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A PHYLOGENETIC ANALYSIS OF THE CAMINALCULES.
I. THE DATA BASE

ROBERT R. SOKAL

*Department of Ecology and Evolution, State University of New York at Stony Brook,
Stony Brook, New York 11794*

Abstract.—The Caminalcules are a group of "organisms" generated artificially according to principles believed to resemble those operating in real organisms. A reanalysis of an earlier data matrix of the Caminalcules revealed some inconsistencies and errors which necessitated recoding of some characters. The resulting differences with earlier results are minor. The images of all 77 Caminalcules are featured, those of the 48 fossil species for the first time. The characters of the Caminalcules are defined and a data matrix is furnished for all Recent and fossil species.

A new phenetic standard is proposed for the Caminalcules which divides them into five "genera." The true cladogram is revealed for the first time. Recent Caminalcules have evolved over 19 time periods. Five branches correspond to the phenetic genera but originate at greatly differing time periods. Four lines terminate in fossils.

A series of measures for quantifying evolutionary change is defined, including measures for homoplasy, parallelism, and reversal. A survey is made of these measures and of other statistics of relevance to systematics for 19 data sets from the numerical taxonomic literature. The Caminalcules turn out to be compatible to data sets on real organisms with respect to all these measures, as well as with respect to evolutionary rates and species longevities. Thus, questions raised by an analysis of the Caminalcules should be of interest to systematists concerned with the analysis of data sets on real organisms. [Phenetic classifications; cladistic classifications; estimated cladograms; homoplasy; Wagner trees; Caminalcules; numerical taxonomy.]

This paper, and others to follow, takes advantage of the opportunity afforded by a group of artificial organisms with a known phylogeny, the Caminalcules, to throw light on some of the questions concerning principles and procedures that currently engage the attention of taxonomists. There is considerable disagreement on the relative merits of phenetic and cladistic classifications (Sneath and Sokal, 1973; Eldredge and Cracraft, 1980; Wiley, 1981). Some workers contend that classifications based on phylogenetic principles are empirically better by various criteria of optimality (Farris, 1977, 1979a, b; Mickevich, 1978a, 1980; Schuh and Polhemus, 1980; Schuh and Farris, 1981). These claims have been questioned by others who find the evidence and methodology presented to be flawed (Colless, 1980; Rohlf and Sokal, 1980, 1981; Sokal and Rohlf, 1981a; Rohlf et al., 1983a, b). The empirical studies, and the arguments pro and con phylogenetic classifications derived in such investigations, suffer from a major impediment. All of the phylogenetic classifications reported in the literature are only estimates of the true phylogeny, which is unknown for all real

organisms. By contrast the various results of this study merit serious attention because they can be examined against the benchmark of the true phylogeny of the group.

The Caminalcules are artifacts created by the late Professor Joseph H. Camin of the University of Kansas and in effect represent a single simulation of the evolutionary process by rules that have not been made explicit. However, readers will find that these organisms, which have the advantage over other simulations in presenting a visual record to the investigator, illustrate a variety of evolutionary phenomena and are therefore of considerable pedagogical and heuristic value. The relevance of this data set to currently active issues in systematics will readily become evident to the reader of this series. I shall show that with respect to a substantial array of measurable properties, the Caminalcules are well within the range of empirically observed values for real taxonomic groups and that, conversely, for no property of consequence in numerical taxonomy are the Caminalcules beyond the range of observed values in real organisms.

At the suggestion of the Editor and some

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reviewers, this series of publications is initiated in this paper with the presentation of the data on which previous and succeeding studies have been based. I furnish the images of the previously published 29 Recent species and for the first time the 48 "fossil" species. I also present for the first time the true phylogeny of the Caminalcules as generated by Professor Camin. With these illustrations I provide a list of the descriptions of characters as adopted in my laboratory as well as a data matrix giving the character states for all 106 characters for each of the 77 Recent and fossil Caminalcules. In addition to presenting a new standard phenetic classification, the paper describes a number of measures for taxonomic and evolutionary properties and compares the Caminalcules with data sets on real organisms with respect to these measures. Subsequent studies in this series will treat estimates of the true cladogram, the inclusion of fossils in phenetic and cladistic classifications, congruence and character stability, and OTU stability.

ORIGIN OF THE DATA BASE

The original intention in generating the Caminalcules was to study the nature of taxonomic judgment (eventually published by Sokal and Rohlf, 1980), but work with these animals has led to other developments in numerical taxonomic methodology, such as an early method of numerical cladistics (Camin and Sokal, 1965) and a method for obtaining taxonomic structure by random and systematic scanning of biological images (Sokal and Rohlf, 1966; Rohlf and Sokal, 1967). Other experiments on taxonomic judgment have also been based on the Caminalcules (Moss, 1971; Sokal, 1974; Moss and Hansell, 1980).

Camin drew the Caminalcules using master stencils for ditto machines. The genetic continuity of the Caminalcules was achieved by Camin by tracing successive drawings of the animals, permitting the preservation of all characters except for such modifications as were desired. Xerox copies of the images of the Recent OTUs were made available in the early 1960s, those of the fossil OTUs some years later. Independent xerox copies of all OTUs are in the possession of Dr. Paul A.

Ehrlich of Stanford University and Dr. W. Wayne Moss of the Philadelphia Academy of Sciences in addition to myself. The originals drawn on the ditto masters appear to have been lost following the death of Professor Camin in 1979.

All examinations of the Caminalcules for numerical taxonomic studies have been carried out on the xeroxes of the images. Illustrations of all 29 Recent OTUs have been published three times previously (Sokal, 1966; Rohlf and Sokal, 1967; Sokal and Rohlf, 1980). For this purpose, inked copies of the xeroxed images were photographed. Although the artist's copies of the original xeroxes are quite faithful, inevitably some fine detail has been altered or lost. Thus, not every character state described below can be unequivocally recognized in the featured illustrations. The version of the 29 Recent OTUs published in Sokal (1966) was "beautified" by the publisher's artist and cannot be relied upon for detail. The images of the 48 fossils were newly inked for this study and all differentiating characteristics can be observed in them.

The Recent OTUs, numbered 1 to 29, are shown in Figure 1. The fossil OTUs, given different code names by Camin, were randomly assigned numbers 30 to 77 by me. They are shown in Figure 2.

The true cladogram of the group was communicated to me by Camin in 1970. But although this information was employed in the computations leading to the analysis of taxonomic judgment (Sokal and Rohlf, 1980), access to it was restricted even for workers on this project. I did not become intimately familiar with the phylogenetic tree until 1981 during the final analyses leading to this manuscript.

Readers of this paper and of subsequent ones in this series should note that I use the term *cladogram* in the sense in which I originally coined it (Camin and Sokal, 1965; also independently coined with the same meaning by Mayr, 1965). One definition of this meaning (Sneath and Sokal, 1973:29) is as "A branching ... network of ancestor-descendant relationships." This definition differs from the several meanings attached to the term cladogram by various cladists (e.g., El-
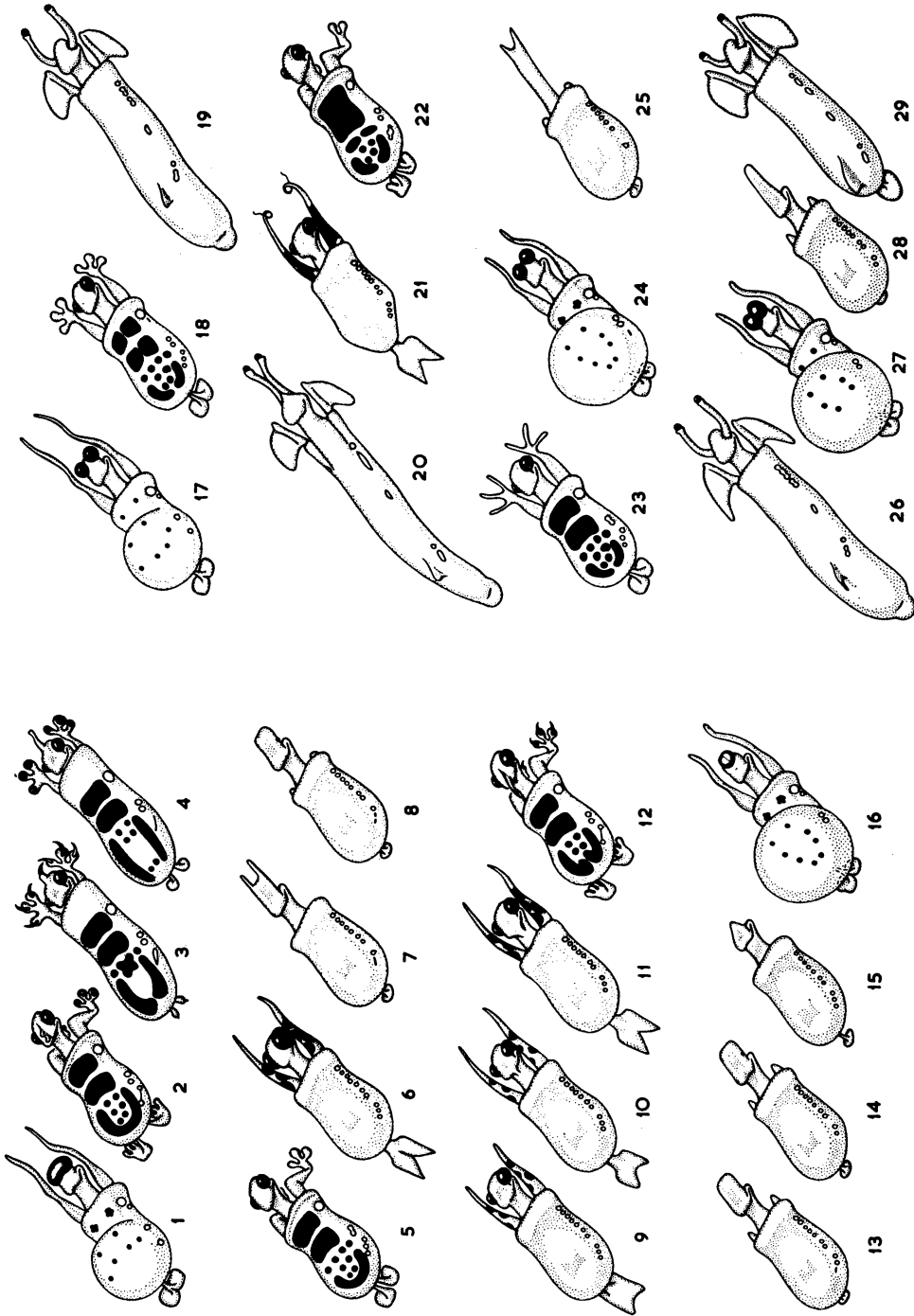
Fig. 1. Images of the 29 Recent species of the Caminalcules, an imaginary group of animals, generated by J. H. Camin. The phenetic classification adopted in this paper divides these into the following "genera": Genus A comprises species 7, 8, 13, 14, 15, 25, 28; B comprises 6, 9, 10, 11, 21; C comprises 1, 16, 17, 24, 27; DE comprises 2, 3, 4, 5, 12, 18, 22, 23; and F comprises 19, 20, 26, 29. Earlier studies (e.g., Sokal and Rohlf, 1980) placed species 3 and 4 in a genus D separate from E, which comprised the balance of the species in the current genus DE.
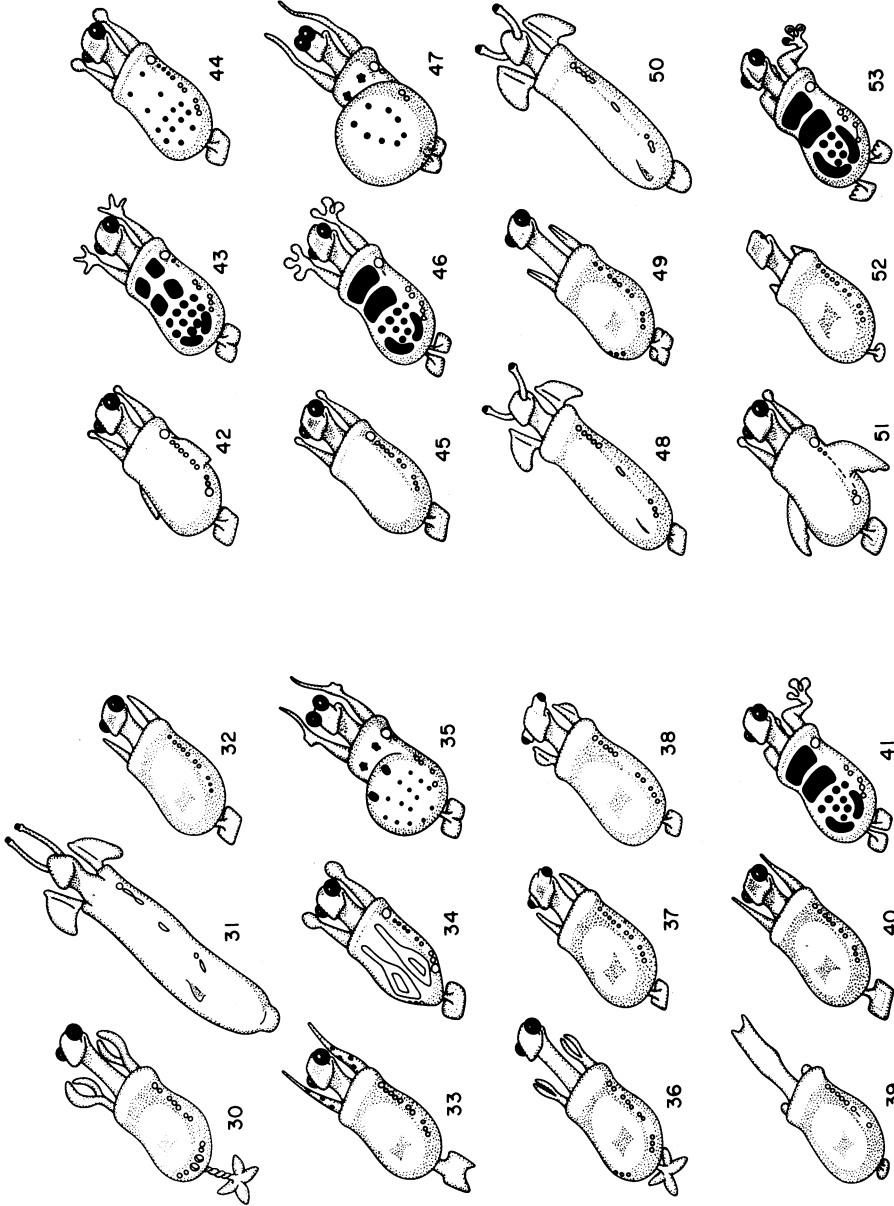
FIG. 2. Images of the 48 fossil species of the Caminalcules, an imaginary group of animals, generated by J. H. Camin. The species were assigned numbers 30 through 77 at random. The common ancestor of the entire group is species 73. Their phylogenetic relations can be learned from Figure 4.
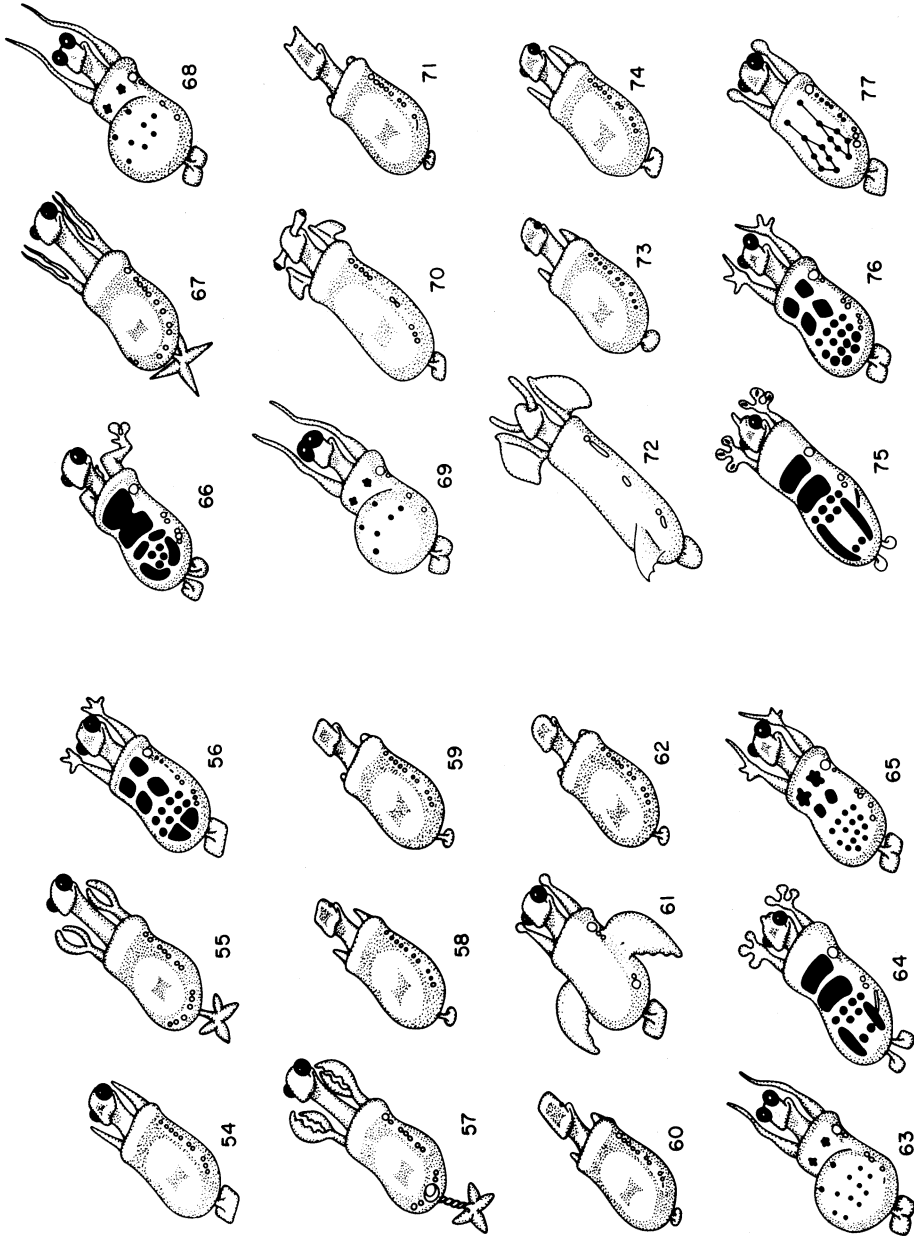
FIG. 2. Continued.

dredge and Cracraft, 1980; Nelson and Platnick, 1981; Wiley, 1981; see also Sneath, 1982). Thus, cladogram as used in this and succeeding papers refers to a branching sequence depicting the actual or hypothesized genealogy of the OTUs. It does not include length of branches of the tree and is not a statement about the evolution or pattern of character states akin to "nested synapomorphy schemes."

Camin did not keep a written record of character changes. In the 1960s, A. J. Boyce and I. Huber prepared a data matrix for a numerical 'phenetic study of the 29 Recent OTUs, describing 86 characters. This data matrix was the basis of various phenetic analyses of the Caminalcules (Sokal, 1966; Sokal and Rohlf, 1966, 1980; Rohlf and Sokal, 1967). For the present study it became necessary to map the coded characters onto the now known cladogram and during this process each character was re-evaluated for the 29 Recent OTUs. This re-examination of the images led to the discovery of several inconsistencies in the Boyce and Huber data matrix. Altogether 13 of the 2,494 entries in that 29 × 86 matrix seemed to be in error and were corrected. Original character 58 was deleted because it was discovered to be invariant. All measurement characters were remeasured and small differences with earlier measurements were recorded. Because the images available during my current studies are poorer quality xerox copies than those available to Boyce and Huber, the resolution of some of the more minute morphological features was more difficult and in a few cases characters were recoded into fewer, coarser classes.

Remeasurements, changes in logic, and revision of character state coding accounted for changes in 33 of the 85 characters. To account for the features of the fossil OTUs, which had not been coded previously, another 12 characters were redefined and 21 new characters were added. This augmented data matrix comprises 77 OTUs and 106 characters of which 65 are binary, 31 are ordered integer characters, and 10 are measurement characters. From this matrix an 85 character × 29 OTU subset was extracted for the Recent OTUs. This matrix has 48 binary characters, 27 ordered integer characters and 10 measurement characters. Both the 106 character × 77 OTU matrix and the 85 character × 29 OTU matrix contain characters with NCs (no comparison codes). All NCs in this study are logical (i.e., presence of a given state for character h making it impossible to define a state for character i) rather than due to missing information. In the larger matrix, 79 of the 106 characters contain NC codes; in the smaller, 59 of the 85 characters have NCs. The measurement characters are available in two versions. One is as direct measurements in millimeters, the other is coded as ordered integer states but with gaps omitted. The range of measurements for one character was divided into 10 equally wide classes coded 0 to 9. Each character state was then assigned to one of these classes, but classes lacking observed character states were ultimately omitted. Thus, if there were no OTUs with measurements in class 3, the subsequent class 4 was renumbered 3. The number of states in the 10 characters resulting from this procedure ranges from four to nine. A list defining the states of each character is furnished in the Appendix. The actual data matrix (integer coded version) is shown in Table 1.

The consequences of recoding the measurement characters in integer scale were minimal. Matrix correlations for the 29-OTU study between the resemblance matrices based on these two methods of character coding are very high (0.998 and 0.997, respectively, for r and d, the correlation and taxonomic distance coefficients). The classifications resulting from these two coding methods are identical. In this and subsequent papers, only the data matrix using integer scale coding of measurement character states is featured, since this is the simpler coding preferred for the several cladistic methods employed.

The effects of correcting and recoding the original Boyce and Huber data matrix for the 29 OTUs were minor. Matrix correlations between the two versions of the resemblance matrices are high (0.980 for r, 0.969 for d). UPGMA phenograms based on these resemblance matrices are close; the strict consensus index CI_C for the classifications based on the

two correlation matrices is 0.889, for those based on the two distance matrices 0.815. This index (Rohlf, 1982) ranges between 0 for no consensus and 1 for perfect consensus. It is identical to the consensus fork index of Colless (1980) and the proportional consensus index of Sokal and Rohlf (1981a).

The differences between the classifications based on correlations and distances computed from the original Boyce and Huber data matrix (see fig. 3 of Rohlf and Sokal, 1967) and those based on the updated, integer-coded version all involve taxonomic affinities at the "species" level. The "generic" classification is the same for both versions. When the new classifications were compared to 49 subjective classifications of the Caminalcules produced by 22 experimental subjects (Sokal and Rohlf, 1980), the new phenograms of the Caminalcules were found to be no more (and no less) similar to these intuitive classifications than the earlier Boyce and Huber classifications.

A NUMERICAL PHENETIC CLASSIFICATION

For phenetic analyses the data were subjected to standard taxometric procedures using the NTSYS system of numerical taxonomic computer programs (Rohlf et al., 1980). Characters were standardized before computation of correlation and taxonomic distance coefficients between OTUs.

Rohlf and Sokal (1967) noted that phenograms based on distances and correlations of the Caminalcules differ substantially in the specific as well as generic affinities indicated. Previous work by Rohlf and Sokal (1967) and by Sokal and Rohlf (1980) showed that the classification based on the correlation matrix corresponded more closely than that based on the distance matrix to the taxonomic structure noted by individual taxonomists grouping the Caminalcules by conventional, intuitive methods. This undoubtedly occurs because correlation coefficients are more sensitive to shape than are distance coefficients (Rohlf and Sokal, 1965), and it is shape rather than size on which taxonomists tend to base their judgments on taxonomic affinity. For this reason, the UPGMA clustering (shown in Fig. 3) of the correlation matrix based on the updated, integer-coded data matrix was

the logical choice as a new standard for a phenetic classification of the 29 Recent OTUs to be compared with the true cladogram. This phenogram also has the highest cophenetic correlation coefficient of any phenetic classification of the Caminalcules computed so far (0.965).

Five major clusters, the "genera" of the Caminalcules, can be seen in the phenogram in Figure 3. These fall naturally into two major groups, that containing genera A, B, and F, and a second group containing C and DE. The status of D, consisting of OTUs 3 and 4, is problematical. Only in one previous study, based on a mechanical method of scanning the images (Rohlf and Sokal, 1967: fig. 3A), was D unequivocally separated from E at a level of phenetic similarity equal to that of the other genera—A, B, C, and F. The Boyce and Huber correlation phenogram (Rohlf and Sokal, 1967: fig. 3C) shows D joining E at a level closer than that of at least one member of A joining its genus. Intuitive classifications by various taxonomists (Sokal and Rohlf, 1980) had frequently assigned species 3 and 4 to genus E, although some had singled out the divergence of these two OTUs which are unique in having rudimentary posterior appendages as well as an elongated body obliterating the neck. Since the phenogram in Figure 3 clearly affiliates D with E, it seems appropriate to join the two together into a single genus which I have called DE to preserve continuity with earlier publications.

THE TRUE CLADOGRAM

The true cladogram as furnished by J. H. Camin is shown in Figure 4. The diversity of the taxon was generated over 19 time periods. Lines undergoing evolutionary change are indicated in Figure 4 by slanted (as distinct from vertical) lines. Species that underwent evolutionary change during a given time period are shown as solid circles at the end of that period. Ancestral species that are not continued into the next time period as vertical lines are considered to have become extinct and are indicated by small hollow circles. Five branches leading to Recent forms, corresponding to the five phenetic genera, can be recognized but these originate at

TABLE 1.   Data matrix of 77 Recent and fossil Caminalcules.[a]

	1-5	6-10	11-15	16-20	21-25	26-30	31-35	36-40	41-45	46-50	51-55	56-60	61-65	66-70	71-75	76-77
1	11111	11111	11111	11111	11110	11111	11111	11101	11111	11111	11111	11111	11111	11111	11111	11
2	11111	01110	01111	11111	0111X	11111	11111	111X1	11111	11111	11111	11111	11111	11111	11111	11
3	XXXXX	1XXX0	0XXXX	XXXXX	1XXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XX
4	00110	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00010	00000	00001	00
5	XX10X	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXX0X	XXXXX	XXXX1	XX
6	10000	12200	00220	10011	00004	10310	10000	00050	00000	00001	00000	01002	00001	00010	21000	00
7	X1111	10111	11112	X1122	11110	2X121	21111	11101	11111	1X122	11111	11111	12111	111X1	02111	11
8	XXXXX	XXXXX	XXXX1	XXX01	XXXXX	0XX0X	0XXXX	XXXXX	XXXXX	XXXX0	XXXXX	XXXXX	X0XXX	X0XXX	X0XXX	XX
9	00000	01000	00000	00000	00001	00000	00000	00010	00000	00000	00000	00000	00000	00000	10000	00
10	11111	10111	11010	11111	11110	11011	11111	11101	11111	11111	11111	11101	10111	11111	00111	11
11	20000	0X000	00X0X	30000	0000X	01X00	00000	0X000	00000	01000	00000	000X0	0X000	00010	XX000	00
12	00000	00000	00000	00011	00000	10010	10000	01100	00000	00101	00000	00000	00000	00001	01000	00
13	XXXXX	XXXXX	XXXXX	XXX55	XXXXX	5XX3X	5XXXX	X01XX	XXXXX	XX3X3	XXXXX	XXXXX	XXXXX	XXXX2	X4XXX	XX
14	XXXXX	XXXXX	XXX1X	XXXXX	1XX0X	2XXXX	X00XX	XXXXX	XX0X0	XXXXX	XXXXX	XXXXX	XXXX0	X0XXX	XX
15	12001	10000	02000	01011	01001	10011	10010	10110	11000	00101	10201	01000	10000	11011	00000	XX
16	X1XXX	XXXXX	X0XXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XX0XX	XXXXX	XXXXX	XXXXX	XXXXX	XX
17	01000	00000	01000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00
18	11111	10111	11110	11111	11111	11111	11111	11111	11111	11111	11111	11111	11111	11111	11111	11
19	54444	4X034	4400X	56378	53350	75063	71334	21202	32322	35415	20412	23000	20434	44553	06013	32
20	01001	0X000	0100X	00000	01000	00000	00000	00000	10000	00000	00100	00000	00000	10000	00000	00
21	01111	0X000	0100X	00100	01100	00001	00001	10000	10100	10010	00101	11000	00011	11000	00001	10
22	1XXXX	1X221	1X22X	21X22	0XX12	2222X	2213X	X2222	X3X33	X22X2	32X2X	XX222	321XX	XX122	2222X	X3
23	X1111	XXXXX	X1XXX	XX1XX	X01XX	XXXX0	XXXX1	0XXXX	1X1XX	1XX0X	XX1X0	10XXX	XXX11	10XXX	XXXX1	1X
24	X0100	XXXXX	X1XXX	XX0XX	X0XXX	XXXXX	XXXXX	XXXXX	0XXXX	0XXXX	XX0XX	XXXXX	XXX0X	XXXXX	XXXX0	XX
25	X1010	XXXXX	X0XXX	XX0XX	X0XXX	XXXXX	XXXXX	XXXXX	0XXXX	0XXXX	XX1XX	XXXXX	XXX0X	XXXXX	XXXX1	XX
26	0XXXX	0X000	0X00X	00X11	0XX00	1001X	1000X	X0100	X0X00	X01X1	0X0X0	XX000	000XX	XX001	0100X	X0
27	XXXXX	XXXXX	XXXXX	XXX34	XXXXX	5XX5X	3XXXX	XX0XX	XXXXX	XX2X3	XXXXX	XXXXX	XXXXX	XXXX1	X5XXX	XX
28	XXXXX	XXXXX	XXXXX	XXX23	XXXXX	6XX4X	3XXXX	XX0XX	XXXXX	XX2X2	XXXXX	XXXXX	XXXXX	XXXX1	X5XXX	XX
29	00000	1X011	1000X	00000	10000	00000	00100	00000	00000	00000	00000	00000	00000	00000	00000	00
30	XXXXX	1XX00	1XXXX	XXXXX	2XXXX	XXXXX	XXNXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XX
31	12222	00000	02000	11200	02210	02000	00001	00000	20100	21000	00200	00000	00121	20110	00002	10
32	XXXXX	10011	1X000	XXX00	1XXX0	0X002	0010X	20001	X0X00	XX000	00X02	02000	00XXX	X2XX0	0000X	X0
33	XXXXX	X11XX	XX011	1XX44	XXXX2	4X04X	46X7X	X432X	X6X76	XX464	61X6X	7X111	61XXX	XXXX3	1524X	X7
34	XXXXX	X11XX	XX112	XX000	XXXX1	0X01X	02X2X	X221X	X2X22	XX121	22X2X	2X221	22XXX	XXXX2	1112X	X2
35	XXXXX	2XX00	1XXXX	XXXXX	1XXXX	XXXXX	XX0XX	XXXXN	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XX
36	X2012	XXXXX	X2XXX	XX2XX	X22XX	X2XXX	XXXXX	XXXXX	2XXXX	2XXXX	XX2XX	XXXXX	XXX2X	2XXXX	XXXX1	XX
37	X1XX0	XXXXX	X1XXX	XX0XX	X10XX	X0XXX	XXXXX	XXXXX	0XXXX	0XXXX	XX1XX	XXXXX	XXX0X	1XXXX	XXXXX	XX
38	X1XXX	XXXXX	X1XXX	XXXXX	X0XXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XX1XX	XXXXX	XXXXX	0XXXX	XXXXX	XX
39	01001	22222	21222	10100	21112	01202	02211	22222	10111	11222	02122	12222	02101	12102	20220	11
40	00000	00000	00000	00001	00000	00000	10000	00000	00000	00000	00000	00000	00000	00000	00000	00
41	00000	11111	10111	00000	10001	00101	01100	11011	00000	00010	01011	01111	01000	01000	10110	00
42	01111	00000	01000	00100	01100	00000	00000	00000	10100	10000	00100	10000	00011	10000	00001	10
43	X1111	XXXXX	X1XXX	XX0XX	X21XX	XXXXX	XXXXX	XXXXX	1X0XX	1XXXX	XX1XX	0XXXX	XXX1N	2XXXX	XXXX1	0X
44	10000	00000	00000	11000	00010	01000	00011	00000	00010	01000	00000	00000	00100	00110	00000	01
45	2XXXX	XXXXX	XXXXX	20XXX	XXX2X	X1XXX	XXX12	XXXXX	XXX0X	X2XXX	XXXXX	XXXXX	XX2XX	XX22X	XXXXX	X0
46	11111	00000	01000	11100	01110	01000	00011	00000	10110	11000	00100	10000	00111	10110	00001	11
47	20000	XXXXX	X0XXX	120XX	X002X	X1XXX	XXX03	XXXXX	0X02X	01XXX	XX0XX	0XXXX	XX202	0X22X	XXXX0	02
48	2XXXX	XXXXX	01XXX	XXX0X	0XXXX	XXXX1	XXXXX	XXX1X	X0XXX	XXXXX	XXXXX	XX1X1	XX12X	XXXXX	1X
49	00000	00000	00000	00000	10000	00000	00010	00000	00000	00000	00000	00000	00000	00000	00000	00
50	00000	00000	00000	00011	00000	10010	10000	00000	00000	00101	00000	00000	00000	00000	01000	00
51	XXXXX	XXXXX	XXXXX	XXX13	XXXXX	1XX4X	2XXXX	XXXXX	XXXXX	XX0X1	XXXXX	XXXXX	XXXXX	XXXXX	X4XXX	XX
52	XXXXX	XXXXX	XXXX10	XXXXX	XXXXX	2XX1X	1XXXX	XXXXX	XXXXX	XX1X1	XXXXX	XXXXX	XXXXX	XXXXX	X2XXX	XX
53	10000	00000	00000	11000	00010	01000	00001	00000	00000	01000	00000	00000	00100	00110	00000	00
54	01221	00000	02000	00200	02200	00000	00000	00000	20200	20000	00200	20000	00020	20000	00002	00
55	XX02X	XXXXX	X0XXX	XX1XX	X00XX	XXXXX	XXXXX	XXXXX	1X0XX	0XXXX	XX0XX	0XXXX	XXX3X	0XXXX	XXXX2	XX
56	XX20X	XXXXX	X3XXX	XX1XX	X11XX	XXXXX	XXXXX	XXXXX	1X1XX	1XXXX	XX1XX	XXXXX	XXX0X	1XXXX	XXXX0	XX
57	X1XX0	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XX
58	XXXXX	XXXXX	XXXXX	XXX01	XXXXX	0XX0X	0XXXX	X00XX	XXXXX	XX0X0	XXXXX	XXXXX	XXXXX	XXXX0	X0XXX	XX
59	XX10X	XXXXX	X0XXX	X00XX	XXXXX	XXXXX	XXXXX	XXXXX	0X0XX	0XXXX	XX0XX	0XXXX	XXX0X	0XXXX	XXXX0	XX
60	22023	XXXXX	X1XXX	323XX	X133X	X2XXX	XXXN6	XXXXX	3X44X	33XXX	XX2XX	3XXXX	XX536	1X32X	XXXX3	6N
61	X0X10	XXXXX	XXXXX	XX0XX	XX0XX	XXXXX	XXXXX	XXXXX	0XXXX	0XXXX	XX0XX	0XXXX	XXX1X	XXXXX	XXXX1	XX
62	X1212	XXXXX	X1XXX	XX2XX	X02XX	XXXXX	XXX1X	XXXXX	2X2XX	2XXXX	XX1XX	2XXXX	XXX2X	0XXXX	XXXX2	2X
63	43233	33333	33332	74310	33363	17313	13324	33333	33333	37131	33323	33333	33533	33542	31332	32
64	11111	00000	01000	11100	01110	01000	00011	00000	11111	11000	10100	10000	10111	10110	00001	11
65	01111	11111	11111	10111	11110	11111	11111	11111	11111	11111	11111	11111	N1111	11101	11111	11

[a] Columns are species code numbers. Recent OTUs are species 1-29. Rows are the 106 characters described in the Appendix. The first 85 characters are the integer-coded data for the Recent OTUs. The rest are those necessary for describing the fossils. The character states, ranging numerically from 0 to 8, are in the body of the table. The following two states have special symbols: X—no comparison (NC) code; N—represents negative one (−1).

TABLE 1. Continued.

	1-5	6-10	11-15	16-20	21-25	26-30	31-35	36-40	41-45	46-50	51-55	56-60	61-65	66-70	71-75	76-77
66	X0001	00000	00000	0X011	0010X	10010	10000	00000	00000	00101	00000	00000	X0000	000X1	01000	00
67	XXXX1	XXXXX	XXXXX	XXX00	XX1XX	0XX0X	0XXXX	XXXXX	XXXXX	XX0X0	XXXXX	XXXXX	XXXXX	XXXX1	X0XXX	XX
68	10000	33333	30333	11133	30013	31333	33331	33333	03233	11333	33033	33333	23101	03113	33330	13
69	0XXXX	XXXXX	XXXXX	001XX	XXX0X	X0XXX	XXXX0	XXXXX	XX1XX	10XXX	XXXXX	XXXXX	0X0X0	XX00X	XXXXX	0X ·
70	XXXXX	00000	0X000	XXX11	0XXX0	1X010	1000X	00000	X0X00	XX001	00X00	00000	X0XXX	X0XX0	0100X	X0
71	XXXXX	XXXXX	XXXXX	XXX10	XXXXX	1XX0X	0XXXX	XXXXX	XXXXX	XXXX1	XXXXX	XXXXX	XXXXX	XXXXX	X0XXX	XX
72	XXXXX	XXXXX	XXXXX	XXXX0	XXXXX	XXX1X	1XXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	X0XXX	XX
73	XXXXX	XXXXX	XXXXX	XXX0X	XXXXX	1XXXX	XXXXX	XXXXX	XXXXX	XXXX0	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XX
74	13333	33333	33323	01333	33311	30233	33332	33313	33333	30333	33333	33333	23233	33113	33333	33
75	0XXXX	XXXXX	XXX0X	X0XXX	XXX10	XX0XX	XXXX0	XXX0X	XXXXX	XXXXX	XXXXX	XXXXX	0X1XX	XX00X	XXXXX	XX
76	X1111	01100	011X0	XX011	010XX	1XX10	1000X	000X0	10000	1X001	10100	00001	X0X11	10XX0	11001	00
77	X0110	X10XX	X00XX	XXX11	X1XXX	1XX1X	1XXXX	XXXXX	0XXXX	0XXX1	0X0XX	XXXX0	XXX10	1XXXX	11XX1	XX
78	XX0XX	XXXXX	XXXXX	XXXXX	X1XXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXX0X	XXXXX	XXXX0	XX
79	XX11X	X0XXX	XXXXX	XX00	X1XXX	0XX0X	0XXXX	XXXXX	XXXXX	XXXX0	XXXXX	XXXXX	XXX1X	1XXXX	00XX1	XX
80	XX02X	X2XXX	XXXXX	XXX10	X0XXX	1XX0X	0XXXX	XXXXX	XXXXX	XXXX1	XXXXX	XXXXX	XXX0X	1XXXX	20XX0	XX
81	X1XX1	XX0XX	X10XX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	1XXXX	1XXXX	0X1XX	XXXX0	XXXX0	XXXXX	XXXXX	XX
82	X0XX1	XXXXX	X0XXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	1XXXX	1XXXX	X0XXX	XXXXX	XXXXX	XXXXX	XXXXX	XX
83	XXXXX	XX2XX	XX0XX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	3XXXX	XXXX0	XXXX1	XXXXX	XXXXX	XX
84	X2222	XXXXX	X2XXX	XX2XX	X20XX	XXXX0	XXXX0	0XXXX	2X0XX	2XX0X	XX2X0	00XXX	XXX20	10XXX	XXXX2	0X
85	00330	00000	00000	00056	00000	50040	50000	00100	00000	01304	00000	00000	00020	00002	04003	00
86	XXXXX	XXXXX	XXXXX	XXXXX	X0XXX	XXXX2	XXXXX	1XXXX	XXXXX	XXX1X	XXXX1	X2XXX	XXXXX	X3XXX	XXXXX	XX
87	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	1XXXX	XXXXX	XXX0X	XXX1	XXXXX	XXXXX	XXXXX	XXXXX	XX
88	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	0XXXX	XXXXX	XXXXX	XXXX1	XXXXX	XXXXX	XXXXX	XXXXX	XX
89	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXX0	XXXXX	XXXXX	XXXXX	XXXXX	XXXX1	X1XXX	XXXXX	XXXXX	XXXXX	XX
90	X0000	XXXXX	X0XXX	XX0XX	XX0XX	XXXXX	XXXX2	XXXXX	0X0XX	0XXXX	XX0XX	0XXXX	XXX02	0XXXX	XXXX0	1X
91	XXXXX	X00XX	XX000	XXX00	XXXX0	0X00X	01X1X	X110X	X1X11	XX110	10X1X	1X000	10XXX	XXXX1	0001X	X1
92	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	X0X0X	X00XX	X0X00	XX01X	0XX0X	0XXXX	0XXXX	XXXX0	XXX0X	X0
93	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXX0	0XXXX	0XXXX	XXXXX	XXXXX	XXXX0	0XXXX	XXXXX	X1XXX	XXXXX	XX
94	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXX1	XXXXX	0XXXX	XXXXX	XXXXX	XXXX1	X1XXX	XXXXX	X0XXX	XXXXX	XX
95	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXX1	XXXXX	XXXXX	XXXXX	XXXXX	XXXX0	X1XXX	XXXXX	XXXXX	XXXXX	XX
96	XXXXX	XXXXX	XXXXX	X0XXX	XXXXX	XXXXX	XXXXX	XXXXX	XXX1X	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	X1
97	10000	XXXXX	X0XXX	110XX	X001X	X1XXX	XXX01	XXXXX	0X01X	01XXX	X0XXX	X0XXX	XX101	0X11X	XXXX0	10
98	0XXXX	XXXXX	XXXXX	00XXX	XXX0X	X0XXX	XXX10	XXXXX	XXX0X	X0XXX	XXXXX	XXXXX	XX0XX	XX00X	XXXXX	X1
99	XX000	XXXXX	X0XXX	XX0XX	X00XX	XXXXX	XXXXX	XXXXX	0X0XX	0XXXX	XX0XX	1XXXX	XXX0X	0XXXX	XXXX0	XX
100	00000	00000	00000	00000	00000	00000	00000	00000	01000	00000	10000	00000	10000	00000	00000	00
101	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	X0XXX	XXXXX	1XXXX	XXXXX	2XXXX	XXXXX	XXXXX	XX
102	X000X	00000	00000	0X0XX	00X0X	X00X0	X0000	00010	00000	00X0X	20000	00000	X0000	001XX	0X000	00
103	XXXXX	00000	0X000	XXX00	0XXX0	0X000	0XXXX	00000	X0X00	XX000	10X00	10X00	X0XXX	X0XX0	0000X	X0
104	X0000	00000	00000	XX000	000X0	0X001	00010	00000	01000	0X000	10000	01000	10000	00XX0	00000	01
105	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXX1	XX0X	XXXXX	X0XXX	XXXXX	0XXXX	X1XXX	XXXXX	XXXXX	XXXXX	X0
106	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	XXXX0	XXXXX	XXXXX	XXXXX	XXXXX	XXXXX	X1XXX	XXXXX	XXXXX	XXXXX	XX

greatly differing time periods. There are also four lineages that underwent evolutionary change before becoming extinct. The extinct terminal species of these fossil lines are shown as large hollow circles. I have indicated the amount of evolutionary change (path length of the internode) based on 85 characters by the length of the thickened bars along the slanted lines. Note that path lengths for lines leading to fossils are based on only 85 characters to make them comparable to path lengths of Recent forms. Path lengths based on all 106 characters will be illustrated in paper III of this series.

MEASURES OF PHENETIC AND
EVOLUTIONARY CHANGE

To describe evolutionary changes in this and succeeding papers, various statistics based on the characters and the true clado-gram are needed. They are summarized in Table 2. Some terms need to be defined. An entire taxon consists of t OTUs and is described by n characters. OTUs are labelled as $1, \ldots, j, k, \ldots, t$ and characters as $1, \ldots, h, i, \ldots, n$. The most recent common ancestor of all of the OTUs is o. $\sum_j$ is summation over all OTUs indexed by j, usually t OTUs.
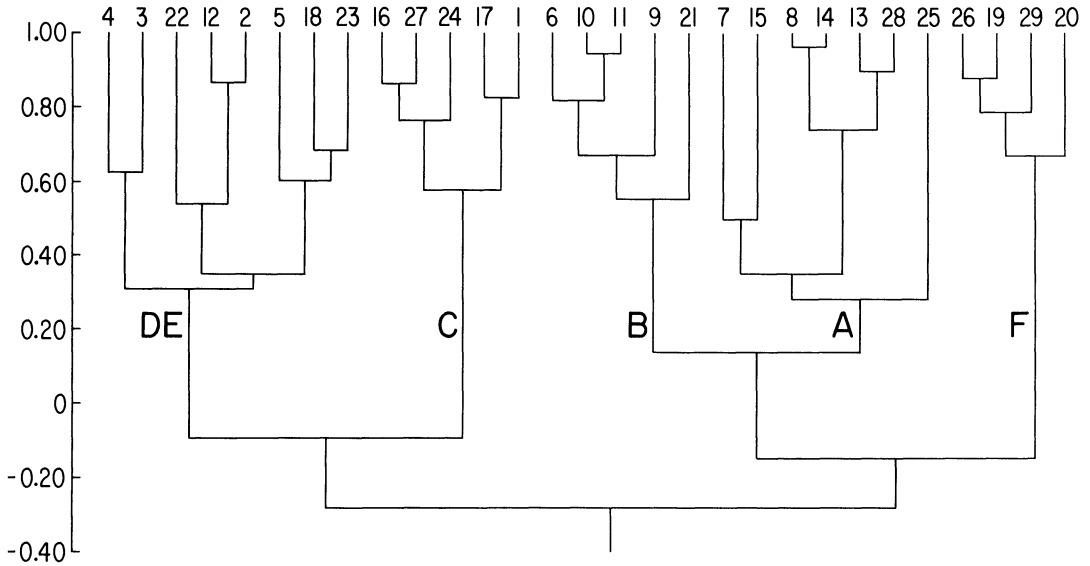
FIG. 3. Standard phenogram of the 29 Recent Caminalcules based on the updated data set of this study. It is based on the data matrix with integer codes substituted for the measurements and was obtained by standardization of characters followed by computation of product-moment correlation coefficients and UPGMA clustering. The ordinate is in correlation coefficient scale. The phenetic genera are labeled with capital letters.

Let us assume that we know the true cladogram of the taxon, as is the case in the Caminalcules. The nodes of the tree will be the Recent OTUs and their ancestors, and the internodes will be the lines of descent connecting these taxa. Throughout I shall assume that evolutionary (character state) change occurs only along internodes. Let l_{jo} be the sum of the lengths in character state changes over all internodes along the directed path from OTU j to o, the most recent common ancestor (root) of the taxon, summed over all characters. Quantity l_{jo} has been called the patristic length of OTU j by Farris (1969) and others. I shall refer to it by the neutral term "path length," since it measures homoplastic as well as patristic resemblance (Sneath and Sokal, 1973). Next, let us define $L_{max(u)} = \sum_j l_{jo}$ as the sum of such lengths over all t OTUs. The quantity $L_{max(u)}$ is the maximal length which the true cladogram could assume if it were rearranged so that every OTU evolves singly and independently from the ancestor o, with the OTUs diverging from that ancestor in bushlike fashion and repeating separately for each OTU the changes in character states that actually occurred along the common evolutionary stems in the true cladogram. Thus $L_{max(u)}$ is a measure which indicates the upper possible bound of parallelism and reversals

$\longrightarrow$

FIG. 4. True cladogram of the Caminalcules as furnished by J. H. Camin. Morphological change occurred during 19 time periods from time 1 to time 20 along the ordinate. Vertical lines indicate periods without morphological change, slanted lines indicate such change. The amount of evolutionary change (path length of the internode) based on 85 characters is shown by the length of the thickened bars along the slanted lines. To furnish an indication of scale, the length of the internode subtending OTU 54 is one Manhattan distance unit, that subtending OTU 76 is 10 such units. Path lengths based on 106 characters, necessary for differentiating fossil species, are shown in a subsequent publication (Sokal 1983b: fig. 2). Squares identify Recent
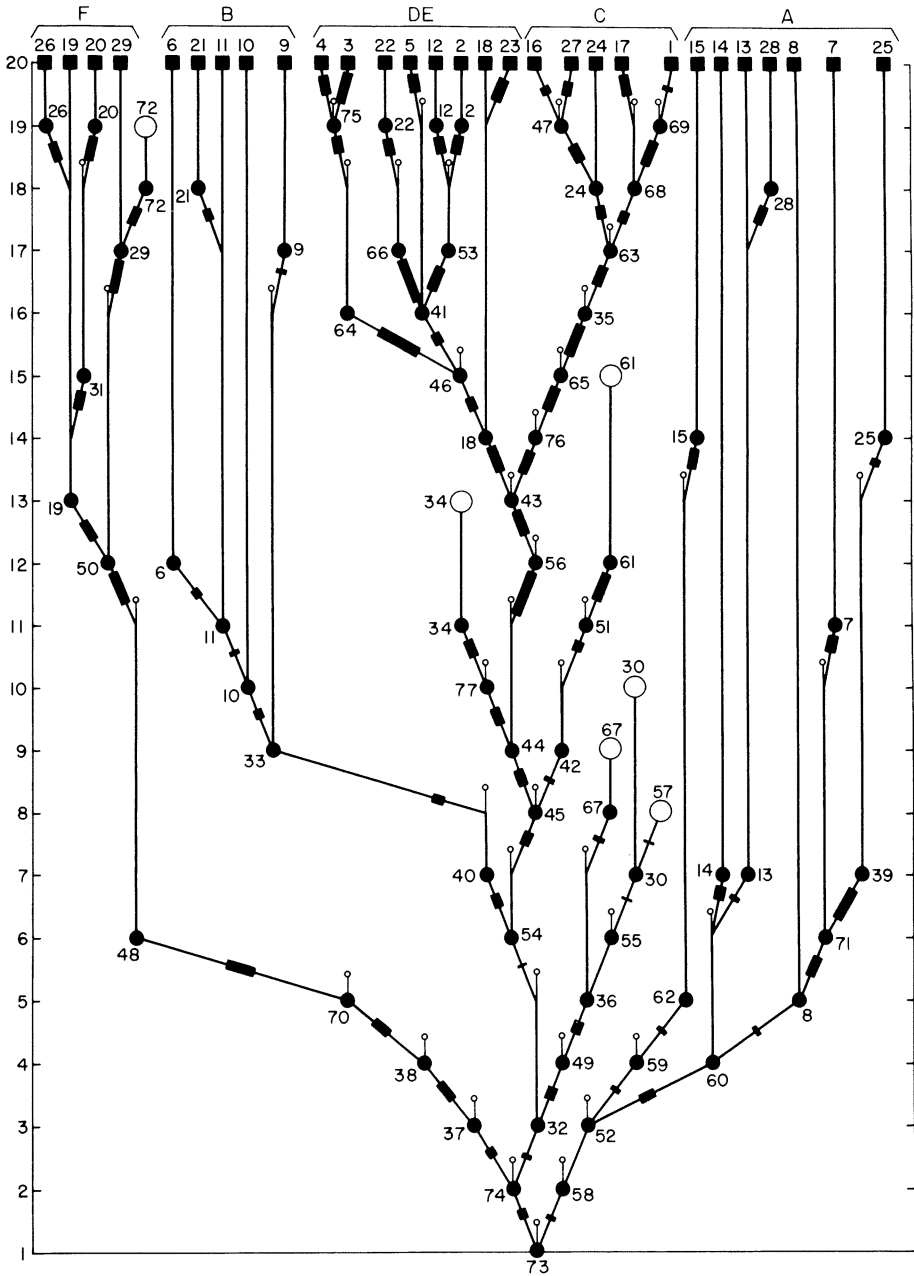
species, black circles fossil species. However, note that some fossil species extend into the Recent (e.g., species 8). Hollow circles indicate extinct species. Large hollow circles terminate extinct lineages whereas the tiny ones symbolize extinct species whose lineages continue with evolutionary change. The numbers next to squares and circles identify the species. Recent species have been given the numbers 1 through 29 familiar from the literature. Fossil species were assigned numbers 30 through 77 at random. Note that, although Camin indicated evolution between species 58 and 52, my coding shows no morphological change between these two forms. The internode between species 36 and 55 appears to be a similar case, but it exhibits morphological change for characters numbered 86–106. The phenetic genera of the Caminalcules are identified by brackets across the top of the tree.

TABLE 2.   Summary of formulas of phenetic and evolutionary change.[a]

l_{jo} = Sum of lengths in character state changes over all internodes along the directed path from OTU j to most recent common ancestor o

$L_{max(u)} = \sum_j l_{jo}$ where $\sum_j$ is summation over all OTUs

$MD_{jo} = \sum_i |X_{ij} - X_{io}|$ where $\sum_i$ is summation over all characters and X_{ij} is the character state for character i and OTU j. OTU o is the most recent common ancestor

$L_{max(l)} = \sum_j MD_{jo}$

$R_1 = L_{max(u)}/L_{max(l)}$

$r_{i(t,o)}$ = Range in character states of character i for the assemblage of t OTUs *plus* the most recent common ancestor o

$L_{min(l)} = \sum_i r_{i(t,o)}$

$L_{min(u)}$ = Minimum length for the taxon, given any tree structure originating from the common ancestor o, and an evolutionary model for allowable types of character state changes

L_{act} = Sum of path lengths over all internodes, given knowledge of the true cladogram

L_{est} = Sum of path lengths over all internodes of an estimated cladogram

$DI = (L_{max(u)} - L_{act})/(L_{max(u)} - L_{min(l)})$ (Dendritic index)

$H = L_{act}/L_{min(l)}$

$H^* = L_{est}/L_{min(l)}^* = 1/C$, where C is the consistency index of Kluge and Farris (1969)

$DR = \sum_{jk} (l_{jk} - MD_{jk})/\sum_{jk} MD_{jk}$, where $\sum_{jk}$ is summation of all OTU pairs except for pairs jj and kk (deviation ratio of J. S. Farris)

$L_{br,avg} = L_{act,M}/(2t_M - 2)$, where the subscript M refers to the subtaxon M

$P_{brl} = L_{br,avg}/(l_{pp'} + L_{br,avg})$, where p is the most recent common ancestor of subtaxon M and p' is the most recent common ancestor of that subtaxon that is also an ancestor of a Recent nonmember of M

[a] Presented in order of appearance in text. Quantities with asterisks are based on estimated rather than true cladograms.

in the data, given the distribution of character states over Recent OTUs and the character states of the fossil OTUs.

A generally shorter length for each OTU j results if one computes

$$MD_{jo} = \sum_i |X_{ij} - X_{io}|, \qquad (1)$$

where X_{ij} is the character state of OTU j for character i and $\sum_i$ is summation over the n characters. Note that MD_{jo} is the Manhattan distance between OTU j and ancestor o. It is the minimum possible evolutionary length for each OTU j from the ancestor o. We can assemble these lengths to form a new upper bound length of the entire tree $L_{max(l)} = \sum_j MD_{jo}$ given a minimal length bush from the ancestor. Note that since $MD_{jo} \leq l_{jo}$, $L_{max(l)} \leq L_{max(u)}$. For any OTU j other than the ancestor o the ratio $R_{jo} = l_{jo}/MD_{jo} > 1.0$ is a measure

of the ratio of unnecessary changes (reversals and repeated forward changes) among the evolutionary steps for that OTU. Consequently,

$$R_1 = L_{max(u)}/L_{max(l)} \geq 1.0 \qquad (2)$$

is a measure of the amount of reversals and repeats in character state changes for the entire taxon considered as a bush. Note that reversals near the base will be repeated in various OTUs and, hence, weighted more heavily.

Two measures of minimum length of the tree were considered. Define $L_{min(l)} = \sum_i r_{i(t,o)}$,

where $r_{i(t,o)}$ stands for the range in character states of character i for the assemblage of the t OTUs in the taxon *plus* its most recent common ancestor o. Length $L_{min(l)}$ is the minimum amount of evolution necessary for producing the taxonomic diversity of the t OTUs in the taxon. It is a theoretical quantity, rare-
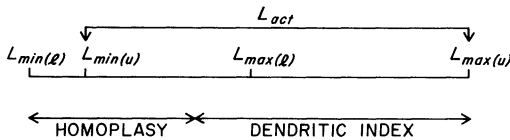
FIG. 5. Schematic to show the relations among the measures of phenetic and evolutionary change discussed in the text. Note that the various statistics have been placed along a line representing the range of possible lengths of an evolutionary tree in positions that they might assume in a "typical" tree. In any actual case, the length of any segments of this line may differ from that shown in the figure and may indeed be zero. The double-arrowed bracket above the line indicates that L_{act} may vary between $L_{min(u)}$ and $L_{max(u)}$ and is undefined with respect to its position vis-à-vis $L_{max(l)}$. The double headed arrows at the bottom of the figure indicate the proportions of the length due to homoplasy and to its dendritic structure. The location of the boundary between these two (the opposed arrowheads) is at the value for L_{act}.

ly, if ever, obtained in real data because of the actual distribution of character states over the OTUs. For $L_{min(l)}$ to be realized, there would have to exist a cladogram for the taxon for which all characters would have to be compatible. In such a case there could be no reversals or parallelisms. Since this is a hypothetical, largely unattainable minimum length, a second minimum length $L_{min(u)}$ needs to be defined as the minimum length for the taxon with t OTUs, given any tree structure originating from the common ancestor o and an evolutionary model for the allowable types of character state changes. Necessarily $L_{min(u)} \geq L_{min(l)}$ since some homoplasy is usually present.

Given knowledge of the true cladogram, the actual length of the tree, L_{act}, is the sum of the lengths over all the internodes. Thus it represents all the evolutionary changes over all characters that have taken place on this tree. Clearly, $L_{min(u)} \leq L_{act} \leq L_{max(u)}$ but L_{act} could be greater or smaller than $L_{max(l)}$. The relations among the various quantities are illustrated in Figure 5.

Quantities L_{act} and $L_{max(u)}$ are computable only in those extremely rare cases, such as the present one, in which the true evolutionary sequence is known; quantities $L_{min(l)}$ and $L_{max(l)}$ require at least knowledge of the most recent common ancestor o. Quantity $L_{min(u)}$, even with knowledge of the common

ancestor, can be computed only by enumeration, which is practical for small numbers of OTUs only. For most real data sets, information is available only for Recent OTUs. In such cases an estimated cladogram is produced by a numerical cladistic algorithm using an outgroup OTU believed to be close to the most recent common ancestor or a vector of character states believed to be primitive. As a result of the cladistic estimation process, the HTU ultimately specified as the most recent common ancestor of the group may be different from the outgroup first furnished. In these cases, the statistics $L_{max(l)}$, $L_{max(u)}$, $L_{min(l)}$, and $L_{min(u)}$ must be defined with respect to the estimated cladogram and the HTU representing the hypothesized most recent common ancestor. To distinguish these statistics based on estimated rather than true cladograms, I have added asterisks to their symbol. The equivalent of the quantity L_{act} for the estimated cladogram obtained by a numerical cladistic procedure such as a Wagner tree algorithm is the length L_{est}. For any given data set and evolutionary model, given a specified root o, $L_{est} \geq L_{min(u)}^*$. This estimate by various computational algorithms will frequently not produce the minimum length $L_{min(u)}^*$. Note that L_{est} can be less than or greater than L_{act}.

These quantities permit computation of the following statistics. The saving in evolutionary length by the known tree structure can be defined as $L_{max(u)} - L_{act}$. Reversals and parallelisms are in both coefficients but they are more numerous in $L_{max(u)}$ since this is a bush-like structure repeating the path length of common shared stems separately for each OTU. A dendritic index can be defined

$$DI = (L_{max(u)} - L_{act})/(L_{max(u)} - L_{min(l)}), \quad (3)$$

which expresses the savings in length due to the tree's dendritic structure departing from that of a bush as a proportion of the tree's maximum possible range in length. If $DI = 0$, then the taxon is a bush and there is no common evolution. If $DI = 1$, then the character states are fully compatible on the cladogram and there are no parallelisms or reversals. Because basal internodes are more often involved in determining l_{jo} than are internodes near the tips of the tree, DI is

more heavily affected by savings in length in the dendritic structure near the base. For data sets with unknown cladogenies one can define

$$DI^* = (L_{max(u)}^* - L_{est})/(L_{max(u)}^* - L_{min(l)}^*). \quad (4)$$

A second quantity, $L_{act} - L_{min(l)}$ describes the excess in evolutionary length over the absolute hypothetical minimum. It may be useful to partition this excess into two parts as follows:

$$L_{act} - L_{min(l)} = (L_{min(u)} - L_{min(l)}) + (L_{act} - L_{min(u)}). \quad (5)$$

The first quantifies the necessary parallelisms to allow for the departure from a fully compatible distribution of character states over OTUs and the second term describes the extra parallelisms and reversals that occurred in the actual evolutionary history of the group over the minimum amount necessary to account for the observed distribution of character states over OTUs. Biologically speaking, however, the two terms may be difficult to distinguish since both describe departures from perfect consistency of character states with the cladogeny. Clearly, $L_{act} - L_{min(l)}$ is a measure of homoplasy as it is conventionally understood and when expressed as a proportion of the maximum possible range of length of the tree $L_{max(u)} - L_{min(l)}$ is simply $1 - DI$ (see Fig. 5).

An alternative statistic, adopted in this paper, is

$$H = L_{act}/L_{min(l)}, \quad (6)$$

which expresses the homoplasy as a ratio, necessarily greater than 1. The amount by which H is greater than unity is the extra length of the actual tree, expressed as a proportion of the minimum tree length necessary for evolution of the character states. For data sets with unknown cladogenies

$$H^* = L_{est}/L_{min(l)}^*. \quad (7)$$

Note that $H^* = 1/C$ where C is the consistency index of Kluge and Farris (1969), also employed by Kluge (1976) and Mickevich (1978a).

A third measure of homoplasy is DR, the deviation ratio featured in Farris' WAGNER 78 program, which is the sum of the pair-

wise homoplastic distances divided by the sum of the Manhattan distances among all pairs of OTUs. The pairwise homoplastic distances for OTUs j and k are found as $l_{jk} - MD_{jk}$, whereas the Manhattan distances are MD_{jk}. Therefore,

$$DR = \sum_{jk} (l_{jk} - MD_{jk})/\sum_{jk} MD_{jk}, \quad (8)$$

where $\sum_{jk}$ is summation of all OTU pairs jk except for pairs jj and kk. This ratio is affected more by homoplasy at the base of the tree, even though the denominator also counts basal lengths repeatedly, because any excess length due to homoplasy will be counted more often for basal than for terminal internodes.

A second measure of character reversal R_2 is analogous to the DR ratio. It is defined as the sum of the pairwise distances due to reversals and nonparallel repeated forward changes divided by the sum of the homoplastic distances among all pairs of OTUs, which is the numerator of DR. It indicates the proportion of homoplasy due to reversals. Its 1-complement is the proportion due to parallelisms.

In studying subtaxa within a larger taxon, as, for example, the genera in the present study, it is useful to define the above statistics also for subtaxa. In such a case when working with subtaxon M, I employ the most recent common ancestor p_M, or simply p, of that taxon, replacing o by p in the above formulas. Summations over OTUs will then be carried out not over the t OTUs of the entire study, but only over the t_M OTUs of subtaxon M.

It is useful to record the path length of the stem of each of the subtaxa. Following the earlier symbolism, this can be defined as $l_{pp'}$, where p' is the most recent common ancestor that is also an ancestor of a Recent nonmember of subtaxon M. An average branch length $L_{br,avg}$ of the internodes subtended by the most recent common ancestor p is also useful. It can be computed by dividing $L_{act,M}$, the observed length of the tree representing the subtaxon, by $2t_M - 2$, the number of its internodes. Comparing $l_{pp'}$ with $L_{br,avg}$ contrasts the evolution on the stem preceding

the most recent common ancestor of the genus with the subsequent evolution within the genus. The average branch length can be expressed as a branch length proportion,

$$P_{brl} = L_{br,avg}/(l_{pp'} + L_{br,avg}). \qquad (9)$$

An additional complication arises whenever NCs are present as in this study. I have adopted two conventions, which are modifications of the Manhattan distance. In "transparent" measure the NC state is thought of as an unknown. For computation of distances between terminal OTUs, character states for OTU pairs, one or both of which had NCs for a given character, were ignored during the computation of the distance and NCs were passed over during computation of path lengths. Thus a $0 \rightarrow NC \rightarrow 3 \rightarrow 4$ path is four units long. In "opaque" measure NCs are considered a distinct character state and changes along the tree from an expressed character state to an unexpressed one (NC) are considered a single step. Successive NC states count as zero steps and a change from an NC to an expressed state is again a single step, regardless of the magnitude of the expressed character state. Thus the path $0 \rightarrow NC \rightarrow 3 \rightarrow 4$ is of length 3. Computing distances between terminal OTUs, the difference between two NCs was considered to be zero, that between any numerical state and an NC was considered to be one. Opaque distance was employed mainly because it made it simple to express path length for any internode along the tree and to partition the path length into homoplastic and reversal distances as needed in the next section of this paper. In transparent measure it is not always possible to uniquely estimate path length for each internode.

RELEVANCE OF CAMINALCULES FOR
SYSTEMATIC INQUIRY

It is of interest to examine in how many ways the Caminalcules resemble data sets on real organisms, since this will strengthen the relevance of results obtained from them for systematic inquiry. Below I inspect as many separate aspects of the Caminalcules as seem to me relevant to systematic methods and principles. I also examine three of these aspects in 19 zoological data sets, ranging from 8 to 97 OTUs and based on from 20 to 139 characters lacking NCs. None of these data sets was subjected to the exhaustive analysis to which the Caminalcules were treated (recounted in subsequent papers of this series) for the obvious reasons that such a project would have taken several additional years, that finding outgroups for them would have taken much specialized knowledge, and that the true cladogenies of the data are of course unknown. As will be seen below, the results for almost all parameters bracket those obtained for the Caminalcules. It is not expected that the differences in tree topology that might be accomplished by repeated application of a cladistic algorithm to the same data set in the hope of finding a shorter tree would alter these relations with respect to homoplasy and other measures. I have summarized my conclusions in Table 3 for homoplasy, tree symmetry and adequacy of characters.

Homoplasy.—Three indices of homoplasy have been mentioned earlier and in the literature. These are the 1-complement of the dendritic index $(1 - DI)$, the homoplasy ratio H, which is the reciprocal of C, the consistency index of Kluge and Farris (1969), and Farris' deviation ratio DR. In the Caminalcules, two values can be obtained for each of these indices. One is based on the true cladogram and should be the correct measure of homoplasy in the group for the given index; the other, comparable to those furnished in the literature on real organisms, is based on the estimated cladogram. As an estimate I employed the approximate Wagner tree obtained with the WAGNER 78 program developed by J. S. Farris, using the distance Wagner procedure and midpoint rooting. Opaque distances were analyzed to permit computation of all homoplasy statistics. However, for the two statistics that can be computed in transparent measure (H and DR), these values are reported as well. Statistics based on estimated cladograms are distinguished by affixing an asterisk to their symbols. Approximate Wagner trees were computed for the 19 data sets, again using the WAGNER 78 program and rooted by the midpoint method. Because these data sets lack

TABLE 3. Minima and maxima of tree statistics for 19 zoological data sets and the Caminalcules.[a]

Tree statistics	Low value	Caminalcules		High value
		Estimated	True	
Homoplasy				
$1 - DI^*$	0.0559[b]	0.1326	0.1745	0.4646[c]
H^*	1.160[b]	1.417	2.327	6.690[d]
C	0.1495[d]	0.7057	0.4298	0.8621[b]
DR^*	0.1124[b]	0.1795	1.3591	1.7395[d]
Symmetry				
BSUM2	0.2597[d]	0.4900	0.3779	0.7714[e]
BSUM3	−0.0976[f]	0.2420	0.0753	0.3462[g]
SHAO2	0.4483[h]	0.6186	0.7720	0.8021[c]
SHAO3	0.3421[h]	0.5225	0.7146	0.6840[c]
COLLESS2	0.1061[f]	0.3331	0.1693	0.4889[g]
Adequacy				
n/t	1.16[h]	2.93	2.93[i]	6.62[j]

[a] High and low values refer to numerical values, not necessarily to the property described. Thus, high values of C indicate low homoplasy, and high values of BSUM2, BSUM3, and COLLESS2 indicate low symmetry (high asymmetry). The values shown are based on means of three runs of the WAGNER 78 program with midpoint rooting for the symmetry measures, and on single estimates for the other measures. Other cladistic estimates were run as well; for details see text. The results conform to those shown in this table. The data sets exhibiting extreme values are identified in footnotes. For explanations of tree statistics see text.
[b] Leptopodomorpha (Schuh and Polhemus, 1980).
[c] Orthopteroid insects (Blackith and Blackith, 1968).
[d] *Hoplitis* complex (Michener and Sokal, 1957).
[e] Western *Bufo* (Feder, 1979).
[f] *Drosophila* (real set; Throckmorton, 1968).
[g] Hemoglobin β (Dayhoff, 1969).
[h] Dasyuridae (Archer, 1976).
[i] Is 5.34 if binary coded data are considered.
[j] Pygopodidae (binary coding; Kluge, 1976).

NCs, the distinction between opaque and transparent measure does not apply to them. As an experiment, I also tried trees with an outgroup rooting using OTU 1 as the outgroup (clearly not a recommended procedure, although it has been used by some numerical cladists; e.g., Mickevich, 1978b; Farris, 1979a). Only midpoint rooting is reported in Table 3. Results for the OTU 1 rooting procedure were similar.

It is worth emphasizing again that, both for the Caminalcules and the 19 real data sets, the above method provides only approximate Wagner trees. Better estimates could have been obtained with further work and were indeed obtained for the Caminalcules (see Sokal, 1983a). I am employing the "cruder" estimate for the Caminalcules, since it is comparable to the estimates in the 19 data sets. Presumably homoplasy would decrease if the length of the trees could be shortened algorithmically. But, on the average, this would occur proportionately for all data sets and, since the Caminalcules are cur-

rently bracketed by the data sets on real organisms, they presumably would still be so bracketed after the length of all trees had been reduced.

In the Caminalcules $1 - DI = 0.1745$ and $1 - DI^* = 0.1326$. In the 19 data sets $1 - DI^*$ ranges from 0.0559 in the Leptopodomorpha (Schuh and Polhemus, 1980) to 0.4646 in 12 orthopteroid insects (Blackith and Blackith, 1968). Because the true trees for these real organisms are not known, the proper comparison with the Caminalcules is with $1 - DI^*$ from the approximate Wagner estimate.

For the true cladogram $H = 2.327$, and for the Wagner estimate $H^* = 1.417$ and 1.261 for opaque and transparent estimates, respectively, yielding corresponding consistency indices of 0.4298, 0.7057, and 0.8048. Mickevich (1978a) reported a range of consistency indices from 0.33 for *Aedes* and papilionids to 0.86 for cytochrome C and globin. In the 19 data sets, H^* ranges from 1.160 in the Leptopodomorpha to 6.690 in bees of the *Hoplitis* complex (Michener and Sokal, 1957),

corresponding to consistency indices of 0.8621 and 0.1495, respectively.

The deviation ratio (DR) for the true cladogram is 1.3591, a very high value, but DR^* is 0.1795 and 0.3852 for opaque and transparent Wagner estimates, respectively. This great discrepancy can be accounted for by the numerous reversals in the true cladogram, especially along the stems defining the genera. Remember that the estimate optimizes the position of the HTUs and, in consequence, attempts to minimize homoplasy. The formula for computing the deviation ratio involves all pairwise distances between OTUs and, therefore, repeatedly counts these basal relations. Actually the parallelism component of the homoplasy is relatively low in the Caminalcules. For the lower triangular matrix in opaque measure, the sum of the homoplastic distances is 21,225, of which 17,093 is due to reversals and 4,132 is due to parallelisms. The Wagner tree algorithm in trying to obtain a shortest length tree cancels many of the reversals, so that the deviation ratio actually observed is relatively low, 0.1795, whereas the deviation ratio of the true cladogram is much higher. The range of observed values of DR^* in the 19 data sets is from 0.1124 in the Leptopodomorpha to 1.7395 in the *Hoplitis* complex. If reversals are as common in real organisms as in the Caminalcules and if we knew their true cladograms, real organisms might well exhibit generally higher deviation ratios. Real and apparent homoplasy in the Caminalcules is well within the reported range for real organisms.

Symmetry.—The true cladogram of the Caminalcules is fairly symmetrical. No universally accepted criterion of symmetry has yet been established, but K. T. Shao (pers. comm.), who is investigating this problem, has used five separate indices to describe different aspects of symmetry. These are BSUM2 and BSUM3 (modified from Sackin, 1972), SHAO2 and SHAO3 (Shao, pers. comm.), and COLLESS2 (Colless, 1982). These coefficients were computed for the true cladogram of the Caminalcules as well as for several estimated cladograms of the Caminalcules. The estimated cladograms include one obtained by means of Joseph Felsenstein's PHYLIP

WAGNER program, rooted at the true ancestor, and an estimated Wagner tree obtained with the WAGNER 78 program with midpoint rooting. The latter was replicated three times with randomly permuted input orders of OTUs.

These same statistics were also calculated for similarly estimated cladograms (except for the impossible true ancestor rooting) for the 19 data sets. Again, rooting using OTU 1 was employed additionally on an experimental basis for trees obtained by both programs. Not all data sets were suitable for each estimation method and statistic, but no reported range of values is based on fewer than 14 data sets. In Table 3 results are reported only for estimated cladograms based on the WAGNER 78 program and midpoint rooting, but below the other results are summarized as well. For WAGNER 78 with midpoint rooting, the true cladogram is contained within the range of observed symmetries for all coefficients except SHAO3. But the true cladogram shows more symmetry than the observed range of symmetry values for estimated cladograms based on the PHYLIP WAGNER program and on WAGNER 78 with OTU 1 as an outgroup. Yet, when estimated cladograms are computed for the Caminalcules, these are almost always less symmetrical than the true cladogram. In Table 3 for midpoint rooted Wagner trees the symmetries of estimated cladograms of the Caminalcules are contained within the range of observed values and, when other estimated cladograms are considered as well, this relation holds in 17 out of 20 comparisons. Since the other 19 classifications are all based on estimated cladograms, it is the estimated cladograms of the Caminalcules that must be compared with these data sets rather than the true cladogram. Thus on this basis, also, it appears that the Caminalcules are not atypical.

Adequacy of the characters for resolving the cladogram.—The 29 Recent OTUs in a fully bifurcating tree would derive from 27 bifurcations, not counting the basal bifurcation at the root. Since one of the branching points in the true cladogram is a trifurcation, 26 synapomorphies are minimally needed to resolve the tree. How can we measure the

adequacy of the data set for this task? At the simplest level, one can count characters. Fewer than 26 binary characters cannot resolve the tree. Subjected to additive binary coding, the 85×29 data yield 155 binary characters—superficially a more than adequate number. However, such an approach is too crude since it does not allow for character correlations. In fact, we know that in addition to the single trifurcation, three bifurcations in the true cladogram (19-26, 11-21, 18-23) are not supported by any evident evolutionary change in the stems subtending them. Thus, even though there are more than five times as many binary characters in this data set than are necessary to define the tree, they are distributed across the tree in such a way as to make it impossible to define more than 23 branching points. Most numerical cladistic studies are carried out on far fewer characters and because the true cladograms of real organisms are unknown, it is generally not known whether the data matrix is adequate for resolving the true tree. In the 19 data sets the ratio n/t, where n is the number of characters and t the number of OTUs, ranges from 1.16 in *Dasyurus* (Archer, 1976) to 6.62 for binary coded members of the Pygopodidae (Kluge, 1976). These figures compare with 2.93 and 5.34 for multistate and binary coded Caminalcules, respectively (see Table 3). Since the values for the 19 data sets reflect differences in character coding, they must be interpreted with caution. Nevertheless, it is clear that the Caminalcules fall well within the bounds of data from the literature.

One can examine the true cladogram to determine the number of OTUs subtended by any given furcation. It ranges from 2 to 22 OTUs. These figures should minimally be matched by the numbers of OTUs (greater than one) sharing any one character state to provide synapomorphies for the recognition of these furcations. When the required distribution of OTU numbers is compared to the actual distributions of such numbers, one finds at least as many observed frequencies as are required. However, this is insufficient evidence for the adequacy of a data set because we already know that three bifurcations in the Caminalcules are not resolved in

terms of the characters available, in addition to the known trifurcation—which goes counter to the assumptions of most cladistic methods. Correlated characters undoubtedly define furcations redundantly, and parallelism allows a single character to define furcations in different parts of the tree. Unfortunately, knowledge of this type is virtually impossible to obtain from real data sets, because the true cladograms are unknown. Using estimated cladograms for such inferences would tend to make the argument circular. In any case, it appears that the Caminalcules are unlikely to be less capable of having their cladogram resolved than most data sets in systematics.

Because of the incompleteness of the fossil record, less is known from real organisms of the following three aspects. However, it may be of some interest to treat these topics at least briefly in an effort to describe where the Caminalcules are located with respect to evolutionary parameters—evolutionary rates, species longevities, and speciation-extinction rates—that might be employed in simulation studies. It will be seen that the Caminalcules are not in contradiction with such findings as are reported in the paleobiological literature.

Evolutionary rates.—A frequency distribution of the path lengths (amount of evolutionary change) of each internode for each time period shows extreme clumping. When examined against Poisson expectations (Fig. 6), the overdispersion is highly significant ($P < 0.001$). Thus, there are many more periods of no evolution as well as more periods with substantial amounts of evolution than expected. Two explanations can be advanced for this phenomenon. (1) The Caminalcules are similar to real organisms in that their evolution is of organic form as a whole rather than independent for each character. Changes in form in the Caminalcules involve various correlated characters and thus those segments of the cladogram during which extensive morphological evolution occurred will exhibit greater amounts of change. (2) There also may be local clumping of evolutionary changes on the tree for nonbiological reasons which have an analog in real phylogenetic processes. We must as-
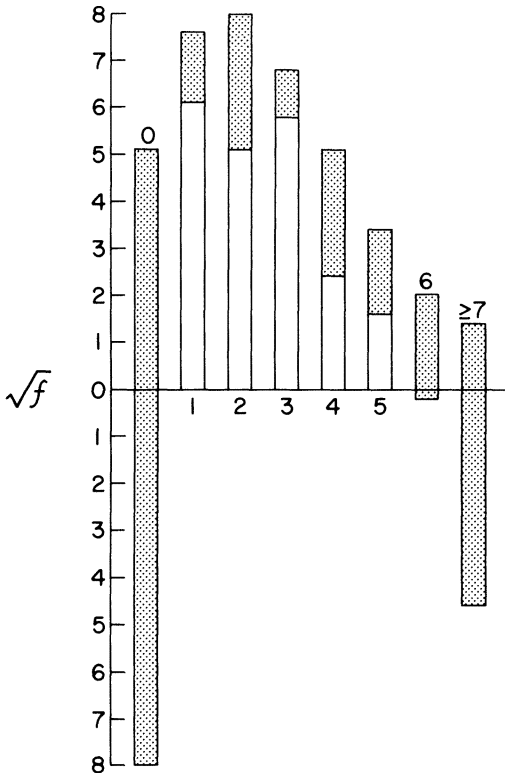
FIG. 6. Observed and expected frequencies of evolutionary rates (path length per evolutionary time period) in the true cladogram of the Caminalcules. These data are based only on those lines leading to Recent OTUs. The bar diagram of the "skyline" (bars above the abscissa) indicates the expected frequencies of a Poisson distribution; the "inverted skyline" (shaded portion of the bars) indicates the observed frequencies. Both frequencies are given in square roots of actual values to emphasize the deviations. Where the inverted skyline does not reach the abscissa, there are fewer observed than expected frequencies. Wherever it reaches below the abscissa, there is an excess of observed frequencies over expected frequencies. The ordinate shows square rooted frequencies, while the abscissa expresses evolutionary rates.

FIG. 7. Average evolutionary rate plotted against time period. The rate is expressed along the ordinate as average path length in the (unit) time interval preceding the point in time shown along the abscissa. The path lengths are computed on the basis of 106 characters. The means of this figure are based on lines leading to Recent OTUs only.

sume that Camin in constructing his tree was at least somewhat goal oriented so that as he evolved any one line he carried it through to some major morphological change rather than abandon the change in midcourse. This process also tends to induce inhomogeneity of rates among the lines which results in clumping of the distribution of evolutionary changes when considered overall. The bio-

logical analog is to assume that major changes in environment or in genetic architecture leading to adaptive radiation are ongoing processes with a momentum of their own. The data in Figure 6 are based on only those lines leading to Recent OTUs. When all internodes including those leading to extinct terminal species are examined, the results are very similar to those already reported and illustrated in Figure 6. Similar data are hard to obtain in real organisms because of the incompleteness of the fossil record, but the observed pattern of evolutionary change is at least biologically plausible.

In Figure 7, I show a graph of the average evolutionary rates over all evolutionary lines for each of the 19 time periods (again, only for lines leading to Recent OTUs; the results including lines leading to extinct species are quite similar). The rates are computed from the 106 character $\times$ 77 OTU data base. There is clear evidence of differential evolutionary rates through time. Between times 7 and 11, rates were generally lower than at other times. By time 7, all genera except for DE and C had already been defined but major within-genus diversity had not yet begun except in genus A. A runs-up-and-down test (Sokal and Rohlf, 1981b), significant at $P <$

0.01, demonstrates the alternating nature of the rate changes. Periods of higher change alternated with periods of lower change more frequently than could be expected by chance alone. Relevant comparisons with real organisms are hard to come by. That evolutionary rates differ over the fossil record has been well established since the work of Simpson (1944, 1949, 1953). Yet, because paleontological series are usually based on few characters and because the fossil lineages are not well known, estimates of evolutionary rates based on multiple characters as in Figure 7 are lacking. For single characters, rates do vary with time within species (Stanley [1979:58ff.] illustrates two examples) as well as within and among genera (Gingerich, 1974, 1979). Clearly, the pattern of evolutionary (phenetic) rates observed in the Caminalcules is not uncharacteristic of observations made on real organisms.

Species longevities.—The known cladogeny of the Caminalcules also permits an examination of the distribution of species longevities. These are shown in Figure 8 separately for the 29 Recent species, as well as for all Recent-and-fossil species in the group. The longevities of Recent species are shown in two different ways. In Figure 8A, I show the actual longevity from the time of origin of each species to the Recent or to the time of extinction. Expressed as a cumulative percentage, it can be read as the percentage of living species that extend backwards by various amounts of evolutionary time. Such curves are generally not used by paleontologists (Stanley, 1979:113), because the incompleteness of the fossil record would make estimates of longevities inaccurate. In the Caminalcules, of course, this graph is fully descriptive and accurate. This curve can be contrasted with that in Figure 8B, a so-called Lyellian curve, which depicts the percentage of Recent species that can be found in faunas of a given age. As expected, with an increase in age of the faunal assembly, the percentage of its species that survive to the Recent decreases. None of the five species extant at time period 4 survived to Recent times, the faunal assembly at time period 5 being the first one to contribute a member species to the Recent faunal assemblage. Although the
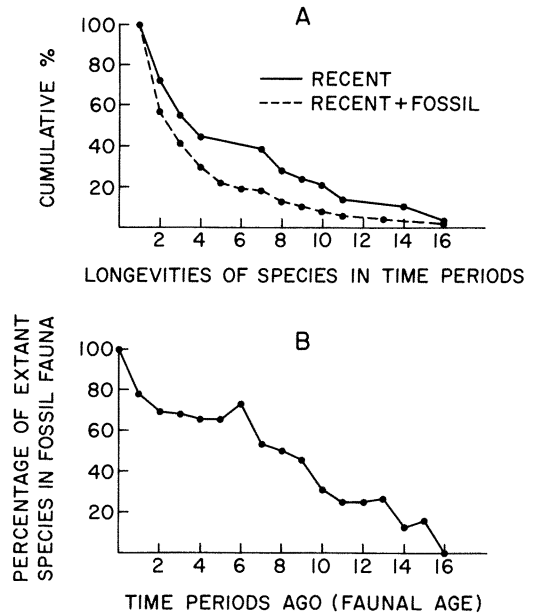

FIG. 8. Species longevities. (A) Longevities of species in given time periods plotted as cumulative percent, i.e., the percentage of living species that extended backwards by various amounts of evolutionary time. Solid line—Recent species only; dashed line—Recent and fossil species. (B) Percentage of Recent species that can be found in faunas of a given age.

total number of species in faunal assemblages was nondecreasing with time, the number of species surviving to the Recent did not increase proportionately. This explains the lack of monotonicity in Figure 8B. Hence, there are time intervals during which the number of species in the faunal assembly increased without a corresponding increase in the number of species surviving to the Recent, producing a lowering of the percentage of extant species in the fossil fauna.

In Figure 8A, the longevity curve for Recent OTUs can be compared with that including both Recent and fossil OTUs. Both curves resemble the hollow curves of similar data from the paleontological literature, with the Recent-and-fossil curve, comprising more data, presenting the smoother appearance as might be expected. Note that both curves decline to zero at time period 16. No Caminalcule species lived for more than that

amount of time. Corresponding graphs in the paleontological literature generally approach an asymptote at a higher percentage because the faunal assemblies are not traced back a sufficient time for all the Recent species to disappear. The Lyellian curve, Figure 8B, is not atypical with respect to those published in the literature (see figs. 5-8 or 9-3 in Stanley, 1979).

The model under which Professor Camin evolved the Caminalcules requires each species to have a longevity of at least one time period. The observed distribution of longevities is highly clumped ($P < 0.001$ against Poisson expectations); there are many more species than expected becoming extinct after a single time interval and substantial numbers survive for quite long periods of time. The latter phenomenon seems to agree with observations on real organisms. The excess of short-lived species is more difficult to demonstrate in real organisms because there would be an inherent bias against observing these species in fossil assemblages. Moreover, real organisms are not limited to discrete time amounts as were the Caminalcules. That is, species existing for less than one time unit clearly must occur in the fossil record. We may conclude, however, that despite some peculiarities due to their mode of generation, the distribution of longevities in the Caminalcules resembles similar distributions observed in real organisms.

Speciation-extinction ratios.—In the Caminalcules, 56.0% of all evolutionary changes are accompanied by extinction, whereas 54.4% of lines showing no evolutionary change (stasis; vertical lines in Fig. 4) lead to extinctions. Thus there is no preference for one or the other type of process leading to extinction built into the evolutionary tree.

The availability of complete records in the Caminalcules permits computation of the net rate of increase in number of species (R), speciation rate (S) and extinction rate (E) for all time periods. In real data, R and E are usually approximated by various indirect approaches and S is estimated as $S = R + E$. Here these values can be directly computed and they are $R = 0.213$, $S = 0.538$ and $E = 0.324$. Note that if R is estimated using an exponential growth model (Stanley, 1979:

104), the resulting value is 0.177, an underestimate of the true rate. The absolute values of R, S, and E cannot be contrasted with those of real organisms since the time intervals chosen for the Caminalcules are arbitrary But the relative magnitudes of these quantities can be compared. The S/E ratio in the Caminalcules is 1.661. This compares with similar ratios estimated under varying assumptions for Plio-Pleistocene mammals of Europe which range from 1.310 to 2.048, and for temperate and subtropical bivalves of the Pacific which range from 1.667 to 3.333 (Stanley, 1979:117). Both of these groups are considered by Stanley to be undergoing active adaptive radiation into the present. By this criterion, the Caminalcules also do not differ markedly from real organisms.

Conclusions.—By the six criteria examined above, the Caminalcules fall well within the range of observed values for real organisms. At least with respect to these criteria, the Caminalcules simulate real organisms, although, of course, this is not to imply that there may not be other aspects of evolutionary change in real organisms that will be found lacking in the Caminalcules. But by these criteria alone the Caminalcules offer considerable scope for analyses of methods and principles of numerical phenetics and cladistics and of taxonomy in general.

sections on evolutionary rates, species longevities, and speciation-extinction ratios were read by Michael Bell, Lev R. Ginzburg, and Jeffrey S. Levinton at Stony Brook, who provided useful comments. Barbara McKay uncomplainingly wordprocessed innumerable versions of this manuscript. Joyce Schirmer prepared the final illustrations. Last but far from least I must acknowledge my debt to the late Professor Joseph H. Camin, my former colleague at the University of Kansas. Without his fanciful imagination coupled with a thorough understanding of systematics, there would not have been any Caminalcules. The computations were carried out on a UNIVAC computer at the Stony Brook Computer Center and on the MODCOMP minicomputer facility at the Department of Ecology and Evolution. This research was supported by grant DEB 80-03508 from the National Science Foundation, whose continued support of my research is much appreciated.

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APPENDIX

List of Characters for 77 Fossil and Recent Caminalcules[a,b]

Head and neck

1. Head junction complex (folded) (1) or not (0). [73, 39]
    2. If complex, degree of folding complete (1) or partial (0). [73, 10]
        3. If partial, secondary junction narrow (0) or broad (1). [10, 21]
4. P (1) or A (0) of horn. [75, 73]
    5. If horn present, pointed (1) or flattened (0). [75, 64]
6. Length of head in mm from rear end of folded section to front, excluding horn and anterior projections. If head not complex, measure from collar. Recoded as integer in the following manner: (0) 9–10.9; (1) 10.9–12.8; (2) 12.8–14.7; (3) 20.4–22.3; (4) 24.2–26.1; (5) 26.1–28. [73, 65, 60, 28, 25, 39]
7. Anterior end of head concave (0), flat (1) or convex (2). [71, 73, 62]
    8. If convex, rounded (0) or sharply pointed (1). [62, 15]
9. P (1) or A (0) of anterior projections. [71, 73]
10. P (1) or A (0) of eyes. [73, 59]
    11. If present, states of fusion of eyes: (0) two separate eyes; (1) grown together but two eyes still discernible; (2) grown together into oblong approximately the size of two eyes; (3) grown together into circle approximately the size of one eye. [73, 47, 1, 16]
12. P (1) or A (0) of eye stalks. [37, 73]
    13. If stalked, length of stalk (excluding eye) in mm. Recoded as integer in the following manner: (0) 3–4.5; (1) 4.5–5.9; (2) 6–7.5; (3) 10.5–12; (4) 13.5–15; (5) 16.5–18. [37, 38, 70, 48, 72, 19]

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[a] These characters were originally defined by A. J. Boyce and I. Huber and were revised by B. Thomson and R. R. Sokal.

[b] Abbreviations and conventions: P—presence; A—absence. Numbers in parentheses are character state codes. Numbers in square brackets following definition of each character are the OTU numbers of representative OTUs that exhibit the character states *in the order described in the list*. Thus for character 1 [73, 39] means that OTU 73 is an example of a complex (folded) head junction and OTU 39 is an example of a not complex head junction. Whenever an "If" statement is denied, as in character 2 for OTUs whose state for character 1 is 0, an NC is recorded for the OTU for that character. Since all measurement characters were recorded to the nearest mm, there is no ambiguity created by shared, more refined class limits of adjacent classes as listed for some characters (e.g., for character 6, a measurement of 10 mm was coded 0, while one of 11 mm was coded 1).

The character numbers 1–85 employed in this list correspond to those employed in earlier studies and originally defined by Boyce and Huber. Characters numbered 86–106 were needed to describe additional observed differences in fossil species. In order to preserve both the old character numbering system and at the same time the logical order of characters in the list, it became necessary to list some char-

acters out of numerical order. The following paragraph gives the location of all characters that are not in strict numerical order in the list.

Characters 26–28 in this list follow upon character 22; 58 follows 13; 59 follows 56; 60 and 61 follow 48; 62 follows 47; 78 follows 80; 84 follows 90 (23); 85 follows 63; 86–90 follow 23; 91 and 92 follow 34; 93–95 follow 35; 96 follows 45; 97 follows 62 (47); 98 follows 61 (48); 99 follows 55; 100 and 101 follow 85 (63); 102 follows 67; 103 follows 69; and 104–106 follow 75.

The following lists of characters comprise the several body regions: head and neck, 1–17, 58 (total of 18); anterior appendages, 18–30, 84, 86–90 (total of 19); posterior appendages, 31–38, 91–95 (total of 13); collar and abdomen, 39–57, 59–63, 85, 96–101 (total of 31); abdominal pores, 64–83, 102–106 (total of 25). The overall total is 106 characters.

The images shown in Figure 1 (OTUs 1–29) were traced from the originals, whereas those in Figure 2 were traced from xeroxes of the originals. In the process and in the reduction necessary for illustration here some detail visible to the data coders was necessarily lost. The states of at least one character (17) are quite indetectable in the published figures. Lengths in millimeters are given in terms of the dimensions of the original images. As reduced in Figures 1 and 2, these measurements must be multiplied by 0.387.

58. If stalked, stalks fused (1) or not (0). [20, 37]
    14. If stalks not fused, tips divergent (0), parallel (1) or convergent (2). [37, 19, 31]
15. Top of head depressed (0), flat (1) or crested (2). [73, 41, 53]
    16. If crested, single (0) or lobate (1). [53, 2]
17. P (1) of A (0) of groove in neck. [12, 73]

Anterior appendages

18. P (1) or A (0) of anterior appendages. [73, 15]
    19. If appendages present, length in mm from tangent to posterior end of abdomen (excluding posterior appendages) up to the anterior end of the longer appendage. Recoded as integer in the following manner: (0) 40–46.3; (1) 46.3–52.6; (2) 52.6–58.9; (3) 58.9–65.2; (4) 65.2–71.5; (5) 71.5–77.8; (6) 77.8–84.1; (7) 84.1–90.4; (8) 96.7–103. [73, 74, 45, 43, 66, 24, 17, 19, 20]
    20. If appendages present, P (1) or A (0) of flexion (elbow) in appendages. [41, 73]
    21. If appendages present, end of appendage divided (1) or not (0). [56, 73]
        22. If not divided, end of appendage is tendril (0), sharply pointed (1), tapered or rounded (2) or knobbed (3). [21, 68, 73, 45]
        26. If not divided, P (1) or A (0) of flange. [38, 73]
            27. If flange present, length expressed as sum of right and left sides in mm. Recoded as integer in the following manner: (0) 17–20; (1) 23–26; (2) 32–34.9; (3) 35–37.9; (4) 38–41; (5) 44–47. [38, 70, 48, 50, 20, 29]
            28. If flange present, width expressed as sum of right and left sides in mm. Recoded as integer in the following manner: (0) 5–6.9; (1) 10.7–12.6; (2) 14.5–16.4; (3) 16.4–18.3; (4) 18.3–20.2; (5) 20.2–22.1; (6) 22.1–24. [38, 70, 48, 31, 29, 72, 26]
        23. If divided, two divisions (0) or three (1). [22, 56]
            86. If two divisions, ending as fingers (0), clamp (pincers without joint) (1), pincers with joint (2) or two wavy spikes (3). [22, 49, 30, 67]
                87. If ending as clamp, closed (0) or open (1). [49, 36]
                    88. If open, clamp is small (0) or large (1). [36, 55]
                89. If ending as pincers with joint, serrated edges P (1) or A (0). [57, 30]
            90. If three divisions, one "finger" much longer than the other two (2), one finger slightly longer than the other two (1) or all fingers the same size (0). [65, 76, 56]
        84. If divided, bulbs on ends of divisions present on all divisions (2), present on some divisions (1) or absent (0). [18, 66, 56]
            24. If bulbs present on all divisions, P (1) or A (0) of claws. [12, 46]
            25. If bulbs present on all divisions, P (1) or A (0) of pads. [75, 46]
    29. If appendages present, P (1) or A (0) of pigment. [9, 73]
        30. If pigment present, distributed in small dots (−1), small circles (0), large circles (1) or very broad areas (2). [33, 9, 11, 21]

Posterior appendages

31. Appendage single (0), partially double (1) or completely double (2). (Completely double means that appendage originates from 2 stalks rather than 1; it does not necessarily mean that the 2 halves are separated.) [73, 43, 18]
    32. If single, disclike (pedestal like) (0), platelike (1) or propellerlike (2). [73, 40, 36]
        33. If disclike, width of disc in mm. Recoded as integer in the following manner: (0) 5–5.7; (1) 5.7–6.4; (2) 6.4–7.1; (3) 7.8–8.5; (4) 8.5–9.2; (5) 9.9–10.6; (6) 10.6–11.3; (7) 11.3–12. [13, 58, 39, 38, 37, 72, 42, 77]
        34. If disclike, stalk long (>3 mm) (2), short (≤3 mm) (1) or absent (0). [74, 73, 28]
        91. If disclike, round (0) or square (1). [73, 74]
            92. If square, P (1) or A (0) of division lines. [49, 74]
        35. If platelike, no indentation (−1), weakly emarginate (curved indentation) (0), cleft (*V*-indentation) (1), or deeply cleft (*V*-indentation continued into division line) (2). [40, 33, 11, 6]
        93. If propellerlike, blades rounded (0) or pointed (1). [36, 67]
        94. If propellerlike, stalk short (<5 mm) (0) or long (>5 mm) (1). [36, 55]
            95. If stalk long, straight (0) or twisted (1). [55, 30]
    36. If completely double, ends pointed (0), clubbed (1) or platelike (2). [3, 75, 18]
        37. If platelike, divided (1) or not (0). [66, 18]
            38. If divided, two divisions (0) or three (1). [66, 53]

Collar and abdomen

39. Rim of abdomen plain (0), narrowly raised (1) or broadly raised (2). [64, 45, 73]
40. Anterior margin of abdomen well delineated (0) or imperfectly delineated (1). [73, 31]
41. P (1) or A (0) of abdominal ridge (raised area on central posterior abdomen). [73, 45]

42. P (1) or A (0) of large areas of color on anterior abdomen. [56, 73]
   43. If present, whole (2), bisected (1), quadrisected and square (0) or quadrisected and irregularly shaped (−1). [66, 46, 56, 65]
44. P (1) or A (0) of spots on anterior abdomen. [44, 73]
   45. If present, small (0), large (1) or large and cross-shaped (2). [44, 27, 35]
      96. If small, 2 (0) or 4 (1) spots. [17, 44]
46. P (1) or A (0) of postabdominal spots. [44, 73]
   47. If postabdominal spots present, large (open circles) (0), medium (>1.5 and ≤2.0 mm avg.) (1), small (>1.0 and ≤1.5 mm avg.) (2) or dots (≤1.0 mm) (3). [56, 47, 44, 35]
      62. If large, anterior lateral spots medially fused (0), posteriorly fused (1) or free (2). [66, 53, 56]
   97. If postabdominal spots present, P (1) or A (0) of a group of four free posterior spots. [44, 56]
      48. If group present, posterior group of four is strongly concave (0), weakly concave (1), or convex (2). [24, 44, 69]
   60. If postabdominal spots present, number of free (not fused) spots on postabdomen: zero (−1), two (0), four (1), six (2), eight (3), ten (4), twelve (5) or fourteen (6). [77, 3, 66, 53, 56, 44, 63, 76]
      61. If six or eight *large* (char. 45), free spots, P (1) or A (0) of gap between second and third rows of spots. [64, 18]
   98. If postabdominal spots present, and anterior abdominal spots (char. 44) also present, spots connected into racquet design (either by lines or by fusion) (1) or not (0). [77, 44]
49. Posterior end rounded (0) or angular (1). [73, 21]
50. P (1) or A (0) of dorsal fin. [50, 73]
   51. If present, length of attachment in mm. Recoded as integer in the following manner: (0) 7–7.7; (1) 7.7–8.4; (2) 8.4–9.1; (3) 9.8–10.5; (4) 13.3–14. [48, 50, 31, 20, 29]
   52. If present, posterior apex projecting beyond rear of attachment (2), not projecting (1) or projecting anterior to rear of attachment (0). [72, 50, 20]
53. Posterior abdomen swollen (1) or not (0). [35, 73]
54. Posterior bars (apparently fused spots) absent (0), single (1) or double (2). [73, 2, 43]
   55. If double, shortest distance between bars in mm. Recoded as integer in the following manner: (0) 1–1.8; (1) 1.8–2.6; (2) 6.6–7.4; (3) 8.2–9. [43, 18, 75, 64]
   99. If double, elongate (0) or fat and roughly triangular (1). [43, 56]
      56. If elongate, straight (0), curved (1), weakly *J*-shaped (posterior ends thickened) (2), or strongly *J*-shaped (3). [64, 43, 3, 12]
   59. If double, P (1) or A (0) of large cross-shaped spot in postabdomen median to anterior tips of bars. [3, 56]
   57. If single, semicircular (0) or *U*-shaped (1). [5, 2]
63. Greatest width of abdomen in mm. Recoded as integer in the following manner: (0) 15.95–17.95; (1) 19.95–21.95; (2) 21.95–23.95; (3) 23.95–25.95; (4) 27.95–29.95; (5) 29.95–31.95; (6) 33.95–35.95; (7) 36. [20, 48, 54, 73, 35, 63, 24, 47]
85. Length of abdomen in mm from base to tip of collar. Recoded as integer in the following manner: (0) 38–42.9; (1) 42.9–47.8; (2) 47.8–52.7; (3) 52.7–57.6; (4) 57.6–62.5; (5) 72.3–77.2; (6) 82.1–87. [73, 47, 64, 75, 50, 19, 20]
100. P (1) or A (0) of lateral flippers. [42, 73]
   101. If present, small (0), medium (1) or large (2). [42, 51, 61]

Abdominal pores

64. P (1) or A (0) of large pore in column 10 (most anterior position). [45, 73]
65. Group II (columns 4 and 5) has zero pores (−1), one pore (0) or two pores (1). [61, 69, 73]
   66. If two pores, fused (1) or not (0). [5, 73]
      67. If fused, fusion complete (0) or incomplete (1). [48, 5]
      102. If not fused, number of pores looking like slits: zero (0), one (1) or two (2). [73, 68, 51]
68. Group III (columns 6–10) has one (0), two (1), three (2) or five (3) pores. [64, 18, 43, 73]
   69. If two or three pores, one pore looks like a slit (1) or not (0). [43, 76]
   103. If five pores, the two pores closest to group II look like slits (1) or not (0). [56, 73]
   70. If five pores, P (1) or A (0) of fusion. [50, 73]
      71. If fusion present, complete (0) or incomplete (1). [29, 50]
         72. If complete, one (0) or two (1) groups of fused pores. [72, 29]
         73. If incomplete, P (1) or A (0) of a group of three fused pores. [26, 50]
74. Group I (columns 1–3) has zero (0), one (1), two (2) or three (3) pores. [47, 24, 35, 73]
   75. If one or two pores, one pore looks like a slit (1) or not (0). [63, 35]
   104. If two or three pores, pore nearest posterior enlarged (1) or not (0). [42, 73]
      105. If three pores present and posterior one enlarged, enlarged pore apparently see-through (1) or not (0). [30, 42]
         106. If see-through, fused with posterior pore from other side's Group I (1) or not (0). [57, 30]

76. If three pores, separated as three open pores of any size (0) or in some way modified (1). [73, 46]
    77. If modified, modified by fusion (1) or some other way (0). [64, 46]
        79. If fusion, two (0) or three (1) pores fused. [50, 64]
        80. If fusion, broad and complete (0), broad and incomplete (1), or slit-like (2). [64, 66, 71]
            78. If broad and complete *and* three pores fused (char. 79), both lateral pores reduced and joining median one (1) or not (0). [22, 64]
    81. If modified in some other way, P (1) or A (0) of line (or slit) connecting pores. [46, 65]
        82. If present, two (0) or three (1) interconnected pores. [53, 46]
        83. If absent, slits in column 1 (0), column 2 (1), columns 1 and 2 (2), or column 3 (3). [60, 65, 8, 51]