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GROWTH AND VARIATION IN *EURYPTERUS REMIPES* DEKAY

By

H. E. Andrews, J. C. Brower, S. J. Gould, and R. A. Reyment

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The statistical analysis of two subspecies of *Eurypterus remipes* shows that both of them display very high integration among all measures considered. The prosomal set of variables are highly integrated with the body set. There is little allometry in bivariate growth sequences. As best known at the present time, trilobites show an analogous level of integration; there is therefore reason to suspect that the growth relationships here recorded are wide-spread among some arthropods. Ontogenetic growth is analysed for *E. remipes remipes*, after the establishment of growth stages by a stepwise multivariate technique. Canonical correlation is used to examine the pattern of integration between head and body. This is, again, exceptionally high. Other methods of multivariate statistics are applied to the analysis of the underlying relationships between variables. The palaeoecology of the Fiddlers Green Member (Bertie Formation, Upper Silurian) is discussed.

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INTRODUCTION

Ever since Mitchill (1818) recorded the first eurypterid from the Upper Silurian of Oneida County, New York, this group of fossils has fascinated palaeontologists. The original *Eurypterus remipes* DeKay came from the Fiddlers' Green Member of the Bertie Formation: this stratigraphical level is still an abundant source of excellently preserved specimens. The original specimen was interpreted as a catfish of the genus *Silurus* (the appendages of the prosoma were identified as the barbels of the fish). Since *E. remipes*, the type species of the genus, was first described by DeKay (1825, p. 375, pl. 29), it has been the object of numerous studies. Noteworthy are those of Hall (1859), Holm (1899), and Clarke and Ruedemann (1912). Kjellesvig-Waering (1958) grouped several taxa, previously considered as species, around *E. remipes* as subspecies. Consequently, according to this revision, the *E. remipes* of DeKay, Hall and Clarke became *E. remipes remipes* and the *E. tetragonophthalmus* of Fischer de Waldheim (synonym *E. fischeri*), the other taxon examined in this paper, became *E. remipes tetragonophthalmus.*

Kjellesvig-Waering (1958, p. 1136), in discussing the high degree of likeness between the two subspecies (for a long time, the European one was referred to the American *remipes*), wrote that "differences between them are minor and probably of a geographic or temporal character" and on p. 1137, "*E. remipes tetragonophthalmus* is closer to *E. remipes remipes* than to any other American subspecies". He noted that the prosomas of the two have the same length-to-width proportions, but the lateral eyes of *tetragonophthalmus* appear to be larger, the prosomal ornament is different, the relative proportions of the sixth and seventh segments of the paddle are reversed and the pre-telson of *remipes* lacks the epimeral spines possessed by the other subspecies. More recently, Størmer (1973) has come to the con-

clusion that differences in the paddles of the European and American forms are great enough to warrant generic separation and has therefore made *tetragonophthalmus* the type of his new genus, *Baltoeurypterus.* Kjellesvig-Waering has informed us that he is in agreement with Størmer.

We have looked into the grounds for this genus and Gould and Reyment think that such slight differences can hardly be of more than minor taxonomic importance. There is a distinct danger that we have here a case of the "key character concept". That is, a certain character is defined as being of "generic" value (rather than "specific" or "varietal") and then one is forced to honour every variation in this character with a high-level taxonomic designation. The variational patterns of the European and American eurypterids are very close indeed. Future study may bring to light more substantial differences, but until then, we have chosen a conservative approach by retaining both taxa as subspecies of *Eurypterus remipes.*

As far as we know, this is the first detailed statistical study of a eurypterid to appear. Indeed, Kjellesvig-Waering (1958) observed that the variability of the eurypterids had yet to be studied. Qualitative observations occur scattered throughout the literature, the most comprehensive being those of Clarke and Ruedemann (1912); most of the growth changes they noted in their qualitative appraisal of *E. remipes remipes* show up clearly in our statistical study.

The purposes of this work are to study the ontogeny and variation of two closely related eurypterids, to contrast and compare the results obtained, and to attempt a palaeoecological analysis for *E. remipes remipes.*

Before making any general statements about the nature of functional integration in eurypterids, we must know whether the patterns discovered in one species can be detected in related taxa. Thus, Brower and Reyment were pleased to learn that Andrews and Gould had done an independent multivariate analysis of a European eurypterid. Because the two groups worked in complete independence and used different measures and methods, a set of similar results would seem all the more compelling. The similarity is striking indeed: the extreme intensity of integration among nearly all measures is also the primary conclusion of Andrews' and Gould's work. Moreover, the few multivariate studies of trilobites that we know (Eldredge, 1972, in particular, and references therein) have independently discovered the existence of very high correlations and little allometry in ontogenetic series. We feel that we may therefore be stating a quite general principle of growth in certain arthropods. Ostracods display a much lower level of integration (Reyment, 1960, 1963, 1966).

Gould and Andrews studied a collection of eurypterids from the upper Silurian of the Baltic island Saaremaa, Estonian S.S.R. The collection was made in 1930 by W. Patten (who used them to help argue his case for an arthropod origin of the vertebrates). Several hundred excellent specimens, ranging from 1 to 30 cm in length, are in the Museum of Comparative Zoology, Harvard University. The analysis was made on 44 specimens evenly spanning the entire range of size; all had complete prosomas as well as the first segment of the mesosoma and seem to be preserved without distortion.

The material studied by Brower and Reyment comes from collections at Colgate University, Hamilton, N.Y. and Syracuse University, Syracuse, N.Y.

ACKNOWLEDGMENTS

Brower and Reyment are indebted to Colgate University for giving them access to a magnificient collection of *E. remipes remipes* and, in particular, to Professor Robert M. Linsley of the Geology Department for giving us a set of prosomal measurements on the Colgate specimens. A great deal of the basic work on the material of *E. remipes remipes* was carried out as a class project by the following students at Syracuse University: Maurice Cucci, John Douglas, Duane Eppler, Susan Siwek, John Kennedy, and Ghan Shyam Srivastava. Acknowledgment is made in the text for the results obtained by them.

Measurements on the Syracuse University *E. remipes remipes* prosomas and *Limulus polyphemus*

were made by Edna S. Kaneshiro (1962, unpublished Master's thesis) who also did much preliminary processing of these data.

The Syracuse University specimens were collected by Adawia Alousi, Nora Kula, Sachiko Nakagawa, E. S. Kaneshiro, Ralph Watson, J. L. Craft and the writers.

We thank Robert M. Linsley, Erik N. Kjellesvig-Waering (Amoco International Oil Co., Chicago, Illinois, USA), C. D. Waterston (Royal Scottish Museum, Edinburgh) and D. F. Merriam (Syracuse University) for reviewing the manuscript and making helpful suggestions for improvement.

The identifications of most of the species occurring with *Eurypterus remipes remipes* were kindly made by Professor John W. Wells of Cornell University (Ithaca, New York), Dr. Erik Kjellesvig-Waering, and Professor Robert M. Linsley.

The text figures were drawn by Mrs. Dagmar Engström and the manuscript typed by Mrs. Eva Eklind, both of the Palaeontological Department, Uppsala University. The Syracuse University and Uppsala University Computer Centers provided computer time; James Wilson of the Syracuse Computer Center aided in APL programming.

Reyment's contribution to the study was made while he was a Visiting Professor at Syracuse University, autumn, 1972, in part sponsored by the Mobil Oil Company.

COMPUTER PROGRAMS USED FOR THE ANALYSIS OF *E. REMIPES*

The computations on *E. r. remipes* were made using standard APL procedures and programs developed by Brower, Reyment and Wilson. The multivariate analyses were made with BMD FORTRAN programs (Dixon, 1970) and FORTRAN programs of Blackith and Reyment (1971). Reference is also made to Veldman (1967) for a program for squared distance coefficients and average linkage cluster analysis. The computations on *E. r. tetragonophthalmus* were made with COVAP, a FORTRAN program (Manson and Imbrie, 1964; Gould, 1967).

ANALYSIS OF *EURYPTERUS REMIPES TETRAGONOPHTHALMUS*

By

Harold E. Andrews and Stephen Jay Gould

Twenty seven measurements were made on each specimen. We attempted to establish a well-spaced grid of general lengths, widths and diagonals; allometric changes produced by gradients of differential growth (Huxley, 1932; Gould, 1966) should have a multivariate expression in the clustering of dimensions expressing a gradient. We also constructed a set of measures for anatomical features of particular interest (the eyes and the first mesosomal segment).

We analyzed our 44×27 matrix with COVAP for R and Q mode principal components factor analysis with options for varimax and oblique rotations. As these techniques assume a linear relationship between pairs of variables, we transformed all measures to their logarithms before the analysis. About the only allometric relationship consistently found in arthropods is the negative differential growth of the eyes. Bivariate plots show that the Saaremaa eurypterids are no exception to this general trend.

The variables are listed in the explanation to Fig. 1, the illustration of the variables measured. Differential allometric relationships found are: Eye length (measure 15) vs. prosoma length (measure 1):

$$EL = 0.64\,PL^{0.73}, \text{ at } r = 0.977,$$

while for eye width (measure 16) vs. prosoma length

$$EW = 0.46\,PL^{0.62}, \text{ at } r = 0.907.$$

Virtually all other bivariate relations are isometric; for prosoma width (measure 2) vs. prosoma length, for example,

$$PW = 1.36\,PL^{0.99}, \text{ at } r = 0.998.$$

Because the logarithmic transformation of the power function is a standard linear equation, operation on logarithms of original data removes the potential dilemma of non-linearity due to allometric power functions.

The first evidence of extremely high integration comes from the correlation matrix (used to

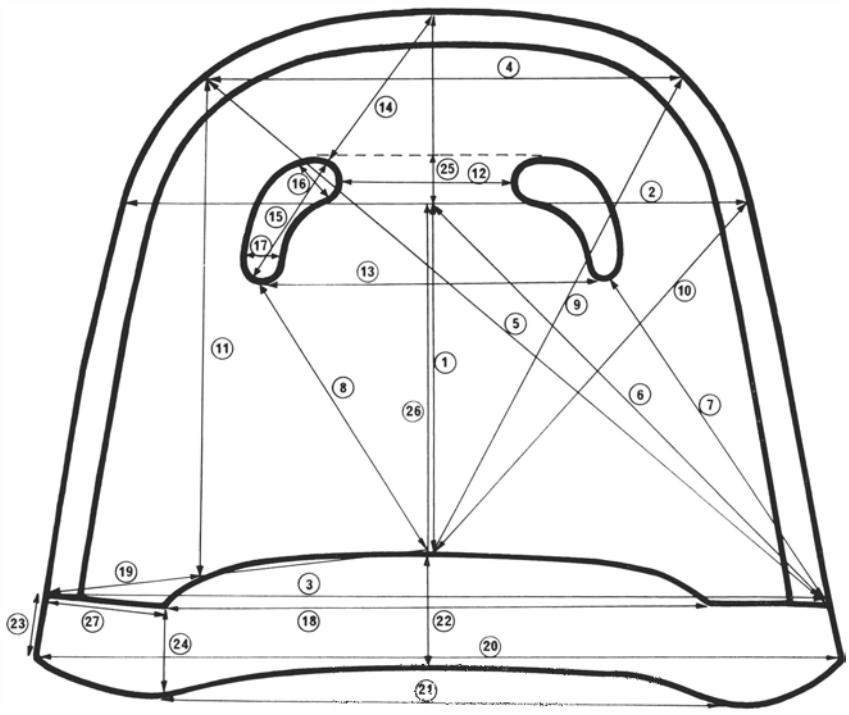

Fig. 1. The 29 variables measured on *Eurypterus remipes tetragonophthalmus* Fischer.

extract eigenvalues in the R-mode analysis). Of 351 elements in the half matrix of correlations (excluding elements of the principal diagonal), 139 (40 %) are greater than 0.99. The lowest value is 0.70 for posterior lateral eye width (measure 17) vs. length of the first mesosomal segment at its lateral border (measure 23). Only 4 correlation coefficients are less than 0.80. In one sense, it is remarkable that COVAP was able to make a significant distinction of functional groups within such a monotonous matrix (see below).

The theme of tight integration is equally evident in the list of eigenvalues; the first eigenvalue explains 95.2 % of all information; 3 eigenvalues encompass 97.7 % of the information and provide the most sensible interpretation (additional components seem to reflect measurement errors or anomalous single values, while fewer axes clearly lump separable and meaningful components of variation).

The lowest communalities over three factors are 0.908 for the two small and inaccurate measures 25 and 27. The factor loadings on principal components are easily interpreted, but not very revealing; all variables load very strongly on the first axis (the lowest projection is 0.84 for eye width measure 17). This is clearly a size axis. As the eurypterid grew, all its measures increased in approximately linear proportion (after logarithmic transformation). This pervasive positive correlation produces a size axis that overwhelms all other components of variation: there is virtually nothing left to load on subsequent axes.

We must rotate our axes to detect the fine structure of variation. The varimax rotation provides some insights, but the constraint that axes be orthogonal limits its utility. The vectors representing variables are so tightly clustered in m-space that a set of orthogonal axes cannot achieve a location very near any of them. If we wish to detect clusters of variables by their projections upon axes, we shall need to "collapse"

Table 1. Triaxial oblique factor solution for the Saaremaa eurypterids; recordered oblique projection matrix.

Measure number	21	17	23
21	1.000	0.000	0.000
18	0.980	0.025	0.004
26	0.933	−0.013	0.089
20	0.918	0.061	0.043
3	0.906	0.075	0.044
12	0.900	0.074	0.050
19	0.889	0.083	0.052
10	0.886	0.047	0.081
2	0.886	0.081	0.060
13	0.885	0.102	0.040
4	0.882	0.058	0.085
7	0.880	−0.006	0.141
6	0.874	0.052	0.100
5	0.869	0.071	0.089
11	0.849	0.045	0.131
14	0.838	0.105	0.087
1	0.835	0.073	0.124
9	0.833	0.115	0.084
8	0.828	0.074	0.127
25	0.792	0.157	0.042
15	0.747	0.288	0.004
22	0.482	0.131	0.425
17	0.000	1.000	0.000
16	0.077	0.770	0.185
27	0.248	0.404	0.392
23	0.000	0.000	1.000
24	0.064	0.449	0.569

See Fig. 1 for the meanings of the measure numbers.

our reference space and use an oblique solution with non-orthogonal axes placed within the vector swarm itself. COVAP performs an oblique rotation using actual vectors (at extreme positions in the swarm) as reference axes.

Table 1 presents a triaxial oblique solution for the Saaremaa eurypterids; each variable is grouped with the reference vector of its strongest projection. The three groups now have a ready and interesting interpretation.

The first and major cluster includes all the general dimensions of the length-width-diagonal grid; it is this system's expression of a size factor. Nonetheless, there is an interesting stratification within it, reflecting some degree of differentiation. The reference axis itself is a width — the most posterior width, measure 21 (the choice of reference axis is of no particular significance in itself). Now, of the 10 highest projections upon the reference axis, 8 are widths — and this includes *all* the width measures. (The exceptions are length measure 26 and diagonal 10). Moreover, of the first 5 widths, four are posterior widths; the latter three are anterior widths. The remaining 11 variables are all diagonal or length measures; the diagonals tend to come first (4 of the first 5). Thus, we see a stratification of this tight cluster into four poorly defined but clear aggregations: posterior widths, anterior widths, diagonals and lengths. There is some tendency for measures of a single direction and place to sort together; this must reflect some slight differentiation (by directional gradients or local effects) within the pervasive isometry of integration.

The second axis includes the two eye widths and the unsatisfactory measure of prosomal end width (measure 27 — its projections are low and nearly equal on all three axes; its placement with one of the three demands no special explanation). Eye length (measure 15), though it groups with the general measures, has the highest projection upon the second axis of any variable outside the cluster of the second axis itself. We repeat that the separate sorting of eye measures is not, *per se*, a result of its negative allometry to general size; for a logarithmic transformation was applied to the raw data. The eye shows a partial independence of general size that is reflected in its correlation with measures of the first group (not in the form of its linear regression). The majority of correlation coefficients lower than 0.9 are between measures of eye width and variables linked with the first axis.

The third axis encompasses the length (but not the widths) of the first mesosomal segment (the third length, measure 22, could just as well group with this axis as with the first; its projections are nearly equal). The width measures for this segment are all firmly allied with the first (general) group. This separation is very revealing: since the width of the first segment is "moulded" as a continuous connection with the prosoma (Fig.

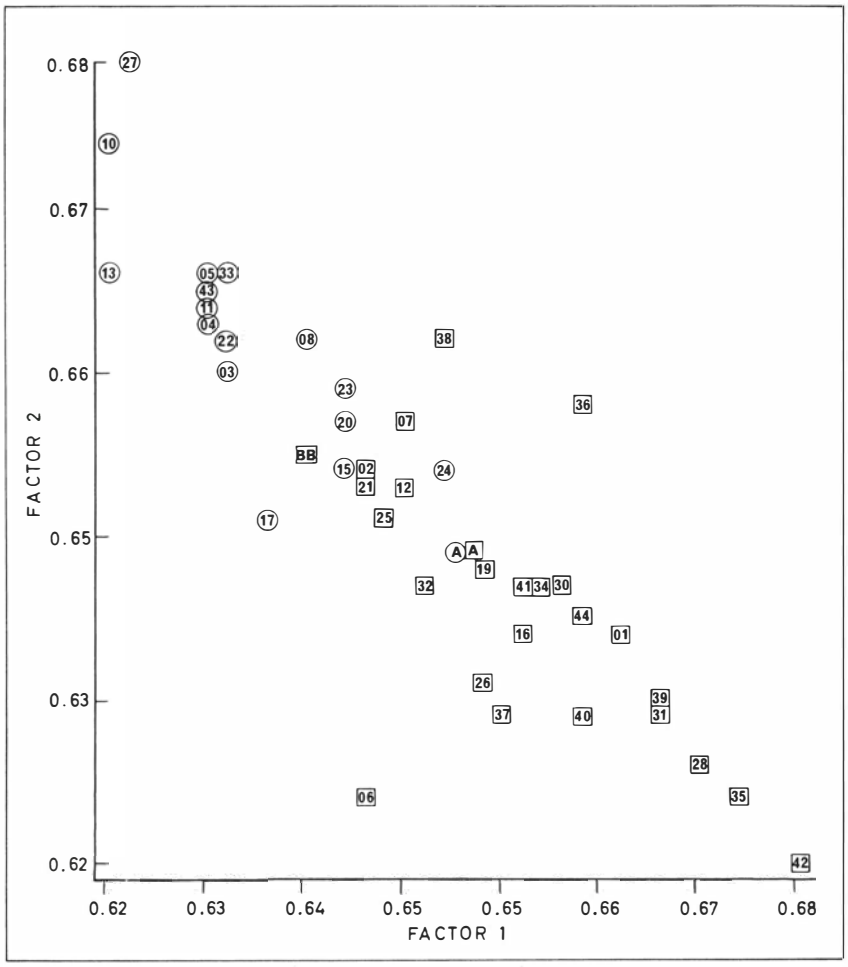

Fig. 2. Plot of all specimens of *Eurypterus remipes tetragonophthalmus* Fischer against the first two varimax axes. The squares represent specimens with measure 1 greater than 20 mm; circles represent specimens with measure 1 less than 20 mm.

1), its control evidently lies with the general factor determining prosomal size. But its lengths are potentially independent of this control, since posterior extension (or curtailment) of the segment does not disrupt the continuity of its lateral margins with the prosoma.

Thus, each of the three axes has an interesting biological interpretation: general prosomal size (with directional gradients and local effects within it), eye size, and mesosomal lengths (but not widths).

The Q-mode analysis is of less interest, but it does display one significant point. COVAP normalizes all samples (individual specimens in this case) before the analysis by dividing each element by the vector length of its sample. This has the effect of scaling all specimens to a common size. The first eigenvector encompasses an overwhelming 99.9 percent of all information: the specimens are morphometrically very similar to one another indeed!

Fig. 2 shows a plot of all specimens against the first two varimax axes. There is a clear separation by size into groups for small and large specimens. This would be of no particular interest if size had remained as an explicit variable in the

analysis. But normalization has removed size *per se.* If the plots still show separation by size, this must reflect the differences in *shape* that correlate to it. Despite the overwhelming similarity of shape among all samples, we can still detect a small allometric component (due primarily to the negative allometry of eye size).

Both R and Q analyses lead us to the same conclusion. The integration of variables is exceedingly strong; it dwarfs that of any comparable set (of measures and ontogenetic range in size) known to us either from our own experiences or from the literature. We do not doubt that it reflects a general principle of arthropod growth. Nonetheless, multivariate methods can still detect small but clearly significant (statistically *and* biologically) distinctions within this pervasive system of integration. In the R mode, eye size and first segment lengths gain separate expression, while the general cluster stratifies by directional gradients and local influences. In the Q mode, allometric consequences of increasing size separate large and small specimens by their shape.

ANALYSIS OF *EURYPTERUS REMIPES REMIPES*

by

James C. Brower and Richard A. Reyment

PALAEOECOLOGY

Speculation on the palaeoecology of eurypterids has been rife. Kjellesvig-Waering (1958) concluded that eurypterids of the genus *Eurypterus* preferred calcareous muds, high in magnesium, and he referred to these sediments as waterlimes. This terminology and interpretation derives from views on the chemistry of the Fiddlers Green member of the Bertie Formation, the type horizon for *E. r. remipes.*

Previous work on the palaeoecology of eurypterids is vast, confusing, and often conflicting; we have no intention of reviewing the literature. Good summaries are available in Caster and Kjellesvig-Waering (1964), Kjellesvig-Waering (1964), Brooks (1957, an annotated bibliography), Størmer (1934, pp. 58—69), and Clarke and Ruedemann (1912, pp. 71—113). These discussions indicate that eurypterids occur in sediments of normal marine salinity that were deposited at various depths, and in brackish and hypersaline environments near, and perhaps in, the intertidal zone. Some eurypterids may have lived in fresh-water environments although we are not convinced by the river hypothesis of O'Connell (1916).

Our specimens come from the Fiddlers Green Member of the Upper Silurian Bertie Formation from the well-known Passage Gulf occurrence on Spohn Road, in Passage Gulf, 0.3 miles south of the junction with Brewer Road, about 1.5 miles southeast of Elizabethtown, Millers Mills 7 1/2′ Quadrangle, New York (see Rickard, 1962, 1969 for reviews of the stratigraphy). Depositional environments of the sequence are summarized by Treesh (1972) and Leutze (1964).

Eurypterids are numerous in several thin beds in the uppermost metre of the Fiddlers Green member. A prominent mud-cracked zone occurs above the eurypterid beds. The Fiddlers Green is a thinly laminated, at least partly clastic, high magnesium rock. The associated materials include detrital quartz, clay minerals, and organic matter. The organic matter is concentrated in certain beds which could represent algal mats. The grain fraction of typical Fiddlers Green sediment contains silt-sized quartz, dolomite, calcite and, or, high magnesium calcite. The matrix consists of a mixture of clay minerals, organic matter, calcite, high magnesium calcite and perhaps dolomite. The most common sedimentary structures are fine laminations, mudcracks, and crossbedding, Graded bedding, scour-and-fill structures, and current ripples are also present. The fine lamination demonstrates that most sediment has not been reworked by burrowing organisms. A few extensively burrowed beds are known, but eurypterids are not found in them. The fauna associated with *Eurypterus remipes remipes* includes the eurypterids *Acutiramus macrophthalmus* (Hall), *Pterygotus juvenis* Clarke & Ruedemann, and *Dolichopterus herkimerensis* Caster & Kjellesvig-Waering, scorpions, leperditid ostracodes, *Tetrameroceras accola* (Ruedemann), "*Gomphoceras*" *ruedemanni* Foerste, a species of gastropod, a phyllocarid, plants,

and several burrows, tracks and trails constructed by unknown organisms and fragments of black material. Although these have not been analyzed, they appear to be carbonaceous and might be remains of algal mats.

The fact that the eurypterids are restricted almost entirely to the upper part of the member suggests that the rock at this level could reflect, in its chemical composition, favourable ecological conditions for them. The chemical variability of the sediment at the Passage Gulf exposure was therefore studied. Seventeen samples were taken at half-metre intervals beginning at the contact between the Bertie Formation and the underlying Camillus Formation. The samples were analysed by atomic absorption spectrophotometry by Maurice Cucci and John Douglas. Taking the standard precautions against interference, they determined nickel, manganese, iron, copper, sodium and zinc on a Perkin-Elmer Model 403 atomic absorption spectrophotometer and magnesium and calcium on a Phillips Unicam SP-90.

The elements, with the exception of iron, show little variation. Most of the elements are present in very small amounts, particularly copper. The strata rich in eurypterids at the top of the section (about 1 m from the top) do not show any remarkable differences from the other strata of the sequence. The topmost bed of the section has a calcium to magnesium ratio very different from all the other samples, probably due to its partial absorption into the soil profile. The occurrence of eurypterids is not correlated with any of the elements considered in this investigation.

The Fiddlers Green member consists on the average of 23 % calcium (range 20.4 %—30.9 %) and 8.2 % magnesium (0.69 %—10.6 %). If the anomalous topmost sample is excluded, the ranges are, for calcium, 20.4 %—24.8 %, and for magnesium 7.0 %—10.6 %. The rock is hardly a pure dolomite but rather a magnesium-rich argillaceous limestone. Other values are: copper (0.0456 %—0.0069 %), iron (0.39 %—0.13 %), sodium (0.028 %—0.021 %), manganese (0.022 %—0.013 %), and zinc (0.0037 %—0.0016 %).

The habitats ranged from shallow water subtidal lagoonal to supertidal flats (denoted by the mudcracks). Eurypterids lived in the subtidal areas where mudcracks are lacking. The environment probably tended to be hypersaline, as indicated by several factors such as the lack of normal marine organisms (all groups found could have tolerated hypersalinity which is consistent with the low faunal diversity); the association of the unit with known evaporites — certainly the gypsum and perhaps the dolomite. The lagoons seem to have been similar to those associated with the *sebkhas* of the Persian Gulf (Friedman and Sanders, 1967, pp. 284—286; Sugden, 1963; Illing, Wells and Taylor, 1965).

The dolomite is primary, penecontemporaneous, or both. This is indicated by several lines of evidence. The grain fraction commonly bears rounded sand and silt-sized quartz. Sedimentary structures, such as crossbedding, indicate that these grains were transported. The origin of such grains must predate their deposition. It is possible they were transported by wind into the lagoons. Dolomite of other beds exhibits mostly euhedral dolomite rhombs; abraded grains are lacking. Virtually all the dolomites are finely laminated. This indicates that the material was either originally deposited as aragonite, or perhaps high magnesium calcite, and dolomitized soon after deposition (for example, see Skinner, 1963; von der Borch, 1965; Illing, Wells and Taylor, 1965).

In summary, we believe that the Fiddlers Green is a primary or penecontemporaneous dolomite, which formed in environments ranging from the supertidal to the shallow subtidal zone. Quiet water conditions prevailed in the subtidal lagoons inhabited by the eurypterids, as witnessed by the fine-grained clastic sediment with a silt-sized grain fraction and a clay-sized matrix. The waters were probably somewhat hypersaline.

It is possible that the occurrences represent mass deaths of eurypterids living near the shore. The fact that the assemblages consist of moulted carapaces, adults, and individuals of all growth stages, showing appendages, argues for this interpretation. This could be analogous to the mass mortality of crustaceans in the modern intertidal environment as a result of sudden, heavy storms. After a sudden storm had struck south-

western Denmark (Ho Bay) on June 13th, 1971, Reyment observed great numbers of dead, largely juvenile crabs spread widely just below the high tide line. R. M. Linsley has drawn our attention to two specimens in the Colgate collection which demonstrate the interment of the eurypterids. One is completely disarticulated, but all the segments are aligned and all the appendages are preserved, thus evidencing the absence of post-mortem disturbances by currents and scavengers. The second specimen is oriented upside down on the bedding plane, with its telson penetrating the underlying sediment. It seems to have been buried while in the act of righting itself.

The eurypterids seem to have been rapidly buried in a catastrophic fashion, which is indicated in several ways. The complete preservation of some entire specimens with all appendages and their eye integuments intact (see later discussion) which apparently represent dead individuals. These views conflict with those of Clarke and Ruedemann (1912, p. 25) and Størmer (1934, p. 57). We also point to the lack of any traces of scavenging activity. Dead *Limulus* are scavenged almost immediately by crabs, shrimp, microbes, and other creatures.

Some of the eurypterids are obviously moults. These include the loose prosomas, often with the first abdominal segment attached, the loose segments, isolated telsons, and pieces of appendages. Probably the complete or nearly complete specimens with damaged eyes are also moults.

Inferred mode of life

Turning to the living habits of *Eurypterus remipes remipes*, we follow the ideas of Clarke and Ruedemann (1912, pp. 71—85) and Størmer (1934, pp. 58—67) in general outline. The presence of well developed walking legs shows that the animals spent some of their lives crawling along and digging in the bottom; this is also consistent with the general body shape, size and position of the eyes, and the *Limulus*-like telson. The paddle appendages may have served in both grubbing and swimming, as do similar legs in the crabs, *Platyonichus ocellatus* and *Callinectes hastatus* (Clarke and Ruedemann, 1912, pp. 71, 75, 76). When swimming, the paddle appendages could have functioned as paddles, as suggested by Clarke and Ruedemann, or as guide planes, as proposed by Størmer (1934) (in Norwegian, Størmer uses the term *svømmeføtter*). Most authors have assumed that *Eurypterus* was either predatory, and ate worms, small arthropods, "soft-shelled" pelecypods, etc., such as does *Limulus*, or that the animals were scavengers. The food could have been taken from the surface or grubbed from within the sediment. In the case of *E. remipes remipes*, "soft-shelled" pelecypods are lacking in the sediment, but the large leperditid ostracods could have provided a comparable diet. Tracks, trails, and burrows testify to the presence of "worms" and other soft-bodied creatures. Such feeding habits are consistent with the nature of the leg bases and the small chelicerae of *E. remipes remipes*. *E. remipes remipes* was a flat-bodied form. It probably spent much time resting on the bottom, covered by a thin layer of sediment, like flounders, skates, and rays of the present day.

STATISTICAL RECOGNITION OF MOULT STAGES

Introduction

In arthropods, such as many ostracods, the moult stages are discrete and these can be easily determined by direct inspection of size-frequency graphs, bivariate scatterplots, scatterplots of principal component scores, scatterplots of principal coordinates, etc. Examples of such discrete moult stages include trilobites: Hunt (1967), Robison (1967) and Whittington (1957, figs. 20, 21); ostracods: Reyment (1960, 1963). Not all arthropods moult with such distances between stages and for these, the moult stages are therefore not clearly discontinuous. Both the living *Limulus* and *Eurypterus remipes remipes* are cases in point; although several of the larger moult stages are in fact discontinuous, the smaller stages tend to intergrade. In such examples, the selection and identification of moult stages may become subjective.

Any procedure for the selection of moult stages must be operational and applicable by the average non-mathematical palaeontologist. Therefore, it

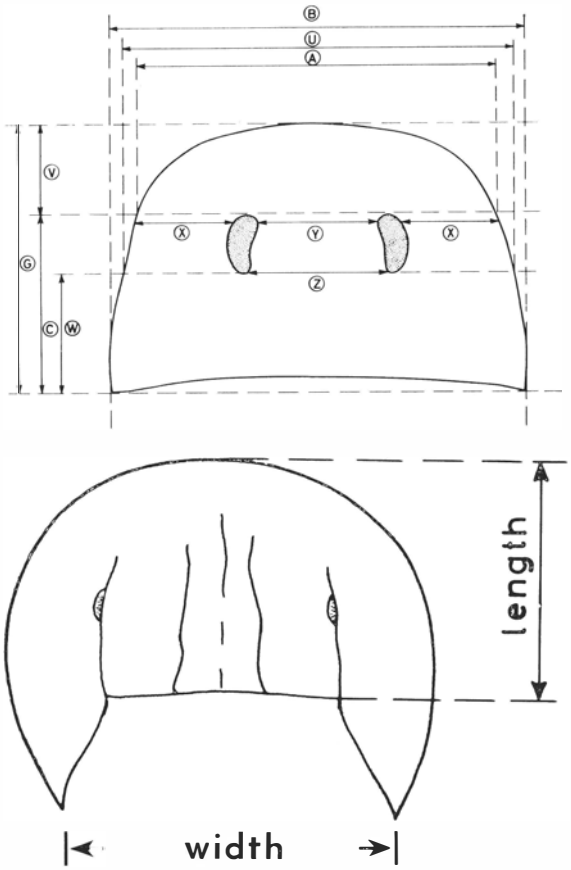

Fig. 3. Variables measured on the prosoma of *Eurypterus remipes remipes* DeKay (above) and *Limulus polyphemus* (below).

seems that the methodology should begin with simple graphics and be followed by univariate, bivariate and then multivariate statistics (cf. Reyment, 1971).

The following samples were examined in this study (see Fig. 3 for measurements):

1. *E. remipes remipes.* Colgate collection, 127 prosomas, measured by Colgate University students. 2. *Limulus polyphemus.* A total of 233 specimens; measurements were made, and the preliminary moult stages defined, by Kaneshiro (1962). The animals were obtained from North Falmouth, Mass., USA and from the supply room at the Marine Biological Laboratory at Wood's Hole, Cape Cod, Mass., USA.

Most of the following discussion is based on the first sample. We have checked Kaneshiro's work on *Limulus polyphemus* and *Eurypterus remipes remipes*, some of which is included for comparative purposes.

Most of the eurypterids are preserved with the dorsal side uppermost, which means that few specimens could be sexed. The measurements were thus made on the dorsal side and these have been pooled into a single group comprising immature individuals and adult males and females. Inspection of the univariate and bivariate plots of all variables failed to disclose significant secondary sexual dimorphism in these dimensions.

Moult stages recognized on single variables

In the first phase, moult stages were selected by trial and error using histograms for prosomal length in *Eurypterus* and *Limulus* in connexion with which, we attempted to maximize the between groups variances in relation to the within groups variances. Several frequency graphs were plotted using various class widths and end-points. Numerous groupings were tried for both *Eurypterus* and *Limulus.* Such a method was necessary because the moult stages, with a few exceptions, do not fall into discrete groups. The moult stages finally inferred with respect to length are shown in Figures 4a and 4c; these are mutually exclusive and there is no overlap. The pertinent statistics for *Eurypterus remipes remipes* and *Limulus polyphemus* are listed in Tables 2, 3, 4, 5.

The data on *L. polyphemus* are incomplete. Moult stages I through VII are relatively continuous (Fig. 4c). The wide gaps between Stages VII, "VIII", and "IX" suggest that there are several missing stages, not represented in the data.

Student's t tests were performed between adjacent moult stages for both the limulid and eurypterid data. In all cases, these are significantly different. Most of the probabilities of larger values of t are less than 0.001, which indicates that the null hypothesis may be rejected with a very minimal risk of 0.1 %.

In the second phase, we examined the moult stages inferred above with respect to the univariate distribution of prosomal width for *Limulus* and

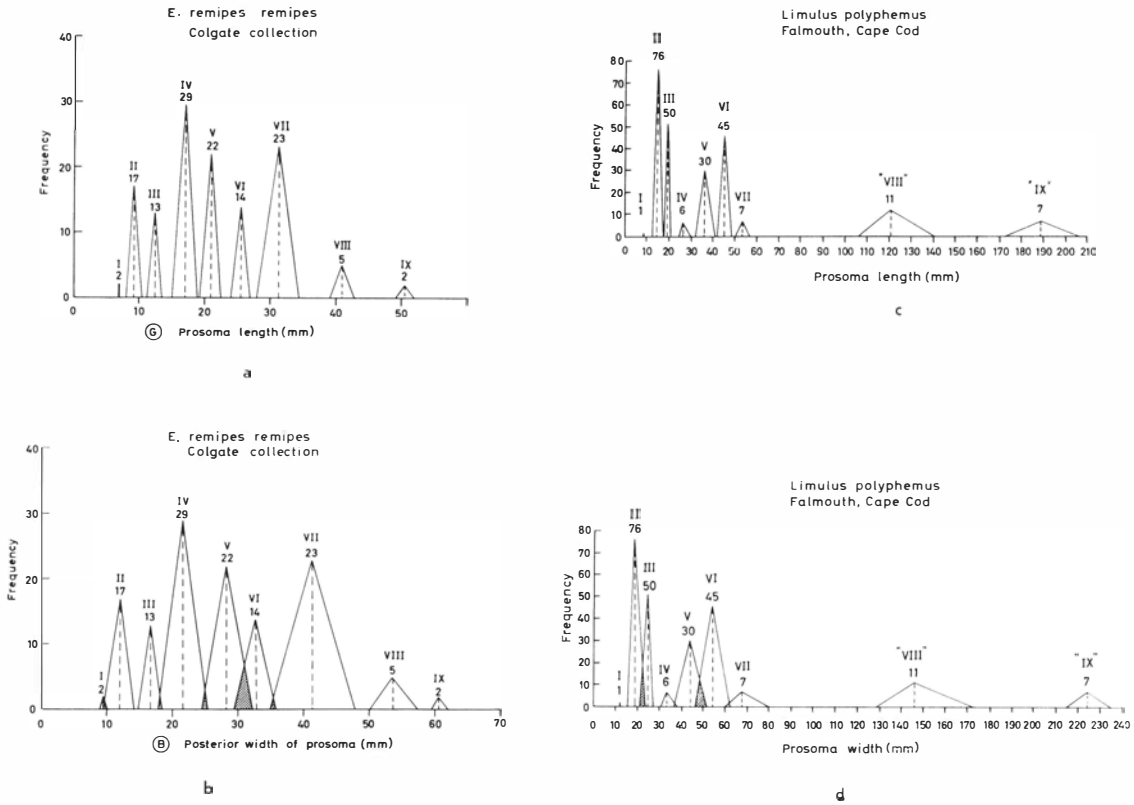

Fig. 4. Size frequency graphs for *E. r. remipes* and *Limulus polyphemus*. The endpoints for the moult stages are the maximum and minimum values for that moult stage. The dashed vertical line is located at the mean of the moult stage and the height of the peak denotes the number of specimens in that stage. Roman numerals stand for the number of the moult stage, Arabic numerals show the number of specimens in the moult stage. Overlapping areas are stippled.

posterior width of the prosoma in *Eurypterus* (Figs. 4b, d). The moult stages now begin to overlap, as indicated by the stippled parts of the figures. For the eurypterids, 14 out of 127 specimens overlap to the extent of 11.0 %. The same *Limulus* values include 25 out of 233 specimens and an overlap of 10.7 %. In general, one would expect the degree of this overlap to be inversely proportional to the correlation coefficient between the two variables. The amount of overlap should decrease as the correlation increases. For *E. remipes remipes*, the correlation coefficient for prosomal length versus posterior width of the prosoma is 0.987 and we see 11 % overlap in the width of the prosoma for the moult stages defined relative to the length of the prosoma. This idea is discussed further in the subsequent section on discriminant analysis of two or more variables.

As for the prosomal length, *t* tests were performed on the prosomal widths for the adjacent moult stages. The *t* values, though highly significant, are slightly lower than those calculated for equivalent moult stages based on prosomal length; this reflects the amount of overlap for the prosomal widths, whereas moult stages are mutually exclusive for prosomal length. The probabilities of higher *t* values are still mostly less than 0.001 for the prosomal widths.

Comparison of frequency distributions for Limulus *and* Eurypterus. The frequency graphs for limulids are right-skewed; young specimens predo-

Table 2. Basic statistics for the moult stages of *Eurypterus remipes remipes*, DeKay (Colgate collection). Measurements in mm.

Stage	Mean	Std. dev.	Number of specimens
	Length of prosoma		
I	7.2	0.07	2
II	9.2	0.73	17
III	12.7	0.75	13
IV	16.7	1.18	29
V	20.7	0.80	22
VI	25.3	1.10	14
VII	31.1	1.65	23
VIII	41.8	1.84	5
IX	50.5	2.33	2
	Posterior width of prosoma		
I	9.4	0.71	2
II	11.6	1.45	17
III	16.8	1.10	13
IV	21.6	2.00	29
V	26.9	1.68	22
VI	32.9	1.83	14
VII	40.8	3.47	23
VIII	54.8	2.29	5
IX	60.6	1.70	2

Table 4. Basic statistics for the moult stages of *Limulus polyphemus*. Data modified from Kaneshiro (1962).

Variable	Stage	Mean	Std. dev.	Number of specimens
Prosomal length	I	8.9 mm	—	1
„ „	II	14.6 mm	1.14 mm	76
„ „	III	18.9 mm	0.82 mm	50
„ „	IV	26.5 mm	1.76 mm	6
„ „	V	36.0 mm	2.30 mm	30
„ „	VI	44.8 mm	1.79 mm	45
„ „	VII	53.8 mm	2.19 mm	7
„ „	"VIII"	120.3 mm	11.30 mm	11
„ „	"IX"	189.1 mm	11.20 mm	7
Prosomal width	I	12.0 mm	—	1
„ „	II	19.3 mm	1.69 mm	76
„ „	III	24.5 mm	1.18 mm	50
„ „	IV	33.6 mm	2.47 mm	6
„ „	V	44.3 mm	3.31 mm	30
„ „	VI	54.3 mm	3.45 mm	45
„ „	VII	68.3 mm	6.31 mm	7
„ „	"VIII"	147.0 mm	13.10 mm	11
„ „	"IX"	225.0 mm	9.30 mm	7

Table 3. *Eurypterus remipes remipes*: comparison of observed moult stage means with predicted values, assuming that the animals moulted each time the volume was doubled.

Variable	Moult stage mean	Moult stage std. dev.	Predicted value, i.e., mean of previous moult stage × 1.26	Student's *t*	Degrees of freedom	Prabability of *t* value with greater magnitude
Prosoma length						
Stage II	9.2 mm	0.73 mm	9.0 mm	0.22	16	above 0.50
III	12.7 mm	0.75 mm	11.6 mm	1.45	12	between 0.20 and 0.10
IV	16.7 mm	1.18 mm	16.0 mm	0.62	28	above 0.50
V	20.7 mm	0.80 mm	21.1 mm	−0.47	21	above 0.50
VI	25.3 mm	1.10 mm	26.1 mm	−0.73	13	between 0.50 and 0.40
VII	31.1 mm	1.65 mm	31.8 mm	−0.45	22	above 0.50
VIII	41.8 mm	1.84 mm	39.2 mm	1.30	4	between 0.40 and 0.20
Posterior width of prosoma						
Stage II	11.6 mm	1.45 mm	11.8 mm	−0.12	16	above 0.50
III	16.8 mm	1.10 mm	14.7 mm	1.85	12	between 0.10 and 0.05
IV	21.6 mm	2.00 mm	21.2 mm	0.20	28	above 0.50
V	26.9 mm	1.68 mm	27.2 mm	−0.16	21	above 0.50
VI	32.9 mm	1.83 mm	33.9 mm	−0.51	13	above 0.50
VII	40.8 mm	3.47 mm	41.5 mm	−0.21	22	above 0.50
VIII	54.8 mm	2.29 mm	51.3 mm	1.37	4	between 0.40 and 0.20

Table 5. Comparison of observed moult stage means for prosomal size of *Limulus polyphemus* with predicted values, assuming that each time the animals moulted, the volume was doubled.

Variable	Moult stage mean	Moult stage std. dev.	Predicted value (=mean) of previous moult stage × 1.26	Student's *t*	Degrees of freedom	Probability of *t* value with higher magnitude
Prosomal length						
Stage III	18.9 mm	0.82 mm	18.3 mm	0.66	49	above 0.50
IV	26.5 mm	1.76 mm	23.8 mm	1.40	5	between 0.40 and 0.20
V	36.0 mm	2.30 mm	33.4 mm	1.13	29	between 0.40 and 0.20
VI	44.8 mm	1.79 mm	45.4 mm	−0.31	44	above 0.50
VII	53.8 mm	2.19 mm	56.4 mm	−1.14	6	between 0.40 and 0.20
Prosomal width						
Stage III	24.5 mm	1.18 mm	24.3 mm	0.15	49	above 0.50
IV	33.6 mm	2.47 mm	30.9 mm	1.02	5	between 0.40 and 0.20
V	44.3 mm	3.31 mm	42.3 mm	0.58	29	above 0.50
VI	54.3 mm	3.45 mm	55.8 mm	−0.44	44	above 0.50
VII	68.3 mm	6.31 mm	68.4 mm	−0.02	6	above 0.50

Growth stages represented by insufficient specimens were omitted.

minate and adults are relatively rare (Figs. 4c, d). In *Limulus polyphemus*, young specimens hatch and live in or near the intertidal zone. Larger specimens are generally found further offshore and in deeper water; for the living habits of *Limulus*, see Waterman (1953), Owen (1872), Fowler (1907), Agassiz (1878), Packard (1871), Laverock (1927), Goto and Hattori (1929), Shuster (1957, 1960). Sexually mature animals (the final moult) migrate shoreward during the spring and summer to reproduce and spawn. Our limulid sample comes from both nearshore and offshore habitats. Although there are numerous gaps in these data, the curves seem to represent, roughly, the entire size-frequency distribution, including the moulting history and mortality of most of the whole population. The *Eurypterus remipes remipes* curves are less asymmetrical than these and young specimens are under-represented. Frequency diagrams of more mature limulids collected from offshore areas resemble those of the eurypterids. Thus, we believe that the eurypterid collections are mainly composed of more mature animals, possibly from offshore habitats.

Size interval between adjacent moults. According to "Dyar's Law" (Thompson, 1942, p. 165), the average linear dimensions of successive moult stages of many arthropods increase at a geometrical rate that is constant throughout ontogeny. "Przibram's rule" is a special case of Dyar's more general "law". Przibram (1931) noted that some crustaceans moulted each time the body weight doubled. Assuming a constant bulk density for the animal, a doubling of weight yields a doubling of volume. Under these conditions, an ideal linear dimension should increase by a factor of 1.26, i.e., by the cube root of 2.00, each time the animal moults. Growth of approximately this sort has been documented by Hunt (1967) for an agnostid trilobite and by Kesling (1951, 1952, 1953) and Reyment (1963) for various ostracods. Other arthropods show different geometrical growth ratios; for example, Palmer (1957, pp. 110—114, 1962, pp. 89—92) calculated the following growth ratios for three trilobite species: *Olenellus gilberti* = 1.13; *Paedeumias clarki* = 1.16; *Aphelaspis* sp. = 1.08.

Growth of *E. r. remipes* and *L. polyphemus* has

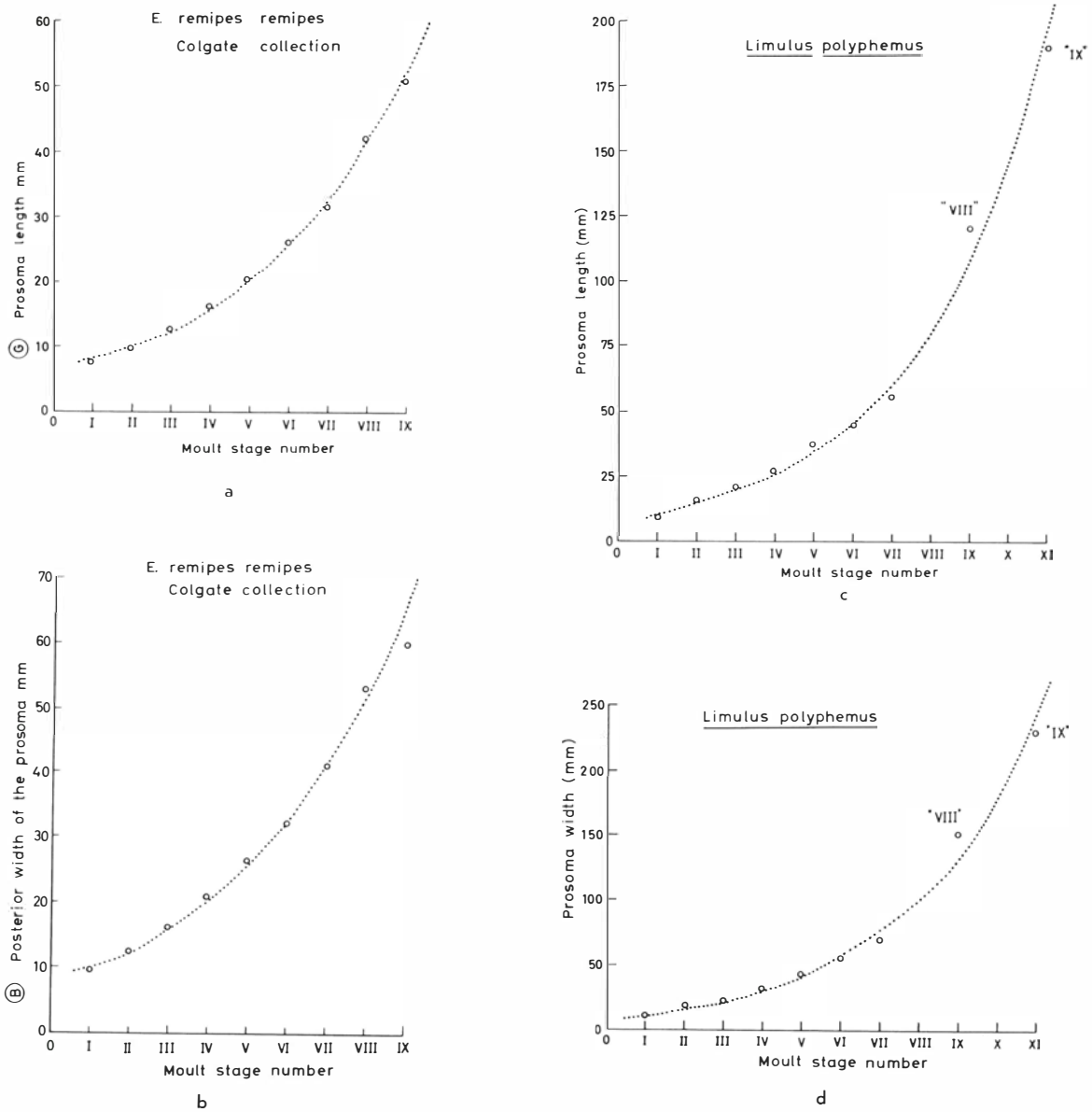

Fig. 5. E. remipes remipes and *L. polyphemus.* Graphs showing growth of prosomal size in relation to moult stages.

been tested with respect to the Przibram hypothesis as follows. The mean of a moult stage is tested against a predicted value, assuming that the animals moulted each time the volume doubled, this value being the mean of the previous moult stage multiplied by 1.26. The results, which were tested by Student's t, are listed in Tables 3 and 5. None of the means differs significantly from the predicted values. In most examples, the probabilities of larger t values are above 0.50. Consequently, it is concluded that the animals moulted each time the volume doubled.

These conclusions were checked by calculating the observed rates of size increase between adja-

Table 6. Regression statistics for the growth of instars in *Limulus polyphemus* and *Eurypterus remipes remipes.*

Independent variable X (=moult stage number)	Dependent variable Y (logarithms)	Slope	Initial intercept	Std. estimate of error for slope
E. remipes remipes	prosomal length	0.105	0.772	0.00256
E. remipes remipes	prosomal width	0.104	0.891	0.00362
Limulus polyphemus	prosomal length	0.129	0.879	0.00424
Limulus polyphemus	prosomal width	0.124	1.000	0.00384

cent moult stages, i.e., (mean of moult stage)/(mean of previous moult stage), for *Limulus* and *E. remipes remipes.* These growth indices are for *E. remipes remipes*, 1.27, for *Limulus polyphemus*, 1.29. Neither differs significantly from the ideal value of 1.26.

Least squares regression analyses were performed for development of the prosomal size parameters versus the moult stage numbers. The prosomal size measures were represented by average values for particular moult stages. The graphs are illustrated in Fig. 5; the regression details are listed in Table 6. In all cases, prosomal lengths and widths grew geometrically with respect to moult stages; as previously noted, the rate of increase of prosomal size does not differ significantly from a factor of 1.26 times the prosomal size of the previous moult. The analysis of variance of regression shows that the best fit equations are of the form (see data in Table 6) $\log Y = a + bX$, where $Y =$ the prosomal size parameter, $X =$ moult stage number; $a = \log Y$ when $X = 0$, i.e. the initial intercept, and $b =$ slope on semi-logarithmic plot. The curvilinear relationship between the two variables implies that growth rates of the prosomal size measures increased throughout ontogeny with respect to moult stages.

For *Limulus polyphemus*, the situation is more complex. As previously mentioned, there are several missing moult stages between VII and "VIII" and "IX". Consequently, equations were fitted to the complete data sets for moult stages I through VII. These were then used to predict the "best" moult stages for the observed Stages "VIII" and "IX"; the "best fit stages" are IX and XI, respectively. Following this, curves were fitted to observed Stages I through VII and the predicted Stages IX and XI.

Numerous observations indicate that *Limulus polyphemus* does not attain sexual maturity until the last moult. The smallest eurypterid with genital appendages that we have seen is a female from Stage V in the Syracuse collection, which suggests that *E. remipes remipes* became sexually mature long before the living *Limulus.* In sexing our eurypterids, we have used the criteria summarized by Kjellesvig-Waering (1958) and Størmer and Kjellesvig-Waering (1969).

Moult stages recognized on multivariate data

The moult stages were initially based on the length of the prosoma (G); these moult stages are mutually exclusive and there is no overlap between adjacent stages. When examined with respect to the width of the prosoma (*Limulus*), or posterior width of the prosoma (B) (*Eurypterus*), the adjacent moult stages overlap to the extent of about 11 % of the total number of individuals.

We may also investigate the number of misidentifications ("misclassifications" of some statisticians) with respect to the joint distribution of two or more variables. This was done with the BMD 07M computer program for generalized and stepwise discriminant analysis (Dixon, 1970, pp. 214a—214t) for the Colgate collection.

The variables are entered into the discriminant analysis in stepwise order. The first variable maximizes the between-groups variance with respect to the pooled within-groups variance in the form of a one way analysis of variance. The second variable entered is the one that maximizes the between-group differences, acting in conjunction with the first variable. The process continues until all variables that make a significant contribution to between-group differences have been entered. The F-ratio is calculated for the differences between all the groups. An F-ratio array with constant degrees of freedom reflecting the "distances" between groups is constructed for all possible pairs of groups. Two group discriminant functions are calculated for all groups. For example, the first group is tested against all other groups

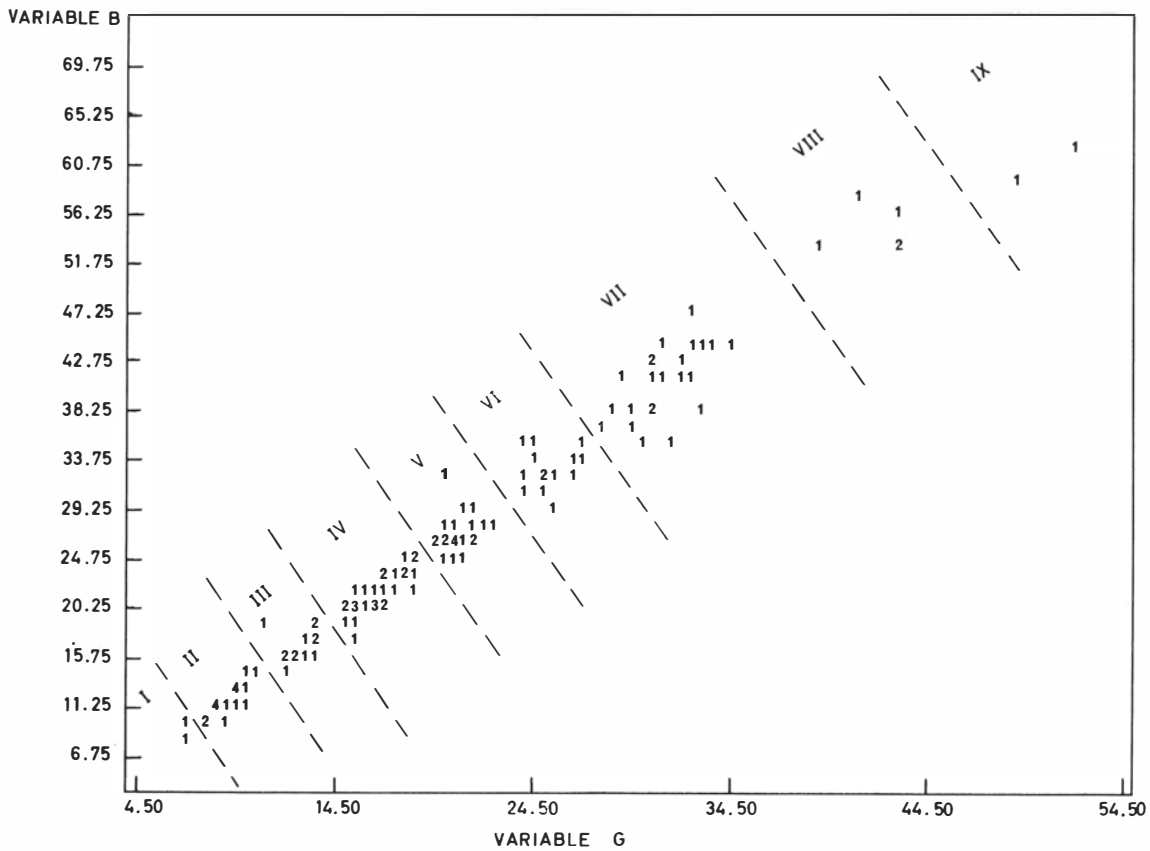

Fig. 6. Bivariate graph for the variables B and G of *E. remipes remipes* (Colgate collection) showing the moult stages subdivided by the dashed lines. The Roman numerals denote moult stages, the Arabic numerals the number of specimens at a particular plotting point.

pooled together, then the second group is similarly tested and so on. Finally, each individual is placed in the group with which it has the highest probability of membership. This is summarized in an identification array showing the group assignments of all individuals. Lastly, canonical variables are computed with a plot of the scores for the first two canonical variables. These illustrate, graphically, the relationships between the various groups and individuals.

In the first stage, two variables, prosomal length (G) and posterior width of the prosoma (B), were investigated. The groups used were the moult stages established on prosomal length. A graph of these two variables is depicted in Fig. 6. The program first entered length, thus indicating that this variable is associated with most of the differences between growth stages (this was expected as the moult stages were based upon length). The posterior width of the prosoma was also entered, which indicates that this variable makes some contribution to between-group differences.

The discriminant functions only misidentified two specimens. A Stage II animal with a relatively narrow prosoma was placed in Stage I and one Stage VII individual was assigned to Stage VI, that is, two out of 127 individuals, relative to the moult stages defined on prosomal length alone. Inasmuch as there are only two variables, there is only one canonical variate, which is:

$$y = 0.11\,B + 0.73\,G.$$

The score plot (Fig. 7) shows that the canonical

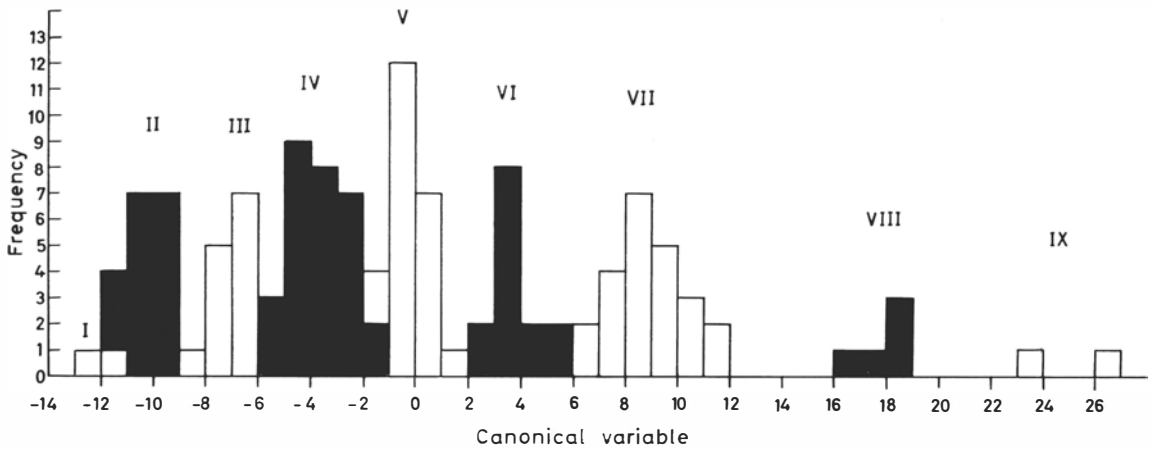

Fig. 7. Histogram of the scores for the first canonical variate of *E. remipes remipes* for the variables: posterior length of the prosoma B, and the length of the prosoma G. The moult stages are denoted by Roman numerals; every second stage is filled in with black for ease of interpretation.

variate is a general size factor, with larger specimens having higher scores. The larger coefficient for prosomal length in the canonical variate reflects the greater discriminating power of this variable. Fig. 7 illustrates that the boundaries between adjacent moult stages correspond to low frequency areas on the first canonical variate scores. Although not shown on the plot, there is no overlap between the canonical variable scores for the different moult stages. Thus, the bivariate analysis sharpens the difference among growth categories.

An increase in the number of variables in the stepwise analysis reproduced the same results as found for two variables, without adding essential information, apart from the loadings of the variables in the discriminant functions, which give a relative idea of the contributions of the variables to the discrimination.

For the three variables, prosomal length (G), posterior width of the prosoma (B), and width of the prosoma anterior to the eyes (C), the first two canonical variates are:

$$y_1 = 0.75\,G + 0.18\,B - 0.09\,C$$
$$y_2 = 0.30\,G - 0.93\,B + 0.75\,C.$$

As before, the differences between all stages, except Stage I versus II, are highly significant; the same two specimens were misidentified. The first two eigenvalues, 69.20 and 0.29, are significantly greater than zero and account for 99.5 and 0.5 % of the dispersion.

The scores show that the first canonical variable represents overall size increase during ontogeny. As before, prosomal length constitutes the most important variable. The second canonical variable contrasts the two prosomal width measurements and tends to separate the two individuals in Stage IX from the other stages. Animals with low scores for the second canonical variable have relatively rectangular prosomas, while those with higher scores tend to have prosomas with more strongly tapering sides. Adding one variable, the width anterior to the eyes, results in relatively little new information, especially with respect to identification of individuals.

Ten variables ($N = 77$) were also analyzed with the discrimination program. The coefficients of the first two canonical variates are shown in Table 7. The results are the same as for two variables, but this time there were no misidentifications of specimens.

The largest first coefficient of the first canonical variate, 0.96, is the prosomal length; the magnitude of the other coefficients is 0.36 or less. Clearly, prosomal length is by far the best separator. The other variables have much lower coefficients in canonical variable I because all are highly correlated

Table 7. Canonical variables for *E. remipes remipes*

Variable	Canonical variate coefficients		Stepwise order of entry into the discriminant analysis
	I	II	
A Prosomal width anterior to the eyes	−0.36	−0.41	5
B Posterior width of the prosoma	0.35	0.59	2
C Length from posterior margin of prosoma to anterior of eyes	−0.21	0.053	4
G Total length of prosoma	0.96	−0.11	1
U Prosomal width posterior to the eyes	0.12	−0.13	9
V Length from eyes to anterior margin of prosoma	−0.12	−0.98	7
W Length from posterior margin of prosoma to posterior margin of eyes	0.14	0.71	8
X Distance from eyes to lateral margin of prosoma	−0.13	1.31	6
Y Anterior distance between the eyes	0.24	−0.19	3
Z Posterior distance between the eyes	−0.22	−0.44	10
Percentage of trace	98 %	1.2 %	

Colgate collection, N = 77.

with the prosomal length; the pertinent correlation coefficients range from 0.94 to 0.98. Consequently, most of the information carried by these variables is redundant — they could be predicted with reasonable accuracy, solely from length of the prosoma.

The second canonical variable is a complex shape factor that separates the two Stage IX animals from the rest. The variables involved are prosomal widths, A and B, and a whole series of variables that deal with eye size, shape, and position, V, W, X and Z. These changes in shape are discussed in detail in subsequent sections on the regression analysis of the prosoma.

Summary

In both *Eurypterus remipes remipes* and *Limulus polyphemus*, moult stages are not discrete and their identification is best accomplished by a trial and error procedure. Initially, we based the moult stages upon the length of the prosoma. Nine moult stages were identified for *E. remipes* and for *Limulus polyphemus.*

The moult stages, defined by prosomal length, were then examined with respect to prosomal width. The adjacent moult stages begin to overlap, and the overlap percentage includes about 11 % of all individuals for both *Limulus* and *Eurypterus.* The low percentage of overlap partially reflects the high correlation between the two variables, 0.987 for. *E. remipes remipes.* In general, overlap of this type should decrease as the correlation between the two variables increases, although some overlap could exist, even with perfect correlation. The distributions of the two variables are also important in dictating the amount of overlap.

Student's *t*-tests between adjacent moult stages show that they differ significantly with respect to both length and width. Both *Limulus polyphemus* and *E. remipes remipes* moulted each time the body volume doubled. Growth in size relative to moult number was geometric in both the limulids and eurypterids. The size-frequency distributions of *E. remipes remipes* resemble those of living *Limulus polyphemus* from offshore habitats. Palaeoecological analysis also suggests that the eurypterids lived in environments below the intertidal zone.

All prosomal variables of *E. remipes remipes* are highly correlated, the correlations ranging from 0.99 to 0.94; therefore, adding new variables to the discriminant analysis produces little new information about differences between moult stages. When dealing with highly correlated variables in arthropods, satisfactory identifications of growth stages can be made on a single variable indicative of overall size. For 127 eurypterids, the best multivariate identifications of the moult stages only improve the identification based on

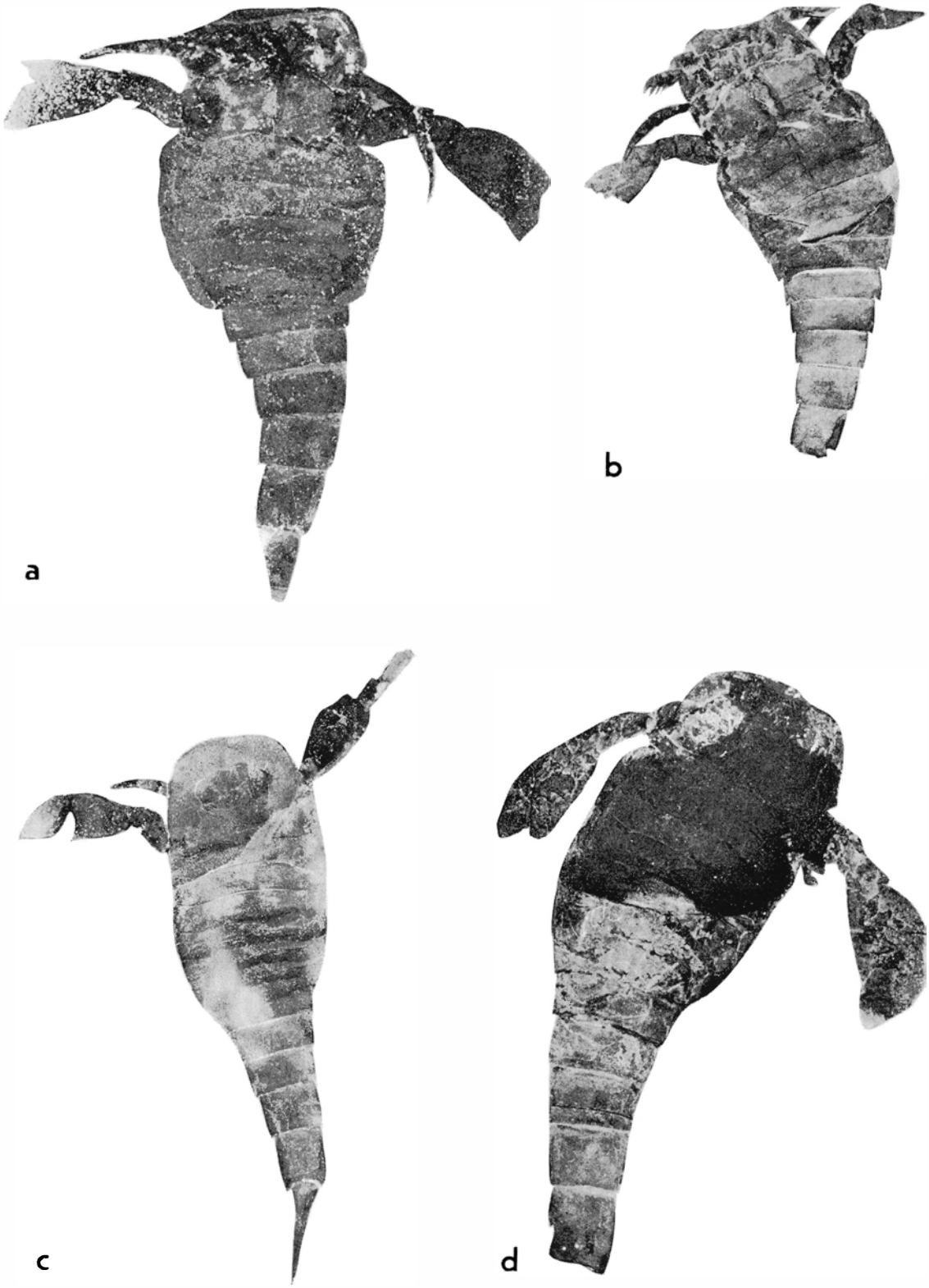

Fig. 8. Photographs of some of the specimens of *E. r. remipes* studied: a) Colgate 221 (× 1.1); b) Uppsala NA 157 (× 1.1); c) Syracuse KWM 20 (× 1.8); d) Syracuse KWM 22 (× 1.3).

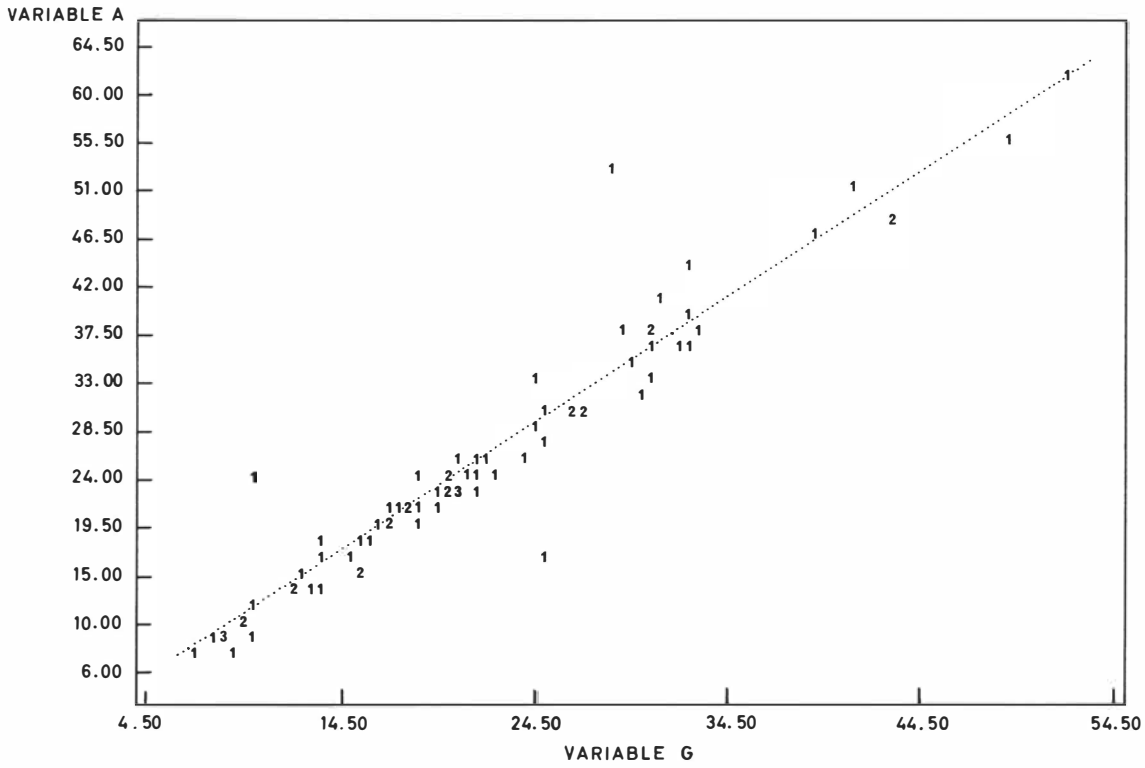

Fig. 9. Plot of the relationship between variables A and G for the prosoma of *E. remipes remipes.*

prosomal length from about 0.0 to about 6.5 percent (depending on the data set and method used). This level of error is easily tolerated.

RELATIVE GROWTH OF THE PROSOMA

Ten measurements were used in the ontogenetic study of prosomal shape. The measurements are illustrated in Fig. 3 and a representative suite of specimens is shown in Fig. 8. Complete data sets were obtained from 77 individuals with a range in prosomal length of 7.2 to 52.2 mm. A plot of one equation for relative growth is given in Fig. 9. Graphs were made of all of the variables of Fig. 3 against G. Since the plots do not differ essentially, we offer Fig. 9 for A against G as a specimen.

Growth grids (Fig. 10) were made by plotting square grids on two small specimens. These were selected to include the range of variation seen in small individuals; one prosoma has a relatively square anterior prosomal outline while the other example is more rounded. The topographic reference points or coordinates for this grid were then plotted on mature specimens. The deformation of the adult grid illustrates changes in proportions. Full discussion of the method is available in D'Arcy Thompson (1942). A word of caution is in order. In relation to arthropods, these grids have been usefully applied to trilobites (Palmer, 1957); trilobite cephalons possess many topographic reference points so that the grids are easily defined and transferred from young to adult specimens with reasonable objectivity. Eurypterid prosomas are comparatively featureless, with only a few good topographic reference points, namely, the eyes and the margin. Nevertheless, the eurypterid grids presented here do portray the main changes in shape occurring during ontogeny. These include reduction of the length and width of the eyes compared to the the total size of the prosoma,

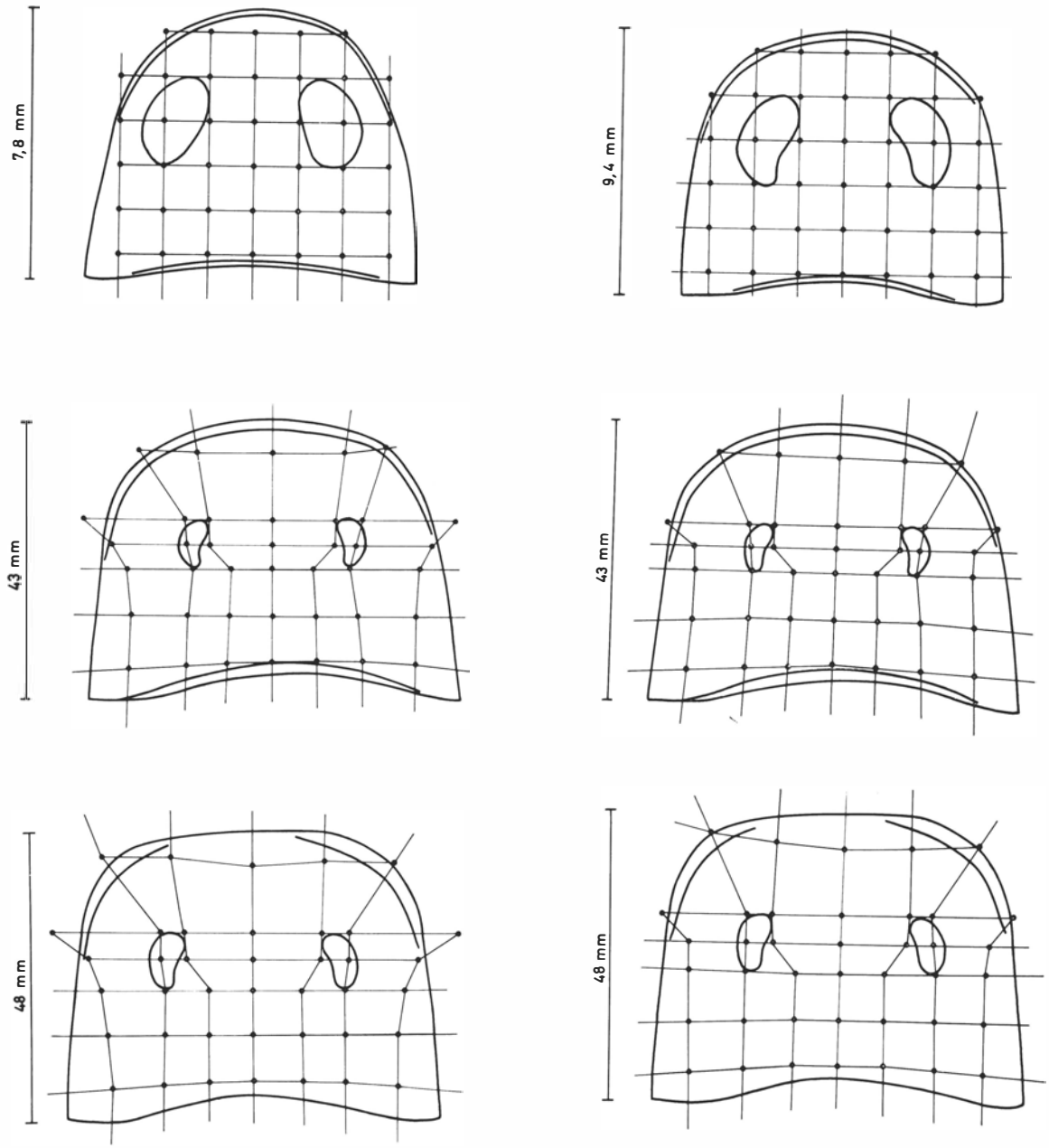

Fig. 10. Growth grids illustrating the ontogeny of the prosoma in *Eurypterus remipes remipes.* All but one specimen (Syracuse KHC 17) from the Colgate collection. The numbers list the specimens used in making the grids, in the order of left to right: KHC 17, 85, 401/KHC 17, 401/85, 90/KHC 17, 90/85.

rotation of the axes of eye length and development of a prominent "brim" in front of the eyes.

The analysis of variance for several selected equations demonstrates that linear equations provide adequate first-approximation fits to the data for prosoma and body shape and power functions are not required.

In this analysis, the slope is considered as the growth rate of Y with respect to unit increments of X. For a linear equation, this growth rate is

constant throughout ontogeny. The initial intercept, a, i.e., Y when $X = 0$, is a location parameter for the line. Regardless of the growth rate, if the intercept is zero, development is isometric and the shape of the two dimensions remains constant throughout ontogeny. If a finite initial intercept is introduced, growth becomes allometric and the shape changes. The amount and nature of the shape changes depends on the signs of the growth rate and initial intercept and the magnitude of the growth rate compared to the intercept. The growth rate and intercept interact to produce the changes in shape described by the equation. Here, the shape changes are expressed as shape ratios, calculated for the smallest and largest specimens: Shape ratio = (Y predicted from the equation)/(X observed).

In the eurypterids examined here, all the slopes or growth rates are positive. With a negative initial intercept and a positive growth rate, the above shape ratio (Y/X) increases with growth. With a positive initial intercept, the shape ratio declines in larger animals. A useful account of these relationships is given in Gould (1972).

The following discussion emphasizes the smallest and largest observed values of the independent variable, X, and the corresponding predicted or equation figures for the dependent variable, Y. Hopefully, this approach shows the ontogeny of the "average" individual. Two-dimensional shape changes are depicted by the ratios of Y (predicted)/X (observed).

Proportions of the prosoma

The development of prosomal widths A, B and U with respect to length was nearly isometric and shape remained roughly constant throughout ontogeny (Table 8, equations 1—3). The U/G ratio was stabilized at 1.2, regardless of age and size. The quotient A/G increased slightly from 1.1 to 1.2, while B/G declined from 1.4 to 1.3. These differentials reflect a slight shift of prosomal shape with progressive age. Young specimens often show prominent rounding of the anterior part of the prosoma, which begins just posterior to the eyes. Consequently, the prosomal width anterior to the eyes A is often less than the width posterior to the eyes U. Many adult specimens have more equal prosomal widths at the anterior and posterior eye levels, which produces a more subquadrate outline of the prosoma. Both types of individuals can be seen at all ages. However, subquadrate specimens predominate among adults while most juvenile prosomas are rounded. Regardless of age, the prosoma is widest at its posterior margin and tapers toward the anterior.

The differential growth patterns of prosomal widths are best illustrated by the ontogeny of widths in the area of the eyes, A and U, relative to the posterior width, B (Table 8, equations 10, 11). The A/B ratio increased from 0.83 to 0.93 while the U/B ratio increased slightly from 0.91 to 0.96. The growth rates for A and U were almost the same, 0.94 or 0.95 mm per 1 mm increase in posterior width B, but A has a greater negative initial intercept.

Ontogeny of eyes relative to prosoma

During growth of the prosoma, the main shape changes occurred in the size and position of the eyes. Due to their smallness and curved outline, the eyes could not be measured with accuracy. Approximate measures of eye size can be obtained by the subtractions C − W; for the length and [A − (Y + 2 X)]/2 for width.

The most important ontogenetic trend is a decrease in eye size relative to prosomal size. Small specimens, distributed over the prosomal length interval of 7.0 to 8.0 mm, have eyes ranging from about 2.5 to 3.0 mm in length and 1.5 to 2.0 mm in width. The same values for the largest available adult are at a prosomal length of 40.4 mm; eye length, 7.9 mm; eye width, 3.5 and 3.7 mm. The juvenile eye length is almost 37 % of the prosomal length; the equivalent value for large specimens is only 20 %. The absolute size of the eyes increased throughout growth, although the size of the prosoma increased relatively more rapidly. (This was detected qualitatively by Clarke and Ruedemann (1912)). *E. remipes tetragonophthalmus* shows the same trend.

The decline of relative eye length also affected the overall geometry of the prosoma. Ontogeny of length from the posterior prosomal margin to

Table 8. Regression statistics showing relative growth of the prosoma in *Eurypterus remipes remipes* DeKay from the Colgate collection (X and Y measured in mm).

Equation number	Independent variable X	Dependent variable Y	Initial intercept *a*	Growth rate of Y relative to 1 mm increments of X (slope) *b*	Xmin	Predicted Ymin	Xmax	Predicted Ymax	Y/X min	Y/X max	Correl. coeff.	Std. est. for error for *b*
1	G Prosomal length	A Width ant. to eyes	−0.52	1.19	7.2	8.06	52.2	61.7	1.12	1.18	0.96	0.040
2	G „ „	B Posterior width	1.09	1.25	„	10.10	„	66.4	1.40	1.27	0.97	0.034
3	G „ „	U Width posterior to eyes	0.40	1.20	„	9.07	„	63.3	1.24	1.22	0.97	0.036
4	G „ „	X Distance from eyes to lateral margin	−0.85	0.28	„	1.14	„	13.6	0.16	0.26	0.94	0.011
5	G „ „	Y Ant. distance between eyes	−1.28	0.48	„	2.20	„	24.0	0.31	0.46	0.97	0.015
6	G „ „	Z Post. distance between eyes	−0.43	0.53	„	3.36	„	27.0	0.47	0.52	0.96	0.017
7	„ „	C Length from post. to ant. of eyes	1.99	0.59	„	6.26	„	32.9	0.87	0.63	0.97	0.018
8	G „ „	V Length from eyes to ant. margin	−1.31	0.38	„	1.40	„	18.3	0.19	0.35	0.97	0.011
9	G „ „	W Length from post. of eyes to post. margin	−0.39	0.43	„	2.70	„	22.0	0.38	0.42	0.98	0.010
10	B Posterior width of prosoma	A Width ant. to eyes	−1.38	0.95	9.9	8.18	61.3	57.1	0.83	0.93	0.98	0.021
11	B „ „	U Width post. to eyes	−0.47	0.94	„	9.00	„	58.6	0.91	0.95	0.96	0.016
12	B „ „	X Distance from eyes to lateral margin	−1.07	0.22	„	1.12	„	12.6	0.11	0.21	0.96	0.007
13	B „ „	Y Ant. distance between eyes	−1.57	0.38	„	2.21	„	22.0	0.22	0.36	0.98	0.008
14	B „ „	Z Post. distance between eyes	−0.75	0.42	„	3.36	„	24.9	0.34	0.41	0.98	0.010
15	C Length from post. margin to ant. of eyes	V Length from eyes to ant. margin	−2.02	0.60	5.2	1.08	31.9	17.0	0.21	0.53	0.95	0.023
16	C „ „	W Length from post. of eyes to post. margin	−1.38	0.69	„	2.23	„	20.7	0.43	0.65	0.97	0.019
17	Y Ant. dist. between eyes	X Dist. from eyes to lateral margin	−0.03	0.56	2.3	1.27	25.8	14.5	0.55	0.56	0.96	0.019
18	Y „ „	Z Post. distance between eyes	1.05	1.08	„	3.53	„	28.9	1.53	1.12	0.99	0.020

the anterior of the eyes, C, length from the eyes to the anterior margin of the prosoma, V, and the length from the posterior of the eyes to the posterior edge of the prosoma, W, relative to total prosomal length, G, was allometric and the shape ratios increased or decreased throughout ontogeny (Table 8, eqns. 7—9). Shape ratios for the youngest and oldest specimens are: C/G, 0.87 and 0.63; V/G, 0.19 and 0.35; and W/G, 0.38 and 0.42. These changes were caused both by the relative decrease in eye length and a shift in eye position with growth. The shape ratios disclose that the change was least marked for W; this suggests that eye position relative to the posterior margin of the prosoma was roughly constant during ontogeny. Compared with prosomal length, V rose and C declined markedly in larger specimens. Therefore, most of the change in eye position involved the anterior margin of the eyes. The eyes seem to have grown more slowly towards the anterior margin than towards the posterior. Young specimens have comparatively large eyes with a small anterior "brim", whereas adults have relatively small eyes with large "brims".

Major changes also occurred in eye widths and the measures of eye position relative to prosomal width. The relative decrease in eye width is best seen in the ontogeny of distance from the eyes to the side of the prosoma, X, distance between the anterior ends of the eyes, Y, and distance between the posterior margins of the eyes, Z, with respect to prosomal length, G, and posterior width of the prosoma B (Table 8, eqns. 4—6, 12—14). All shape ratios increased during growth as tabulated for the smallest and largest specimens: X/G, 0.16 and 0.26; Y/G, 0.31 and 0.46; Z/G, 0.47 and 0.52. The same patterns characterized X, Y, and Z relative to the posterior prosomal width, B (eqns. 12—14).

In summary, development of prosomal shape was approximately isometric. The main allometric changes involved decrease in length and width of the eyes relative to the size of the prosoma and a shift in the orientation of the eye-length axes. The immature eye-length axes converge strongly toward the anterior margin of the prosoma, but the mature axes are roughly parallel to

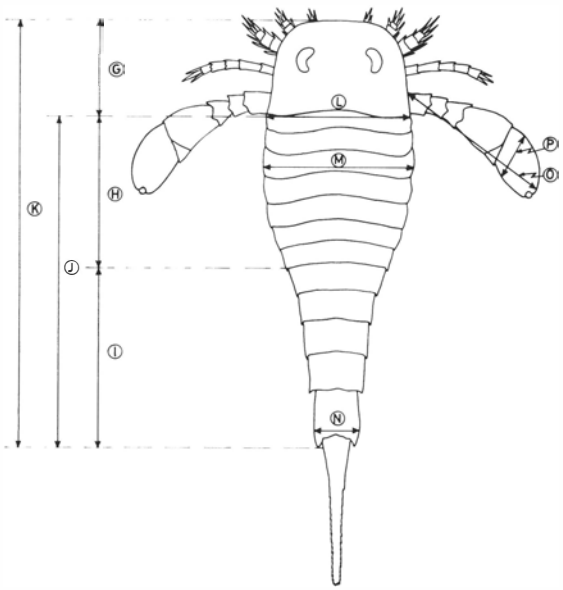

Fig. 11. Measurements made on whole specimens of *Eurypterus remipes remipes.*

one another. The eyes grew faster toward the posterior margin of the prosoma than toward the anterior edge. These growth trends caused allometric changes in the prosoma, the most noticeable being the development of a "brim" anterior to the eyes.

RELATIVE GROWTH OF THE ENTIRE BODY

Due to differences in preservation, only ten measurements (Fig. 11) were made. The sample comprises 19 specimens, ranging from 5.0 to 35 mm in prosomal length. Several specimens are pictured in Fig. 12.

Development of abdominal length J was allometric with respect to the standard measure of size, prosomal length, G, and total body length, K (Table 9, eqns. 3, 4). Throughout ontogeny, the abdominal length became relatively greater. The shape ratios for the youngest and oldest specimens are: J/G, 2.8 and 3.3; K/G, 3.8 and 4.3. In K/G, higher ratios denote a relatively shorter prosoma and a longer abdomen.

The abdomen is divided into two parts, a preabdomen including the anteriormost seven seg-

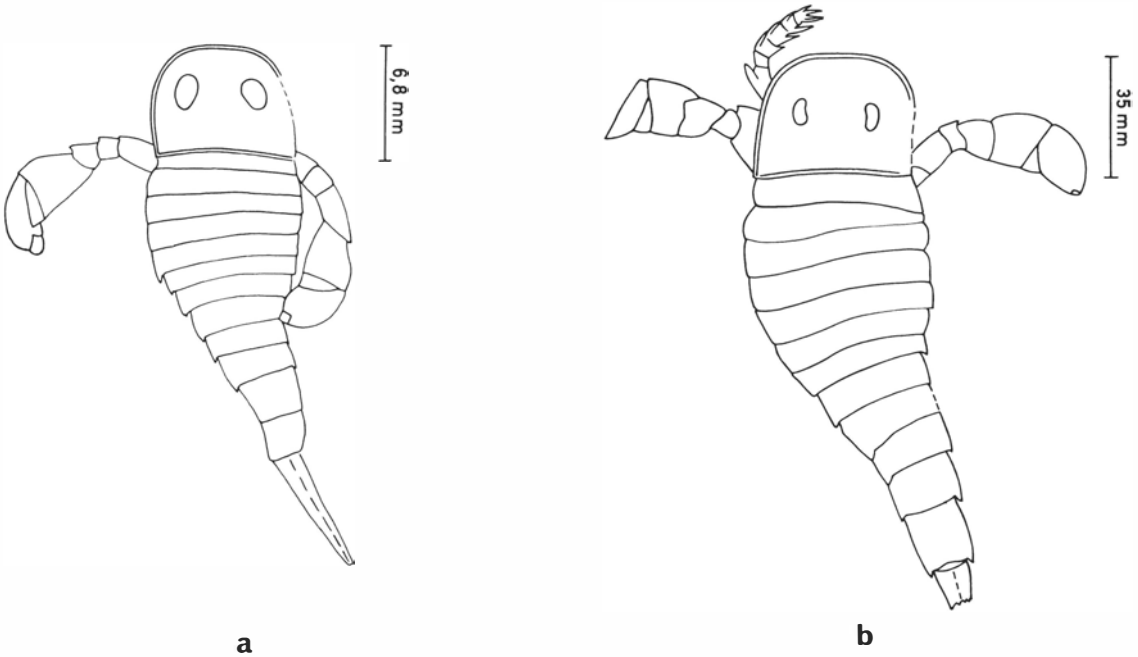

Fig. 12. Eurypterus remipes remipes DeKay. a) a young individual (Colgate 121); b) a large specimen (Syracuse KWM 18) — the left tip of the paddle and the telson are broken.

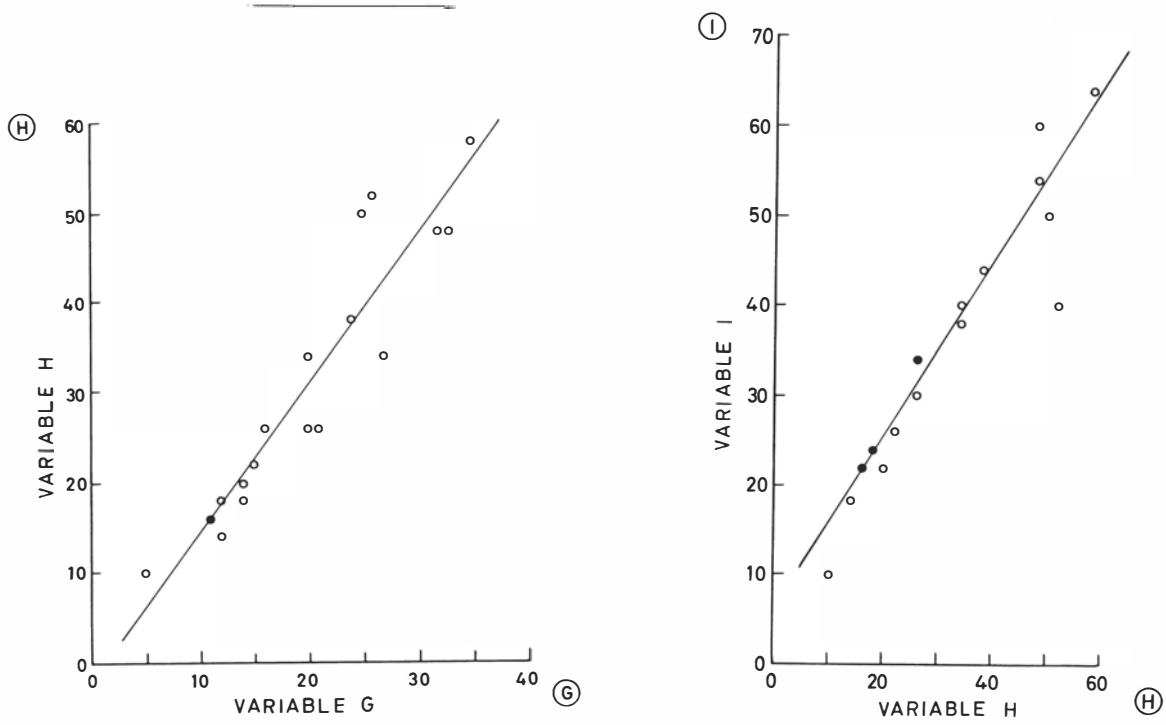

Fig. 13. Plots for the pairs of variables H against G, and I against H (see Fig. 11) for Colgate *E. remipes remipes* to show bivariate relationships in whole individuals.

Table 9. Regression statistics for the relative growth of whole specimens of *E. r. remipes* from the Colgate collection.

Equation number	Independent variable (in mm) X	Dependent variable (in mm) Y	Initial intercept a	Growth rate of Y relative to 1 mm increments of X (slope) b	Xmin	Predicted Ymin	Xmax	Predicted Ymax	Y/X min	Y/X max	Correl. coeff.	Std. est. of error for b
1	G Prosomal length	H Length of preabdomen	−2.65	1.65	5.0	5.61	35.0	55.2	1.12	1.58	0.945	0.139
2	G „ „	I Length of postabdomen	−0.39	1.74	„	8.33	„	60.6	1.67	1.73	0.975	0.096
3	G „ „	J Length of abdomen	−3.04	3.40	„	13.90	„	116.0	2.79	3.31	0.972	0.200
4	G „ „	K Total length	−3.04	4.40	„	18.90	„	151.0	3.79	4.31	0.983	0.200
5	G „ „	L Anterior width of abdomen	−0.21	1.35	„	6.54	„	47.0	1.31	1.34	0.984	0.059
6	G „ „	M Abdomen width at segment 3	0.42	1.47	„	7.78	„	51.9	1.56	1.48	0.982	0.068
7	G „ „	N Abdomen width at last segment	0.90	0.28	„	2.31	„	10.7	0.46	0.31	0.797	0.052
8	L Anterior width of abdomen	M Abdomen width at segment 3	0.80	1.09	8.0	9.49	47.0	51.8	1.19	1.10	0.992	0.032
9	L „ „	N Abdomen width at last segment	0.85	0.21	„	2.55	„	10.8	0.32	0.23	0.824	0.035
10	J Length of abdomen	H Length of preabdomen	−1.66	0.49	18.0	7.24	122.0	58.6	0.40	0.48	0.988	0.019
11	J „ „	I Length of postabdomen	1.66	0.50	„	10.80	„	63.4	0.60	0.52	0.988	0.019
12	J „ „	L Anterior width of abdomen	2.02	0.38	„	8.88	„	48.5	0.49	0.39	0.972	0.023
13	J „ „	M Abdomen width at segment 3	2.65	0.42	„	10.20	„	53.8	0.57	0.44	0.977	0.022
14	J „ „	N Abdomen width at last segment	1.46	0.08	„	2.86	„	11.0	0.16	0.09	0.772	0.015
15	H Length of preabdomen	I Length of postabdomen	4.86	0.97	9.0	13.60	58.0	61.3	1.51	1.06	0.951	0.076

ments, and a postabdomen made up of the last five segments (Figs. 11, 12). These two parts of the abdomen exhibit contrasting developmental patterns. Relative to prosomal length, G, the preabdomen, H, became longer in progressively larger animals (Table 9, eqn. 1); the shape ratios for the smallest and largest animals are: H/G, 1.1 and 1.6. Ontogeny of the postabdomen, I, was isometric with respect to the prosomal length, G, and the I/G shape ratio was stabilized at 1.7 throughout growth (Table 9, eqn. 2). This shows that all relative lengthening of the abdomen resulted from allometric changes of the preabdomen, not the postabdomen. Specimen plots of relationships between variables are shown in Fig. 13.

Development of the two preabdominal widths,

Table 10. Regression statistics for growth of the paddles of *Eurypterus remipes* from the Colgate collection.

Equation number	Independent variable X	Dependent variable Y	Initial intercept a	Growth rate of Y relative to 1 mm increments of X slope b	Xmin	Predicted Ymin	Xmax	Predicted Ymax	Y/X min	Y/X max	Correl. coeff.	Std. est. of error for b
1	G Prosomal length mm	O Total paddle length mm	2.87	0.912	7.0	9.25	35.0	34.8	1.32	0.994	0.907	0.0848
2	G „ „	P Maximum width of paddle mm	0.639	0.407	7.0	3.49	35.0	14.9	0.499	0.426	0.908	0.0377
3	O Total paddle length mm	P Maximum width of paddle mm	0.333	0.398	7.0	3.12	35.0	14.2	0.445	0.407	0.891	0.0406

anterior width, L, and width at the third and widest segment, M, was almost isometric, relative to the prosomal length, G (Table 9, eqns. 5, 6). The L/G ratio is 1.3, regardless of age, but M/G decreased slightly from 1.6 to 1.5. Growth of abdominal width at the last segment, N, was allometric with respect to prosomal size and N/G declined from 0.46 to 0.31 throughout ontogeny (Table 9, eqn. 7).

Changes in abdominal shape are best shown by development of the widths, L, M and N, relative to the total length of the abdomen, J (Table 9, eqns. 12—14) and the ontogeny of abdominal widths compared to one another (Table 9, eqns. 8, 9). The proportions of the anterior width of the abdomen, L, and the maximum width of the abdomen, M, decreased somewhat relative to the length of the abdomen, J; shape ratios for the smallest and largest specimens are: L/J, 0.49 and 0.40; M/J, 0.57 and 0.44. Development of L and M was almost isometric with respect to each other (Table 9, eqn. 8). The main shape change in abdominal widths occurred in the relationships of the last segment, N, with the other abdominal widths, L and M, and the abdominal length, J (Table 9, eqns. 9, 14). In both cases, N declined relative to the other measures. Shape ratios of the smallest and largest animals are N/L = 0.32 and 0.23; N/J = 0.16 and 0.09.

In summary, the major shape changes in the entire body included the relative lengthening of the abdomen, mainly preabdomen compared to the prosoma. The abdomen tended to become progressively more slender, the most intense change occurring in the last segment.

GROWTH OF THE PADDLES

The ontogeny of two paddle dimensions, total length, O, and maximum width, P, was studied for 27 specimens, ranging from 7.0 to 35.0 mm in prosomal length. The measurements are shown in Figs. 11 and 12 and the regression results are listed in Table 10.

The two paddle dimensions, total length, O, and maximum width, P, also decreased relative to overall size, G (Table 10, eqns. 1, 2). The shape ratios for the youngest and oldest animals are: O/G = 1.3 and 0.99; P/G = 0.50 and 0.43. Allometry is indicated by the large positive initial intercepts in conjunction with relatively small positive growth rates. The decrease of overall paddle dimensions relative to body size suggests that adults could have shown less swimming ability and perhaps spent more time on the bottom than the younger specimens. A similar phenomenon occurs in *Limulus*, where immature animals swim more actively and more frequently than the largest individuals. During ontogeny of paddle shape, width decreased somewhat compared to length (Table 10, eqn. 3).

INTEGRATION BETWEEN THE BODY AND PROSOMA

The intuitively most satisfying model for studying the strength of correlation between two sets of variables is that of canonical correlation. Although this method is one of the older ones, it has not been widely applied, as the main interpretations of the analysis lie with the sizes of coefficients of the pairs of equations for each set and it has in practice turned out to be difficult to judge the significance of these (cf. Blackith and Reyment, 1971).

Recently, psychometricians have succeeded in deepening the theoretical background of canonical correlation analysis with an improved means of interpreting the roles of the elements. These improvements have been made in the light of experience arising of recent years in developing the statistical foundations of factor analysis.

Five of the variables were judged as response variables and two of them as predictors, for a total number of 27 individuals from the Syracuse and Colgate collections. The predictor set comprises the width of the prosoma at its base L and the length of the prosoma G, in that order. The response variables are the width at the base of the third segment M, the width at the base of the last segment N, the length of the paddle O, the width of the paddle P, the length from the prosoma to the base of the seventh segment H. The locations of these measures are illustrated in Fig. 11.

We shall first consider the matrix of correlations for the seven variables considered together. It is:

		L	G	M	N	O	P	H	
R_{21}	L	1.00	0.96	0.99	0.96	0.85	0.89	0.93	R_{12}
	G	0.96	1.00	0.95	0.95	0.79	0.91	0.91	
	M	0.99	0.95	1.00	0.96	0.83	0.88	0.93	
	N	0.96	0.95	0.96	1.00	0.71	0.83	0.88	
	O	0.85	0.79	0.83	0.71	1.00	0.85	0.83	
R_{21}	P	0.89	0.91	0.88	0.83	0.85	1.00	0.89	R_{22}
	H	0.93	0.91	0.93	0.88	0.83	0.89	1.00	

With such high correlations, it is to be expected that most of the variation will lie with the first pair of canonical variates.

The dashed lines in the correlation matrix denote its partitioning into four submatrices (for producing the characteristic equation required for finding the correlations between sets).

Table 11. Vector loadings for the first canonical correlation for *Eurypterus remipes remipes.*

Variable	Response weightings		Variable	Predictor weightings	
	Unadjusted	*Adjusted*		*Unadjusted*	*Adjusted*
M	0.56	1.00	L	−1.13	0.93
N	0.26	0.96	G	2.14	0.93
O	0.16	0.85			
P	0.00	0.90	CORRELATION = 0.95		
H	0.02	0.93			

Submatrices R_{11} and R_{22} contain the correlations for the two sets, predictors and responses, respectively. Submatrices R_{12} and R_{21} contain the correlations linking the variables across the two sets. The purpose of this analysis is to present these interrelationship in paired linear combinations of the variables. The rank of the smaller of the submatrices R_{11} and R_{22} determines the number of paired combinations.

We shall begin the analysis of the 27 individuals by briefly considering the direct relationships between the elements of the cross-correlation matrices. Practically all of the variation in the negative definite matrix R_{12} resides in one eigenvalue. Only the first eigenvalue is significant (Bartlett's test yields $\chi^2_{10} = 53.3$). In effect, virtually all of the information contained in the observations is localized to the first eigenvalue and its associated vectors.

A comparison of the raw loadings and the improved "factorial" estimates is presented in Table 11. It will be seen that the raw loadings (unadjusted) are meaningless. If only these were available for interpretation, the analysis would be rejected out of hand by any quantitative biologist, for they are at complete variance with all other information. For example, we have the completely misleading zero coefficients for P and H. The adjusted coefficients give, however, a completely different picture. All weights are roughly the same and, with the canonical correla-

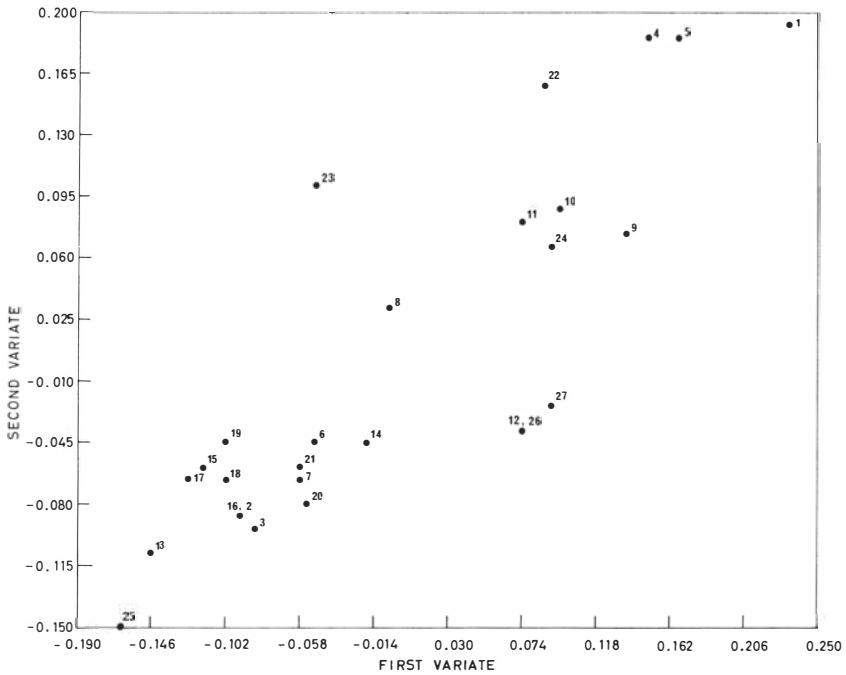

Fig. 14. Plot of the scores for the canonical variates of the first canonical correlation for *E. r. remipes*. The points falling in the upper part of the plot (points 1, 4, 5, 22) are the largest specimens of the sample, those falling in the lower corner (points 25, 13 and 3) are the smallest individuals.

tion of 0.95, the exceptionally high integration between body and head is manifest.

Another instructive result arising from the adjusted weightings is the equal contributions of the predictor variables L and G. In the unadjusted coefficients they are in a negative relationship which is misleading.

The "transformed canonical scores" for the two sets of vectors were plotted (Fig. 14). The most obvious thing arising from this plot is the spread of the values, according to size, across the field, with the smallest falling in the bottom left quadrant and the largest in the upper right quadrant. As a result of the high level of integration, both axes reflect size variation, although the horizontal axis also includes a shape-differentiating element over part of the field (i.e. among more mature specimens).

A redundancy analysis can hardly be expected to furnish any surprises. All variables correlate highly with the original data (0.88 L, 0.88 G) and (0.95 M, 0.91 N, 0.81 O, 0.85 P, 0.89 H). The redundancy coefficients are 0.77 for predictors and responses alike, and also for both total coefficients of redundancy.

There is virtually nothing left over for the second canonical correlation, which is a low 0.14. The raw vector elements give high and apparently meaningful loadings, but these are artifacts. All of the adjusted coefficients are close to zero, with only the length of the paddle approaching a meaningful level. This variable was the most difficult of all to measure, and we suspect that its high coefficient is a reflection of measurement error.

R AND Q MODE ANALYSES

The same seven prosomal and abdominal measurements as used in the canonical correlation as well as the full set of prosomal measures were subjected to an R-mode principal components analysis. Although we consider the canonical correlation model to be more appropriate to the biological problem at hand, it is well known, that an *in toto*

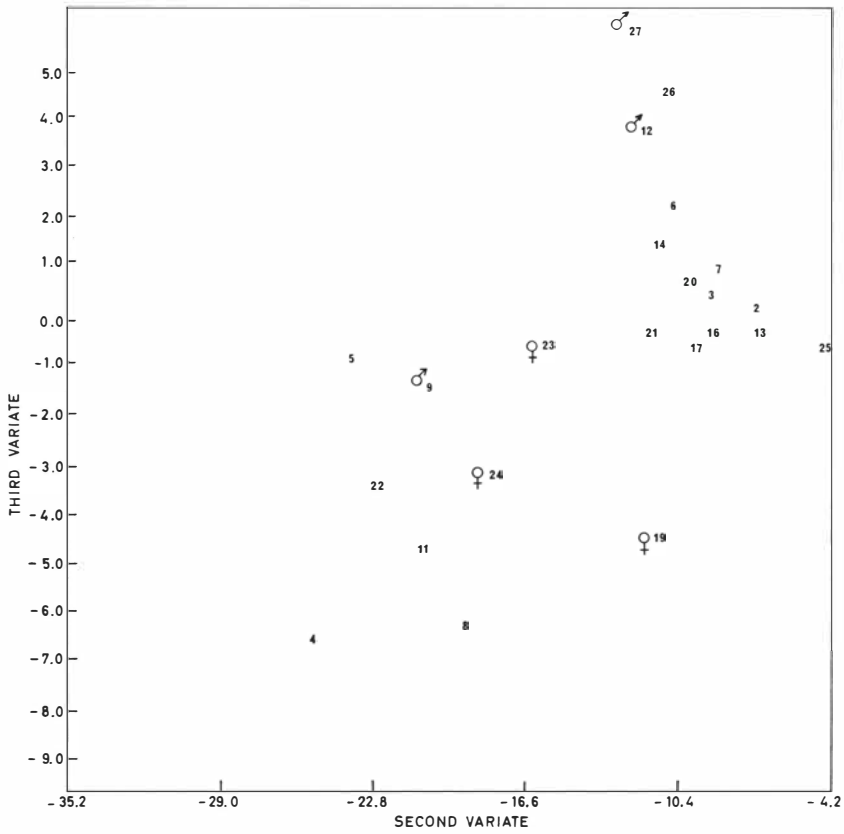

Fig. 15. Graph of the scores of the second and third principal components for *Eurypterus remipes remipes.* The numbering of the points is the same as for the plot of the canonical correlation scores of Fig. 14. Observe the locations of the sexable specimens.

consideration of the data often yields useful information that might otherwise be overlooked.

Should the matrix of correlations or the matrix of covariances serve as a base for the eigenanalysis? There are several arguments that speak in favour of the former. Firstly, we are interested in examining the morphological integration of the eurypterid. The correlations are clearly, then, the obvious starting point. Secondly, the correlations are in themselves a form of standardization. In the present study, this is a necessary consideration, as the variables have widely differing ranges of variation. In fact, the first eigenvector of the covariance matrix turns out to reflect, faithfully, the sizes of the respective standard deviations. We could have standardized our observations by the usual method of dividing the deviate from the mean by the appropriate standard deviation; this would have given much the same result as the correlations.

The first principal component of the correlation matrix is connected to more than 90 % of the total variation. All of its elements are close in value (0.39, 0.39, 0.39, 0.38, 0.35, 0.37, 0.38), showing the remarkably even contributions of each of the variables and, consequently, the exceptionally close-knit integration. The second principal component, including only 5 % of the variation, contrasts mainly the width of the paddle with the width of the base of the last segment; this is possibly a dimorphic characteristic. This principal component has the structure:

$$z_2 = 0.2\,G - 0.2\,M - 0.5\,O + 0.8\,P + 0.3\,H.$$

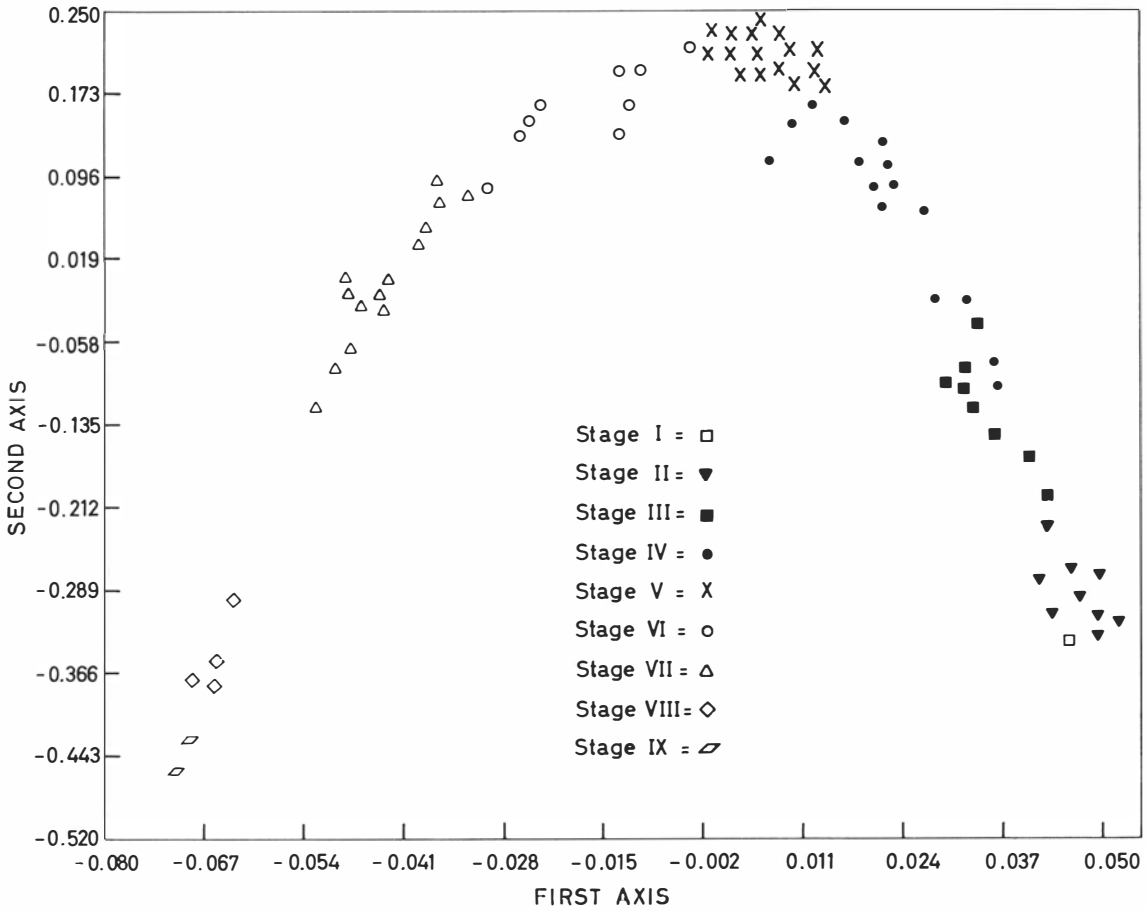

Fig. 16. Plot of the first two sets of coordinates for the principal coordinates analysis of prosomas of *E. r. remipes* from the Colgate collection. This plot gives a remarkably good ordination into moult stages. The parabolic form of the plot is in part a result of the high degree of correlation between the variables of the prosoma, in part indicatory of a quadratic relationship between the first and second eigenvectors of the association matrix.

The plot of the first two transformed scores also reflects a growth-size relationship, as one might expect. The grouping of the observations into two fields found in our data is difficult to explain, but it might bear some relationship to sexual dimorphism. Too few sexed specimens were available for a detailed analysis, but these do seem to have a tendency to segregate. This is most clearly indicated on the plot of the second and third transformed variables, shown in Fig. 15. The second and third eigenvalues represent together almost 7 % of the total variation. The possible indication of dimorphism suggested by the paddle to pre-telson relationship does, therefore, appear to receive a measure of support in the graphical analysis. The third principal component (2 % of the variance) has the structure:

$$z_3 = -0.\,\mathrm{L} + 0.2\,\mathrm{G} - 0.3\,\mathrm{M} - 0.2\,\mathrm{N} - 0.4\,\mathrm{O} + 0.8\,\mathrm{P}.$$

It is mainly a measure of shape variation in the paddle.

The principal components of the correlation matrix of the ten prosomal measurements were extracted (the first three components are shown in Table 12). The first component is a growth factor, the second and third components reflect shape differences, particularly in the shape and

Table 12. Principal components for the prosoma of *Eurypterus remipes remipes* from the Colgate collection.

Variable	Principal component I	II	III
A Prosoma width anterior to the eyes	0.319	0.041	−0.197
B Posterior width of the prosoma	0.318	−0.058	−0.171
C Length from posterior margin of prosoma to anterior of eyes	0.312	−0.515	0.597
G Total length of prosoma	0.318	−0.135	0.142
U Prosomal width posterior to the eyes	0.317	0.016	−0.160
V Length from eyes to anterior margin of prosoma	0.315	0.423	0.218
W Length from posterior margin of prosoma to posterior margin of eyes	0.317	−0.163	0.234
X Distance from eyes to lateral margin of prosoma	0.312	0.674	0.219
Y Anterior distance between the eyes	0.317	−0.057	−0.404
Z Posterior distance between the eyes	0.316	−0.221	−0.465
Percent of correlation matrix trace associated with the listed component	97.6 %	0.8 %	0.5 %

positioning of the eyes. This agrees with the results for *E. r. tetragonophthalmus.*

The prosomal observations on 77 prosomas in the Colgate collection were analysed by the Q-mode technique introduced by Gower (1966). For biological interpretations, see Blackith and Reyment (1971). This analysis succeeds in ordinating the individuals into successive size classes, which represent moult stages. The graph of values of the principal coordinates for the 77 individuals, shown in Fig. 16, has a paraboloid form, a reflection of the very high correlations between variables and a quadratic relationship between the eigenvectors forming the first and second axes. The residual, after two eigenvalues had been extracted, was only 31.8 %, a low value for studies of his type. After "size variation" had been removed from the observations, using the principal components model, the plots of the new set of principal coordinates yielded a completely haphazard picture, reflecting largely random variability. A few points forming an attenuated cluster away from the main body could not be interpreted meaningfully.

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