties of the shell material in the formation, according to a system consistent for the whole family, of plates limited in size and guided also by geometrical, *i.e.*, mechanical, limitations in the arrangement of these plates in certain areas said to be more "plastic" than other areas because manifesting the changes induced by the internal force.

29. There is also some suggestion that it may be the changes themselves in the environment which indirectly induce certain of these skeletal changes, since the asymmetrical patterns, especially of the dorsal side, and the sudden transformation from one pattern to another usually occur in species found under unusual conditions of the environment, and in species which often show other features, such as the abortion of antapical horn, indicating the shock of the reaction of the organism to an unaccustomed environment.

30. While for species in their natural habitat the skeletal patterns seem to be on the whole a good and convenient species character as well as one of sound phylogenetic basis, the occurrence of these occasional sports indicates that it is not an infallible character, especially in regions where a mixture of water from widely different sources occurs or some other marked deviation from an accustomed environment.

31. These conclusions in regard to the mutationary behavior of these skeletal characters perhaps carry an added interest from the occurrence of these phenomena in this group of marine Protozoa, living under an environment very different in many respects from that of land plants and animals which have been the usual subjects of variational studies, contributing perhaps support for the normal occurrence of a method of species formation by means of mutations.

32. Though these observations may furnish some information upon the behavior of the discreet elements of the dinoflagellate skeleton, they do not contribute definite information upon the process of plate growth in these organisms. This problem will require a different method of attack, probably involving the continued observation of single isolated specimens of dinoflagellates through considerable periods of time.

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EXPLANATION OF PLATES

PLATE 17

Peridinium granii Pauls

Fig. 1. Ventral view of type from Sausalito, California, September 24, 1913. × 1500.

Fig. 2. Ventral view of type from Union Bay, Bayne Sound, Alaska, May 14, 1906. × 1500.

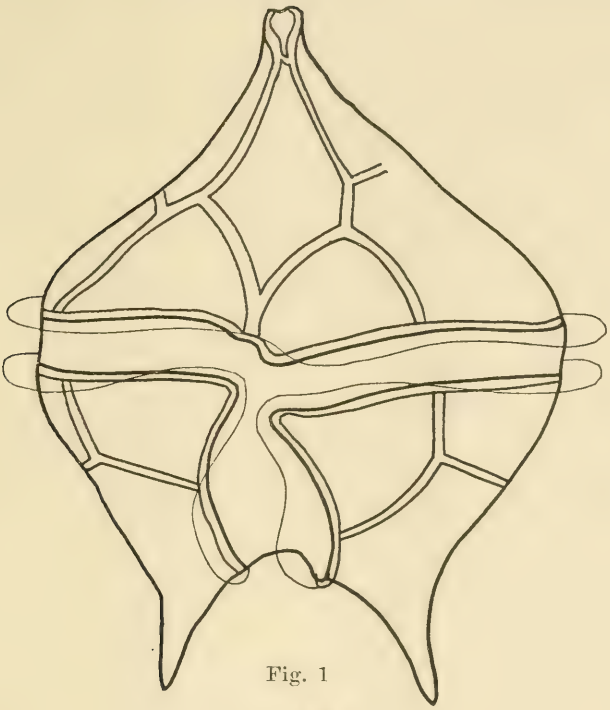

Fig. 1

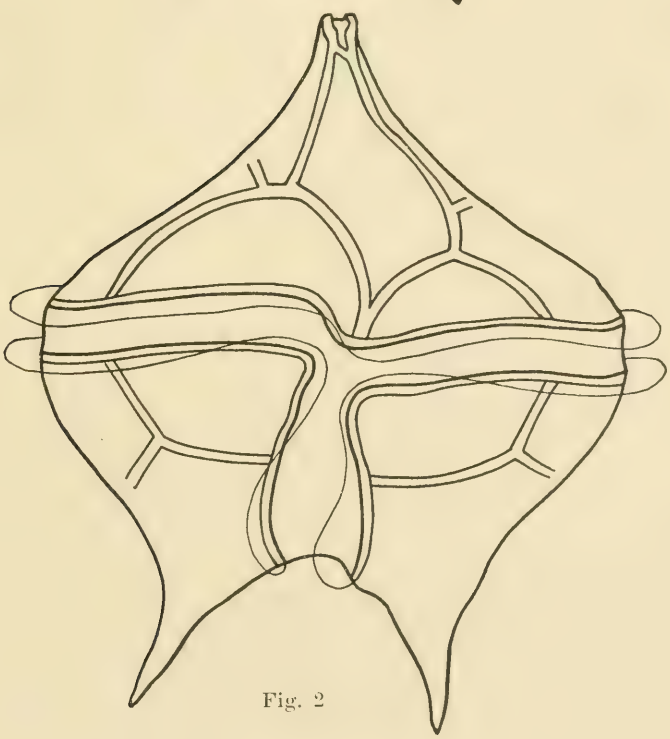

Fig. 2

PLATE 18

Peridinium granii Pauls

Fig. 3. Dorso-apical view of the same specimen shown in figure 1, plate 17. × 1500.

Note that the dorsal epithecal plate pattern is that which has been termed the left oblique pattern. The ventral plate pattern is that of the subgenus, *Metaperidinium*.

Fig. 4. Dorso-apical view of the same specimen shown in figure 2, plate 17. × 1500.

Note that the dorsal epithecal plate is asymmetrical and the reverse of that found in a similar form from Sausalito, California. The dorsal plate pattern of the form from Union Bay corresponds to the form of *P. granii* described by Paulsen (1908, p. 52, fig. 66) from the Baltic Sea, but the ventral plate pattern figured for the Baltic Sea is that of the subgenus, *Paraperidinium*.

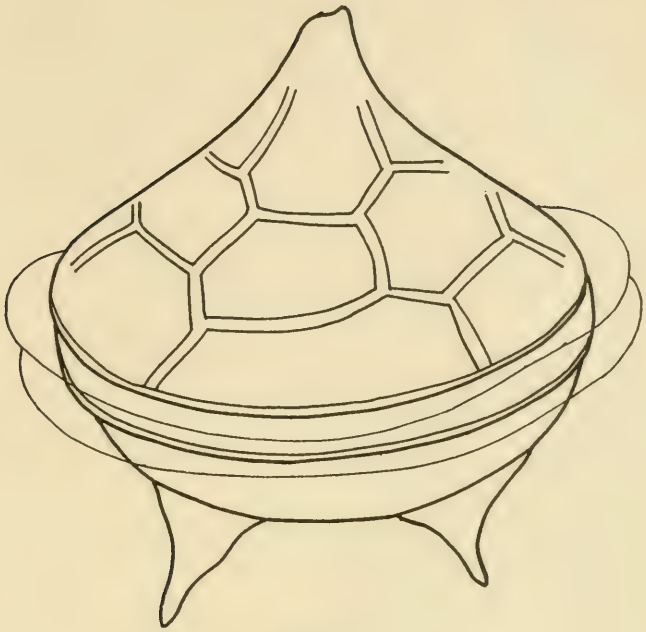

Fig. 3

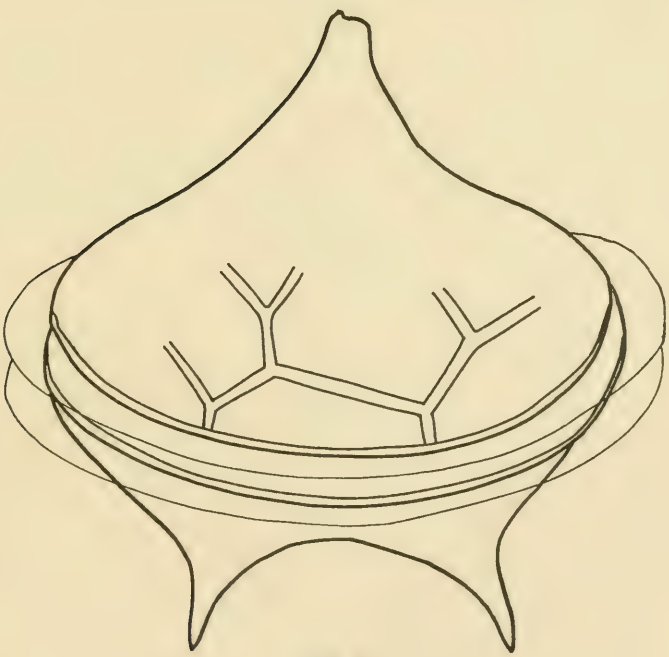

Fig. 4

PLATE 19

Peridinium claudicans

From Sausalito, California, September 24, 1913

Fig. 5. Ventral view. × 1400.

Fig. 6. Dorsal view. × 1400.

Note that the dorsal epithecal plate pattern is of the asymmetrical type termed right oblique instead of the usual symmetrical type for this species, shown in text-figure 5.

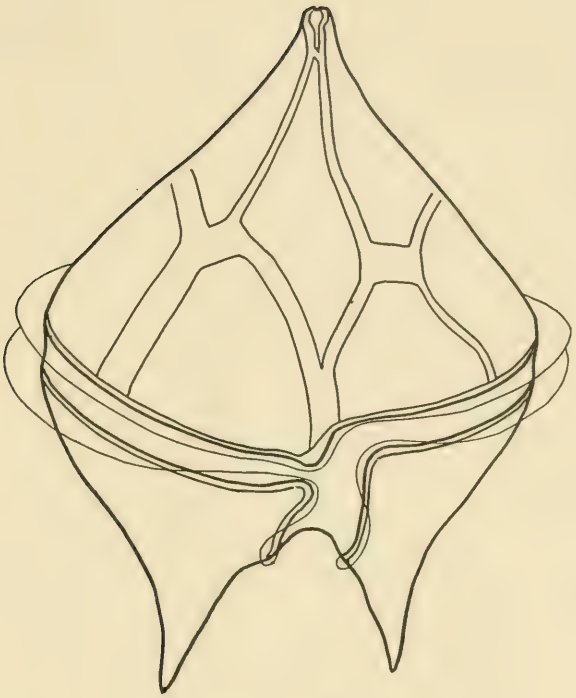

Fig. 5

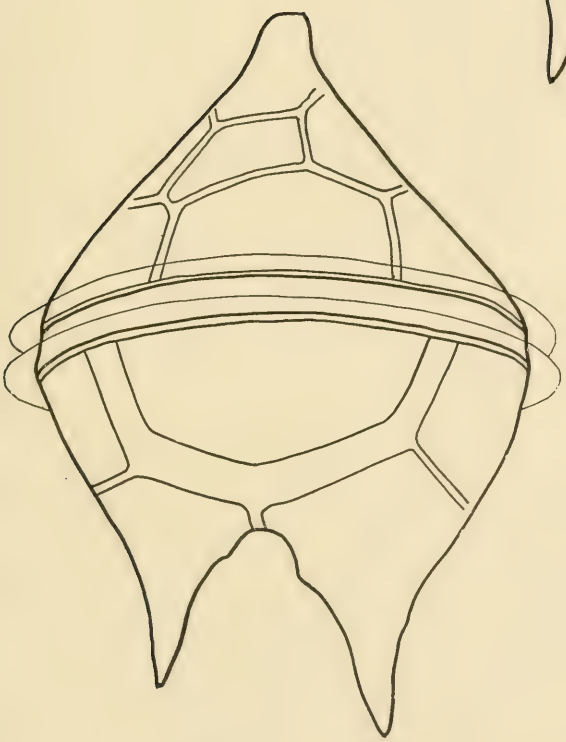

Fig. 6

PLATE 20

Peridinium oceanicum Van H.

From Sausalito, California, February 13, 1912

Fig. 7. Ventro-apical view. × 1500.

Fig. 8. Lateral view. × 1500.

Note that the ventral epithecal plate pattern is that of the subgenus, *Paraperidinium,* rather than that of the subgenus, *Orthoperidinium,* usually found in *P. oceanicum.* It is possible that this particular specimen may be more closely related to a race of *P. depressum* Bail. than to a race of *P. oceanicum* Vanh.

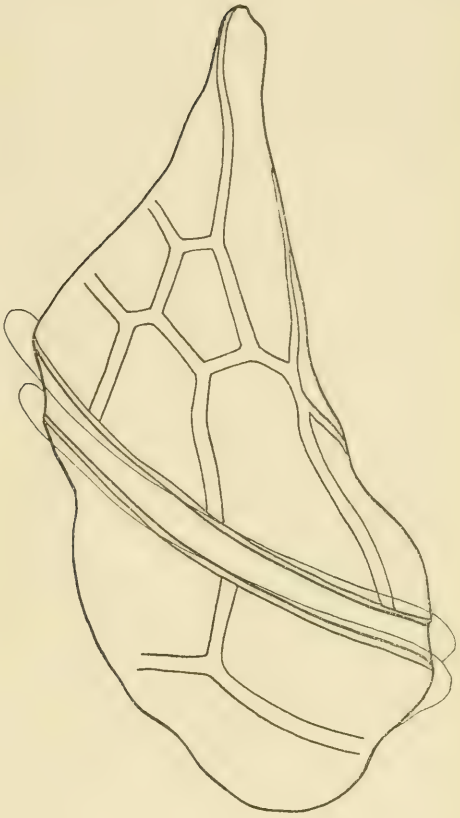

Fig. 7

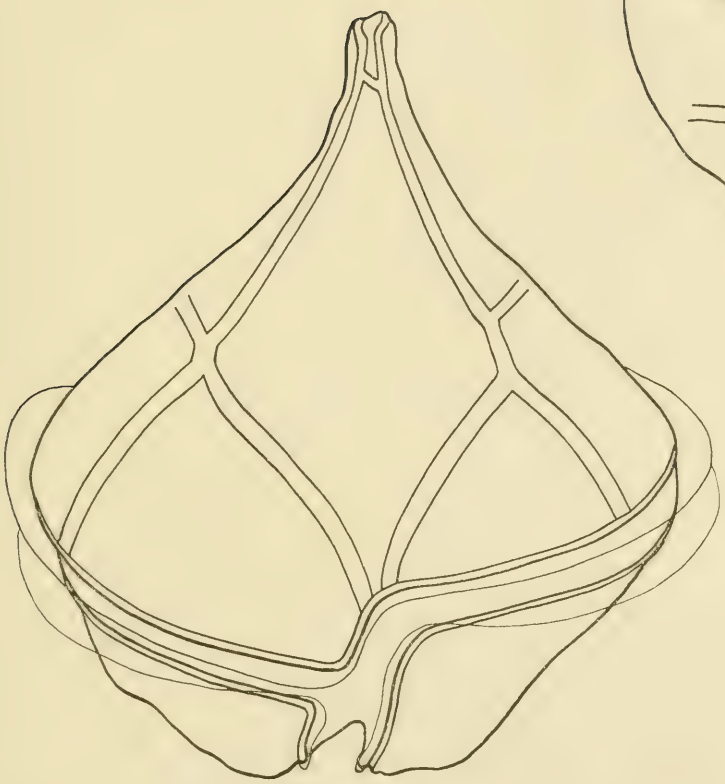

Fig. 8

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5. Notes on the Tintinnoina. 1. On the Probable Origin of *Dictyocysta tiara* Haeckel. 2. On *Petalotricha entzi*, sp. nov., by Charles Atwood Kofoid. Pp. 63-69, 8 figures in text. December, 1915 ..... .05
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Nos. 6 and 7 in one cover. December, 1915 ..... .25
8. On *Blepharcorys equi*, sp. nov., a New Ciliate from the Caecum of the Horse, by Irwin C. Schumacher. Pp. 95-106, plate 13. December, 1915.... .10
9. Three New Helices from California, by S. Stillman Berry. Pp. 107-111. January, 1916 ..... .05
10. On *Trypanosoma triatomae*, a New Flagellate from a Hemipteran Bug from the Nests of the Wood Rat *Neotoma fuscipes*, by Charles Atwood Kofoid and Irene McCulloch. Pp. 113-126, plates 14-15. February, 1916 ..... .15
11. The Genera *Monocercomonas* and *Polymastix*, by Olive Swezy. Pp. 127-138, plates 16-17. February, 1916 ..... .10
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Nos. 1 and 2 in one cover. August, 1916 ..... .10
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Nos. 14 and 15 in one cover. April, 1918 ..... .15
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3. Description of Some New Species of *Polynoidae* from the Coast of California, by Christine Essenberg. Pp. 45-60, plates 2-3. October, 1917 ..... .20
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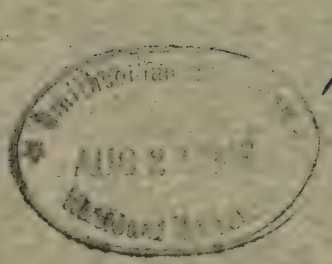
BY
J. FRANK DANIEL



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THE SUBCLAVIAN VEIN AND ITS RELATIONS IN ELASMOBRANCH FISHES

BY
J. FRANK DANIEL

Smithsonian Inst.
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Introduction

C. F. O'Donoghue (1914) has called attention to the confusion in the literature on the subscapular and subclavian veins of the elasmobranch fishes, and has in a way straightened out the difficulty by showing that the subscapular enters the postcardinal sinus and that the subclavian, formed by the union of the brachial and lateral abdominal veins, enters the duct of Cuvier.

In my study of the Elasmobranchs I have been attracted to this problem, since in different types the subscapular varies in extent and the subclavian differs greatly as to the relative amount of blood which it receives. In certain cases the condition in both of these vessels is as O'Donoghue and T. Jeffrey Parker (1886) have shown for *Scyllium canicula* and *Mustelus antarcticus* respectively. In these types the subscapular vein enters the postcardinal sinus and therefore none of its blood passes to the heart by way of the subclavian. In others, however, the subclavian may receive all of the blood from the whole of the subscapular system. In still others an intermediate condition may obtain in which a subscapular vein bridges postcardinal and lateral abdominal systems, so that blood entering it may go to the heart by either of these systems, depending upon whether it enter the subscapular dorsally or ventrally.

Material

As material for study I have had access to *Heptanchus* (*Notorhynchus*) *maculatus* ranging from two to nine feet in length and *Squalus sucklii* and *Mustelus henlei* of about two feet in length.

Method

For this study the body was transected two to four inches back of the pectoral fins, and the anterior segment then cut in sagittal plane from the tip of the nose to the place of severance of the body. By the latter cut, right or left halves of the head and pectoral regions may be

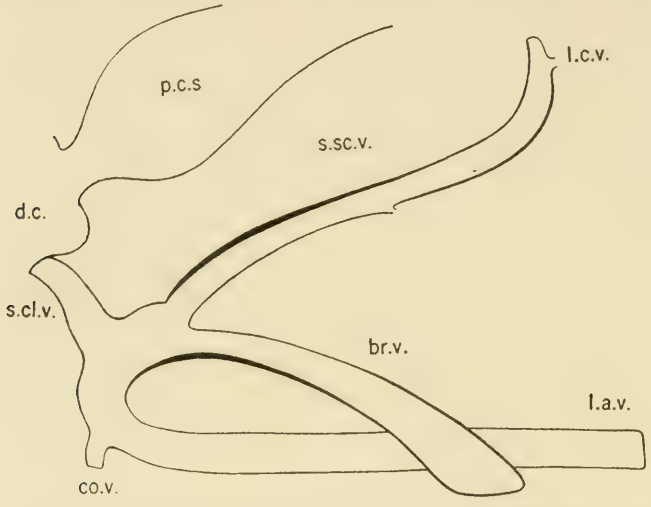

Fig. 1. The subclavian vein and its relations, *Heptanchus maculatus*, lateral view.

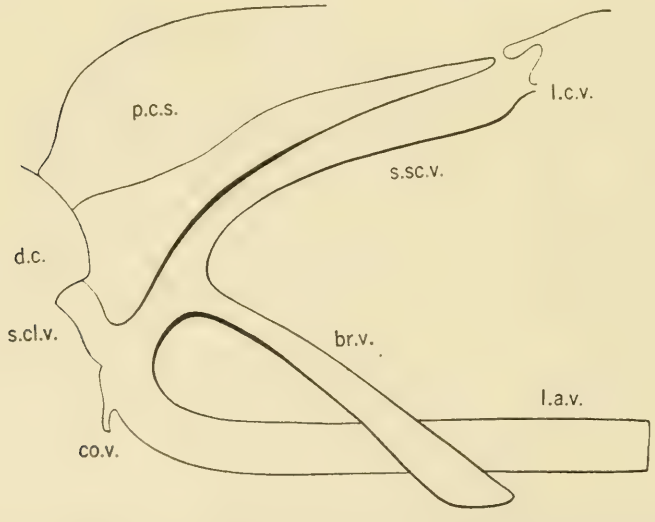

Fig. 2. The subclavian vein and its relations, *Squalus sucklii*, lateral view. *br. v.*, brachial vein; *co. v.*, coracoid vein; *d. c.*, duct of Cuvier; *l. a. v.*, lateral abdominal vein; *l. c. v.*, lateral cutaneous vein; *p. c. s.*, postcardinal sinus; *s.cl.v.*, subclavian vein; *s. sc. v.*, subscapular vein.

studied in median view. From such a section the lateral abdominal and subscapular veins are seen to advantage, and all vessels may be dissected without great difficulty. When color is needed a starch mass may be injected into the large brachial vein as it leaves the fin. In this injection the mass is prevented from running out at the cut ends of the vessels either by plugging the ends with cotton or by ligature. After the mass has hardened for two days the material is ready for dissection.

Observations

The conditions which I have found in *Mustelus henlei,* are in the main so much like those given for the Australian form of *Mustelus* as not to require refiguring. The subscapular sinus receives the lateral cutaneous vein and empties into the postcardinal sinus; none of its blood, therefore, reaches the heart by way of the subclavian vein. The brachial vein from the pectoral fin joins the lateral abdominal and the two form the subclavian which enters the duct of Cuvier, but not in common with the inferior jugular as reported for *Scyllium* by O'Donoghue.

In one important respect, however, my observations differ from those recorded for *Mustelus antarcticus* and *Scyllium.* In addition to, but separate from the subscapular sinus at the distal part of the scapular cartilage, there is an abbreviated subscapular vein which extends along the ventral and posterior margin of the scapula and enters the brachial vein. In other words the subscapular vein is made of two distinct components: first, a distal sinusoid around the tip of the scapular cartilage, which receives the lateral cutaneous vein and joins the postcardinal sinus, and secondly an abbreviated portion of the subscapular vein, which as a smaller vessel passes down the postero-median margin of the scapular cartilage to join the brachial vein. From this subscapular vein blood enters the duct of Cuvier through the subclavian vein.

In *Heptanchus* the subscapular (fig. 1, *s. sc. v*) begins at the tip of the scapula as a large sinus, passes unbroken down the entire length of the postero-medial margin of the scapula and enters the brachial vein (*br. v.*) at a place where the latter crosses obliquely over the shoulder girdle. The principal tributary of the subscapular is the lateral cutaneous vein (*l. c. v.*) which receives blood from the skin and empties it into the dorsal part of the subscapular sinus. But since the

subscapular joins only the brachial vein, and has no relation to the postcardinal sinus (*p. c. s.*) all of its blood enters the lateral abdominal vein (*l. a v.*) and passes by the large subclavian trunk (*s. cl. v.*) through the duct of Cuvier (*d. c.*) to the heart.

A second vessel in *Heptanchus* joining the lateral abdominal almost opposite the place of entrance of the brachial vein, should be further described. This I wish to call the coracoid vein (*co. v.*) since it passes downward along the posterior margin of the coracoid cartilage. It soon leaves the cartilage, however, and passes directly downward toward the midventral line. In this part of its course it runs in the tissue lying at the base of the pericardio-peritoneal septum. At the midventral line it joins a similar vein from the opposite side and is joined by the ventral cutaneous vein.

From this it is apparent that the condition in *Heptanchus* differs radically from that in *Mustelus* as described by Parker. In *Heptanchus* the lateral abdominal is the main stem receiving blood from all of the lateral vessels associated with the paired fins and their girdles. From the pectoral fin it is joined by the large brachial; while dorsally from the girdle it receives the subscapular and its tributary, the lateral cutaneous; ventrally from the girdle it receives the coracoid and its tributary, the ventral cutaneous vein.

An extremely interesting condition is found in *Squalus sucklii* which completely bridges these two extreme types. In it the subscapular (fig. 2, *s. sc. v.*) is a continuous vein, as in *Heptanchus,* and as such belongs to the lateral abdominal system; but dorsally this vessel comes in contact with and may actually have an opening into the postcardinal sinus (*p. c. s.*), so that the subscapular connects the postcardinal and lateral abdominal (*l. a. v.*) systems. Since the lateral cutaneous (*l. c. v.*) joins the subscapular sinus near the union of the latter with the postcardinal, blood from the lateral cutaneous after entering the subscapular might pass dorsally a short distance into the postcardinal sinus, or ventrally into the lateral abdominal vein. In other words: if the subscapular vein in *Squalus sucklii* were not secondarily connected with the postcardinal sinus, *Squalus* would be of the heptanchid type; while on the other hand if that segment of the subscapular, or any part of it, between the entrance of the lateral cutaneous and the brachial were dropped out, the subscapular, with its lateral cutaneous, would be a tributary of the postcardinal, and hence independent of the lateral abdominal system.

Discussion

From the work of Parker and O'Donoghue it is clear that the subclavian vein of Elasmobranchs enters the duct of Cuvier and not the postcardinal sinus as stated by Rabl (1892). But the character of the blood which it receives depends in great part on the subscapular vein and its relations.

I am of the opinion that the lateral abdominal, as is postulated by the lateral fin-fold theory, should be regarded as the main vessel in relation to the paired fins. As such it should receive the veins of the paired fins and also of their girdles. This case is realized in *Heptanchus* where anteriorly the lateral abdominal receives the brachial from the fin and the subscapular and coracoid veins from the girdle. Furthermore the subscapular and the coracoid increase the importance of the lateral abdominal by receiving all of the blood from the lateral and ventral cutaneous veins.

The finding of Parker for *Mustelus* and O'Donoghue for *Scyllium*, that the subscapular with its lateral cutaneous tributary empties into the postcardinal sinus doubtless represents the most usual condition; but that this is not universal, and that it is brought about secondarily has, I think, been shown in the present paper. Whether the postcardinal receive any of the blood from the lateral cutaneous depends upon the subscapular vein. If the subscapular is unbroken and unconnected with the postcardinal, as in *Heptanchus* (fig. 1), all of its blood reaches the heart by way of the lateral abdominal and subclavian. In *Squalus* (fig. 2) where the subscapular vessel, although continuous, is secondarily connected to the postcardinal there is a transition from the more generalized heptanchid type to a more specialized type like that of *Mustelus* in which the subscapular is divided into two parts, a distal sinusoid surounding the tip of the scapular cartilage, and a proximal more or less abbreviated portion. In this more specialized case, blood entering the distal part from the lateral cutaneous vein has but one course open to the heart and that through the postcardinal sinus.

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6. Binary and Multiple Fission in *Hexamitus*, by Olive Swezy. Pp. 71-88, plates 9-11.
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   Nos. 6 and 7 in one cover. December, 1915 ..... .25
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Index in preparation.

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   Nos. 1 and 2 in one cover. August, 1916 ..... .10
3. *Spelerpes platycephalus*, a New Alpine Salamander from the Yosemite National Park, California, by Charles Lewis Camp. Pp. 11-14. September, 1916 ..... .05
4. A New Spermophile from the San Joaquin Valley, California, with Notes on *Ammospermophilus nelsoni nelsoni* Merriam, by Walter P. Taylor. Pp. 15-20, 1 figure in text. October, 1916 ..... .05
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14. Six New Mammals from the Mohave Desert and Inyo Regions of California, by Joseph Grinnell. Pp. 423-430.
15. Notes on Some Bats from Alaska and British Columbia, by Hilda Wood Grinnell. Pp. 431-433.
    Nos. 14 and 15 in one cover. April, 1918 ..... .15
16. Revision of the Rodent Genus *Aplodontia*, by Walter P. Taylor. Pp. 435-504, plates 25-29, 16 text figures. May, 1918 ..... .75
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    Index in preparation.

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2. An Unusual Extension of the Distribution of the Shipworm in San Francisco Bay, California, by Albert L. Barrows. Pp. 27-43. December, 1917. .20
3. Description of Some New Species of *Polynoidae* from the Coast of California, by Christine Essenberg. Pp. 45-60, plates 2-3. October, 1917 ..... .20
4. New Species of *Amphinomidae* from the Pacific Coast, by Christine Essenberg. Pp. 61-74, plates 4-5. October, 1917 ..... .15
5. *Crithidia euryophthalmi*, sp. nov., from the Hemipteran Bug, *Euryophthalmus convivus* Stål, by Irene McCulloch. Pp. 75-88, 35 text figures. December, 1917 ..... .15
6. On the Orientation of *Erythropsis*, by Charles Atwood Kofoid and Olive Swezy. Pp. 89-102, 12 figures in text. December, 1917 ..... .15
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13. A Quantitative Analysis of the Molluscan Fauna of San Francisco Bay, by E. L. Packard. Pp. 299-336, plates 12-13, 6 figs. in text. April, 1918..... .40
14. The Neuromotor Apparatus of *Euplotes patella*, by Harry B. Yocom. Pp. 337-396, plates 14-16 ..... (*In press*)
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Vol. 18, No. 17, pp. 485-507, 3 figures in text
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January 4, 1919

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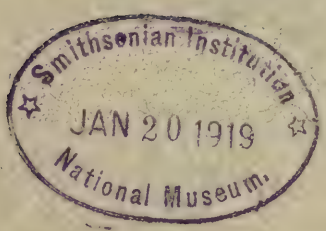
18. NOTES ON THE EGGS AND MIRACIDIA OF THE HUMAN SCHISTOSOMES

BY
WILLIAM W. CORT



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Index in preparation.

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THE CERCARIA OF THE JAPANESE BLOOD FLUKE, *SCHISTOSOMA JAPONICUM* KATSURADA

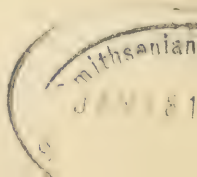
BY
WILLIAM W. CORT

CONTENTS

PAGE
Historical 485
Material 489
Method of study 490
Characters of the schistosome cercariae 491
Structure of the cercaria 492
Oral sucker and cephalic glands 496
Activity of the cercaria 502
Literature cited 504

HISTORICAL

The discovery of the intermediate stages and methods of entrance into man of the human blood flukes is of very recent date. Guided by the knowledge of the life cycles of related forms, numerous workers attempted without success to find intermediate hosts for these species. After repeated efforts to find the larval stages of the Egyptian blood fluke, *Schistosoma haematobium*, in Egyptian molluses, Looss finally advanced the hypothesis that no intermediate host was needed in the life cycle of this species and that man was infected by the miracidium penetrating through the skin. According to this hypothesis, the intermediate stages developed in the liver of man. Looss supported his contention in a number of articles (1894, 1905, 1908, 1909), but without adducing any positive experimental evidence. In fact, numerous attempts to infect experimental animals directly with the miracidia of the human schistosomes were entirely without success (Looss, 1905;



Tsuchiya, 1913; Conor, 1914). Looss explained these failures by stating that since man was the only known host for this parasite experiments on other animals were without significance. Looss's hypothesis of direct infection received the support of many parasitologists and undoubtedly delayed the final discovery of the life cycle of these forms.

The first successful experiments on the method of transmission of the human schistosomes were carried on in 1909 by Japanese workers with the Japanese species, *Schistosoma japonicum*. Katsurada and Hashegawa (1910) showed that cats and dogs could be infected through the skin with *S. japonicum*, by immersion in canal water in a district where schistosomiasis was prevalent. Fujinami and Nakamura (1909) succeeded in infecting calves through the skin with this same parasite. The first article by these authors was in Japanese, but their results were included in a later publication by Fujinami (1914) in German. In their first experiments the Japanese workers accepted Looss's hypothesis that the infective stage which penetrated the skin of the host was the miracidium. Further studies, however, began to throw doubt on this conclusion. Miyagawa (1912, 1913) studied the infective stage just after penetration through the skin. In his description he noted the presence of suckers and other differences between this stage and the miracidium. He therefore concluded that *S. japonicum* must have an intermediate host. Matsuura and Yamamoto (1912 and 1912*a*) studied infective stages of *S. japonicum* before they entered the skin and Fujimami (1914, p. 22), with the aid of Nakamura and Narabayashi, studied newly penetrated schistosome larvae in sections of new-born mice and rats. All of these workers noted differences between the infective stage and the miracidium. Fujinami (1914, p. 23) concluded from his studies that the miracidium did not penetrate the skin in infection with *S. japonicum*. Tsuchiya (1913) also came to the conclusion that the Japanese schistosome must require an intermediate host for its development, since all attempts to produce direct infection with the miracidium were without success. Katsurada (1913, p. 371) in a summary of research on Japanese schistosomiasis, abandoned Looss's hypothesis of penetration by the miracidium, in favor of a relatively simple metamorphosis of the miracidium prior to skin infection. In this same paper published in December, 1913, Katsurada (1913, p. 378) added a note to the effect that he had just been informed that Miyairi of Kinshu had found the intermediate stage of *S. japonicum* in a species of *Lymnaea*.[1] Fujinami (1914,

[1] This early identification was later corrected.

p. 23) soon after this also published the statement that the intermediate host had been discovered by Miyairi in a new species of *Blanfordia.* These statements were the first hints to scientific workers outside of Japan that this problem has been solved.

Credit for the discovery of the intermediate host and the first study of the larval stages of the Japanese blood fluke goes to two Japanese workers, Miyairi and Suzuki (1913, 1914). Miyairi and Suzuki solved the problem experimentally by infecting snails of the species *Blanfordia nosophora* with the miracidia of *S. japonicum.* They found that development of sporocysts containing cercariae followed. The cercariae when fully developed escaped from the snails and produced schistosomiasis by penetration through the skin of mice exposed to the water containing infected snails. These authors also described and figured the structure of the stages found in the snails. Two years later Leiper and Atkinson (1915) also produced experimentally the development of the cercariae of *S. japonicum* in the Katayama snail, *Blanfordia nosophora* (Robson). Adults of *S. japonicum* were experimentally developed in mice after skin penetration of cercariae so produced. Leiper and Atkinson (1915) briefly described the sporocysts and cercariae and figured the snail intermediate host and the larval stages. Appended to their account is the description of the intermediate host by G. A. Robson as *Katayama nosophora* nov. gen nov. spec. Fujinami (1914, p. 23) stated that this snail is a new species of the genus *Blanfordia.* Miyagawa (1916, p. 97) discussed fully the question of the systematic position and name of the intermediate host of *S. japonicum.* He placed it in the genus *Blanfordia* A. Adams, and accepting the priority of Robson's specific name designated it as *Blanfordia nosophora* (Robson). Since the discovery of the intermediate host and cercaria of *S. japonicum* additions to the knowledge of this stage have been made by a number of Japanese workers. In 1916 Fujinami, Tsuchiya and Miyagawa (1916) published in Japanese an extensive monograph on Japanese schistosomiasis. In this monograph Fujinami contributed the discussion on the history of the subject and the pathological anatomy, Tsuchiya the part on symptomology, and Miyagawa the part on the etiology. In his part of this monograph Miyagawa (1916) gives the most extensive account of the intermediate host and larval stages of *S. japonicum* to be found in the literature. He also included a critical analysis of the Japanese work along this line which proved to be very helpful. Parts of the papers of Fujinami

(1916, part V) and of Miyagawa (1916) have been translated for me by F. T. Konno, a Japanese student in the University of California. It has been from this translation, from the reviews in the *Tropical Disease Bulletin,* and from the reviews of Japanese medical literature by Mills in the *China Medical Journal,* that material was obtained for the discussion of Japanese papers which were not accessible. Other Japanese writers who have contributed to the knowledge of the structure of the cercaria of *S. japonicum* are Ogata (1914) and Narabayashi (1914, 1916). Notwithstanding the amount of work which has been done on the intermediate stages of *S. japonicum* there is still considerable confusion and difference of opinion in regard to the structure of the cercaria.

The discovery of the intermediate hosts and larval stages of the other two species of human blood flukes, *S. haematobium* and *S. mansoni* followed closely after that of *S. japonicum.* Leiper (1915, parts I, II, III) working in the same laboratory from which Looss tried so long in vain to solve the life history of the Egyptian blood fluke found the intermediate host of that species and studied its larval stages. At first Leiper did not distinguish between the cercariae of *S. haematobium* and *S. mansoni.* In later publications, however, Leiper (1916, 1918) distinguished between the cercaria of *S. haematobium* which develops in *Bullinus contortus* and *Bullinus dybowski* and the cercaria of *S. mansoni* which develops in *Planorbis boissyi.* Leiper did not attempt to make a critical structural analysis or comparison of the cercariae of these two species. Cawston (1915, 1916, 1917) reported the larval stages of *S. haematobium* in *Physopsis africana* from South Africa. His descriptions and figures of this and the other forked-tailed cercariae which he described are so entirely inadequate that it seems to me that his entire work needs verification by more competent observers. In the new world the intermediate host of *S. mansoni* has been discovered in Venezuela by Iturbe and Gonzales (1917) in *Planorbis guadelupensis* Sowerby and by Lutz (1916 and 1917) in *Planorbis olivaceus* Spix. Lutz so far has published only preliminary reports of his work, but promises the full account soon in the *Memorias do Instituto Oswaldo Cruz.* A second paper by Iturbe (1917) contained a fuller account of the anatomy of this cercaria. It is very probable, as stated by Lutz (1916, p. 387), that *Cercaria blanchardi* from *Planorbis bahiensis* was the cercaria of *S. mansoni.* Da Silva's description of this form is too brief to make certain determination possible, but agrees as far as it goes with the description of

the cercaria of *S. mansoni*. Lutz (1916, p. 387) considers *Planorbis bahiensis* to be a synonym of *Planorbis olivaceus* Spix. In a footnote to a review of Lutz's second preliminary report (Trop. Dis. Bull., **11**, 79) Leiper makes the following statement: "*Planorbis guadelupensis* more recently implicated by Iturbe in Caracas is very similar to, if not identical with, *Planorbis olivaceus*." The solving of the exact systematic relations of these hosts will have to await further work. As can be gathered from this brief review of the literature there still remains much work to be done on the larval stages of the human schistosomes.

Studies on the human schistosomes are of peculiar importance to California and the other Pacific coast states on account of immigration from countries where schistosomiasis is prevalent. Records of the United States Public Health Service and case records show that schistosomiasis has been brought into this country. If suitable intermediate hosts could be found this disease might become established, especially since it can develop in cats, dogs, rats, cattle, and other animals. In previous publications I have pointed out this danger and have shown that trematodes of this type show considerable adaptability in intermediate hosts (Cort, 1918*b*, 1918*c*). Recently Reed (1918) has also considered this subject. He discusses five cases of schistosomiasis from California and mentions others which have come to his attention. His conclusions in regard to the dangers to California from this disease are similar to my own. One of the purposes of the present paper is to aid investigations, which are being carried on to determine whether the human schistosomes have found suitable intermediate hosts in this country, by clearly defining the cercaria of *S. japonicum*.

MATERIAL

The material of the larval stages of *S. japonicum* on which the studies included in this paper are based was obtained from living specimens of the Katayama snail, *Blanfordia nosophora* (Robson), which were sent to Professor C. A. Kofoid by Professor A. Fujinami of Kyoto, Japan. To both of these gentlemen my sincerest thanks are due for making possible this work. *Blanfordia nosophora* is an operculate snail, and is very resistant to drying. The snails were shipped across the Pacific Ocean in dust, and appeared, on arrival, to be entirely dry and dead. They were placed in water in an aquarium in the evening and the following morning were found to be actively

moving. A few of the original lot are still alive, having lived more than a year in an aquarium. Since only a small percentage of these snails were infected with cercaria of the Japanese blood fluke, the material available for study was small. To make sure that the cercariae found in the snails belonged to *S. japonicum,* two white rats were infected through the skin. Post-mortem examination of these rats made six weeks later revealed specimens of *S. japonicum.* On account of the limited amount of material no extensive infection experiments or studies of the developmental stages between the cercariae and the adult were attempted. In all, sporocysts and cercariae from five infected snails were utilized in this study.

METHOD OF STUDY

The greater part of my observations of the cercaria of *S. japonicum* were made from living specimens. The method used in this study of the living cercaria is the same that I have utilized in all my recent studies on larval trematodes. It is discussed in detail in previous publications (Cort, 1917, pp. 49–50 and 1918*a*, pp. 129–130). The snails intended for study were carefully opened and the viscera removed, so that the digestive gland was as little crushed as possible. If the snail were infected with the cercariae the digestive gland would have a yellowish diseased appearance, since it would be literally riddled with the sporocysts. Snails were opened early in the morning and the cercariae which would be present in an infected host in large numbers could be kept alive a whole day in ordinary tap water. Therefore each infected snail found, gave material for a whole day's intensive study of living cercariae. The cercariae, freed in a Syracuse watch glass, were first studied with the lower powers of the microscope to make an analysis of locomotion. Several cercariae were then transferred to a slide in a small drop of water and covered with a No. 1 cover glass. In order to slow down the movements sufficiently for study it was necessary to remove slowly the water from the preparation with a piece of blotting paper until the cover glass pressed on the living cercaria. The cercaria could then be studied until the drying and pressure of the cover glass caused it to go to pieces. I usually found it convenient to make a half dozen or more of these preparations at a time. A single day's study required the use of several hundred preparations. The use of a compound binocular microscope is indispensable for this type of work. The best results were obtained

with an oil immersion lens and low oculars. This method of study is tedious, hard on the eyes, and requires long practice to use effectively, but gives extremely satisfactory results. Miyagawa (1916, p. 64) noted the difficulty of observing the living cercariae on account of their great activity. He advocates the method of intravitam staining as employed by Narabayashi. I have, however, found no advantage in intravitam staining in the study of a cercaria such as that of *S. japonicum* in which the structures are clearly differentiated. To check my observations on the living cercaria, serial sections were made of a piece of a snail's liver containing the sporocysts and cercariae. These sections were cut five micra in thickness and stained with Delafield's haematoxylin with a counterstain of erythrosin. The study of the sections served to corroborate the observations made from the living animals and added certain important details.

CHARACTERS OF THE CERCARIAE OF THE HUMAN SCHISTOSOMES

The cercaria of *S. japonicum* agrees with the cercariae of the two other species of human schistosomes in a number of definite particulars. Certain specific differences will be noted, but in the present state of our knowledge it is difficult to discriminate clearly in morphological characters between these three species of cercariae. This is undoubtedly due more to the limitations of our knowledge than to lack of specific differences. The cercariae of the human schistosomes are very small and develop in elongate motile sporocysts. They are fork-tailed forms in which the divided lobes of the tail are less than half the length of the main stem and definitely constricted from it. They are without eyespots and pharynx and have a very rudimentary digestive system. The whole surface of the body is covered with fine, backward pointing spines. The ventral sucker is very small and in the posterior third of the body length. The posterior half of the body is filled with large unicellular glands, the ducts of which open at the anterior tip after passing through a highly modified oral sucker containing a central glandular reservoir. The reproductive organs of the adult are represented by a small group of nuclei back of the ventral sucker. The excretory system contains a very small number of flame cells and a tubular bilateral type of bladder extending into the tail. To sum up: the adult structures of the cercariae of the human schistosomes are only slightly developed, and adaptive larval characters for locomotion and penetration predominate.

STRUCTURE OF THE CERCARIA

Measurements of the cercaria of *S. japonicum* are very unsatisfactory data for comparison, since the length of the living animal varies greatly with extension and contraction. Preserved specimens are much contracted and vary in length with the method of killing and the contraction state when killed. Further, there is no evidence that all cercariae of the same species will develop to the same size in different sporocysts or different host individuals. Figure 1 is an enlargement from a camera lucida drawing of a slightly compressed cercaria and gives an idea of the size and shape at an average state of extension. The body of the cercaria has the power of extension to almost twice its contracted length and the stem of the tail is capable of even greater changes in length. The body of the cercaria and the stem of the tail are cylindrical in cross-section. When the body is fully extended its diameter may be reduced to that of the tail. Miyagawa (1916, p. 64) gives the length of the body in well extended specimens as 0.09 to 0.21 mm. Leiper (1915, p. 202) gives the body length of the specimens of the cercaria of *S. japonicum* measured by him as about 0.1 mm. This measurement agrees with Miyagawa's measurement on preserved material. Leiper, however, does not state the condition of the specimens which he measured.

The whole surface of the body and tail of the cercaria of *S. japonicum* is covered with backward pointing, cuticular spines. Beneath the delicate cuticula are found two layers of muscles, an outer circular and an inner longitudinal (figs. 1, 2). The individual strands of the longitudinal layer have about twice the thickness of those of the circular layer. The body of the cercaria is so completely filled with the various organs that the parenchymatous tissue is limited to a very thin superficial layer (figs. 1, 2). Since the flame cells and tubules of the excretory system develop in the parenchymatous tissue they are also limited to this superficial region of the body.

The tail of the cercaria of *S. japonicum* has well developed muscular layers, especially in the stem region (fig. 1, *st*). The strength of these muscles is shown clearly by the power of vibration, extension and contraction which the tail possesses. The main stem of the tail is round in cross-section, while the divided lobes which are definitely constricted off from the stem are somewhat flattened. The parenchymatous tissue of the tail is dense, containing numerous nuclei obscur-

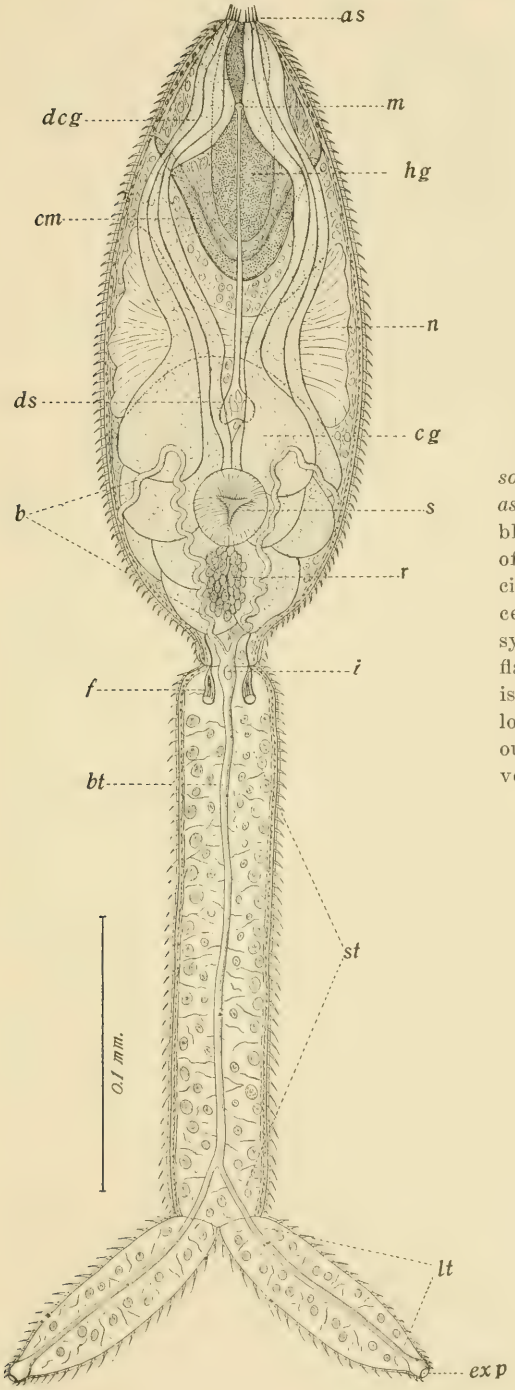


Fig. 1. Cercaria of *Schistosoma japonicum*, ventral veiw; *as*, anterior spines; *b*, excretory bladder; *bt*, excretory bladder of tail; *cg*, cephalic glands; *cm*, circular muscles; *dcg*, ducts of cephalic glands; *ds*, digestive system; *exp*, excretory pore; *f*, flame cell; *hg*, head gland; *i*, island in excretory bladder; *lt*, lobe of tail; *m*, mouth; *n*, nervous system; *st*, stem of tail; *s*, ventral sucker.

ing the tubes of the excretory system, which can only be followed with difficulty. In the main stem of the tail (fig. 1, *st*) there are two lateral rows of large, fairly regular nuclei. The tail is an effective muscular organ and is so attached that it is readily lost when the cercaria starts to penetrate into its final host.

The ventral sucker (figs. 1, 2, *s*) is located at a point about three-fourths of the distance from the anterior to the posterior end of the body. It is circular in ventral view with a depth considerably greater than its diameter (fig. 2). In the living animal the ventral sucker can be protruded so that it has almost the appearance of a proboscis. The sucker functions strongly in locomotion and is able to hold the cercaria against considerable pressure.

I have already given in a previous publication (Cort, 1917, p. 52) a preliminary description of the excretory system of the cercaria of *S. japonicum*. The bladder (figs. 1, 2, *b, bt*) is composed of elongate tubes and extends from the body into the tail. As in all fork-tailed cercariae I have ever observed, there are two excretory pores (fig. 1, *exp*), one on each of the divided lobes of the tail. The sides of the V-shaped, bladder tubes of the body unite at the posterior end and pass into the main stem of the tail as a single tube, which divides to send branches to the pores at the tips of the bifurcations of the tail. At the pores the tubes are slightly enlarged (fig. 1, *exp*). There is a characteristic anastomosis in the tube of the bladder just where it enters the tail, forming a little island (fig. 1, *i*). The bladder in the body (figs. 1, 2, *b*) which after the loss of the tail becomes the bladder of the adult, is V-shaped. The sides of the V extend from their point of union at the posterior end of the body along the ventral surface to a region in front and to each side of the ventral sucker. They then turn dorsad and pass along the sides of the cercaria still in the superficial layer of parenchymatous tissue to the points on each side where they receive the anterior and posterior collecting tubes (fig. 2, *act, pct*). Two ciliated areas (fig. 2, *ca*) are present on each side near the ends of the sides of the bladder. The collecting tubes (figs. 2, 3, *act, pct*) are short and each receives the capillaries from two flame cells, making four flame cells on each side, three in the body and one in the anterior part of the stem of the tail (figs. 2, 3, *f*). The positions of the flame cells are clearly indicated in figure 2. . The complete excretory system of the cercaria of *S. japonicum* is shown diagrammatically from the ventral side in figure 3. The cercaria of *S. japonicum* has the smallest number of flame cells that I have ever observed

in a fully developed cercaria or seen recorded in the literature. The whole system in the body is limited to the superficial layer of parenchymatous tissue, and almost all of the anterior half of the body of the cercaria is without flame cells. However, the total mass of the body of the cercaria is so small that no part is far from a flame cell. I will not discuss here the general homologies of the excretory system of the forked-tailed cercariae, since this subject was taken up in previous publications (Cort, 1917, 1918). Previous knowledge of the excretory system of the cercaria of the human schistosomes is very slight. Miyagawa (1916, p. 67, pl. 4, fig. 30) saw only the main tubules of the excretory system in the body and missed its connections in the tail. Miyairi and Suzuki (1914) stated that the excretory system of the cercaria of *S. japonicum* has five pairs of flame cells. Ogata (1914) found two paired, laterally symmetrical flame cells with vessels. Iturbe (1917, p. 433, fig. 1) located five pairs of flame cells in the cercaria of *S. mansoni*, including one pair in the tail, but neither describes nor figures the rest of the system. From my knowledge of the homologies of the excretory systems of the fork-tailed cercaria in general I would expect to find this system in the cercariae of *S. mansoni* and *S. haematobium* corresponding closely to the conditions just described for the cercaria of *S. japonicum*.

The central nervous system of the cercaria of *S. japonicum* (figs. 1, 2, *n*) is a bilobed mass back of the oral sucker and dorsad to the ducts of the cephalic glands. No attempt was made to trace the nerve trunks leading from this mass.

It was not possible to distinguish morphologically between male and female cercariae, and the only trace of the complicated reproductive systems of the adult is a small mass of nuclei on the ventral side back of the acetabulum (fig. 1, *r*). The extreme immaturity of this type of cercaria is emphasized when we consider how completely the structure of the adult schistosomes is dominated by secondary sexual characters and the complex reproductive systems.

The digestive system of the cercaria of *S. japonicum* is in a very rudimentary condition (figs. 1, 2, *m, ds*). The mouth is situated on the ventral surface a little distance back of the anterior tip. A very narrow buccal cavity passes through the oral sucker. The esophagus extends from the posterior limit of this cavity to about the midline of the body dorsad to the cephalic glands, where it widens into a heart-shaped structure which represents the beginnings of the bifurcations of the intestinal caeca. The remarkable thing about this

digestive system is that the mouth is located on the ventral surface quite a little distance back of the anterior tip and not at the anterior tip, as believed by other workers on this species. Ssinitzin (1909) noted this same relation in the digestive system of *Cercaria ocellata* La Valette, which is a schistosome cercaria of the group with eyespots. His description and figures of the digestive system in this form (Ssinitzin, 1909, p. 317, pl. 10, figs. 22, 23) agree almost exactly with the description just given for the cercaria of *S. japonicum*. Miyagawa (1916, pl. 4, fig. 30) notes the same rudimentary condition of the esophagus and intestinal caeca in his studies on the cercaria of *S. japonicum*. He, however, considers that the mouth is at the anterior tip, although he does not adequately describe or figure its relations to the digestive tract in the oral sucker. Leiper (1915, fig. 2) figures the intestinal caeca as very wide tubes extending to each side of the ventral sucker. The esophagus he shows to be very short. In fact, his description and drawing of this structure are very different from Miyagawa's and my own. I believe that Leiper must have confused the lobes of the nervous system with the digestive caeca, since he does not show these structures. In view of Ssinitzin's finding in *Cercaria ocellata* and my own in the cercaria of *S. japonicum*, I would expect to find such a rudimentary digestive tract as that described above in all fully developed schistosome cercariae.

ORAL SUCKER AND CEPHALIC GLANDS

The oral sucker (figs. 1, 2) of the cercaria of *S. japonicum* is so remarkably modified by adaptive larval characters that it has little resemblance to the oral sucker of the adult into which it develops. It has a length of more than one-third the length of the body, and has distinctly separated anterior and posterior regions. In its anterior region it is in direct contact with the cuticula. The layers of circular and longitudinal muscle fibers of the body wall, which are strengthened in this region, form its outer limits. The posterior region of the oral sucker does not come into contact with the body wall, but is separated from it by a considerable layer of parenchymatous tissue, and tapers posteriorly in the shape of a blunted cone. This posterior region is surrounded by a thick layer of circular muscles (figs. 1, 2, *cm*), the fibers of which appear in the drawings in optical section. Within the circular muscle layer is a thinner layer of longitudinal muscles. The line of separation between the anterior and posterior regions of

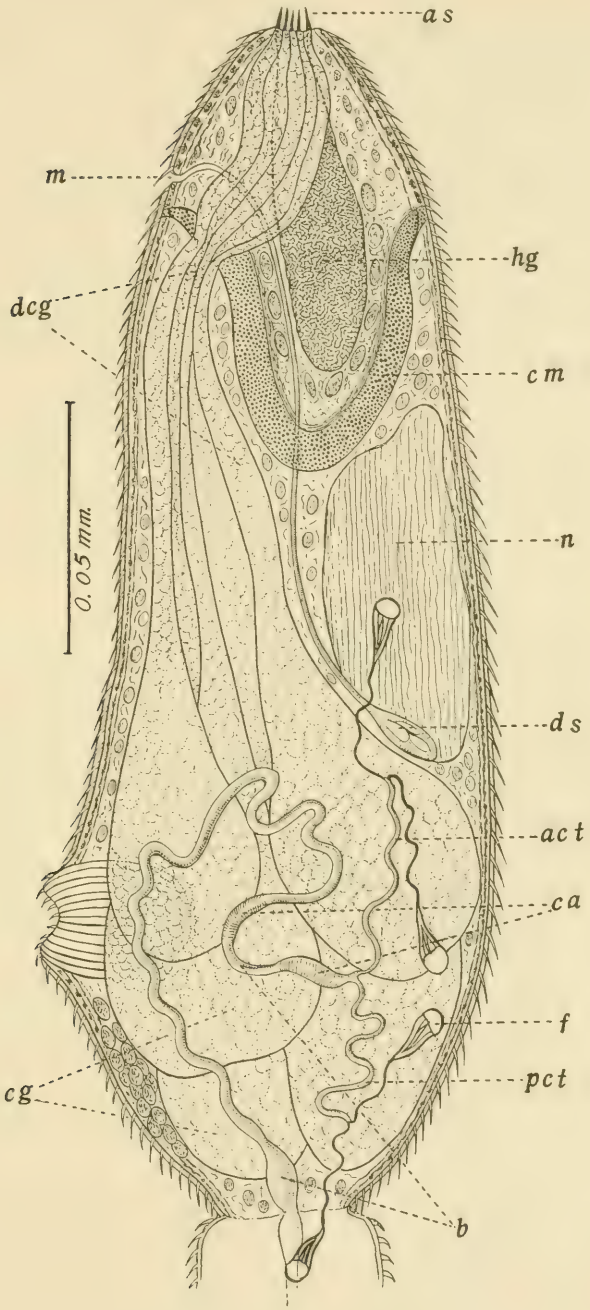


Fig. 2. Cercaria of *Schistosoma japonicum*, side view; letters as before; also *act*, anterior collecting tube; *ca*, ciliated areas; *pct*, posterior collecting tube.

the oral sucker is very clearly defined in a living cercaria or toto mount. Under certain conditions this line appears as a constriction which separates the so called "head" of the cercaria from the body proper.

The center of the oral sucker contains a large reservoir-like gland (fig. 1, 2, *hg*) which opens almost exactly in the middle of the anterior tip. This is called the "head-gland" by Miyagawa (1916, p. 67). As noted by Miyagawa it is more coarsely granular than the cephalic glands which fill the posterior half of the body. I will include a translation of the discussion in Miyagawa's paper (1916, p. 67) in regard to this gland:

> Head-gland = Kopfdruse (of Narabayashi).
>
> This gland occupies about half of the head at the dorsal part of the center. It contains coarse granular material and is stretched or compressed with the movements of the cercaria. It opens at the anterior end of the oral sucker. This sac-like gland has been confused by many investigators with the buccal cavity. In larvae examined after entering the skin it was found to be pressed to one side and later disappeared.

Since the head-gland degenerates soon after the cercaria has penetrated through the skin of its final host, Miyagawa considered that it is an adaptive larval structure which has some function connected with penetration. Its position would also seem to support this view. A layer of large nuclei surround the gland and are evidently a part of it. The contrast between the head-gland and the cephalic glands (figs. 1, 2, *cg*) is shown very clearly by reactions of their glandular substances to stains. The head-gland in the sections studied took the red stain (erythrosin), while the cephalic glands were stained a light blue with haematoxylin.

The remainder of the oral sucker is filled with parenchymatous tissue and the anterior portions of the ducts of the cephalic glands (figs. 1, 2, *dcg*). The consistency of the oral sucker is such that its shape can be greatly distorted by contraction of its muscles. The ducts from the cephalic glands (figs. 1, 2, *dcg*) pass into the oral sucker on each side near its ventral surface. They pass directly through the muscular boundary of the sucker and run forward along each side to open at the anterior tip of the cercaria. Near the openings of these ducts at the anterior tip are located on each side four or five, forward pointing spines (figs. 1, 2, *as*). The relations of the different parts included in the oral sucker are shown clearly in figures 1 and 2. The oral sucker is not radially symmetrical as is usually the case, but has

a dorsoventral differentiation depending on the position of the ducts of the cephalic glands, the mouth and buccal cavity. This dorsoventral differentiation is also clearly indicated by the shape of its posterior region. That this unusual differentiation of the oral sucker is probably common to all true schistosome cercariae is suggested by the description of a similar differentiation of the oral sucker of

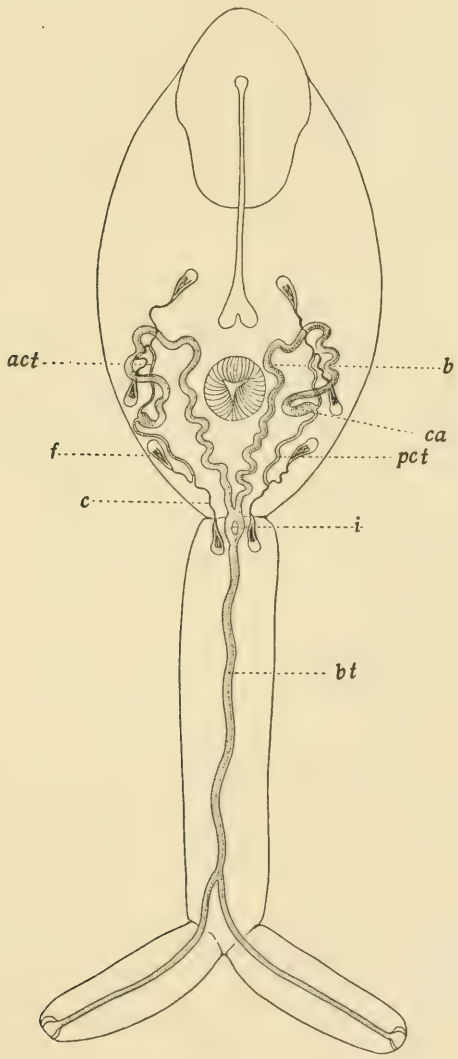


Fig. 3. Diagrammatic representation of the excretory system of the cercaria of *Schistosoma japonicum*, ventral view; letters as before.

Cercaria ocellata La Valette as described by Ssinitzin (1909, p. 316, pl. 10, figs. 22, 23, 26). This author shows clearly the layer of circular muscles of the posterior region of the oral sucker, the positions of the ducts of the cephalic glands passing through the sucker and the position of the mouth on its ventral surface. Most of the descriptions of schistosome cercariae do not show the details of this organ. In my figures (Cort, 1915, p. 50, pl. 7, figs. 59–62) of the oral sucker of *Cercaria douthitti* the passage of the ducts of the cephalic glands through the oral sucker is clearly brought out, although the other parts are not entirely clear. In recent studies of an undescribed species of schistosome cercaria with eyespots I found the structures of the oral sucker to be much the same as in the cercaria of *S. japonicum,* including the thick circular muscular layer of the posterior region, the head-gland, and the spines at the openings of the ducts of the cephalic glands.

The cephalic glands (figs. 1, 2, *cg*) are unicellular with large nuclei filling almost all of the posterior half of the body. I counted five of these glands on a side. The ducts from the cephalic glands pass forward in two groups ventrad to the central nervous system and digestive tract and enter the oral sucker as described above. These glands are loose in texture, the bulk of each gland apparently consisting of secretory products and are pushed into all sorts of shapes by changes in the shape of the body of the cercaria. It is not easy to distinguish clearly the outlines of the cephalic glands and to determine their exact number. Leiper (1915, p. 202) stated that there are five or more of these glands on each side. I have, however, never noted any variation in their number in different cercariae. Miyairi and Suzuki (1914), Ogata (1914), and Miyagawa (1916, p. 66, pl. 4, fig. 30) noted only three pairs of these glands in their descriptions of the cercaria of *S. japonicum.* Miyagawa's figure (1916, fig. 30) shows the cephalic glands as six small bodies between the digestive caeca and the acetabulum, filling only a small part of the posterior body region. My observations lead me to believe that Miyagawa's drawing is incorrect in this particular.

The total bulk of these glands and their ducts, which is more than half the total bulk of the body of the cercaria, indicates that they perform an important function. The cephalic glands of the fork-tailed cercariae appear to be homologous to the stylet glands of the xiphidio-cercariae which open at the base of the stylet or piercing organ, and to which the function of dissolving tissue in connection

with the penetration of the cercaria into its host has been ascribed by certain authors. A full account of the functioning of the stylet glands in penetration was given almost twenty-five years ago by Looss (1894, pp. 127, 238). Faust (1918, p. 34), following La Rue's analysis (1917, p. 5) of similar glands in an agamodistome, calls the cephalic glands of the fork-tailed cercariae mucin glands. Miyagawa (1916, p. 366), following Miyairi and Suzuki (1914), called the cephalic glands of the cercaria of *S. japonicum* "poison glands." I prefer the term cephalic gland, since the ducts of these glands open at the anterior tip of the cercaria. My studies lead me to believe that these cephalic glands function in penetration, probably by dissolving tissue. Instead of a single stylet as in the xiphidio-cercariae, the schistosome cercariae have a number of spines around the openings of the cephalic glands which perform the same function as the stylet in penetration. Besides producing a cytolytic secretion which dissolves the tissues of the host and thus aids the cercaria in penetration, it seems probable that the secretions of these glands neutralize the toxic secretions that the host produces in its attempt to combat the entrance of the cercariae. Miyagawa (1916, p. 66) stated that these glands must have something to do with penetration since, according to his observations, they disappear soon after the cercaria has entered the body of the host. Leiper (1915, part III, p. 260) also suggested that these glands in the cercaria of *S. haematobium* function in penetration. The head-gland which also disappears after the cercaria has entered the body of its host, seems also to function in penetration. The productions of eosonophil cells by the host in connection with the penetration of the schistosome cercaria, suggests that the host is actively combating the entrance of the parasite by the production of toxins. This may be taken as evidence of the battle which is waged between the host and the entering parasite. It seems to me very probable that the head-gland and the cephalic glands are the batteries of the cercaria in this fight, which in the offensive of the human schistosome cercariae give such striking success to the invaders. Certain of the movements of the anterior end of the cercaria of *S. japonicum* observed in connection with the activities of the living animal support the theory that the cephalic glands function in penetration. This evidence will be brought out in connection with the discussion of the activity of the living cercaria.

ACTIVITY OF THE CERCARIA

The cercaria of *S. japonicum* when freed from its sporocysts in a watch glass swims freely for a short time and then settles down to the surface where it moves by a looping movement. It has a strong positive thigmotropism, so that whenever any part of its body touches a surface the cercaria immediately adheres to it and starts moving on it. In fact, this cercaria is apparently better adapted for locomotion on a substratum than for free swimming. In swimming the movement of the cercaria of *S. japonicum* consists of a vibration of both the body and the tail which carries the animal either forward or backward in an irregular course through the water. The movement is more often backward than forward. During the vibration the body is slightly contracted, but the stem of the tail is considerably elongated. The posterior end of the body and the point of bifurcation of the tail are relatively constant points, while the anterior end of the body and the middle of the stem of the tail vibrate backward and forward so rapidly that they disappear from view.

The method of locomotion on a substratum is also very characteristic. It is a modification of the ordinary looping movement common to so many distome cercariae (see Cort, 1915). The cercaria is able to take hold both with the ventral sucker and the anterior tip. Its method of taking hold with the anterior tip is very characteristic. In trematodes, both cercariae and adults, in which the oral sucker is fully developed, the suction which allows this sucker to take hold is produced by the action of the muscles of the sucker in connection with the mouth and buccal cavity. In the cercaria of *S. japonicum* the sucking action of the anterior end is developed in an entirely different way and has no connection with the mouth or buccal cavity. As long as a cercaria is alive the anterior tip keeps rolling in and out by the interaction of the strong circular and longitudinal muscles of the anterior region of the oral sucker, and the circular muscles of the posterior region. The exact mechanism of this rhythmic action is not clear but the sequence of movements is about as follows: The strong contraction of the circular muscles of the posterior region of the oral sucker presses this organ forward and causes the anterior end to be thrust out with the openings of the cephalic glands and the spines surrounding them at the anterior extremity. This is followed by a rolling-in of the tip for a considerable distance. This rolling-in

pushes the ends of the ducts of the cephalic glands with their spines well back into the middle of the sucker and produces a cavity at the anterior tip lined with the surface spines. It is this rolling-in action of the anterior tip which makes suction possible.

The locomotion on a substratum of the cercaria of *S. japonicum* consists of an alternate taking-hold and loosening of the ventral sucker and the anterior tip. In initiating locomotion on a substratum the cercaria takes hold with its ventral sucker and stretches out its body to about one and one-half times the normal length. The extended body may sway backward and forward and reach around as if it were exploring. At greatest extension the body, which at this time has a width no greater than the width of the tail, bends over and the anterior tip takes hold, then the ventral sucker is loosened and is pulled forward to take hold just back of the anterior tip; this causes the body to arch up. After the ventral sucker takes hold the anterior tip is loosened and the preacetabular region is again extended and takes hold. Each time the body is bent up for the ventral sucker to take a new hold the tail is vibrated. Quick repetitions of this movement produce a fairly rapid locomotion. The bending-up of the body and the taking hold by the ventral sucker are accomplished so quickly that the cercaria gives the impression of moving across the surface by a series of jumps. Even if the anterior tip does not get a hold, as is often the case in movement on a smooth surface, the cercaria will make progress, since the ventral sucker, aided by the vibration of the tail, will gain a hold in advance of its previous hold. At the initiation of the movement when the anterior end is at its greatest extension the openings of the ducts of the cephalic glands with their spines are just at the anterior tip, but when the worm bends over to take hold the anterior tip is rolled in, so that the openings of these ducts point toward the center of the oral sucker and the surface which catches hold is covered with spines.

Certain of the activities of the cercaria of *S. japonicum* show direct correlation with penetration into the human host. The tendency of the cercaria to adhere and move on the surface of any object with which it comes in contact would tend to bring it into relation to this host. In several instances cercariae were watched when attached by their ventral suckers to pieces of snail tissues. When in this position the preacetabular region reaches out in all directions in an exploring movement. This movement, combined with the rhythmical pushing out and rolling in of the anterior tip made the cercariae look as if

they were exploring with the anterior end to find a point where they could push in. That the pushing out of the anterior tip exerts considerable force was shown by the observation that when the cercaria was in contact with loose pieces of débris it would push them away by this movement. I also saw cercariae forcing their way through the loose tissue of the snail or disintegrating sporocysts. The extension of the body combined with the pushing out of the anterior tip forced the tip of the worm into the tissue. The backward pointing, cuticular spines of the body held what was gained and the new extensions of the body produced further progress. Several times in connection with the progress of cercariae through tissue, bubbles of secretions from the cephalic glands were seen to be forced out when the anterior tip was extended to its utmost. The above observations and a consideration of the relations of the adaptive larval characters of the cercaria of *S. japonicum* gives us an idea of how it penetrates the human host. The cercariae freed from the snail in the rice fields would be stirred into activity by the passage of the host. Coming in contact with the surface of the skin the cercaria would catch hold with the ventral sucker and by the extension of its body and the butting with the spines of the tip would produce a slight opening. Aided by the cytolytic secretions of its glands, the backward pointing spines and its movement, the cercaria would rapidly take advantage of the opening to penetrate through the skin of the host. In fact, the cercaria of *S. japonicum* is primarily a machine for skin penetration and its structure is completely dominated by those adaptive larval characters which make possible its penetration into the human host.

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NOTES ON THE EGGS AND MIRACIDIA OF THE HUMAN SCHISTOSOMES

BY
WILLIAM W. CORT

INTRODUCTION

During the spring of 1917 through the kindness of Dr. J. P. Hickey of the United States Public Health Service, I obtained fecal samples from three cases of schistosomasis. One of these samples contained eggs of *Schistosoma mansoni* and the other two contained eggs of *S. japonicum*. This material was used primarily for experimental work, but gave an excellent opportunity for careful study of the eggs and miracidia in the living condition. An examination of the literature shows that, although the structure of the miracidium of *S. haematobium* had been carefully worked out twenty-five years ago (Looss, 1893, 1894), the descriptions and figures of this stage in *S. mansoni* and *S. japonicum* are still inadequate.

THE EGG AND MIRACIDIUM OF *SCHISTOSOMA MANSONI*

Figure 1 is a microphotograph of an egg of *Schistosoma mansoni* showing its general shape and the position of the spine, and figures 2, 3, and 4 are drawings of the miracidium of this species, showing the details of structure as they appear in optical section of the living animal. It is interesting to note that in the egg the position of the miracidium may be either with the anterior papilla toward the spine (fig. 3) or away from the spine (fig. 4). Conor (1910, p. 533) noted this same difference of position of the miracidium of *S. haematobium* within the egg. In forty counts of this species he finds the anterior papilla toward the spine and in one hundred and seventy, away from

it. The shell of the egg of *S. mansoni* is very tough and resistant. Attempts were made to break open the eggs and free the miracidia by pressure on the cover glass. Often the egg would be pressed to twice its normal diameter before the shell would break. Even then, in a number of instances, the miracidium escaped undamaged. The inside of the shell is lined with a thin vitelline membrane (fig. 4, *vm*). In several instances when the shell was broken by pressure, the vitelline membrane came away intact, surrounding the miracidium like a veil, and it required considerable activity of the miracidium to free itself from the membrane. Looss (1893, pp. 521, 522) described the vitelline membrane in the egg of *S. haematobium* as a colorless, finely granular

Fig. 1. Microphotograph of the egg of *Schistosoma mansoni*. Photograph taken by Dr. J. P. Hickey.

membrane with projecting nuclei here and there. The space between the vitelline membrane and the embryo contains granules and oil globules. These oil globules are secreted by the anterior ducts (fig. 2, *ad*). Holcomb (1907, pp, 66, 67) speaks of these oil globules as opalescent bodies and considers them to be food for the embryo. The anterior ducts and their secretion will be discussed more fully in connection with the description of the miracidium of *S. japonicum*.

When freed from the egg the miracidium swims actively, rotating on its long axis. The shape assumed in swimming is similar to that of the miracidium of *S. japonicum* (fig. 5). The miracidium is very mobile and changes its shape greatly when pushing through the débris on a slide. I have seen no such extreme elongation as Holcomb (1907, fig. 4) figured, and believe it very improbable that the miracidium of *S. mansoni* could possibly assume such a shape while swimming. The anterior papilla, which is the only part of the surface of

the body without cilia, is constantly pushed forward and withdrawn when the miracidium is moving in débris. The firm nature of this papilla was shown by the way it could push aside the particles with which it came in contact.

The cephalic glands (figs. 2, 3, 4, *cg*) of the miracidium of *Schistosoma mansoni* are somewhat larger in proportion to the length of the

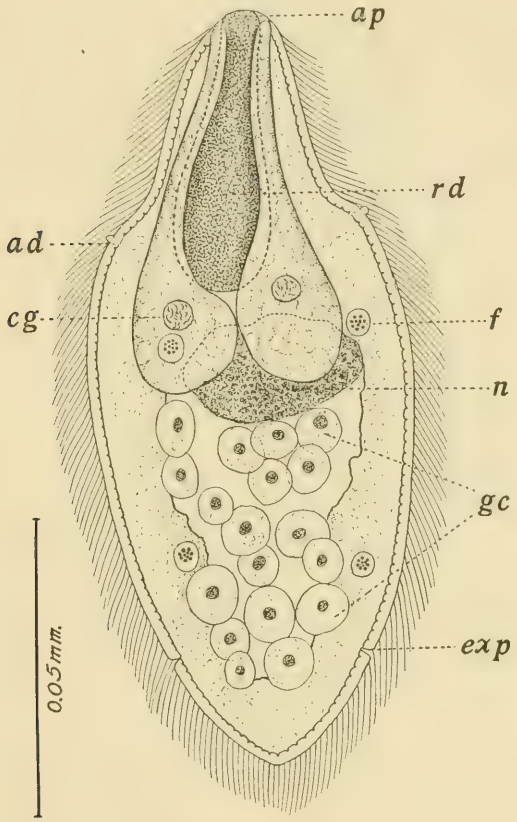

Fig. 2. Miracidium of *S. mansoni*, from glandular surface; *ad*, anterior ducts; *ap*, anterior papilla; *cg*, cephalic gland; *exp*, excretory pore; *f*, flame cell; *gc*, germ cell; *n*, central nervous mass; *rd*, rudimentary digestive sac.

body than in the miracidium of the other two species of human schistosomes. The position of their ducts and their similarity to the cephalic glands of the schistosome cercariae suggest that their secretions may aid in the penetration of the miracidium into the intermediate host, either by dissolving the tissue or by neutralizing the secretions of this host. The cephalic glands are unicellular, with large nuclei.

The central nervous system is an oval, slightly irregular mass lying about the center of the body (figs. 2, 3, 4, *n*). My observations on the living animal did not reveal the nerve fibers going out from this central mass as shown by Looss (1896, p. 165, pl. 11, fig. 113). Holcomb (1907, p. 68) entirely misses the significance of this structure,

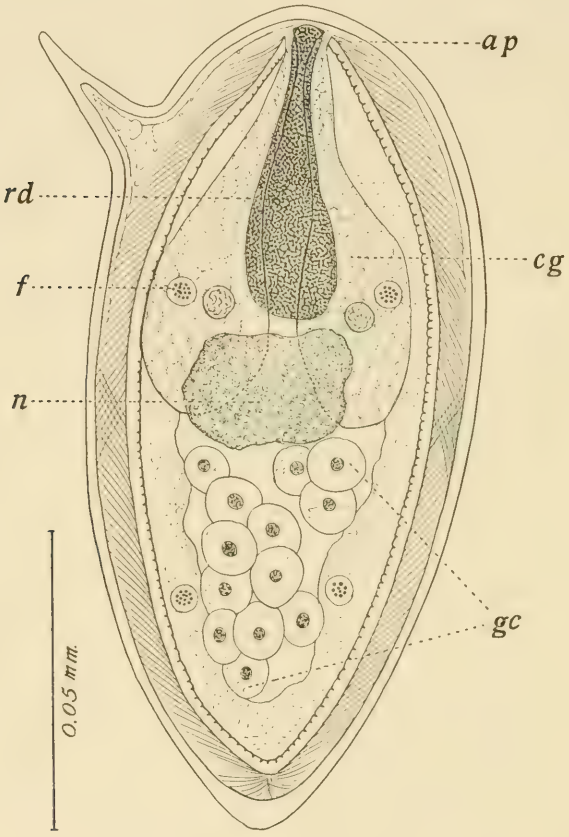

Fig. 3. Miracidium of *S. mansoni* within the egg, from neural surface; letters as in figure. 2.

and calls it a viscus or stomach connected with the anterior end by an esophagus. He was also confused in regard to the structures of the posterior part of the body. His errors are surprising, since an acquaintance with the general structure of the miracidium stage of the trematodes or with the description or figures of the miracidium of *Schistosoma haematobium* would have made them impossible. It is unfortunate that his figures have found their way into some of the

standard textbooks, since they give an entirely erroneous picture of the structure of the miracidium of *S. mansoni.*

I was unable to trace completely the connections of the tubules of the excretory system in this miracidium. The excretory pores (fig. 2, *exp*) are located on each side of the body near the posterior end.

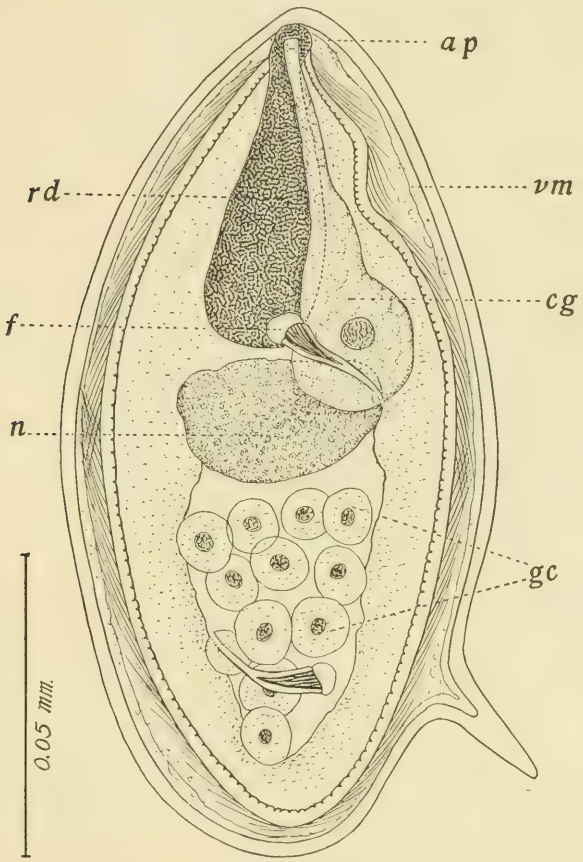

Fig. 4. Miracidium of *S. mansoni* within the egg, lateral view; letters as in figure 2; also *vm,* vitelline membrane.

Four large flame cells (fig. 4, *f*) are present, draining the anterior and posterior regions on each side. The individual flame cell is very large in proportion to the size of the miracidium, having a length of about one-third the width of its body. The flame cells in the miracidium of *Schistosoma mansoni* differ in position from those of the miracidia of *S. haematobium* and *S. japonicum,* since they lie almost perpendicular to the long axis (cf. figs. 4, *f*; 6, *f*). For this

reason they appear, except in side view in optical section of the living miracidium, merely as ciliated holes (figs. 2, 3, *f*). This appearance confused Holcomb (1907, p. 68) who misinterpreted them entirely. Only the beginnings of the capillaries were made out. I could distinguish coiled tubules on each side, but could not trace their connections. In view of the position of the excretory pores and flame cells it is very probable that the excretory system in this miracidium is similar to that of the miracidium of *S. japonicum* (fig. 6, 7).

Functionally the schistosome miracidium appears to have no dorsoventral or lateral differentiation, since it is round in cross-section and revolves on its long axis in locomotion. Structurally, however, this differentiation is very striking. The arrangement of the excretory system and cephalic glands gives a very clear bilateral symmetry. The cephalic glands lie nearer one surface of the body, and the central nervous body and rudimentary digestive sac lie nearer the other. Since the use of the terms dorsal and ventral are meaningless for such a type as this miracidium, I propose that these surfaces be designated respectively the glandular and neural surfaces. The symmetry can be understood most clearly by a comparison of figure 4, a lateral view with figure 2, which is a view from the glandular surface, and with figure 3, which is drawn from the neural surface.

THE EGG AND MIRACIDIUM OF *SCHISTOSOMA JAPONICUM*

The egg and miracidium of *Schistosoma japonicum* are smaller than those of *S. mansoni* or *S. haematobium* (cf. figs. 4, 6). The eggs of *S. japonicum* from the two cases which I studied showed no trace of the rudimentary spine which is so often found on the eggs of this species.[1] The most characteristic form of this spine is described by Leiper (1911, p. 134) as follows:

> In many of the ova the spine appears to rise from the center of a slight navel-like depression in the egg shell. The base of attachment is thickened in all and spreads out upon the shell for a short distance in a manner somewhat similar to the attachment of a thorn to the stem of a rose.

Leiper examined about fifty eggs in all from seven different cases, four in man and three in dogs, and came to the conclusion that the presence of a rudimentary spine is a specific character. Katsurada

[1] In a sample of feces obtained recently from another case of Japanese schistosomiasis about fifty per cent of the eggs showed no spine, while the rest showed it in varying degrees of development.

(1913, p. 370, figs. 4, 6, 7) found either a spine or a thickening of the shell in all the eggs which he examined, and concluded that it was a constant feature. Looss (1911), in the examination of an extensive series of eggs to determine whether the rudimentary spine is a constant feature, found all degrees of variation and a considerable percentage of eggs in which no spine was present. He therefore concluded that the presence of this spine is a variable feature and not a specific character. Wooley and Huffman (1911, p. 131), in examinations of several hundred eggs of *S. japonicum,* found in no instance the least appearance of a blunt protuberance or spine on the outer envelope

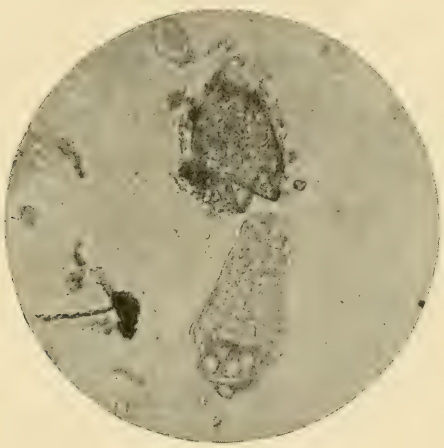

Fig. 5. Microphotograph of miracidium of *S. japonicum* just after it has escaped from the egg. Photographed by Dr. J. P. Hickey.

of the egg. These observations suggest that the lateral spine of the ova of *S. japonicum* is variable and cannot be considered as a specific character. The surface of the shells of the eggs of this species which I examined appeared to be covered with some sort of a sticky substance. This is shown by the fact that the egg never showed a clear-cut outline as in *S. mansoni* (fig. 1), but always had particles of débris adhering to it (fig. 5).

When eggs were first examined fresh from the feces the miracidia, which at this time completely filled the shells, were practically motionless. After a few hours in fresh water the egg shell expanded, leaving a considerable space between the shell and the miracidium, which at this stage was moving actively. In this space were collected granules and oil globules. The globules of oil were extruded from

the anterior ducts (fig. 6, *ad*) which open on each side of the body between the so-called cephalic region and the body proper. The internal relations of these ducts were not clear, but extrusion from them of the oil globules was observed both in *S. japonicum* and *S. mansoni*. Holcomb (1907, fig. 3) figures the anterior ducts in *S. mansoni* as if connected with the cephalic glands. My studies gave no evidence of this relation.

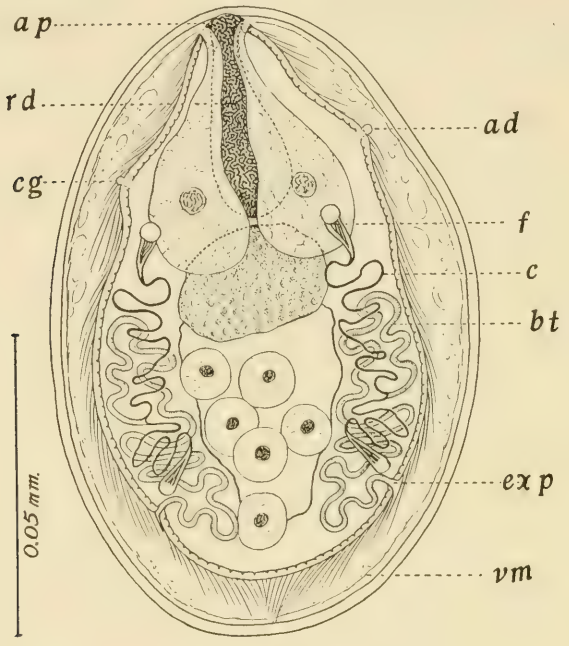

Fig. 6. Miracidium of *S. japonicum* within the egg, from glandular surface; letters as in figures 2 and 4. The reference line from *cg* is incorrectly drawn. It should be extended to the cephalic gland on the left side.

The exact process of the hatching of the egg I did not follow, nor did I see the miracidium escape. The remarkable microphotograph shown in figure 5 was taken by Dr. J. P. Hickey and I am much indebted to him for its use. In the photograph the split through which the miracidium has just escaped is across the end of the egg. The process of hatching of the embryo from the egg has been described for *S. haematobium* by Seligmann (1898, pp. 386–388) and by Conor (1910, p. 533). Smith (1911, p. 64) described this process for the egg of *S. japonicum*. The accounts agree with my observations in that the egg shell begins to swell soon after the egg is placed in water and

the miracidium becomes active, often turning completely around. Finally the egg bursts by splitting, allowing the miracidium to escape. The bursting of the shell seems to be due to the swelling caused by the action of the water and not by any activity of the embryo. I will quote Smith's description (1911, p. 64) of the hatching of the egg of *S. japonicum:*

> The specimens shown [eggs of *S. japonicum*] are in the early unexpanded state. At about 30° C, in the course of ten to twenty hours these eggs expand to nearly or quite double their capacity and the miracidium, now in the quiescent stage, moves actively about within the enclosure and with further enlargement, the wall of the ovum splits and the embryo escapes, a free-swimming ciliated organism.

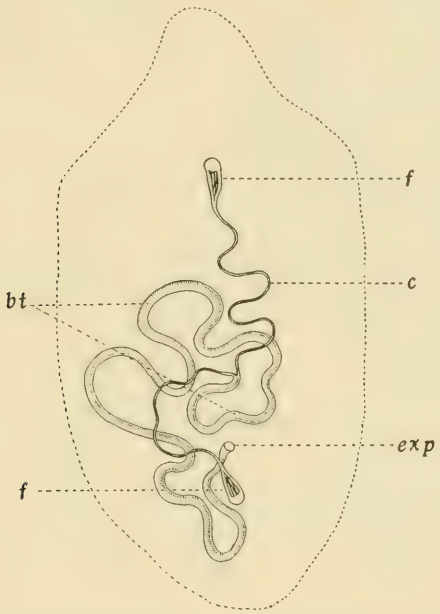

Fig. 7. Diagrammatic representation of one side of the excretory system of the miracidium of *S. japonicum,* from the lateral view; *bt,* bladder tubule; *c,* capillary; *exp,* excretory pore; *f,* flame cell.

The freed miracidium in the microphotograph (fig. 5) shows certain of the structural characters very clearly. The anterior region is somewhat contracted. The non-ciliated anterior papilla shows very clearly at the anterior tip. A short distance back from this, are visible the depressions which mark the openings of the anterior ducts and near the posterior end the openings of the excretory pores are also marked by depressions. Some idea can also be gained of the character

of the glandular structures of the anterior end and the germ cells near the posterior end.

The cephalic glands in the miracidium of *Schistosoma japonicum* are smaller in proportion to the length of the body than in *S. mansoni* (cf. fig. 2, *cg;* 4, *cg*). Also fewer germ balls are present in the posterior body region than in the miracidium of *S. mansoni.* The figures of both miracidia represent optical sections and therefore cannot show the total number of germ cells or their exact relation.

The excretory system of *Schistosoma japonicum* is shown in figures 6 and 7. Excretory pores are located near the posterior end on each side (figs. 6, 7, *exp*). The two sides of the system are entirely separate. From the pores on each side the main tubules coil backward and then forward and again back to the points on each side where they receive the capillaries from the flame cells (figs. 6, 7, *f*). The capillaries of the flame cells are of distinctly smaller caliber than the main tubules. The positions of the flame cells are shown in figure 6.

Looss's descriptions and figures (1893, p. 189) of the excretory system of the miracidium of *Schistosoma haemotobium* differ in two particulars from the above description of this system in *S. japonicum.* Looss showed all the tubules of the same caliber. He also figured the capillaries of the posterior flame cells as much shorter than those of the anterior flame cells.

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Index in preparation.

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Nos. 1 and 2 in one cover. August, 1916 ..... .10
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Nos. 14 and 15 in one cover. April, 1918 ..... .15
16. Revision of the Rodent Genus *Aplodontia*, by Walter P. Taylor. Pp. 435-504, plates 25-29, 16 text figures. May, 1918 ..... .75
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18. Excavations of Burrows of the Rodent *Aplodontia*, with Observations on the Habits of the Animal, by Charles Lewis Camp. Pp. 517-536, 6 figures in text. June, 1918 ..... .20

Index in preparation.

Vol. 18. 1. Mitosis in *Giardia microti*, by William C. Boeck. Pp. 1-26, plate 1. October, 1917 ..... .35
2. An Unusual Extension of the Distribution of the Shipworm in San Francisco Bay, California, by Albert L. Barrows. Pp. 27-43. December, 1917. .20
3. Description of Some New Species of *Polynoidae* from the Coast of California, by Christine Essenberg. Pp. 45-60, plates 2-3. October, 1917 ..... .20
4. New Species of *Amphinomidae* from the Pacific Coast, by Christine Essenberg. Pp. 61-74, plates 4-5. October, 1917 ..... .15
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Nos. 17 and 18 in one cover. January, 1919..... .35

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