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## Prairie Dog Food Preference and the Photosynthetic Pathway-Selective Herbivory Hypothesis

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*Abstract.* — Black-tail prairie dogs (*Cynomys ludovicianus*) at the Tulsa Zoological Park were offered diets consisting of  $C_3$  and  $C_4$  plant species under conditions of controlled food species abundance and availability, in order to test whether the photosynthetic pathway-selective herbivory hypothesis is predictive of foraging behavior. The  $C_4$  species tested were *Setaria italica*, *Zea mays*, *Eragrostis curvula*, and *Salsola kali*. The  $C_3$  species tested were *Arachis hypogea*, *Daucus carota*, *Helianthus annuus*, and *Lactuca sativa*. Four experiments were performed. I. Each food was presented separately to test whether *C. ludovicianus* would eat each species. II. All four  $C_3$  species were presented simultaneously to test for preferences within the  $C_3$  plant food group. III. All four  $C_4$  species were presented simultaneously to test for preferences within the  $C_4$  food group. IV. Finally, all four  $C_3$  and all four  $C_4$  species were presented simultaneously to test for preferences between  $C_3$  and  $C_4$  food groups. Data demonstrated that prairie dogs have significant food preferences within both the  $C_3$  and  $C_4$  species groups tested. However, predictions of the photosynthetic pathway-selective herbivory hypothesis were not met. No statistical preference for either  $C_3$  or  $C_4$  species existed.

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The black-tail prairie dog, *Cynomys ludovicianus*, inhabits shortgrass prairies from eastern Montana through southwest North Dakota south to western Texas, New Mexico, and southeastern Arizona. The North American prairie supported approximately five billion black-tail prairie dogs during the 19th century (Coppock et al. 1983), at which time *C. ludovicianus* formed one of the region's largest mammal populations. Prairie dog populations have now been greatly reduced in the wild. Presently, *C. ludovicianus* occupies less than 10% of its former range (Hoogland 1981), and existing populations are less than 2% of what they were a century ago (Coppock et al. 1983).

Herbivory, pasture disturbance, and potentially explosive population growth have made the black-tail prairie dog incompatible with both agriculture and ranching. The observed population decline is largely the result of intentional eradication by man. Means of extermination have been developed that are inexpensive and effective (i.e., suffocation by gasoline; Kansas ranchers, personal communication). Relict populations in a few reserves (e.g., Wind Cave National Park, Devils Tower National Monument, and a reserve at Lubbock, Texas), and colonies maintained in Zoological parks, therefore, figure heavily in survival of the species. Determining black-tail prairie dog food preference is, thus, one important component in their preservation and management.

*C. ludovicianus* is strictly herbivorous. Natural diet of the black-tail prairie dog

includes seeds, shoots, and roots (Fagerstone and Williams 1982). Potential herbivore forage in temperate North America includes both  $C_3$  and  $C_4$  plants. The photosynthetic pathway-selective herbivory hypothesis predicts that herbivores should tend to feed on  $C_3$  rather than on  $C_4$  plants in temperate climates when a choice exists, given that both types are palatable (Caswell et al. 1973). The selective herbivory hypothesis is based upon the assumption that  $C_4$  plants, statistically, are a nutritionally poorer food resource than  $C_3$  plants in temperate regions.

Evidence that a general nutritional food difference for herbivores exists between  $C_3$  and  $C_4$  plants in temperate climate comes from two types of study. First, data from plant composition experiments depict a trend in which nitrogen and phosphorus contents tend to be greater in  $C_3$  plants than  $C_4$  plants in temperate regions (National Research Council 1958; Wilson and Haydock 1971; Caswell et al. 1973). Other plant composition studies show a trend in which the ratio of digestible to non-digestible carbohydrates tends to be greater in temperate climate  $C_3$  plants than  $C_4$  plants (National Research Council 1958; Wilson and Ford 1971; Wilson and Haydock 1971; Minson 1971), and that herbivores select species greater in digestible carbohydrates (Spalinger et al. 1988). These nutritional differences may be related to carbon assimilation efficiencies of  $C_3$  and  $C_4$  species in temperate regions (Percy and Pjorkum 1983; Tolbert and Zelitch 1983), since transport and phloem unloading of nutrients (both carbon and nitrogen) from leaves is linearly dependent on the rate of carbon assimilation (Giaquinta 1980; Thorne 1985). Correspondingly, fruit and seed nutritive stores have been shown to be affected by the rate of leaf carbon assimilation during development of reproductive structures (Pate 1984).

The second type of data supporting the hypothesis that a general nutritional difference exists between  $C_3$  and  $C_4$  plants in temperate regions comes from studies of herbivore survival and fecundity responses under laboratory conditions. These experiments generally use domesticated plants as food for native herbivore species in order to minimize palatability complications. The data show a trend of increased survival and/or fecundity when the diet consists of  $C_3$  rather than  $C_4$  plants (Smith et al. 1952; Wilbur 1954; Barnes 1955; Mulkern et al. 1962; Putnam 1962; Pickford 1962, 1963; Coupe and Schultz 1968; Delvi and Pandian 1971).

Existence of a reward (nutritional) difference does not automatically mean that the difference can be perceived by a foraging animal (Wenner 1971; Wells and Wells 1983). Data from both field and laboratory herbivore food preference studies, however, lend credibility to the proposal that nutritional differences between  $C_3$  and  $C_4$  plants actually affect herbivore foraging. Herbivores from temperate regions, in taxa ranging from insects to mammals, tend to select  $C_3$  over  $C_4$  plants as food when a choice exists in both lab preference tests and in observations of natural diets (Scharff 1954; Jantz 1962; Thompson 1965; Shade and Wilson 1967; Pruess 1969; Hansen and Ueckert 1970; Ueckert and Hansen 1971; Evans and Tisdale 1972; Flinders and Hansen 1972).

Furthermore, the photosynthetic pathway-selective herbivory hypothesis appears to be a robust model in two respects. First, the selective herbivory theory is not phylum specific. Second, the feeding preference of specific herbivores appears to be the result of evolution to selectively forage on  $C_3$  plants in general, rather than only selection to feed on specific  $C_3$  plants with which a particular herbivore has locally evolved. Eurasian herbivores given North American  $C_3$  and

C<sub>4</sub> plant species tend to select C<sub>3</sub> over C<sub>4</sub> species, as do North American herbivores given Eurasian C<sub>3</sub> and C<sub>4</sub> plant species (Scharff 1954; Thompson 1965; Jantz 1962; Pruess 1969; Evans and Tisdale 1972). This is not surprising since the ability of generalist foragers to detect reward quality as well as quantity differences is central to optimal foraging theory and would be predicted evolutionarily (Schoener 1971; Cody 1974; Pulliam 1975; Pyke et al. 1977; Krebs 1978; Belovsky 1986). In fact, animal selection of food based upon ability to determine qualitative nutrient differences has been observed in a wide range of taxa (Moss et al. 1972; Pulliam 1975; Rozin 1976; Gross-Custard 1977; Wells and Wells 1984, 1986; Belovsky 1986; Provenza et al. 1987).

This study was designed to test whether the photosynthetic pathway-selective herbivory hypothesis is predictive of black-tail prairie dog food preference under controlled conditions of plant species availability and abundance.

### Methods

The study was conducted at the Tulsa Zoological Park, Tulsa, Oklahoma. Experiments I, II, and III were conducted from March through May, while experiment IV was performed from May to October, 1988. The colony of prairie dogs consisted of seven animals in a natural outdoor exhibit, without vegetation. Food for the prairie dogs prior to this study was Purina Monkey Chow.

Prairie dog food preferences were tested using four C<sub>4</sub> plant species and four C<sub>3</sub> plant species. Domestic plant species were used to minimize unpalatability problems that can result from secondary plant compounds (Owen-Smith et al. 1983), following the design of prior experiments using other organisms (Scharff 1954; Jantz 1962; Pruess 1969). Each food used in a particular experimental trial was weighed prior to being offered to the animals, and a time limit was set for feeding the animals. The time limit was 30 minutes per trial in experiments I, II, and III and 60 minutes per trial in experiment IV. After that interval had elapsed, any remaining food was removed and weighed.

Plant species were selected for this study on the basis of year-round availability and general palatability to herbivores. None are found naturally in the prairie dog range; thus specific co-evolved relationships between animals and plants should not confound the study. The C<sub>3</sub> species tested were *Lactuca sativa* (lettuce leaves; 56 g/trial = 8 g/animal-trial), *Arachis hypogea* (unshelled peanuts; 28 g/trial = 4 g/animal-trial), *Daucus carota* (carrot roots; 56 g/trial = 8 g/animal-trial), and *Helianthus annuus* (unshelled sunflower seed; 14 g/trial = 2 g/animal-trial). The C<sub>4</sub> species tested were *Setaria italica* (millet seed; 56 g/trial = 8 g/animal-trial), *Zea mays* (dry corn seed removed from cob; 56 g/trial = 8 g/animal-trial), *Eragrostis curvula* (lovegrass seed; 28 g/trial = 4 g/animal-trial), and *Salsola kali* (Russian thistle seed; 56 g/trial = 8 g/animal-trial). Amounts of each food species were chosen such that 100% could be consumed by the prairie dogs in a trial, and so that volumes were approximately equal. Thus, abundance of a food would not affect prairie dog food preferences. Food was placed in ceramic bowls when given to test animals. Each plant species was placed in a separate bowl. Experiments were run at normal feeding periods. Only one experiment (food offering) was performed per day. There were four parts to this study.

I. *One plant species presented per trial.*—First, prairie dogs were tested to see if they would eat each species of plant chosen for the experiment. Each of the

four  $C_4$  plant species and each of the four  $C_3$  plant species of food were presented to the test animals five times. Only one plant species was presented at a time, only one species per day, and the order in which plant species were presented was random. The animals were presented food for 30 minutes during each trial.

II.  *$C_3$  plant species presented simultaneously.*—The second part of this study was to determine prairie dog food preference among the species of  $C_3$  plants. Animals were presented samples of the four  $C_3$  species simultaneously, once each day, for ten consecutive days. Preference was determined by ranking the  $C_3$  species, based on percentage of each plant species eaten. Animals were presented food for 30 minutes during each experimental trial.

III.  *$C_4$  plant species presented simultaneously.*—The third experiment was identical in design to the second, with the exception of plant species used. The four  $C_4$  species were offered simultaneously to the animals on ten consecutive days, once each day. Preference was determined by ranking within the  $C_4$  species, based on percentage of each plant species eaten. Animals were presented food for 30 minutes during each experimental trial.

IV.  *$C_3$  and  $C_4$  plant species presented simultaneously.*—Finally, the animals were offered, simultaneously, all four  $C_3$  and all four  $C_4$  plants chosen for this study. This part of the study was also conducted for a total of ten days, with feeding limited to once each day. Preference was determined by ranking species offered, based on percentage eaten. Animals were presented food for 60 minutes during each experimental trial.

The Kruskal-Wallis one-way analysis of variance by ranks was used in experiments II, III, and IV to test whether the responses to food species within an experiment were different (Siegel 1956; Leach 1979). The null hypothesis in each experiment predicted that no difference in response to different species of foods existed.

Data from experiment IV were partitioned into two groups:  $C_3$  species and  $C_4$  species. If no preference by prairie dogs exists overall between  $C_3$  and  $C_4$  plants, then the rank sums of the two groups should be approximately equal. The null hypothesis that there is no preference for either group was tested using the Mann-Whitney  $U$  statistic, of which the Kruskal-Wallis statistic is a direct extension for more than two groups (Leach 1979).

Multiple comparison tests were used to supply detail about the differences detected by the ANOVA. Two statistics were used. The first test, the REGWQ multiple-stage statistic, controls maximum experimentwise error rate ( $\alpha = 0.05$  overall) under any complete or partial null hypothesis (Ryan 1959, 1960; Einot and Gabriel 1975; Welsch 1977). The second statistic was Fisher's unprotected LSD test in which comparisonwise error rate is controlled ( $\alpha = 0.05$  each comparison), but not experimentwise error rate (Miller 1981; SAS/STAT 1988).

Finally, food preference was compared to food composition. Published data on forage composition exist for all species used except *E. curvula* and *S. kali* seeds (Henry and Morrison 1922, 1959; USDA Handbook 8-11 1980). Composition of *E. curvula* seed and *S. kali* seed were determined by laboratory analysis, following the methods established by the Association of Official Analytical Chemists (Williams 1984). Whole seeds of these two species were weighed, and then dried at 60°C to a constant mass. Dried seeds of each species were assigned to one of three groups. Neutral lipids were extracted from ground seeds of the first group

of each species using a Goldfish lipid extractor (Labconco Model 35001) for eight hours with petroleum ether as a solvent. The second sample of seeds from each species was ground and analyzed for total nitrogen using an ammonia selective electrode and an Orion microprocessor ionalyzer (Model 901) following Kjeldahl digestion. Total protein was estimated by multiplying total nitrogen by a factor of 6.25 following Williams (1984). The third group of seeds from each species was ashed at 550°C for 24 hours in a Thermolyne ashing furnace. Carbohydrate was estimated by subtraction of the combined estimates of protein and lipid from ash free dry seed mass. Kendall rank correlations (Siegel 1956) were performed to examine the relation of forage composition to food preference.

## Results

I. *One plant species presented per trial.*—The prairie dogs ate 100% of the single species of plant presented each day, regardless of the plant species or whether the food was a C<sub>3</sub> or C<sub>4</sub> plant. Therefore, *C. ludovicianus* will eat all plant species used in this set of experiments. Furthermore, the animals in this study can regularly consume the quantity of any one of the food species used in experiments II, III, and IV.

II. *C<sub>3</sub> plant species presented simultaneously.*—Black-tail prairie dogs showed a distinct food preference among the C<sub>3</sub> group of plants (Table 1). Based on rank sums, peanut appears to be most favored, and lettuce least favored.

III. *C<sub>4</sub> plant species presented simultaneously.*—Food preference by black-tail prairie dogs exists within the C<sub>4</sub> group of plants (Table 2). Again based on rank sums, thistle appears to be preferred, and corn least favored. Furthermore, the similar values of the Kruskal-Wallis statistic (H) in parts II and III suggest that approximately equal disparity in preference exists within the C<sub>3</sub> group as within the C<sub>4</sub> plants.

IV. *C<sub>3</sub> and C<sub>4</sub> plant species presented simultaneously.*—Food preference exists, as predicted from parts II and III, within the combined group of C<sub>3</sub> and C<sub>4</sub> plants (Table 3). However, a general preference either for C<sub>3</sub> or for C<sub>4</sub> plants does not appear to exist (Table 3).

Both multiple pairwise comparison test results (Figs. 1 and 2) show *A. hypogea* (C<sub>3</sub>) being the preferred food, followed by *H. annuus* (C<sub>3</sub>), *S. italica* (C<sub>4</sub>), and *S. kali* (C<sub>4</sub>). Fisher's LSD test separates *A. hypogea* into a unique most preferred group (Fig. 2), whereas the REGWQ test combines the first three taxa into a single group, and places *S. kali* into the less preferred food groupings (Fig. 1). *Zea mays* (C<sub>4</sub>), *E. curvula* (C<sub>4</sub>), and *L. sativa* (C<sub>3</sub>) are placed into groupings in both analyses representing foods that tend to be avoided (Figs. 1 and 2). *Salsola kali* (C<sub>4</sub>) and *D. carota* (C<sub>3</sub>) in both Fisher's LSD and the REGWQ methods are intermediate in preference (Figs. 1 and 2). Thus, the multiple pairwise comparisons do not separate the C<sub>3</sub> and C<sub>4</sub> plants into distinct groups, or even segregate C<sub>3</sub> seeds from C<sub>4</sub> seeds, based on daily quantities eaten.

The observed feeding preference of the black-tail prairie dog is partially explained by food composition. The correlation of *C. ludovicianus* food preference to forage percentage lipid content is  $\tau = 0.50$  (significance level:  $P = 0.054$ ), and to percentage protein content is  $\tau = 0.61$  ( $P = 0.031$ ); based on percentage wet mass (dry mass results were  $\tau = 0.47$  and  $0.31$  respectively). The two preferred foods correspond to forage with highest lipid and protein composition. However,

Table 1. Results of prairie dog food preference when only C<sub>3</sub> plant species were presented simultaneously. Data are expressed as percent by weight of food consumed. Significant food preferences existed ( $H = 20.57$ ,  $df = 3$ ,  $P < 0.001$ ).

| Day      | Percent food consumed each day |                 |                  |                  |
|----------|--------------------------------|-----------------|------------------|------------------|
|          | <i>A. hypogea</i>              | <i>H. annus</i> | <i>D. carota</i> | <i>L. sativa</i> |
| 1        | 100                            | 29              | 39               | 66               |
| 2        | 100                            | 64              | 18               | 29               |
| 3        | 79                             | 43              | 02               | 43               |
| 4        | 86                             | 00              | 00               | 39               |
| 5        | 100                            | 75              | 63               | 47               |
| 6        | 88                             | 88              | 03               | 13               |
| 7        | 100                            | 50              | 81               | 50               |
| 8        | 100                            | 63              | 47               | 59               |
| 9        | 81                             | 75              | 06               | 06               |
| 10       | 100                            | 75              | 100              | 13               |
| Mean %   | 93.4                           | 56.2            | 35.9             | 36.5             |
| Rank sum | 343                            | 200             | 140              | 137              |

food preference differences in feed with lower protein and lipid content are not explained by comparing either percentage protein, lipid, or carbohydrate content (Table 4).

The reason *S. italica* (C<sub>4</sub>) seed is a preferred food, while *Z. mays* (C<sub>4</sub>) and *E. curvula* (C<sub>4</sub>) are avoided, is not known. Seed size does not appear to be the deciding factor since *Z. mays*, *H. annus*, and *A. hypogea* all have large seed, while *S. kali*, *E. curvula*, and *S. italica* all have small seed.

### Discussion

Herbivore foraging behavior under natural conditions can be dependent on several factors related to forage. The cumulative effects of these factors, in turn, determine optimal foraging in a particular habitat. Forage availability, handling

Table 2. Results of prairie dog food preference when only C<sub>4</sub> plant species were presented simultaneously. Data are expressed as percent by weight of food consumed. Significant food preferences existed ( $H = 19.09$ ,  $df = 3$ ,  $P < 0.001$ ).

| Day      | Percent food consumed each day |                   |                   |                |
|----------|--------------------------------|-------------------|-------------------|----------------|
|          | <i>S. kali</i>                 | <i>S. italica</i> | <i>E. curvula</i> | <i>Z. mays</i> |
| 1        | 38                             | 14                | 04                | 11             |
| 2        | 66                             | 80                | 39                | 18             |
| 3        | 52                             | 23                | 04                | 09             |
| 4        | 57                             | 09                | 00                | 09             |
| 5        | 78                             | 13                | 13                | 00             |
| 6        | 100                            | 78                | 31                | 34             |
| 7        | 75                             | 06                | 06                | 03             |
| 8        | 81                             | 44                | 38                | 16             |
| 9        | 72                             | 03                | 13                | 00             |
| 10       | 100                            | 50                | 38                | 47             |
| Mean %   | 71.9                           | 32.0              | 18.6              | 14.7           |
| Rank sum | 336.5                          | 204.5             | 148.5             | 130.5          |



Table 3. Results of prairie dog food preference when C<sub>3</sub> and C<sub>4</sub> plant species were presented simultaneously. Data are expressed as percent by weight of food consumed. Significant food preferences existed ( $H = 40.71$ ,  $df = 7$ ,  $P < 0.001$ ), but not between the groups C<sub>3</sub> and C<sub>4</sub> plants ( $U = 717.5$ ,  $n_1 = n_2 = 40$ ,  $P = 0.156$ ).

| Day              | Percent food consumed each day |                          |                  |                  |                   |                          |                |                   |  |
|------------------|--------------------------------|--------------------------|------------------|------------------|-------------------|--------------------------|----------------|-------------------|--|
|                  | C <sub>3</sub>                 |                          |                  |                  | C <sub>4</sub>    |                          |                |                   |  |
|                  | <i>A. hypogea</i>              | <i>H. annus</i>          | <i>D. carota</i> | <i>L. sativa</i> | <i>S. italica</i> | <i>S. kali</i>           | <i>Z. mays</i> | <i>E. curvula</i> |  |
| 1                | 81                             | 75                       | 00               | 06               | 50                | 41                       | 13             | 13                |  |
| 2                | 100                            | 100                      | 25               | 06               | 47                | 56                       | 16             | 31                |  |
| 3                | 100                            | 75                       | 56               | 16               | 84                | 91                       | 19             | 75                |  |
| 4                | 81                             | 75                       | 47               | 00               | 94                | 63                       | 06             | 19                |  |
| 5                | 88                             | 75                       | 22               | 16               | 72                | 31                       | 34             | 23                |  |
| 6                | 100                            | 63                       | 44               | 19               | 41                | 53                       | 38             | 38                |  |
| 7                | 81                             | 63                       | 94               | 28               | 56                | 88                       | 84             | 38                |  |
| 8                | 100                            | 63                       | 69               | 25               | 100               | 59                       | 63             | 44                |  |
| 9                | 100                            | 63                       | 25               | 13               | 59                | 44                       | 50             | 19                |  |
| 10               | 100                            | 63                       | 100              | 06               | 100               | 97                       | 91             | 56                |  |
| Mean %           | 93.1                           | 71.5                     | 48.2             | 13.5             | 70.3              | 62.3                     | 41.4           | 35.6              |  |
| Species rank sum | 697.5                          | 539.5                    | 362.5            | 105.0            | 519.5             | 456.0                    | 306.0          | 254.0             |  |
| Group rank sum   |                                | C <sub>3</sub><br>1704.5 |                  |                  |                   | C <sub>4</sub><br>1535.5 |                |                   |  |

time, and secondary plant compounds, as well as nutritional value, can be important in determining foraging behavior (Eloff 1983; Owen-Smith et al. 1983; Garnett et al. 1985; Jonsdottir-Vivaas and Saether 1987; Provenza et al. 1987; Spalinger et al. 1988). Foraging behaviors of specific species appear in some instances to have evolved primarily in response to only a single factor. Presumably, some environments present conditions in which a single factor is of disproportionate selective importance. Innate behavior resulting from selection in these instances can result in non-optimal foraging in alternative environments (Horn et al. 1986; Provenza et al. 1987). Other herbivore species seem to respond to all of these factors, and to generally forage as predicted by optimal foraging theory

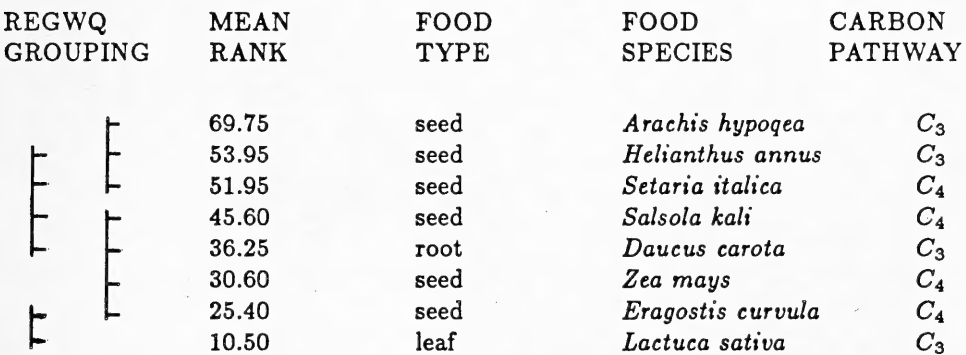


Fig. 1. REGWQ multiple-stage pairwise comparison test. Maximum experimentwise error rate under any complete or partial null hypothesis is controlled ( $\alpha = 0.05$ ), but not comparisonwise error rate. Neither C<sub>3</sub> forage in general nor only C<sub>3</sub> seeds are separated from C<sub>4</sub> forage (seeds).

| LSD GROUPING                       | MEAN RANK | FOOD TYPE | FOOD SPECIES             | CARBON PATHWAY |
|------------------------------------|-----------|-----------|--------------------------|----------------|
| <br> <br> <br> <br> <br> <br> <br> | 69.75     | seed      | <i>Arachis hypogea</i>   | C <sub>3</sub> |
|                                    | 53.95     | seed      | <i>Helianthus annuus</i> | C <sub>3</sub> |
|                                    | 51.95     | seed      | <i>Setaria italica</i>   | C <sub>4</sub> |
|                                    | 45.60     | seed      | <i>Salsola kali</i>      | C <sub>4</sub> |
|                                    | 36.25     | root      | <i>Daucus carota</i>     | C <sub>3</sub> |
|                                    | 30.60     | seed      | <i>Zea mays</i>          | C <sub>4</sub> |
|                                    | 25.40     | seed      | <i>Eragostis curvula</i> | C <sub>4</sub> |
|                                    | 10.50     | leaf      | <i>Lactuca sativa</i>    | C <sub>3</sub> |

Fig. 2. Fisher's LSD multiple pairwise comparison test. Comparisonwise error rate ( $\alpha = 0.05$ ), but not experimentwise error rate is controlled. Neither C<sub>3</sub> forage in general nor only C<sub>3</sub> seeds are separated from C<sub>4</sub> forage (seeds).

(Belovsky 1984a, b). Non-optimal foraging of some herbivores regardless of the environment has also been observed, and appears to be explainable by overriding selective forces such as competition, social learning, and predation risk avoidance behavior (Belovsky 1981; Meserve 1981; Grubb and Greenwald 1982; Holmes 1984; Carey and Moore 1986; Peacock and Jenkins 1988).

Prairie dog diet in natural populations, determined by gut contents, has been reported to be extremely diversified both in plant taxa and parts of plants eaten. However, the authors, by limiting analysis to the grass portion of the diet, concluded that prairie dogs did not avoid C<sub>4</sub> plants (Fagerstone and Williams 1982). Rather, the data subset showed an actual preference for some C<sub>4</sub> plants. Two C<sub>4</sub> grass species, in particular, *Bouteloua gracillis* and *Aristida longiseta*, were found to predominate in gut contents. However, prairie dogs tended to switch from C<sub>4</sub> to C<sub>3</sub> plants seasonally. *C. ludovicianus* showed a preference for C<sub>3</sub> plants in spring. During the summer, fall, and winter months C<sub>4</sub> plants were preferred (Fagerstone et al. 1981; Fagerstone and Williams 1982). The parts of a plant eaten also varied

Table 4. Food composition: percent wet mass/percent dry mass. Species are presented in the order they appear in Table 3.

| Species                    | H <sub>2</sub> O | Ash      | Protein   | Lipid     | Carbo-<br>hydrate |
|----------------------------|------------------|----------|-----------|-----------|-------------------|
| C <sub>3</sub>             |                  |          |           |           |                   |
| <i>A. hypogea</i> (seed)   | 5.3/5.6          | 2.3/2.4  | 30.5/32.2 | 47.7/50.4 | 14.2/15.0         |
| <i>H. annuus</i> (seed)    | 4.5/4.7          | 3.8/4.0  | 27.2/28.3 | 41.4/43.1 | 23.5/24.6         |
| <i>D. carota</i> (root)    | 88.3/754.7       | 1.2/10.3 | 1.2/10.3  | 0.2/1.7   | 9.1/77.7          |
| <i>L. sativa</i> ** (leaf) | 95.7/2175.0      | 0.5/11.4 | 1.0/22.7  | 0.2/4.5   | 2.7/61.4          |
| C <sub>4</sub>             |                  |          |           |           |                   |
| <i>S. italica</i> (seed)   | 10.2/11.3        | 5.6/6.2  | 10.7/11.9 | 4.7/5.2   | 68.8/76.6         |
| <i>S. kali</i> * (seed)    | 3.8/4.0          | 5.8/6.0  | 20.6/21.4 | 36.0/37.4 | 33.8/35.1         |
| <i>Z. mays</i> (seed)      | 9.3/10.3         | 1.8/2.0  | 11.5/12.7 | 7.9/8.7   | 69.5/76.6         |
| <i>E. curvula</i> * (seed) | 7.7/8.3          | 3.4/3.7  | 19.7/21.3 | 4.9/5.3   | 64.3/69.7         |

From: Henry and Morrison (1922, 1959).

\* Laboratory analysis by authors (N = 5 samples).

\*\* USDA Handbook 8-11, 1980.

seasonally (Fagerstone et al. 1981). A large percentage of the prairie dog's diet was leaves from grasses in spring, the proportion of seeds in the diet increased throughout summer, and roots were a large portion of their diet in winter. Changes in gut contents observed could reflect differences in availability rather than changing tastes or nutritional needs, although the relationship of prairie dog diet to available forage has been reported to be weak (Uresk 1984). Social influences involved in risk avoidance behavior is another reported factor that could lead to the changing diets recorded in prairie dog populations (Devenport 1989).

Prairie dogs can unquestionably differentiate between plant food species, and preferentially select certain species as food both in field and experimental situations. The results of the present study, however, suggest that earlier field study results, depicting a trend to feed on  $C_4$  plants, may have resulted from changing availability, social learning, and/or risk avoidance behavior, rather than preference by the black-tail prairie dog. According to the photosynthetic pathway-selective herbivory hypothesis, prairie dogs should forage selectively on  $C_3$  plants. According to the field studies cited above, they prefer  $C_4$  plants, at least seasonally. According to the present study, food preferences are unrelated to carbon cycle.

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## Revision of Two Dorvilleid Species From the Pacific Coast of North America (Annelida: Polychaeta)

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*Abstract.*—Two species of *Protodorvillea* described from California and Washington have been reexamined and determined to belong to the genus *Pettiboneia*. Structures originally described as branchiae have been determined to bear internal aciculae and are actually dorsal cirri. The numerous rows of accessory denticles originally noted as specific characters are generic level characters in *Pettiboneia*. The two species, *P. pugettensis* and *P. dibranchiata*, are redescribed and compared with related species of *Pettiboneia*.

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In 1978, Armstrong and Jumars described two new species of *Protodorvillea* from the Santa Catalina Basin (California) and Puget Sound (Washington): *P. dibranchiata* and *P. pugettensis*. In the following year, Blake (1979) reported on the discovery of *Pettiboneia sanmatiensis* Orensanz, 1973 in Tomales Bay, California; this genus and species was heretofore known only from Argentina. Upon examination of the two papers it became apparent to us that both of Armstrong and Jumars' *Protodorvillea* species were very similar to *Pettiboneia* in the composition of the jaw apparatus. *Pettiboneia* is an unusual genus in having maxillae with numerous rows of denticles and no basal plates. We recently reexamined the type material of Armstrong and Jumars and have confirmed that both species do indeed belong to the genus *Pettiboneia*. In order to clarify the position of these two species, we present complete redescrptions and comparisons with related species that have been described in subsequent years (Campoy and San Martin 1980; Westheide and von Nordheim 1985; Wolf 1987; Hilbig and Ruff 1990). A key to all known species of *Pettiboneia* is presented in a companion paper (Hilbig and Ruff 1990).

Type specimens examined as part of this study are now deposited in the Los Angeles County Museum of Natural History and include the former type designations of the Allan Hancock Foundation (AHF). Two non-type specimens are deposited in the Royal British Columbia Museum (RBCM).

*Pettiboneia pugettensis* (Armstrong & Jumars, 1978), new comb.

Figure 1

*Protodorvillea pugettensis* Armstrong & Jumars, 1978:133-135, fig. 1.

*Material examined.*—Puget Sound, Washington, intertidal, holotype (AHF Poly 1259) and 11 paratypes (AHF Poly 1260-63).—British Columbia, Chemainus Bay, subtidal, 11-12 m, sand-gravel, 30 September 1974, coll. K. D. Hobson, 2 specimens (BCPM).

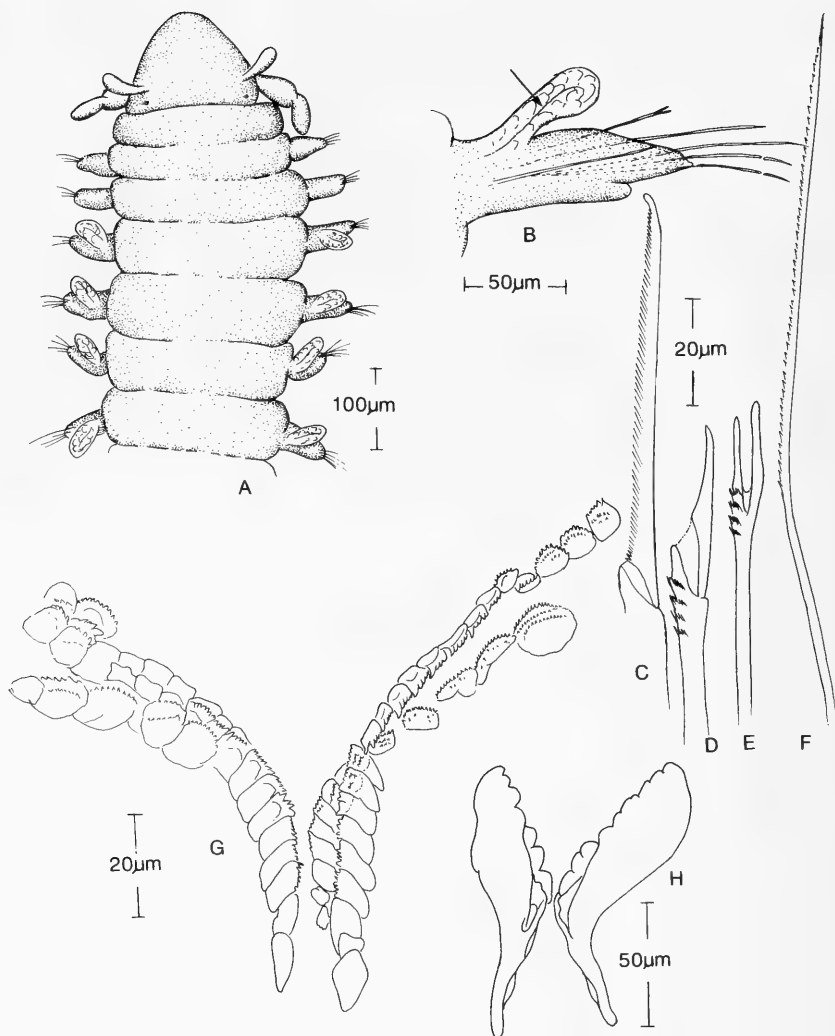


Fig. 1. *Pettiboneia pugettensis* (Paratypes, AHF Poly 1261-3): A, anterior end, dorsal view; B, parapodium, setiger 8 (arrow denotes notopacilla); C, uppermost compound falciger; D, lowermost compound falciger; E, furcate seta; F, capillary seta; G, maxillae; H, mandibles. A-G from paratypes, H from Anderson and Jumars (1978).

*Description.*—Holotype 4.6 mm long, 0.3 mm wide for 48 setigers. Prostomium bluntly triangular, wider than long, recessed into achaetous peristomial ring; one pair faint eyes located at bases of antennae; antennae small, simple, clavate; palps well-developed, about twice as long as antennae, biarticulate (Fig. 1A). Peristomium with two achaetous rings, fused dorsally.

Parapodia uniramous in setigers 1-2, subbiramous in setigers 3-10(-14), uniramous in remaining setigers. Notopodia elongate, glandular, with fine notopacilla (Fig. 1B); some notopodia with very distinct vessel loops; neuropodia long, pointed apically and longer than notopodia when fully extended, truncate and shorter than



neuropodia when retracted. Ventral cirri short, inconspicuous (Fig. 1B), absent in posterior parapodia.

Supraacicular fascicle with 1–2 subdistally serrated capillaries (Fig. 1F) and 1–2 furcate setae with slender, tapering, subequal tines and 3 rows of fine serrations at base of shorter tine (Fig. 1E). Subacicular fascicle with 2–3 compound falcigers (Fig. 1C, D); blade of uppermost seta elongate, tapering to hook-shaped tip, with very fine, long serrations along edge; often appearing spinigerous (Fig. 1C). Blades of lower compounds smooth, much shorter and wider (Fig. 1D); shafts of all compound setae with 1–2 subdistal rows of oblique serrations. Inferiormost compound seta emerging from tip of retractable setal lobe (Fig. 1B); in far posterior setigers occasionally accompanied by very fine, smooth capillary.

Pygidium rounded, bearing 4 short clavate anal cirri.

Maxillae composed of two main rows of free denticles on each side (Fig. 1G) and additional rows in apical part of pharynx; maxillary carriers and basal plates absent. Basal teeth of main rows elongate plates with main fang and coarsely serrated cutting edge; apical teeth of main rows rounded plates covered with surficial spines, with finely serrated cutting edge. Denticles of additional rows large, delicate, rounded plates with surficial spines. Mandibles curved, anteriorly flared, with scalloped cutting edge; posterior handle short and narrow (Fig. 1H).

*Remarks.*—The original description of *P. pugettensis* contains some misinterpretations of morphological characters. The structure addressed as “branchia” is clearly identifiable as a notopodium due to the presence of an acicula. The notopodia may, however, function as gills because large vessel loops are usually present. The “cirrus-like protuberance” at the ventral neuropodial edge is not a consistent structure and is probably an artifact of preservation. The maxillae do not include maxillary carriers and basal plates or any fusion product; the four main rows are free from one another and contain only free denticles. The basal structure depicted in Armstrong and Jumars (1978: Fig. 1I) is most likely a ligament-like structure connecting the jaws to the pharyngeal muscles.

*Pettiboneia pugettensis* is readily distinguished from its congeners by the occurrence of notopodia from setiger 3 rather than 2. The species is most closely related to *P. sanmatiensis* Orensanz from Argentina and California as redescribed by Blake (1979). Two specimens from British Columbia identified as *P. sanmatiensis* by Blake (1979) have been reexamined. Both have the notopodia beginning on setiger 3 rather than setiger 2 and are therefore referred to *P. pugettensis*. In *P. pugettensis* the peristomial rings are fused dorsally instead of being separate, and the blades of the short-bladed compound setae are smooth instead of serrated.

*Pettiboneia dibranchiata* (Armstrong & Jumars, 1978), new comb.

Figure 2

*Protodorvillea dibranchiata* Armstrong & Jumars, 1978:135–137, fig. 2.

*Material examined.*—Santa Catalina Basin, California, bathyal: holotype (AHF Poly 1264) and paratype (AHF Poly 1265).

*Description.*—Holotype 5.8 mm long, 0.4 mm wide for 47 setigers. Prostomium bluntly triangular, wider than long, with two clavate to indistinctly biarticulate antennae and two biarticulate palps (Fig. 2A); antennae as long as greatest prosto-

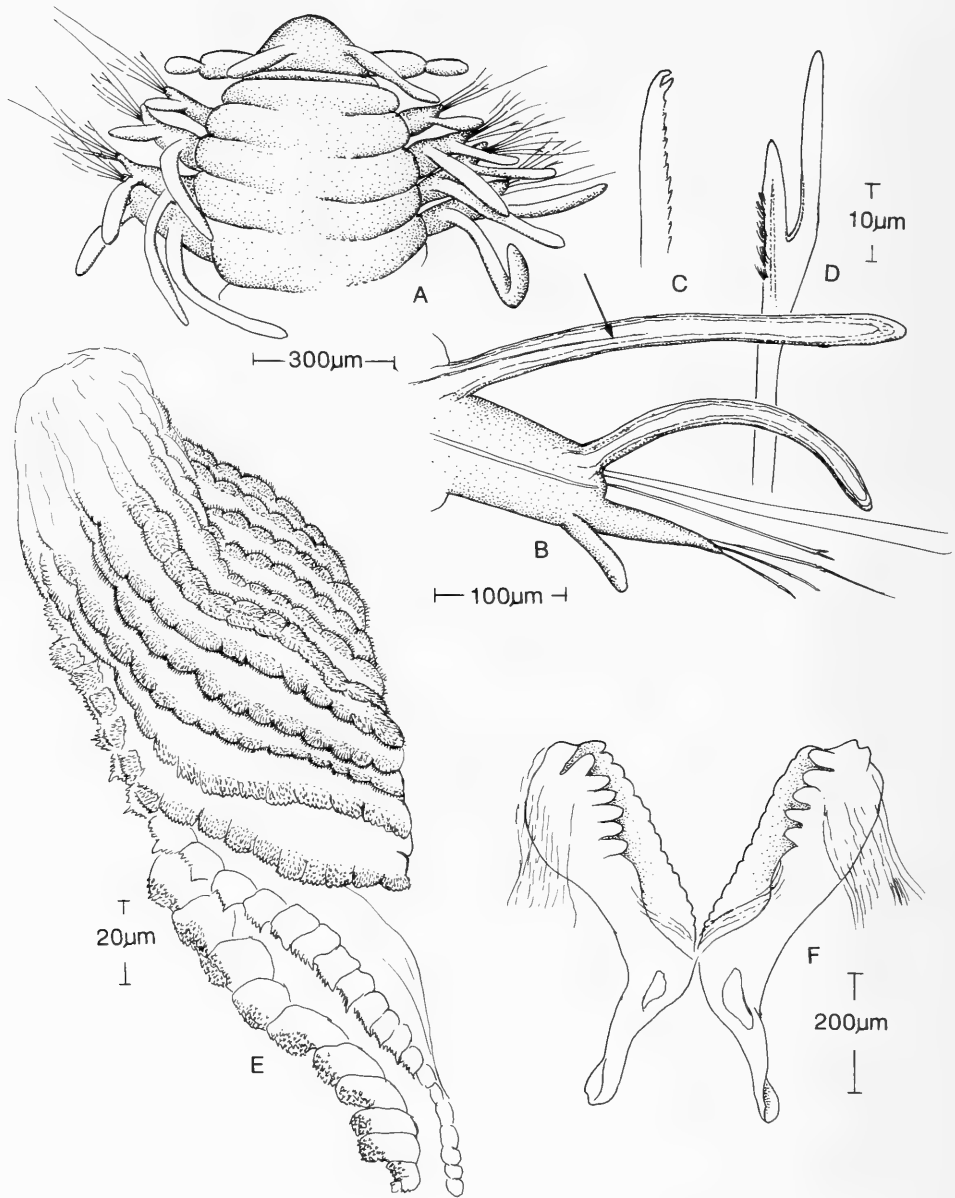


Fig. 2. *Pettiboneia dibranchiata* (Paratype, AHF Poly 1265): A, anterior end, dorsal view; B, parapodium from anterior setiger (arrow denotes notoacicula); C, bifid tip of compound falciger; D, furcate seta; E, maxillae; F, mandibles.

mial width, palps slightly longer; eyes absent. Peristomium with two rings, the first one much shorter and narrower than the second (Fig. 2A).

Parapodia uniramous in setiger 1, subbiramous from setiger 2 through 13–17 and uniramous in remaining setigers. Notopodia very long, extending well beyond neuropodia, with distinct vessel loops and heavy ventral ciliation. Notopodial acicula very thin, visible only at notopodial base (Fig. 2B). Neuropodia blunt or

apically pointed if fully extended; ventral cirri short, digitiform, present from setiger 2 (Fig. 2B). Dorsal branchiae present from setiger 1 through setiger 13–17, decreasing on subsequent parapodia to an inconspicuous protuberance of the dorsal neuropodial margin.

Supraacicular setae comprising 1–2 finely serrated capillaries with long, hairlike tips and 1 furcate seta with slender, unequal tines; short tine with 3 rows of basal serrations and narrow wing along inner side (Fig. 2D). Subacicular fascicle consisting of 3–4 compound setae with bifid, finely serrated blades (Fig. 2C); blade longest on seta closest to acicula; inferiormost seta emerging from tip of setal lobe when parapodium fully extended.

Pygidium rounded, with two clavate dorsal anal cirri and two shorter ventral ones.

Maxillae consisting of two main rows of denticles and approximately 12 additional rows on each side (Fig. 2E); maxillary carriers and basal plates absent. Denticles of row I large, delicate, rounded plates covered with surficial spines; proximal denticles of row II small, rectangular plates with main fang and coarsely serrated cutting edge; distal denticles of row II rounded, with surficial spines. Denticles of additional rows rounded, with surficial spines. Mandibles weakly sclerotized, with elongate, scoop-shaped, scalloped cutting edge and short, narrow handle (Fig. 2F).

*Remarks.*—Some misinterpretations in the original description by Armstrong and Jumars (1978) are corrected in this redescription. The structure originally named “proximal branchia” contains a fine acicula and can therefore be identified as a notopodium. It may function as an additional gill, however, because of its very distinct vessel loop and ciliation. The “distal branchia” is a true gill. Wolf (1987) described a similar arrangement for *P. duofurca*; he found that the gills of *P. duofurca* are not present in all specimens. This might prove to be true for *P. dibranchiata* if additional material were available for examination. None of the *Protodorvillea*-like structures of the maxillary apparatus, such as fused maxillary carriers and basal plates, are present in the jaws of the paratype; instead, the main denticle rows are free from each other and consist only of free denticles.

The two branchiate *Pettiboneia* species differ most obviously in the following characters: (1) notopodia are present from setiger 2 through 13–17 in *P. dibranchiata* and from setiger 2 through 8–9 in *P. duofurca*; (2) gills are present from setiger 1 in *P. dibranchiata* and from setiger 3 in *P. duofurca*; (3) the furcate setae have unequal tines in *P. dibranchiata* and subequal tines in *P. duofurca* (adults); (4) the dorsal anal cirri are slightly longer than the ventral ones in *P. dibranchiata* and about 6–7 times longer in *P. duofurca*; (5) the mandibles are scoop-shaped in *P. dibranchiata* and flat, slightly curved in *P. duofurca*. The number of additional denticle rows seems to differ greatly between the two species; however, it should not be used as a diagnostic specific character because the apparent number of denticle rows may differ substantially even among specimens of the same species due to differences in the way the pharyngeal wall is spread on the slide (see Hilbig and Ruff 1990).

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## Remarks on the Genus *Pettiboneia* (Polychaeta: Dorvilleidae) with Descriptions of Two New Species

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*Abstract.*—Two new species of the genus *Pettiboneia* Orensanz, 1973, are described from the North Pacific and North Atlantic Oceans. Comments on within-species variability, generic relationships, and species distributions are presented, and a key to the species of *Pettiboneia* is provided.

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The genus *Pettiboneia* Orensanz, 1973, was originally described from seven specimens found in shallow water in the Gulf of San Matías, Argentina. Members of the genus are very small, typically averaging only about 5 mm in length, and are easily overlooked. However, within the last decade an additional four species have been discovered, all in intertidal to shelf depths, and in tropical or subtropical waters. Blake and Hilbig (this issue) are transferring two additional species originally described as *Protodorvillea* to the genus. In this paper two new species from Alaska and from the western North Atlantic are described. These species are from deeper and more northern waters than previously reported, raising the number of species of *Pettiboneia* to nine.

The Alaskan specimens were collected as part of a monitoring study conducted in two southeast Alaska fjords between 1979–1983. The Atlantic specimens were collected on the continental slope and rise between Cape Cod, Massachusetts, and Cape Lookout, North Carolina, between 1982–1986.

The holotype and some paratypes are deposited in the U.S. National Museum of Natural History (USNM). Additional paratypes are deposited in the British Museum of Natural History (BMNH) and in the Zoological Museum of the University of Hamburg (ZMH). Some specimens have been retained by the authors or have been transferred to the Smithsonian Institution.

### *Pettiboneia brevipalpa* n. sp.

Figure 1

*Pettiboneia* sp.—VTN Consolidated, Inc., 1980.

*Material examined.*—Boca de Quadra, Alaska: Sta. 200, 55°18.1'N, 130°30.6'W, 150 m, Apr 1980, 3 paratypes (USNM 130085); Jul 1980, 1 paratype (USNM 130086). Sta. 201, 55°18.3'N, 130°30.9'W, 145 m, Apr 1980, 1 paratype (USNM 130087). Sta. 277, 55°18.1'N, 130°30.6'W, 150 m, Sep 1983, 1 paratype (USNM 130088). Sta. 400, 55°16.7'N, 130°31.9'W, 150 m, Apr 1980, 3 specimens. Sta. 401, 55°16.7'N, 130°32.1'W, 140 m, Apr 1980, 1 paratype (USNM 130089); Jul

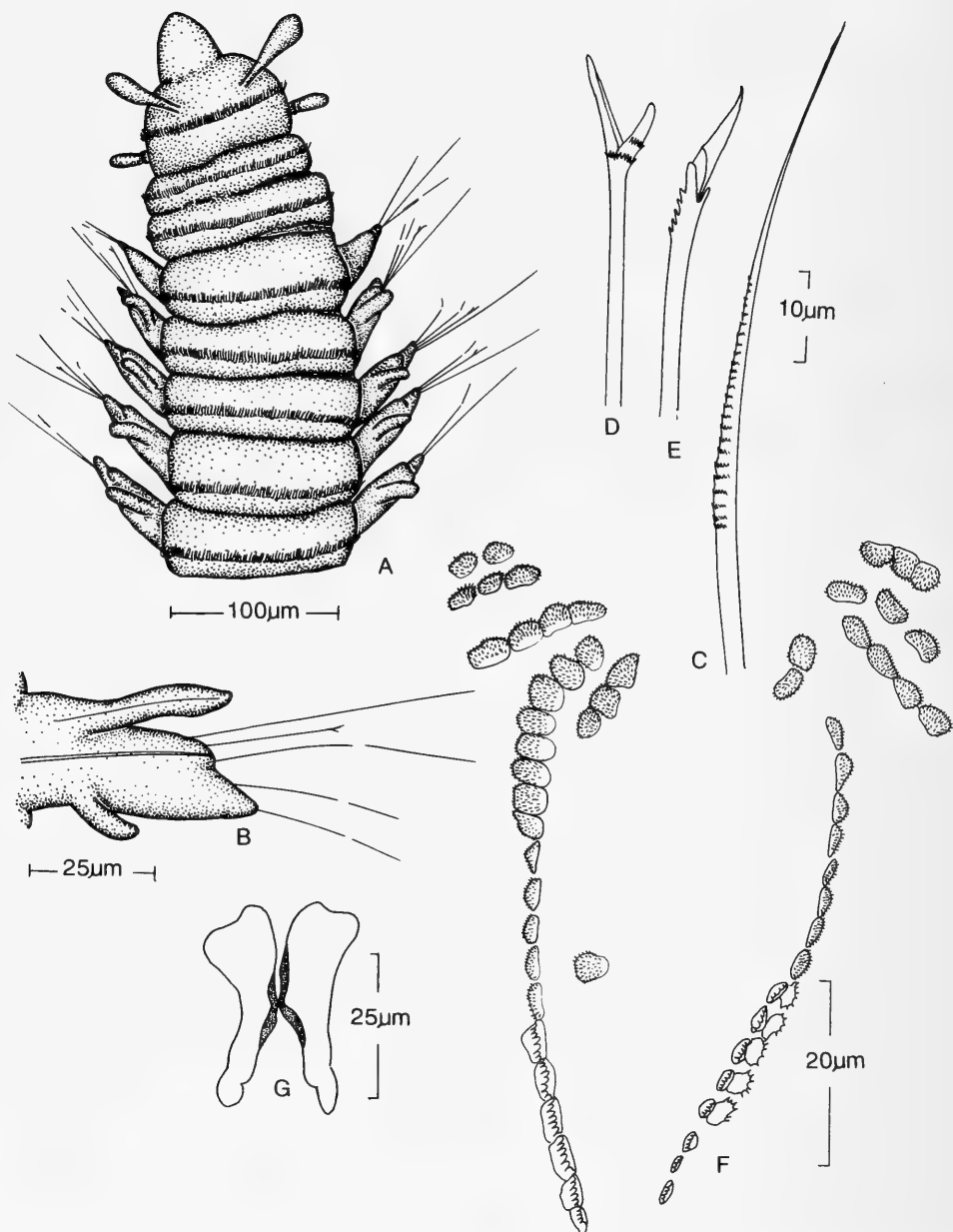


Fig. 1. *Pettiboneia brevipalpa*: A, anterior end, dorsal view; B, parapodium; C, capillary supraacicular seta; D, furcate supraacicular seta; E, subacicular seta; F, maxillae; G, mandibles.

1980, 2 paratypes (ZMH P-20324). Sta. 500, 55°15.1'N, 130°33.1'W, 210 m, Apr 1980, 2 specimens; Jul 1980, 3 specimens. Sta. 501, 55°15.0'N, 130°32.8'W, 195 m, Jul 1980, 1 specimen. Sta. 502, 55°14.9'N, 130°32.6'W, 195 m, Jul 1980, 1 specimen. Sta. 600, 55°12.4'N, 130°35.8'W, 280 m, Jul 1980, 1 specimen. Sta. 601, 55°12.6'N, 130°36.1'W, 275 m, Jul 1980, 3 specimens. Sta. 602, 55°12.3'N,

130°35.5'W, 275 m, Jul 1980, 3 paratypes (BMNH ZB 1990.29–31). Sta. 700, 55°10.2'N, 130°39.3'W, 280 m, Apr 1980, holotype (USNM 130084); Jul 1980, 5 paratypes (USNM 130090). Sta. 800, 55°05.9'N, 130°43.5'W, 330 m, Apr 1980, 3 paratypes (USNM 130091). Sta. 801, 55°06.1'N, 130°43.9'W, 330 m, Apr 1980, 1 specimen. Sta. 802, 55°05.7'N, 130°43.3'W, 380 m, Jul 1980, 1 paratype (ZMH P-20325).—Smeaton Bay, Alaska. Sta. 010, 55°18.7'N, 130°41.4'W, 241 m, Oct 1980, 1 paratype (BMNH ZB 1990.32).

*Description.*—Holotype complete, 2.4 mm long, 0.1 mm wide for 35 setigers. Other complete specimens up to 4.5 mm long for 66 setigers. Body slender, fragile, unpigmented in alcohol. Prostomium pear-shaped, about as long as wide (Fig. 1A); antennae clavate, about as long as greatest prostomial width; biarticulate palps half antennal length, inserted ventrolaterally behind antennae, with short, inconspicuous palpophores; eyes absent; narrow band of cilia encircling prostomium between antennae and palps; large yellowish-brown nuchal organs on posterior margins of prostomium. Two subequal asetigerous peristomial rings, shorter than setigerous segments; complete ciliary bands on both rings and on anterior setigers.

Cirriiform notopodia with embedded acicula present from setiger 2 through setigers 8–11; absent posteriorly; as long as or slightly longer than neuropodial acicular lobe. Neuropodia with conical acicular lobe and inferior retractable setal lobe supported by inferiormost seta (Fig. 1B); ventral cirri short, cirriiform.

Supraacicular setae include 1–3 serrated capillary setae (Fig. 1C) and 1 (occasionally 2) furcate seta with unequal tines and 1–2 rows of fine serrations below shorter tine; longer tine with delicate wing on inner side (Fig. 1D). Subacicular fascicle with 2–4 compound setae having long to short unidentate, finely serrated blades; shafts bifid with coarse subdistal serrations (Fig. 1E). Far posterior setigers occasionally with simple pointed inferior setae.

Pygidium rounded, longer than preceding setigers, with 2 pairs of clavate sub-terminal cirri.

Maxillae with two main rows of free denticles and about six additional rows on each side; maxillary carriers and basal plates absent (Fig. 1F). Basal teeth of main rows smooth, delicate, rounded plates with serrated cutting edge; middle and upper teeth rounded plates covered with surficial spines. Teeth of additional rows including smooth, anteriorly serrated plates proximally and spinose plates distally. Mandibles elongate, slightly curved, anteriorly flared, smooth and weakly incised (Fig. 1G).

*Remarks.*—*Pettiboneia brevipalpa* is similar to *P. sanmatiensis* in the number of notopodia, the shape of the prostomium, the number of maxillary rows, and the size and shape of the pygidial cirri. It differs from the latter species in lacking eyes and in having long rather than short notopodia. In addition, *P. brevipalpa* differs from all other known species in possessing palps that are much shorter than the antennae, and palpophores shorter than the palpostyles.

Of the 42 specimens examined, eight were gravid females and ten appeared to be developing or mature males. There are up to 8 round or elongated eggs per setiger averaging 40  $\mu\text{m}$  in length and 27  $\mu\text{m}$  in width. The eggs are first present between setigers 14–21, and the sperm appear between setigers 15–19. The gametes are associated with the bases of the parapodia and continue for most of the length of the worm.

*Etymology.*—The specific name refers to the unique short palps which distinguish this species from its congeners.

*Distribution.*—Known only from Boca de Quadra and Smeaton Bay in the Alaskan panhandle, 140–380 m, in fine silts. This is the northernmost record for the genus.

*Pettiboneia bathyalis* n. sp.

Figure 2

*Pettiboneia* sp. 1.—Blake et al. 1987; Maciolek et al. 1987a, b.

*Material examined.*—U.S. Atlantic Continental Slope and Rise Program, off New England, Sta. N2, 40°57.2'N, 66°13.9'W, 2100 m, Nov 1984, 1 specimen; Apr 1986, 1 specimen. Sta. N8, 40°10.3'N, 67°37.4'W, 2180 m, Nov 1984, 1 paratype (USNM 130093); Apr 1986, 1 paratype (ZMH P-20326). Sta. N13, 39°48.4'N, 70°54.3'W, 1250 m, Nov 1985, 1 specimen. Sta. N14, 39°41.0'N, 70°54.3'W, 2105 m, Nov 1984, 1 specimen.—Off Delaware and New Jersey: Sta. M1, 38°36.0'N, 72°53.0'W, 2195 m, Aug 1984, 1 specimen; Dec 1984, 2 paratypes (USNM 130094); Aug 1985, 1 paratype (USNM 130095). Sta. M2, 38°35.8'N, 72°53.7'W, 2020 m, Aug 1984, 2 specimens; Aug 1985, 1 specimen; Nov 1985, holotype (USNM 130092), 2 paratypes (USNM 130096). Sta. M3, 38°36.8'N, 72°51.4'W, 2055 m, May 1984, 1 specimen; Dec 1984, 1 specimen. Sta. M4, 38°44.5'N, 72°33.0'W, 2100 m, May 1984, 1 specimen; Dec 1984, 1 specimen. Sta. M5, 38°50.5'N, 72°33.0'W, 2065 m, Nov 1985, 1 specimen. Sta. M6, 39°05.5'N, 72°03.0'W, 2090 m, Nov 1984, 1 specimen. Sta. M7, 38°27.4'N, 73°03.4'W, 2100 m, Dec 1984, 1 specimen; Aug 1985, 2 paratypes (BMNH ZB 1990.33–34), 1 specimen. Sta. M9, 38°17.3'N, 73°14.5'W, 2105 m, May 1984, 4 paratypes (ZMH P-20327); Aug 1984, 2 specimens; Nov 1984, 5 paratypes (USNM 130097), 2 specimens; May 1985, 4 specimens; Aug 1985, 3 paratypes (USNM 130098); Nov 1985, 1 specimen. Sta. M10, 37°51.8'N, 73°19.8'W, 2095 m, May 1984, 1 specimen; Aug 1985, 1 specimen. Sta. M11, 38°40.2'N, 72°42.2'W, 1515 m, Aug 1984, 1 specimen; Dec 1984, 1 specimen. Sta. M12, 38°29.3'N, 72°42.2'W, 2505 m, Dec 1984, 1 specimen. Sta. M13, 37°53.3'N, 73°45.1'W, 1613 m, Nov 1984, 3 specimens; May 1985, 3 specimens; Nov 1985, 1 specimen.—Off North Carolina: Sta. S3, 34°14.8'N, 75°40.1'W, 1500 m, Mar 1984, 1 specimen. Sta. S4, 34°11.4'N, 75°38.8'W, 2000 m, May 1984, 1 specimen; Sep 1985, 2 paratypes (USNM 130099); Nov 1985, 6 paratypes (BMNH ZB 1990.35–40). Sta. S6, 34°49.5'N, 75°13.4'W, 2004 m, May 1984, 5 specimens; July 1984, 3 specimens. Sta. S10, 35°26.3'N, 74°41.4'W, 2003 m, Nov 1985, 4 specimens. Sta. S12, 33°00.3'N, 76°07.4'W, 1996 m, Nov 1985, 1 paratype (USNM 130100). Sta. S14, 32°23.6'N, 77°01.1'W, 805 m, Nov 1985, 1 specimen.

*Description.*—Holotype complete, 5.5 mm long, 0.3 mm wide for 65 setigers. Other complete specimens to 6.0 mm long with up to 70 setigers. Body stout, dorsoventrally compressed, unpigmented in alcohol.

Prostomium broadly rounded anteriorly, slightly wider than long, with two ciliary bands straddling antennae (Fig. 2A); antennae short, smooth, slightly clavate, half as long as prostomial width; palps longer, biarticulate, with elongate palpostyles; eyes absent. First peristomial ring short, about as wide as prostomium, often telescoped beneath the second, wider, longer ring; each ring with ciliary band close to posterior margin.



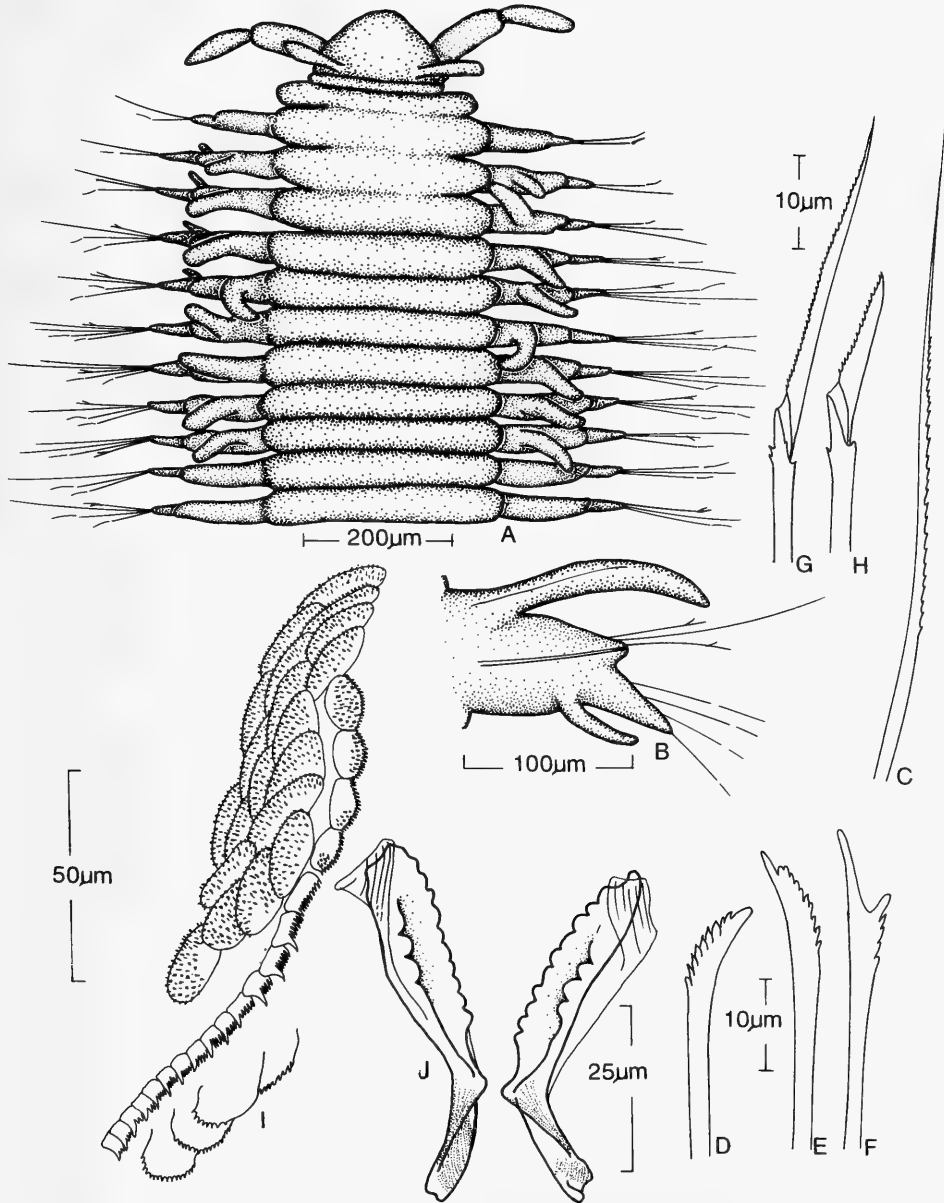


Fig. 2. *Pettiboneia bathyalis*: A, anterior end, dorsal view, ciliation not shown; B, parapodium; C, capillary supraacicular seta; D, geniculate supraacicular seta, setiger 1; E, geniculate supraacicular seta, setiger 3; F, furcate supraacicular seta, setiger 5; G, subacicular seta, middle position; H, subacicular seta, inferiormost position; I, maxillae; J, mandibles.

Cirriiform aciculate notopodia present from setiger 2 through setigers 7–9. Neuropodia with acicular lobe and retractable inferior setal lobe; filiform ventral cirri inserted subdistally, extending beyond acicular lobe (Fig. 2B).

Supraacicular fascicles with 1–3 capillary setae (Fig. 2C) and 1–2 bifid, serrated geniculate setae in anteriormost parapodia (Fig. 2D); geniculate setae progressively

changing within anterior 5 setigers to furcate setae having unequal truncate tines (Fig. 2E, F); shaft coarsely serrated below shorter tine. Subacicular fascicles with 3–4 compound setae having finely serrated falcigerous blades; serrations longer than blade width; inferior blades shortest; shaft with a few coarse subdistal teeth (Fig. 2G, H). Posterior setigers occasionally with simple cultriform seta in ventralmost position.

Pre-pygidial setigers short. Pygidium wider than long, with 2 pairs of clavate subterminal cirri; dorsal pair longest.

Maxillae consisting of two main rows of free denticles and numerous additional denticles arranged in 6–8 rows on each side; maxillary carriers and basal plates absent (Fig. 2I). Basal teeth of main rows smooth, rounded plates with finely serrated cutting edge; middle teeth smooth, rectangular, with proximal main fang and coarsely serrated cutting edge; anterior teeth oval plates with surficial spines, proximal main fang and coarsely serrated cutting edge; main fang lacking in last 1–4 denticles. Denticles of additional rows large, delicate, rectangular to oval plates with surficial spines and finely serrated cutting edge, arranged in several imbricated distal rows and one proximal row on each side. Mandibles L-shaped with short, sclerotized handle and long, delicate, scoop-shaped cutting edge with 10–12 rounded teeth in one row and 2–3 teeth in additional rows (Fig. 2J).

*Remarks.* — *Pettiboneia bathyalis* appears to be close to *P. urciensis* in prostomial shape and number of notopodia. It differs from the latter species in lacking eyes and in having elongated palpostyles. *P. bathyalis* differs from its congeners in possessing geniculate rather than furcate setae in the anteriormost setigers.

Of the 83 specimens examined, 8 were gravid females and 19 were males. The eggs are irregularly polygonal in shape, averaging 116  $\mu\text{m}$  in the longest dimension. There are about 8 eggs per segment after setiger 10 packed across the ventrum and extending into the parapodia. Sperm occur from setigers 13–20, continuing to near the end of the body.

*Etymology.* — The species name refers to the bathyal regions where it was collected.

*Distribution.* — *P. bathyalis* is distributed from Cape Cod, Massachusetts, to Cape Lookout, North Carolina, 800–2500 m, in muddy sands. This is the first deep-sea species of *Pettiboneia* discovered, and the first record for the western North Atlantic.

### Discussion

The diagnostic characters delineating the genus *Pettiboneia* were provided by Orensanz (1973), and the structure of the jaw apparatus was elucidated by Blake (1979). The two new species conform well to the genus concept as reviewed by Wolf (1987) with the exception that in *P. brevipalpa* the biarticulate palps are distinctly shorter than the antennae. The generic diagnosis should therefore be emended to encompass this feature.

Abundant material permitted a detailed assessment of within-species character variability. Many features, such as the shape of the prostomium, the length of the palps and antennae, and the length of the notopodia relative to the neuropodia, were found to be relatively constant within each species. The ciliary bands also appeared to be invariable, although these features were not always discernible.

Examination of the jaw apparatus of at least ten specimens of each species

revealed very different appearances of the maxillary arrangement. The apparent number of maxillary rows varied between 8 and 14, and in most cases these rows were only discernible in the anterior part of the pharynx. The differences seemed to be a function of the maceration of the very thick pharyngeal muscle rather than reflecting a real morphological variability. The arrangement of maxillary plates as a diagnostic character on the species level should therefore be used with caution until the true morphology of the jaw apparatus can be revealed. Examination of dissected and dorsally opened pharynges with SEM may be an appropriate technique.

Anterior notopodia begin on setiger 2 and generally extend through setiger 11 in *P. brevipalpa* and through setiger 9 in *P. bathyalis*. However, in a number of specimens the posteriormost 1 to 3 notopodia were not observed (Table 1). Since these structures are supported by an internal acicula and do not tend to be deciduous, the variability in the total number of notopodia appears to be a real feature rather than an artifact.

All of the neuropodia possess an inferior setal lobe supported by the ventralmost seta, a feature that has not been reported in the descriptions of other species within the genus. The length of this lobe was often variable in adjacent parapodia, and at times it was inconspicuous. This feature appears to reflect the degree of extension of the ventral seta, and the length is therefore an artifact of preservation.

The inferior setal lobe is supported by a simple pointed seta rather than a compound falciger in the posterior setigers of about half of the examined specimens of *P. brevipalpa* and about a quarter of the *P. bathyalis* material. The setiger of its first occurrence varies greatly, and the seta is not always present in all consecutive setigers. Similar simple inferior setae have also been noted in other dorvilleid genera such as *Ophryotrocha* (Hilbig and Blake in press). The retractable setal lobe is also present in many of the species within that genus, although it has often been overlooked in the past (Hilbig and Blake in press). These two features appear to be widespread among dorvilleids and may represent plesiomorphic characters.

The change from serrated bidentate geniculate setae to short-tined furcate setae noted in the anterior region of *Pettiboneia bathyalis* is also known from *Dorvillea rudolphi* and an undescribed Atlantic deep-sea species of *Meiodorvillea* reported in Blake et al. 1987, and Maciolek et al. 1987a, b, indicating a close relationship between these genera. The relationship between *Pettiboneia* and *Meiodorvillea* is further confirmed by the absence of maxillary carriers and basal plates and the presence of surficial spines on the anteriormost maxillary plates of *Meiodorvillea minuta*.

With recent discoveries, it appears that the genus *Pettiboneia* is widely distributed throughout the world's oceans (Fig. 3). A total of nine species are now known from tropical habitats to boreal waters, and from the shallow subtidal to depths exceeding 2500 m.

#### Key to the known species of *Pettiboneia*

- |   |  |
|---|--|
| 1a. Eyes present .....  | 2  |
| 1b. Eyes absent .....   | 5  |
| 2a. Notopodia beginning on setiger 3; peristomial rings fused dorsally .... |  |
| .....   | <i>P. pugettensis</i> (Armstrong & Jumars, 1978) |

- 2b. Notopodia beginning on setiger 2; peristomial rings distinct and not fused dorsally ..... 3
- 3a. Notopodia shorter than neuropodia; furcate setae with subequal tines ..... *P. sanmatiensis* Orensanz, 1973
- 3b. Notopodia as long or longer than neuropodia; furcate setae with unequal tines ..... 4
- 4a. Prostomium pear-shaped; eyes large, situated behind antennae ..... *P. blakei* Wolf, 1987
- 4b. Prostomium rounded; eyes small, situated in front of antennae ..... *P. urciensis* Campoy & San Martin, 1980
- 5a. Prostomium pear-shaped; palps shorter than antennae . *P. brevipalpa* n. sp.
- 5b. Prostomium rounded; palps longer than antennae ..... 6
- 6a. Notopodia longer than neuropodia; anterior neuropodia with superior branchiae ..... 7
- 6b. Notopodia subequal to neuropodia; anterior neuropodia without superior branchiae ..... 8
- 7a. Branchiae beginning on setiger 1; notopodia extending through setigers 13–17; all anal cirri short ... *P. dibranchiata* (Armstrong & Jumars, 1978)
- 7b. Branchiae beginning on setiger 3; notopodia extending through setigers 8–9; dorsal anal cirri long ..... *P. duofurca* Wolf, 1987
- 8a. Notopodia extending through setiger 9; furcate setae in median setigers serrated, with unequal tines ..... *P. bathyalis* n. sp.
- 8b. Notopodia extending through setiger 19; furcate setae in median setigers smooth, with subequal tines ..... *P. australiensis* Westheide & von Nordheim, 1985

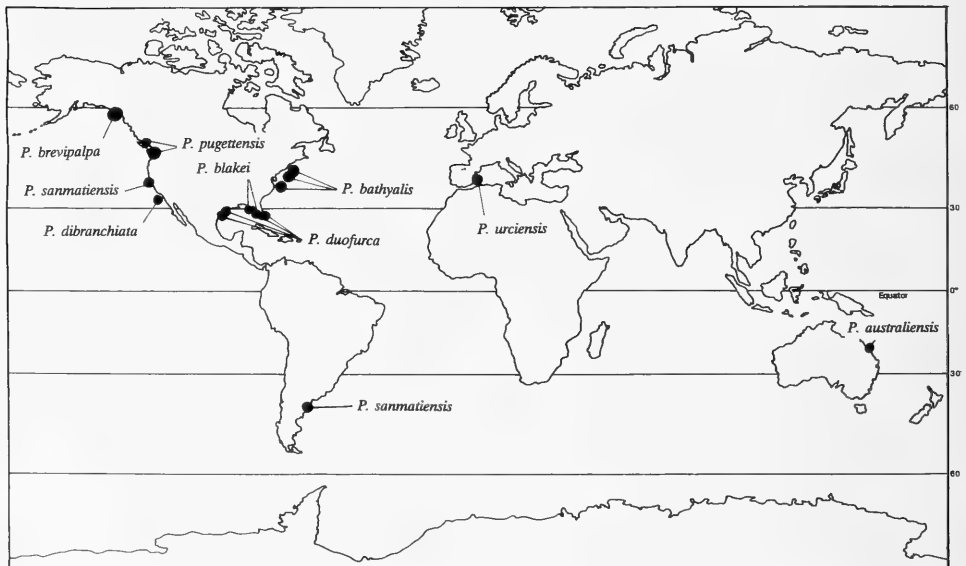


Fig. 3. Worldwide distribution of species of *Pettiboneia*.

Table 1. Distribution of notopodia in the anterior setigers of *P. bathyalis* and *P. brevipalpa*.

| Last setiger bearing notopodia | Number of specimens |                      |
|--------------------------------|---------------------|----------------------|
|                                | <i>P. bathyalis</i> | <i>P. brevipalpa</i> |
| 7                              | 6                   | —                    |
| 8                              | 9                   | 4                    |
| 9                              | 39                  | 12                   |
| 10                             | —                   | 7                    |
| 11                             | —                   | 17                   |

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## A New Species of Marine Amphipod (Gammaridea: Ampeliscidae) from the Sublittoral of Southern California

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*Abstract.*—A new species of ampeliscid amphipod, *Ampelisca brachycladus*, is described from southern California. The species is distinctive in having the inner ramus of uropod 1 approximately one-half the length of the outer ramus. *Ampelisca brachycladus* occurs along the southern California bight in shallow water (10–50 m) on a variety of substrates.

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The genus *Ampelisca* Krøyer 1842 is at present represented by 34 species on the continental shelf of the northeastern Pacific and 214 worldwide. This genus is exclusively marine and estuarine (Enequist 1949) and found on sublittoral sand and mud bottoms. Approximately 80% are sublittoral and 20% are bathyal to abyssal (Barnard 1969). The genus *Ampelisca* has been examined in many major studies along the eastern Pacific coast (Holmes 1908; Barnard 1954, 1960, 1967, 1971; and Dickinson 1982) and will not be reviewed in this paper.

Only those diagnostic characters in combination that distinguish the new species from all known species of *Ampelisca* are illustrated. All illustrations and descriptions are based on type material.

### *Ampelisca brachycladus* n. sp.

Figures 1–3

*Description.*—Female holotype, 7.3 mm. Head (Fig. 1) as long as first three pereonites combined; lower front margin of head oblique; oblique margin slightly concave; frontal margin of head not incised. Two corneal lenses on each side; lower cuticular lens positioned at lateral angle of head. Antenna 1 short, slender, not reaching end of peduncle of antenna 2; peduncular article 1 one-half length of article 2; article 3 short, flagellum subequal to peduncle. Antenna 2 of moderate length; article 3 short; article 4 longer than article 5; flagellum bearing sparse medium setae. Upper lip with median apical notch. Mandibular palp (Fig. 2A) 3-articulate; first article borne on medial elevated process bearing patch of minute setules, and armed with 2 lateral setae. (Note: stippled area on medial surface of first article of Fig. 2A indicating cuticular fold not intersegmental arthrodivial membrane.) Left lacinia with 4–5 cusps; spine row with 8 large spines; molar toothed and ridged. Lower lip with mandibular lobe weak or lacking; inner lobe well developed. Maxilla 1 (Fig. 2B) outer lobe with 10 denticulated spines; palp with 4 strong apical spines. Maxilla 2 (Fig. 2C) inner plate setose. Maxillipedal palp (Fig. 2D) 4-articulate; outer lobe with 10 spines (medial group of spines spatulate and terminal ones long and slender); inner lobe setose and with a single apical spatulate spine. Pereonal segments dorsally smooth. Coxae 1–4 longer than broad;

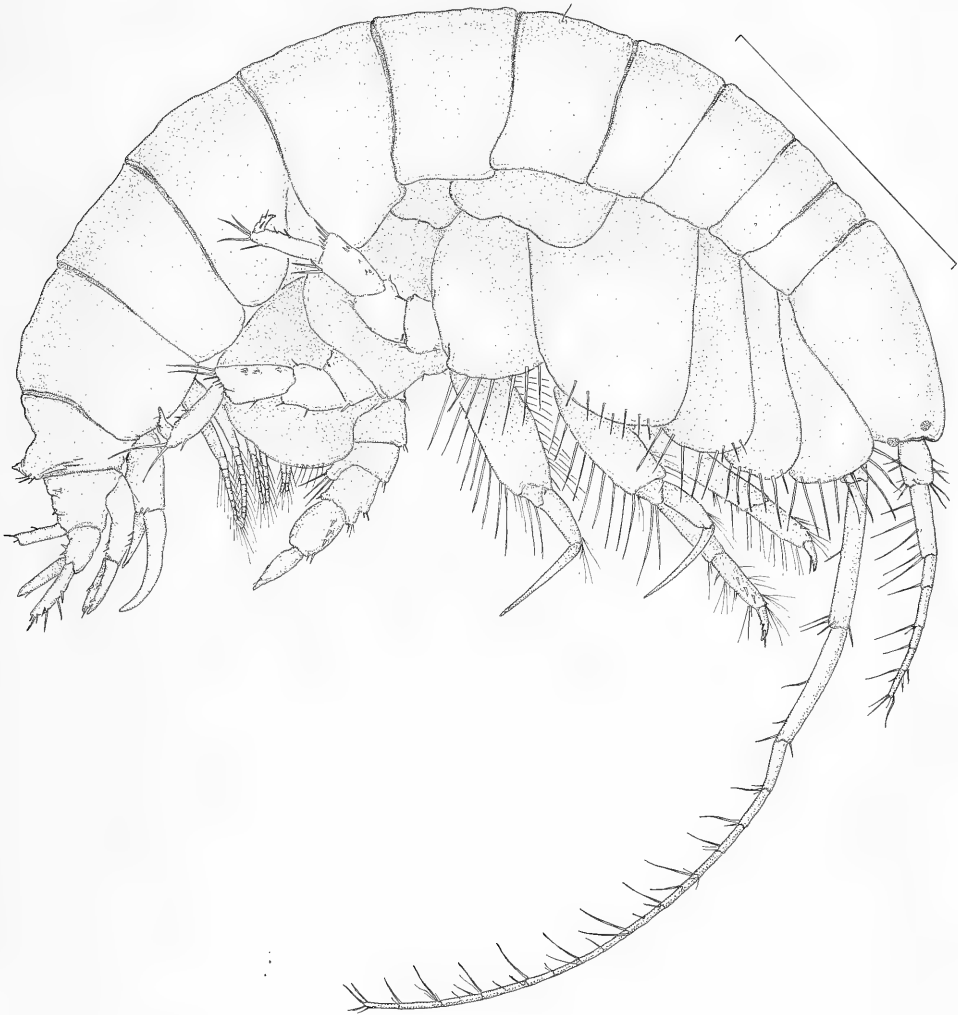


Fig. 1. *Ampelisca brachycladus* n. sp., female paratype, Santa Monica Bay, California. Scale: 1.0 mm.

lower posterior corners untoothed. Coxa 1 expanded distally. Coxae 1–2 with a single row of plumose setae along entire ventral margin. Coxa 3 with sparse plumose setae on posterior ventral margin. Coxa 4 with sparse short setae along ventral margin; upper one-third strongly excavate posteriorly.

Gnathopods 1 and 2 simple; both pereopods with pectinate setae. Gnathopod 1 moderately setose along posterior margin of articles 5 and 6, and setose on distal half of anterior margin of articles 5 and 6. Gnathopod 2 articles 5 and 6 moderately setose along posterior margin. Pereopods 3 and 4 similar to each other; pereopod 3 article 4 with setae only on anterior distal margin; pereopod 4 article 4 with setae along the entire anterior margin. Pereopods 5 and 6 similar (see Fig. 3A); article 6 with two spines on posterior margin, with setal tuft on distal end; article 5 with three sets of spines on posterior edge, with setal tuft at distal end; dactyl short, hooklike, and reversed. Pereopod 7 (Fig. 3B) lower lobe of article 2 reaching joint between articles 4 and 5; lower posterior edge of lobe oblique; article 4



Fig. 2. *Ampelisca brachycladus* n. sp.: A, right mandible; B, first maxilla; C, second maxilla; D, maxilliped; symbols: LFT MD = left mandible; PROX ART = proximal article. Scales: 0.1 mm for B, C; 0.2 mm for A, D.



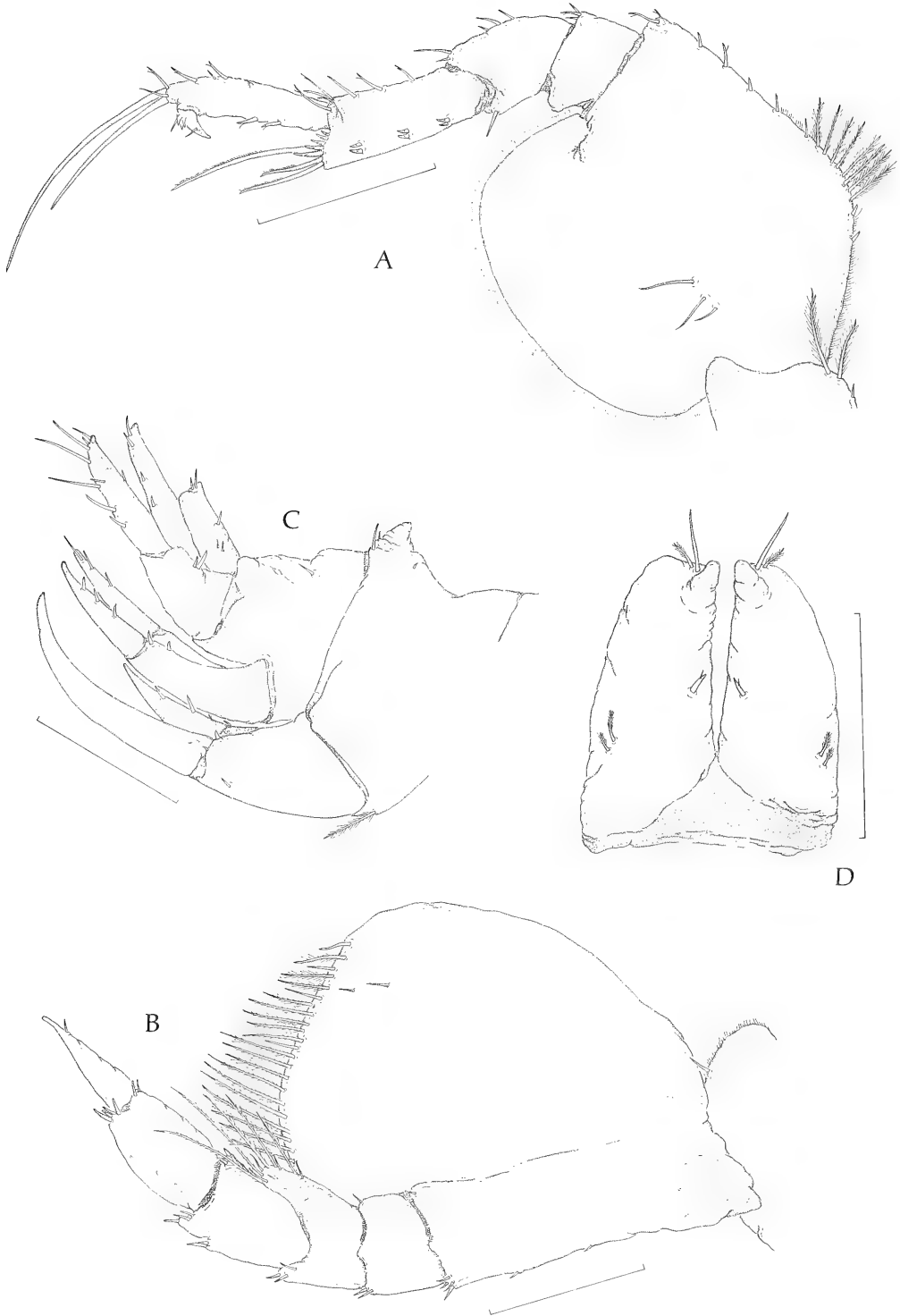


Fig. 3. *Ampelisca brachycladus* n. sp.: A, pereopod 6; B, pereopod 7; C, urosome; D, telson. Scales: 0.5 mm for A; 0.3 mm for B, C; 0.6 mm for D.

posterior lobe reaching more than halfway along hind margin of article 5; article 4 posterior lobe setose; article 5 distal anterior edge notched; article 6 longer than article 5; article 7 equal in length to article 5. All pleonal segments dorsally smooth. Epimera 2 and 3 posterodistal corners subquadrate. Urosomite 1 (Fig. 3C) dorsally a pointed hood. Urosomites 2 and 3 dorsally smooth. Uropod 1 reaching end of uropod 2; inner ramus one-half length of outer ramus; peduncle short and stout. Uropod 2 outer ramus lacking subapical spine. Uropod 3 rami lanceolate. Telson (Fig. 3D) deeply cleft, with terminal spine and seta on each lobe; each lobe with single spine halfway along median edge, and two spines inserted on outer margin  $\frac{1}{4}$ th distance from proximal end.

*Relationship.*—*Ampelisca brachycladus* n. sp. is most closely related to *Ampelisca agassizi* (Judd 1896) (see Dickinson 1982) in having subquadrate epimera 2 and 3 and in having the urosome compressed lengthwise. However, they are distinguishable by article 5 of pereopod 7 of the new species being anterodistally notched; their telsons are also quite dissimilar. *Ampelisca brachycladus* is distinguished from all known congeners by the short inner ramus of uropod 1.

*Material examined.*—All specimens deposited in the Los Angeles County Museum of Natural History. LACMNH No. 85-199.1, Aliso Beach, California (33°28'06"N, 117°44'06"W), Jan 1985, 35 m, 1 holotype female (7.3 mm); LACMNH No. 88-116.1, Santa Monica Bay, California (33°58'47"N, 118°30'27"W), July 1985, 27 m, 8 paratypes; LACMNH No. 85-200.1, Santa Monica Bay, California (33°52'34"N, 118°26'02"W), July 1985, 26 m, 3 paratypes.

*Distributional ecology.*—Geographic range—Santa Monica Bay, California to San Diego, California. Bathymetric range—sublittoral 10 m to 50 m depth. Sediment preference—mixed bottom areas of silt and sand.

*Etymology.*—The specific epithet, *brachycladus*, is a combination of the Greek words brachys (=short) and klados (=branch), alluding to the short inner ramus on uropod 1. It is a masculine noun in apposition to the generic name.

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Contribution Number 1 of the Southern California Association of Marine Invertebrate Taxonomists.

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**Two Medusae New to the Coast of California:  
*Carybdea marsupialis* (Linnaeus, 1758), a Cubomedusa and  
*Phyllorhiza punctata* von Lendenfeld, 1884,  
a Rhizostome Scyphomedusa**

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*Abstract.*—The cubomedusa *Carybdea marsupialis* and the rhizostome scyphomedusa *Phyllorhiza punctata* are reported from waters of California and the eastern Pacific for the first time. Previously, *C. marsupialis* was only known from the Atlantic Ocean. It apparently is native to this area but was confused with *Carybdea rastoni* which is known from Hawaii and the central and western Pacific. *P. punctata* was recently found in San Diego Bay, previously it was known in the Pacific from Hawaii and the tropical Indo-Pacific. Its recent appearance in California was probably due to transport of polyps on the hulls of ships. A synopsis of cubomedusae and scyphomedusae from the waters of California is presented; a total of 19 species are known.

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Although the marine fauna of California is relatively well studied some invertebrate groups are in need of further work. The scyphomedusae are one such group. Nearly one-half of the 18 known species from California were reported after 1960 (Table 1). Most of these new records are for deep water species. Alvaríño (1967, 1976) added two previously unreported coronates, *Atorella vanhoeffeni* Bigelow, 1909 and *Nausithoe rubra* Vanhöffen, 1902, to the fauna of California and Russell (1967) and Smith (1982) found two previously unreported mesopelagic semeanostomes, *Deepstaria enigmatica* Russell, 1967 and *Poralia rufescens* Vanhöffen, 1902, which were collected using submersibles. Some neritic species have also been recently found. Two new stauromedusae, benthic scyphozoans which generally live subtidally attached to algae, were recently described from California. Larson (1988) described *Kyopoda lamberti*, which represents a new family, and Larson and Fautin (1989) described a new species belonging to the genus *Manania*. Here we report on the recent collection of two medusae, *Carybdea marsupialis* (Linnaeus, 1758), and a cubomedusan *Phyllorhiza punctata* von Lendenfeld, 1884, previously was not known from the eastern Pacific. Most recently, a darkly pigmented, undescribed species of *Chrysaora*, up to 25 cm diameter, has appeared in waters of southern California (J. Martin, pers. comm., 1989).

Cubomedusae can be common in warm marine waters. Two species occur in inshore waters of the east coast of the U.S. *Tamoya haplonema* Müller 1859 has been collected along the north coast of the Gulf of Mexico (Phillips and Burke 1970), along the Georgia coast (Kraeuter and Setzler 1975), and as far north as Long Island (Mayer, 1910). *Chiropsalmus quadrumanus* (Müller, 1859) is known

Table 1. Checklist of Cubomedusae and Scyphomedusae known from the coast of California.

| Taxon  | References*       |
|--|-------------------|
| Class Cubozoa  |                   |
| <i>Carybdea marsupialis</i> (Linnaeus, 1758)         | 6, 11, 13, 17, 18 |
| Class Scyphozoa                                      |                   |
| Order Stauromedusae                                  |                   |
| Suborder Eleutherocarpidae                           |                   |
| <i>Haliclystus octoradiatus</i> (Lamarck, 1816)      | 7                 |
| <i>Haliclystus</i> "californiensis"                  | 7                 |
| "Stenoscyphopsis vermiformis"                        | 7                 |
| <i>Kyopoda lamberti</i> Larson, 1988                 | 15                |
| Suborder Cleistocarpida                              |                   |
| <i>Manania gwilliami</i> Larson and Fautin, 1989     | 16                |
| Order Coronatae                                      |                   |
| <i>Atolla wyvillei</i> Haeckel, 1880                 | 4, 9, 12          |
| <i>Atorella vanhoffeni</i> Bigelow, 1909             | 12                |
| <i>Nausithoe rubra</i> Vonhöffen, 1902               | 9                 |
| <i>Periphylla periphylla</i> (Péron & Lesueur, 1809) | 4, 9, 12          |
| Order Semaestomeae                                   |                   |
| <i>Aurelia aurita</i> (Linnaeus, 1758)               | 1                 |
| <i>Chrysaora fuscescens</i> Brandt, 1835             | 1, 2, 3, 17       |
| <i>Chrysaora</i> sp.                                 | 17                |
| <i>Deepstaria enigmatica</i> Russell, 1967           | 10                |
| <i>Pelagia colorata</i> Russell, 1964                | 7, 17             |
| <i>Phacellophora camtschtica</i> Brandt, 1835        | 1, 4, 17          |
| <i>Poralia rufescens</i> Vanhöffen, 1902             | 14                |
| Order Rhizostomeae                                   |                   |
| <i>Phyllorhiza punctata</i> von Lendenfeld, 1884     | 18                |
| <i>Stomolophus meleagris</i> L. Agassiz, 1862        | 5, 6              |

\* References: 1 = Agassiz (1862), 2 = Fewkes (1889), 3 = Kishinouye (1899), 4 = Bigelow (1913), 5 = Bigelow (1914), 6 = Stiasny (1922), 7 = Gwilliam (1956), 8 = Russell (1964), 9 = Alvaríño (1967), 10 = Russell (1967), 11 = Gladfelter (1973), 12 = Alvaríño (1976), 13 = Satterlie (1979), 14 = Smith (1982), 15 = Larson (1988), 16 = Larson and Fautin (1989), 17 = Larson unpubl., 18 = this report.

from the northern Gulf of Mexico (Guest 1959; Phillips and Burke 1970), and along the east coast of the U.S. from Florida (Larson, unpublished observations), Georgia (Kraeuter and Setzler 1975), and North Carolina (Mayer 1910).

Several other species, i.e., *Carybdea alata* Reynaud, 1830 and *Carybdea marsupialis*, although common in the Caribbean (Mayer 1910; Bigelow 1938), have not been reported in neritic waters of the U.S. east coast.

Surprisingly, no cubomedusae are known from the coast of the tropical eastern Pacific even though one species, *Carybdea rastonii* Haacke, 1886, has been reported from California. The first report of this species from the west coast of the U.S. was based on material collected at La Jolla (Stiasny 1922). Additionally, this species has been collected at Santa Barbara (Gladfelter 1973; Satterlie 1979).

Rhizostomes are also mainly subtropical/tropical, reaching their greatest diversity in the Indo-Malayan region (Kramp 1970). In the tropical Indo-Pacific these medusae are so abundant that they are harvested for their collagenous bell (Omori 1978, 1981). Only a single species, *Stomolophus meleagris* L. Agassiz, 1862, was previously known from California (Bigelow 1914; Stiasny 1922).

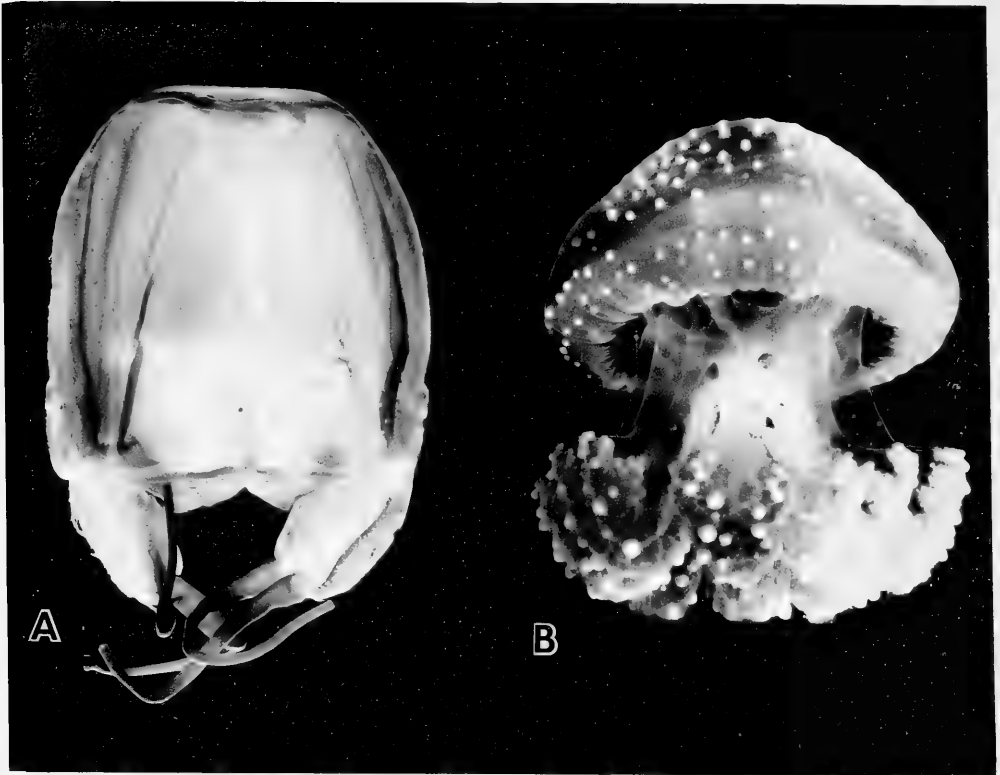


Fig. 1. A. Side view of preserved *Carybdea marsupialis*, 40 mm bell height, collected off Point Moremesa, Santa Barbara, California, 10 August 1985. B. Side view of live *Phyllorhiza punctata* (oral arm appendages not shown), 50 mm bell diameter, collected in Mayaguez Harbor, Puerto Rico, August 1975.

## Results

### *Carybdea marsupialis* (Linnaeus, 1758)

**Material examined:** Thirteen specimens. One specimen 25 mm bell height; collected off Scripps pier, La Jolla, 7 October 1961; collector: R. Cutter. Five mature specimens, 36–40 mm bell height; collected off Point Moremesa, Santa Barbara; 10 August 1985; 5 m depth; collectors: S. Anderson and J. McCullach. Seven mature specimens, 28–35 mm bell height collected off Point Moremesa, Santa Barbara; 11 November 1984; collectors: S. Anderson and J. McCullach.

For comparison, we examined *C. rastoni* specimens collected at the type locality, the Gulf of St. Vincent, Australia. In addition, *C. marsupialis* specimens from the Bahamas were studied.

**Discussion:** The California material fits the diagnosis of *C. marsupialis* as described by Bigelow (1938) in his revision of the family Carybdeidae. The interradial phacellae are single stalked. These specimens most closely resemble the Mediterranean morph which is larger and has more obvious exumbrellar sculpturing than medusae from the western Atlantic (Mayer 1910; Bigelow 1938) (Fig. 1).

*Carybdea marsupialis* is distinguished from the closely related *C. rastoni*, in

size and arrangement of the gastric cirri. In the larger *C. marsupialis*, reaching 4 cm bell height, the phacellae (dendritic gastric cirri present at each of the 4 interradial stomach corners), originate from a single trunk, or rarely from two adjacent trunks (Bigelow 1938, text-figs. 3-5). Whereas, *C. rastoni* is usually less than 3 cm bell height and has gastric cirri that originate from multiple trunks arranged in four interradial rows in the stomach corners (Haacke 1886, fig. 4b; Bigelow 1909, plate 10, fig. 7).

*Carybdea marsupialis* was previously known only from the tropical/subtropical Atlantic and Mediterranean.

Although, two species of *Carybdea* may occur along the coast of southern California, we believe that there is only one. We have examined material from the same locations along the coast of California where *C. rastoni* was previously reported and all specimens were *C. marsupialis*. It is possible that Stiasny (1922) made an incorrect determination. The first author examined Stiasny's specimen which is in the Zoologiske Museum, Copenhagen. The specimen was a *C. marsupialis*. Evidently, Stiasny had not examined the phacellae closely because the bell apex had not been dissected open to expose them. Stiasny probably identified the specimen as *C. rastoni* after only a cursory examination because that species was then the only known cubomedusan from the eastern Pacific since it was known from Hawaii.

Although, Gladfelter (1973) and Satterlie (1979) examined living *Carybdea* material there is no indication on what they based their determinations. Based on the material available to us, there is only one species of *Carybdea*, namely *C. marsupialis*, from the California coast.

It is enigmatic that *C. marsupialis* has not been reported from other areas of the eastern Pacific because in the Atlantic it is widely distributed and relatively common. Possibly the California population represents a recent introduction from the Atlantic as polyps attached to a ship hull or as medusae in bilge water. Yet, this seems unlikely because the polyps are small and delicate (Studebaker 1972) and probably could not have survived the trip. The medusae are also sensitive to water quality.

More likely, *C. marsupialis* is a resident species of the eastern Pacific, having occurred in the contiguous waters of the Caribbean and eastern Pacific prior to the emergence of the Isthmus of Panama about 3 million years ago (Woodring 1966). Why this species was not previously reported in the eastern Pacific is unknown, but it may be that *C. marsupialis* is not as common there as it is in the Caribbean, and the medusan fauna of the tropical/subtropical eastern Pacific has not been as well studied as that of the Caribbean.

The distribution of *C. marsupialis* is apparently unique among medusae, being widespread in the subtropical/tropical Atlantic but restricted in the Pacific to the eastern region. The fact that the specimens from the Pacific more closely resemble the Mediterranean morph is puzzling but may be due to ecological factors, e.g. lower temperatures and/or higher prey concentrations.

*Carybdea marsupialis* is common near Santa Barbara where it occurs from September to November (Gladfelter 1973; Satterlie 1979; S. Anderson and J. McCullugh, pers. comm. 1986). It is mostly seen in the water column a few meters above the bottom in about 10 m of water. Gladfelter (1973) reports that it feeds on mysids. Satterlie (1979) has described aspects of its neurophysiology.

*Phyllorhiza punctata* von Lendenfeld, 1884

Material examined: One specimen (7 cm bell diameter); collected in Mission Bay (30 July 1981; surface). Numerous live specimens have also been observed by one of us (A. Arneson) in San Diego Bay.

Discussion: This species is readily identified when alive by its bluish exumbrella with white spots (Fig. 1) and by its long oral-arm clubs with blue and white tips.

The taxonomy of *P. punctata* is highly confused, mainly owing to poorly preserved or damaged material. As suggested by Cutress (1971), *P. punctata* is probably synonymous with a number of *Mastigias* species (i.e., *M. albipunctata* Stiasny, 1920; *M. andersoni* Stiasny, 1926; and *M. scintillae* Soares Moreira, 1961) and probably also with *Cotylorhiza pacifica* Mayer, 1915 and *Cotylorhizoides pacifica* Light, 1921. The life history of *P. punctata* has been elucidated by Cutress (1971).

*Phyllorhiza punctata* was previously known in the Pacific, only from the Indo-Pacific (Mayer 1910). But recently, it was found in Hawaii (Devany and Eldredge 1977) as well as in the western tropical Atlantic, i.e., Brazil (Soares Moreira 1961), Puerto Rico (Cutress 1971), and Jamaica (Larson unpublished). Its recent appearance in these areas was probably due to transport of polyps on the hulls of ships, as previously suggested by Cutress (in Doty, 1961). This hypothesis is supported by observations that *P. punctata* medusae are mostly confined to harbors used by ocean-going ships. The San Diego Bay and adjacent Mission Bay populations may have originated from polyps carried from Honolulu Harbor by naval vessels. It is unlikely that medusae were the dispersal stage since they are very active and therefore have high food demands that would probably not be met in oligotrophic oceanic waters between Hawaii and California.

Similarly, scyphistomal introduction has been hypothesized for the recent appearance of another rhizostome, *Anomalorhiza shawi* Light, 1921, in Hawaii. Cooke (1984) postulated that this species was transported to Hawaii from the Philippines as part of the ship-borne fouling community.

Apparently, *P. punctata* has become well established in San Diego Bay, judging by the seasonal presence of large numbers of medusae.

## Synopsis of California Scyphomedusae

One species of cubomedusa and 18 species of scyphomedusae are now known from California (Table 1). Since about half of these species have been reported only in the last 20 years, it is likely that additional species may be discovered when further collecting is done in offshore waters and when material from existing collections is examined.

## Acknowledgments

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## Research Notes

### The Tropical Colonial Stony Coral *Tubastrea coccinea* at Cabo San Lucas, Mexico

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Three coralla of the tropical stony coral *Tubastrea coccinea* Lesson, 1829 (see Wells 1983 for list of junior synonyms) were collected on July 17, 1989 at 4 m depth from the north side of a granite islet at Cabo San Lucas, Baja California Sur, Mexico. The live specimens were brilliant orange in color. The two largest coralla are 10 cm (Fig. 1) and 15 cm in diameters and each has approximately 100 corallites. The smallest corallum is 3 cm in diameter and has 15 corallites.

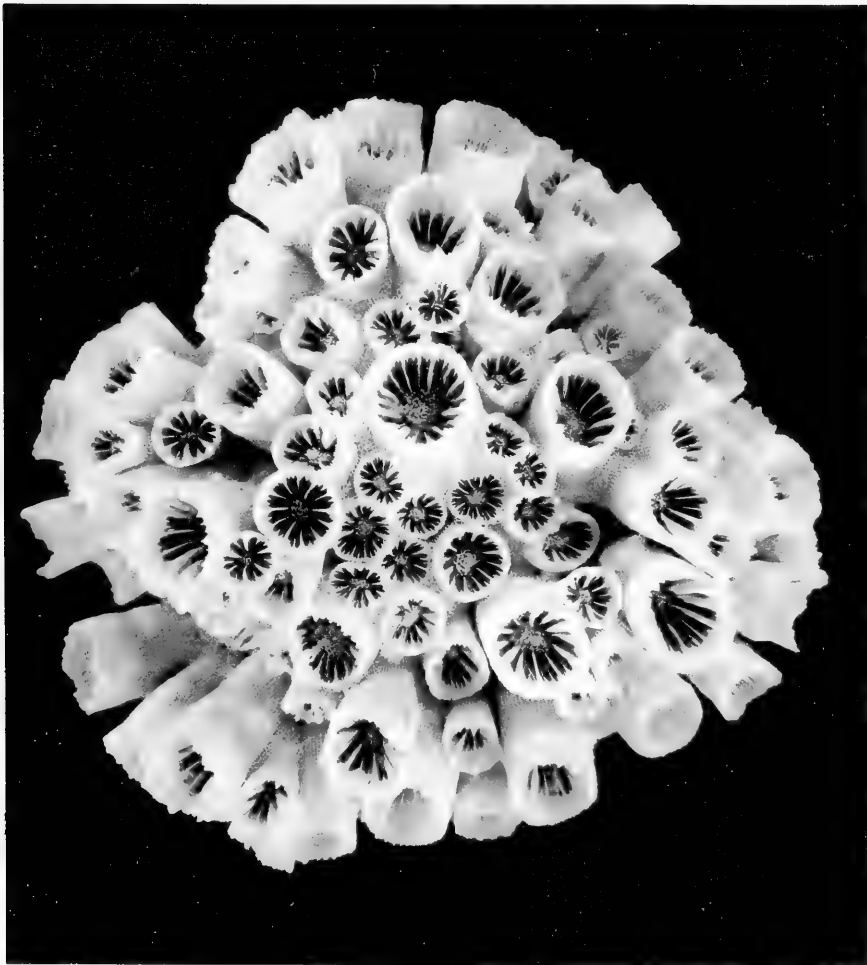


Fig. 1. Colonial stony coral *Tubastrea coccinea*.

The coralla of *Pocillopora* spp. reported by Wilson (1988) occur on the south side of the same islet.

This report extends the known range of *Tubastrea coccinea* from Bahía Pulmo in the Gulf of California (Brusca and Thompson 1977) approximately 80 km SSW to the border of the Pacific Ocean. The previous known range in the eastern Pacific Ocean extended from Bahía Pulmo north into the Gulf of California and south along the mainland shores and islands of Mexico, Costa Rica, Panama, Ecuador, and the Galapagos Islands; in the western Pacific Ocean, *T. coccinea* has been recorded from the Hawaiian Islands west to Murray Island, Australia (Brusca 1980; Durham 1947; Durham and Barnard 1952; Horst 1922; Squires 1959; Wells 1983). Squires' (1959, table 3) indication of a western coast of Baja California occurrence apparently is an error because there are no recorded localities for the species in that region.

The specimens were deposited in the Invertebrate Zoology Section, Natural History Museum of Los Angeles County. Permission to collect kindly was obtained through M. en C. Jorge Garcia P. of the Departamento de Biología Marina, Universidad Autónoma de Baja California Sur, through the courtesy of M. en C. Oscar Arizpe C. of the same department. I am indebted to Srs. Paulino Perez G. and Hector Reyes B. of La Paz for assistance in collecting.

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## Harbor Porpoises Utilize Tidally-induced Internal Waves

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Little information exists to associate small cetaceans with physiographical phenomena known to affect oceanic prey distribution. We present data which suggest that harbor porpoises, *Phocoena phocoena*, feed in surface slicks generated by tidally-induced internal waves.

Internal waves are evident at the water surface as parallel streaks of flat water ("slicks") surrounded by rippled water in coastal areas and harbors when the wind is light (Ewing 1950; LaFond 1959). Internal waves and the resultant surface slicks are common features in many ocean basins (Ewing 1950; LaFond 1959; Cairns 1967; Hendrickson 1973; Lepley et al. 1977; Shea and Broenkow 1982; Chereskin 1983). The waves often result in areas of increased levels of biological activity due to their tendency to concentrate small organisms (Zelids and Jillett 1982; Kingsford and Choat 1986; Shanks and Wright 1987) and to transport pelagic larval invertebrates and fish (Norris 1966; Shanks 1983, 1988). Fish that feed on plankton concentrated in the internal waves are also aggregated in these areas (Norris 1966; Kingsford and Choat 1986). In addition, cetaceans exhibit affiliations with surface slicks and these animals may feed within the waves as well. Silber (1990) noted that Gulf of California harbor porpoises, *Phocoena sinus*, tended to be sighted more often in slicks caused by internal waves than in surrounding waters. However, there is little quantitative documentation of cetaceans associating with slicks of internal wave origin, nor are there data which suggest that cetaceans feed within the subsurface waves.

In offshore areas, slicks may be caused by different factors, such as windrowing, fronts, and eddies, where waters of differing physical properties converge (Bowman and Esaias 1978). Smith et al. (1986) found that ribbons of increased biomass, represented by intermediate levels of the food web, along fronts or convergent zones were exploited by foraging cetaceans. Researchers in the western North Atlantic reported that sei, *Balaenoptera borealis*, and right whales, *Eubalaena glacialis*, followed offshore slicks as a source of concentrated planktonic prey (Watkins and Schevill 1976, 1979, 1982). Feeding humpback, *Megaptera novaeangliae*, and fin whales, *Balaenoptera physalus*, were also associated with slicks in areas where concentrated schools of fish prey were correlated with dense plankton patches (Watkins and Schevill 1979). Other pelagic cetaceans are known to utilize surface slicks, including pygmy killer whales, *Feresa attenuata* (Pryor et al. 1965), rough-toothed dolphins, *Steno bredanensis*, and false killer whales, *Pseudorca crassidens* (K. S. Norris, Long Marine Lab, 100 Shaffer Drive, Santa Cruz, California 95060, pers. comm.).

During recent field studies on the behavior of harbor porpoises in Monterey Bay, California, we observed that porpoises surfaced most frequently in or near surface slicks. To quantify the association between surface slicks and behavioral activity, a subsequent study was conducted in which harbor porpoise behavior was monitored from a 67.5 meter bluff at Sunset Beach State Park overlooking

Monterey Bay, from 10 September to 1 November 1988, during sea states of Beaufort 2 (no whitecaps, windspeed 7–11 km/hour). The study area consisted of water less than 20 m deep with a sandy substrate. At one-minute intervals, the most recent behavioral state of a focal group (milling or traveling) observed within the previous minute was noted, as was the nature of the water surface (slick or rippled) within which the activity occurred. The first porpoise(s) observed within 1.5 km of the study site was selected as the focal group. If a porpoise group traversed between slick and interslick areas, which occurred rarely, the group was categorized as having surfaced in the water type that it appeared in during its ultimate surfacing. Each surfacing sequence by a porpoise group was treated as an independent event, because we could not be sure whether or not the group under observation had been previously sampled. The minimum observation period for a focal group was set at three minutes for analysis. The width of the slicks was not measured, because the location and dimensions of the slicks and interslick areas were dynamic and constantly shifting.

Traveling was defined as unidirectional movement for at least three surfacings. Milling was defined as nondirectional movement for three consecutive surfacings, generally consisting of criss-crossing or circling movement. Although milling behavior may represent a wide variety of activities in cetaceans and the exact function of milling could not be established in our work, foraging activity in harbor porpoises apparently occurs during milling (Goetz 1983; Watson and Gasikin 1983; Sekiguchi 1987). We saw fish jumping at the water surface near milling harbor porpoises on three occasions, which corroborates, but does not confirm a connection between milling and feeding.

A total of 532 behavioral and associated water surface states was collected on 96 porpoise groups during a total of 19.4 hours on 15 days. Harbor porpoises were generally common within 3 km of shore, but we focused our attention on those animals closest to shore (<1.5 km from the observation site), because they were easiest to observe. We used seven power binoculars to spot porpoises.

While in slicks ( $N = 222$ ), harbor porpoises spent significantly more time milling ( $N = 139$ ) than traveling ( $N = 83$ ) (Chi-square = 13.6,  $df = 1$ ,  $P < 0.001$ ). No significant difference was found between the amount of time spent milling ( $N = 142$ ) or traveling ( $N = 168$ ) within rippled (non-slick) water ( $N = 310$ ) (Chi-square = 2.02,  $P > 0.10$ ). When the two habitats (slick versus non-slick) were compared, a significantly greater tendency for milling while in slicks was found (Chi-square = 24.2,  $df = 1$ ,  $P < 0.001$ ).

Most harbor porpoise prey items are relatively small gregarious species (Jones 1981), that may be drawn to internal waves to feed on aggregated larvae or zooplankton. In an analysis of harbor porpoise stomach contents from Monterey Bay, Sekiguchi (1987) reported that market squid (*Loligo opalescens*), the northern anchovy (*Engraulis mordax*), the spotted cusk eel (*Chilara taylori*), rockfishes (*Sebastes* spp.), the plainfin midshipman (*Porichthys notatus*), the jack mackerel (*Trachurus symmetricus*), and the shiner surfperch (*Cymatogaster aggregata*) were the numerically dominant prey. Jones (1981) reported that two-thirds of all fish found in stomachs of harbor porpoises from north-central California live in open ocean or are inshore schooling species. The Pacific hake (*Merluccius productus*), the Pacific tomcod (*Microgadus proximus*), rockfishes, and northern anchovies accounted for 97% of all otoliths in harbor porpoise stomachs sampled. Inver-

tebrates, mostly *Loligo opalescens*, were found in 40% of all stomachs examined by Jones (1981).

The tendency for harbor porpoises to affiliate with slicks and to mill while in slicks, suggests that porpoises may be feeding on higher localized prey densities as a result of concentrating properties of internal waves. It is likely that the porpoises were feeding on fish, squid, or other organisms attracted to zooplankton assemblages in the slicks.

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## The Aquatic Dryopoid Beetles of Pinnacles National Monument: *Optioservus canus* Revisited (Coleoptera: Dryopoidea: Elmidae)

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Early in 1985 I was contacted by the Sacramento, California offices of the U.S. Fish and Wildlife Services. They were interested in what species of California riffle beetles might warrant listing on the national register. One potential candidate was *Optioservus canus* Chandler, 1954, the type locality of which is Pinnacles National Monument (PNM), in San Benito County, California. During the summer of 1946 Harry Chandler collected four specimens of *O. canus* from Chalone Creek, in PNM. In his description of the species Harry also included two additional specimens collected by F. E. Winters in Santa Barbara and Riverside. Thus the type series included only six specimens. Despite careful collecting in California by such noted aquatic coleopterists as Hugh Leech and Harley Brown, no one recollected the species. Obviously this was a potentially endangered species.

In August 1985, I traveled to PNM to obtain a collecting permit and to begin searching for this elusive species. The first two attempts to collect *O. canus* were fruitless despite searching the few permanent water sources and along the mostly dry bed of Chalone Creek. Several other species of dryopoids were collected however. On discussing things with the rangers, one recalled that Chalone Creek had been channelized to control erosion. It appeared that *O. canus* had perhaps gone extinct due to man's lack of attention to "lesser" organisms.

The one mitigating circumstance was that while traveling to and from the PNM area, I had collected a new and quite distinct species of *Optioservus* in Tres Pinos Creek, about 30 miles to the north. This new species was also found in the Arroyo Seco River some 20 miles to the south of PNM. Since it was unkeyable in the recent revision of *Optioservus* (White 1978), I set about describing this species. After examining many specimens among which the elytral coloration varied greatly (from all dark to almost all light), I began to notice some were similar to White's illustration of *O. canus*. This led to reexamination of the types of *O. canus*. Happily, I can report that *O. canus* still exists, although under a different appearance than furnished by the type series and published illustrations. One last collecting trip to PNM, in December 1985, disclosed that *O. canus* still existed in Chalone Creek, the type locality. This population occurs in a very small area and is well hidden under an overstory of watercress. At this site surfacing bedrock forces water in Chalone Creek out of the bed sediments and over the bedrock for a few feet.

In the original description and the first inclusion of *O. canus* in a key to *Optioservus* (Leech and Chandler 1956) the elytral maculae were noted but their shape was not even described. The most distinctive feature for the species was that the elytral pubescence gave a "grizzled look" to the specimens. Collier (1969) was the first to refer to the shape of the maculae. In his key he called them vittae, but in his description he called them spots. His illustration shows an elongate vitta in the lateral half of each elytron (Plate II, fig. 15). Collier examined three specimens from Pinnacles (all of which were in the California Academy of Sciences

collection). His couplet in which *O. canus* is separated does include the "grizzled appearance." Brown (1972) repeated Collier's couplets and illustrations in his manual on the United States' species of dryopoids. In the latest revision of *Optioservus* (White 1978) *O. canus* is again illustrated with a vitta in the lateral half of each elytron. However, the couplet separating *O. canus* omits mention of the "grizzled appearance" even though it is mentioned in the description given later. White notes having seen the holotype and his questioning of the paratypes collected by F. E. Winters (which by then were also in the California Academy of Science collection) implies that he examined them also. White concluded the Winters paratypes were general *O. divergens* (LeConte), 1874.

After examining five of the six specimens in the type series and many other specimens, I am unable to explain the vittate pattern illustrated by Collier, Brown, and White. As mentioned earlier, the elytral coloration varies from entirely brassy-black to almost entirely yellow or dark orange. Humeral spots may be absent, very small, or fairly large. However, when vittate the maculae extend along the medial half of each elytron (not the lateral half as had been earlier illustrated). Sometimes the elytral suture is involved so the elytral disc is all light in color. However, the sides of the elytra are always dark. The type specimens examined appear to me to be of the bimaculate form and not at all vittate. The grizzled appearance, a product of the long pubescence, is characteristic of all color morphs and is the most distinctive character of this species. Chandler is vindicated! Specimens from PNM have a higher frequency of bimaculate forms than other populations. This may be an effect of a genetic bottleneck that perhaps occurred during a severe summer which killed all but a few individuals. Alternatively, it could be a founder effect.

The aquatic dryopoid fauna of Pinnacles National Monument has thus been found by this author to include the following species:

#### Psephenidae

*Eubrianax edwardsii* (LeConte), 1874

#### Dryopidae

*Helichus productus* LeConte, 1852

*Helichus striatus* LeConte, 1852

non *H. columbianus* Brown, 1931

*Helichus suturalis* LeConte, 1852

#### Elmidae

*Optioservus canus* Chandler, 1954

Elsewhere I have found *O. canus* associated with *Psephenus falli* Casey, 1893, *Zaitzevia parvula* (Horn), 1870, *Ordobrevia nubifera* (Fall), 1901 and *Microcylloepus similis* (Horn), 1870. Streams in which I have found *O. canus* include: Monterey Co.—Piney Creek, Juan Higuera Creek, Grimes Canyon Creek, Partridge Creek, and Arroyo Seco River; San Benito Co.—Tres Pinos Creek, Chalona Creek, and San Benito River.

### Acknowledgments

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## INDEX TO VOLUME 89

- Ampelisca brachyclaus* n. sp., 124  
Arneson, A. Charles, see Ronald J. Larson  
Austin, Jorja, see George W. Cox
- Blake, James A. and Brigitte Hilbig: Revision of Two Dorvilleid Species from the Pacific Coast of North America (Annelida: Polychaeta), 109  
Blood, Brad R.: Taxonomy and Distribution of *Sigmodon* in California, 86  
Breen, Robert T. and Mary K. Wicksten: Movement and Habitat Selection in Tagged Rock Crabs (*Cancer antennarius*) in Intertidal Channels at James V. Fitzgerald Marine Life Refuge, California, 10  
Brasher, Anne M., see Daniel L. Castleberry  
Bright, Donald: Management of Hazardous Substances: An Overview, 49  
Bursey, Charles R., see Stephen R. Goldberg
- Castleberry, Daniel L., Jack E. Williams, Georgina M. Sato, Todd E. Hopkins, Anne M. Brasher, and Michael S. Parker: Status and Management of Shoshone Pupfish, *Cyprinodon nevadensis shoshone* (Cyprinodontidae), at Shoshone Spring, Inyo County, California, 19  
Cox, George W. and Jorja Austin: Impacts of a Prescribed Burn on Vernal Pool Vegetation at Miramar Naval Air Station, San Diego, California, 67
- Davis, Stephen D., see Roy Stoddard
- Frost, Patrick, see Ingo H. Gaida
- Gaida, Ingo H. and Patrick Frost: A New Host in the Northern Hemisphere for the Parasitic Marine Isopod *Ceratothoa gaudichaudii* (Crustacea: Isopoda: Cymothoidae), 94  
Goldberg, Stephen R. and Charles R. Bursey: Prevalence of Larval Cestodes (*Mesocestoides* sp.) in the Western Fence Lizard, *Sceloporus occidentalis biseriatus* (Iguianidae), from Southern California, 42
- Hilbig, Brigitte and R. Eugene Ruff: Remarks on the genus *Pettiboneria* (Polychaeta: Dorvilleidae) with Description of Two New Species, 115  
Hilbig, Brigitte, see James A. Blake  
Hopkins, Todd E., see Daniel L. Castleberry
- Larson, Ronald J. and A. Charles Arneson: Two Medusae New to the Coast of California: *Carybdea marsupialis* (Linnaeus, 1758) a Cubomedusa and *Phyllorhiza punctata* von Lendenfeld, 1884, a Rhizostome Scyphomedusa, 130
- Mason, Waynelle, see Harrington Wells

Parker, Michael S., see Daniel L. Castleberry

*Pettiboneia bathyalis* n. sp., 115

*Pettiboneia brevipalpa* n. sp., 115

Reynolds, Robert E., see Barry Roth

Roney, James D.: A New Species of Marine Amphipod (Gammaridea: Ampeliscidae) from the Sublittoral of Southern California, 124

Roth, Barry and Robert E. Reynolds: Late Quaternary Nonmarine Mollusca from Kokoweef Cave, Ivanpah Mountains, California, 1

Ruff, R. Eugene, see Brigitte Hilbig

Sato, Georgina M., see Daniel L. Castleberry

Shepard, William D.: The Aquatic Dryopoid Beetles of Pinnacles National Monument: *Optioservus canus* Revisited (Coleoptera: Dryopoidea: Elmidae), 143

Silber, Gregory K. and Mari A. Smultea: Harbor Porpoises Utilize Tidally-induced Internal Waves, 139

Smultea, Mari A., see Gregory K. Silber

Stewart, James R., see Harrington Wells

Stoddard, Roy and Stephen D. Davis: Comparative Photosynthesis, Water Relations, and Nutrient Status of Burned, Unburned, and Clipped *Rhus laurina* after Chaparral Wildfire, 26

Wells, Harrington, Waynelle Mason, and James R. Stewart: Prairie Dog Food Preference and the Photosynthetic Pathway-Selective Herbivory Hypothesis, 97

Wicksten, Mary K., see Robert T. Breen

Williams, Jack E., see Daniel L. Castleberry

Wilson, Edward C.: Mass Mortality of the Reef Coral *Pocillopora* on the South Coast of Baja California Sur, Mexico, 39

Wilson, Edward C.: The Tropical Colonial Stony Coral *Tubastrea coccinea* at Cabo San Lucas, Mexico, 137



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**The literature cited:** Entries for books and articles should take these forms.

McWilliams, K. L. 1970. Insect mimicry. Academic Press, vii + 326 pp.

Holmes, T. Jr., and S. Speak. 1971. Reproductive biology of *Myotis lucifugus*. J. Mamm., 54:452-458.

Brattstrom, B. H. 1969. The Condor in California. Pp. 369-382 in *Vertebrates of California*. (S. E. Payne, ed.), Univ. California Press, xii + 635 pp.

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## CONTENTS

|  |     |
|--|-----|
| Prairie Dog Food Preference and the Photosynthetic Pathway-Selective Herbivory Hypothesis By <i>Harrington Wells, Waynelle Mason, and James R. Stewart</i> .....   | 97  |
| Revision of Two Dorvilleid Species From the Pacific Coast of North America (Annelida: Polychaeta) By <i>James A. Blake and Brigitte Hilbig</i> .....   | 109 |
| Remarks on the Genus <i>Pettiboneia</i> (Polychaeta: Dorvilleidae) with Descriptions of Two New Species By <i>Brigitte Hilbig and R. Eugene Ruff</i> .....   | 115 |
| A New Species of Marine Amphipod (Gammaridea: Ampeliscidae) from the Sublittoral of Southern California By <i>James D. Roney</i> .....   | 124 |
| Two Medusae New to the Coast of California: <i>Carybdea marsupialis</i> (Linnaeus, 1758), a Cubomedusa and <i>Phyllorhiza punctata</i> von Lendenfeld, 1884, a Rhizostome Scyphomedusa By <i>Ronald J. Larson and A. Charles Arneson</i> ..... | 130 |
| Research Notes   |     |
| The Tropical Colonial Stony Coral <i>Tubastrea coccinea</i> at Cabo San Lucas, Mexico By <i>Edward C. Wilson</i> .....   | 137 |
| Harbor Porpoises Utilize Tidally-induced Internal Waves By <i>Gregory K. Silber and Mari A. Smultea</i> .....  | 139 |
| The Aquatic Dryopoid Beetles of Pinnacles National Monument: <i>Optioservus canus</i> Revisited (Coleoptera: Dryopoidea: Elmidae). By <i>William D. Shepard</i> .....  | 143 |
| Index .....  | 147 |

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