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EVOLUTION OF MIDDLE DEVONIAN SPECIES OF *EUGLYPHELLA*
AS INDICATED BY CLADISTIC ANALYSIS

BY

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CONTRIBUTIONS FROM THE MUSEUM OF PALEONTOLOGY

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VOLUME 24

1. A new species of *Porocrinus* from the Middle Ordovician Kimmswick Limestone of Missouri, by Robert V. Kesling. Pages 1-7, with 2 plates and 8 text-figures.
2. *Strataster devonicus*, a new brittle-star with unusual preservation from the Middle Devonian Silica Formation of Ohio, by Robert V. Kesling. Pages 9-15, with 2 plates and 3 text-figs.
3. Coccoliths and related calcareous nannofossils from the Upper Cretaceous Fencepost Limestone of northwestern Kansas, by John M. Huh and Charles I. Smith. Pages 17-22, with 2 plates.
4. Ordovician vertebrates from Ontario, by Kathleen Anne Lehtola. Pages 23-30, with 2 plates and 1 text-figure.
5. New *Botryocrinus* and *Glossocrinus* from the Middle Devonian Bell Shale of Michigan, by Robert V. Kesling. Pages 31-46, with 8 plates and 2 text-figures.

EVOLUTION OF MIDDLE DEVONIAN SPECIES OF *EUGLYPHELLA* AS INDICATED BY CLADISTIC ANALYSIS

SABEEKAH ABDUL-RAZZAQ

ABSTRACT—By the Prim network and the Wagner groundplan-divergence method, a cladistic analysis of *Euglyphella* species produces an evolutionary tree indicating unsuspected relationships. As a result of detailed inspections of hundreds of specimens and calculations of the characters of hypothetical intermediate operational taxonomic units, a much better understanding of the genus is obtained.

INTRODUCTION

ONE OF THE MORE DIFFICULT PROBLEMS in paleontology is the evolution of animals, arranging the members of a taxon into lineages which logically, at least, seem to reflect their natural descent through time. Evolution is particularly hard to determine at the species level, since the discrimination of species themselves is based on minute morphological differences which, more often than not, exhibit individual variations. If one is concerned with only a few species and two or three characteristics, it is possible to keep all the data in mind while shifting the species into a sensible scheme of derivation. Such situations are rare. Most species possess numerous characteristics, and many evolutionary trees involve several species. Some kind of numerical treatment is necessary to bring the mass of data into condensed and usable form.

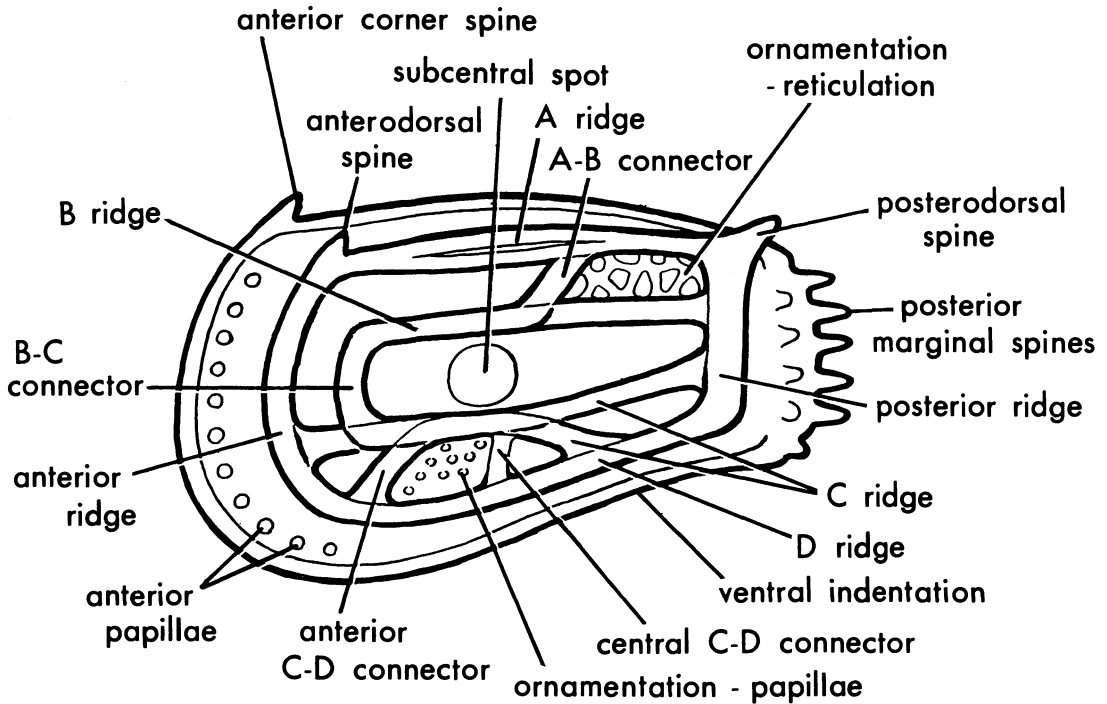
This brings us to the time factor. Chronology is an ever-present bias. Whatever trends are apparent within the group of species after mathematical manipulation, the evolutionary succession must finally conform to the known geologic sequence of occurrences in most respects. Some latitude is usually regarded as permissible; some time discrepancies are excused on the assumption that the paleontologic record is incomplete.

When all the procedures have been completed and the final evolutionary tree is presented, the truth of the lineages suggested must rest on the accuracy with which genetic relationships are reflected in phenetic expression and on the reliability of the numerical treatment to assess phenetic differences. Of these two factors, the first remains, for the present at least, outside the scope of paleontologic investigation.

In this paper, I follow the procedures used

by Kesling & Sigler (1969). These involve the methods first introduced in the Prim (1957) network and the Wagner (1954) groundplan divergence. Simply stated, as many characters as can be observed in all species are coded as consistent numerical values for each species (as outlined by Sneath, 1964, p. 43-45), the phenetic differences between all pairs of species are determined, the species are linked together in a tree or network such that the least possible phenetic difference is used, the tree is arranged to conform to time sequence insofar as possible, possible hypothetical intermediate species are sought among triads of species in close proximity on the tree, the values assigned to coded characters are weighted according to their significance in the formation of the tree, and the procedure is repeated with the revised values to produce a final tree. If fortune is kind, the final tree will coincide with the first; this would signify that the characters selected for the study were all of nearly the same evolutionary merit. If the final tree differs from the first, then the numerical procedure will have disclosed which of the characters has little evolutionary significance.

Euglyphella is an ostracod that includes many species. Because the genus is restricted to Middle Devonian time, its evolution must be considered as rapid, if not explosive, radiation. Several factors combine to make *Euglyphella* an ideal subject for cladistic analysis. First, the carapaces of the species contain a variety of complex ridges, ornamentation, proportions, and sizes; in all, I used 29 different characters in the study. Second, for most species, specimens are plentiful; for several, hundreds of specimens are available to show the individual ranges of characters. Third, the species of *Euglyphella* have already received taxonomic attention; although I am confident



TEXT-FIG. 1.—Composite sketch of *Euglyphella* showing location and terminology of features occurring in various species.

that at least one species is still undescribed, I restricted this investigation to the species present in literature. Fourth, the Middle Devonian formations which yield *Euglyphella* have been searched sufficiently to discover at least the common species. And fifth, the locations of collecting sites in northern Michigan, northwestern Ohio, Ontario, and western New York offer a chance to determine if some of the evolution proceeded in isolation.

For her patient washing of samples and arduous picking of *Euglyphella* specimens, I am much indebted to Ruth Berner (Mrs. William) Chilman, Research Associate in the Museum of Paleontology. Mr. Karoly Kutasi assisted in preparation of the illustrations, Mrs. Helen Mysyk typed the manuscript, and Mrs. Gladys Newton read the proofs. All deserve my deep gratitude.

SPECIES

Ostracods of the genus *Euglyphella* all have the left valve conspicuously larger than the right, overlapping it particularly strongly on the dorsal, anterodorsal, and ventral borders. In the left valve the diagnostic characters are more clearly defined. In selecting ostracods for study, I eliminated *Euglyphella trialis* described and figured by Peterson (1966, p. 11, pl. 1, fig. 16) from the Windom Formation,

inasmuch as the only known specimen is the holotype, a right valve. It appears to be directly descended from *Euglyphella simplex*.

Aside from this species, we can distinguish 11 Middle Devonian species of *Euglyphella* that are sufficiently well represented to show the essential characters of the left valve. They are the operational taxonomic units (OTUs) in this paper.

EUGLYPHELLA ABDITA Peterson

E. abdita Peterson, 1966, p. 5, pl. 1, figs. 3, 11, 12, text-fig. 1.

EUGLYPHELLA ASAPHA Stover

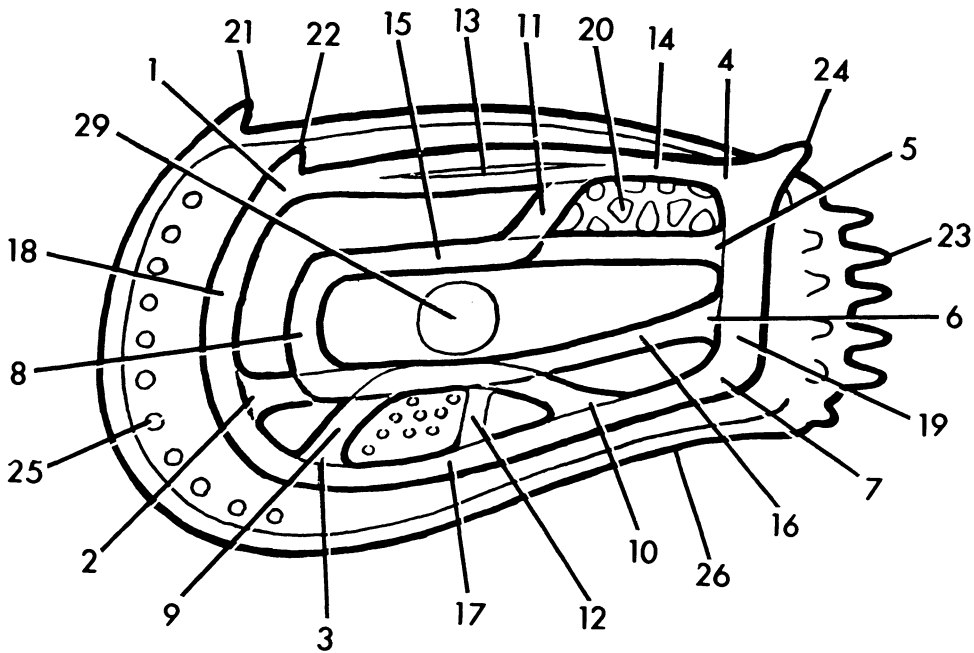
E. asapha Stover, 1956, p. 1128, pl. 118, figs. 17, 18, text-fig. 2. Kesling *et al.*, 1959, p. 19, table 1. Peterson 1966, p. 4, pl. 2, figs. 2, 3, 6, 21, text-fig. 1.

EUGLYPHELLA COMPRESSA Coryell & Malkin

E. compressa Coryell & Malkin, 1936, p. 7, fig. 19. Warthin, 1945, card 74. Kesling & Weiss, 1953, p. 58, pl. 4, fig. 16. Kesling *et al.*, 1959, p. 19, pl. 1, figs. 25-42; pl. 4, figs. 20-27, text-fig. 2.
E. jenningsi Coryell & Malkin, 1936, p. 8, fig. 20. Warthin, 1945, card 75.
E. compressa compressa Peterson, 1966, p. 3, pl. 1, figs. 6, 24, 26, 27; pl. 2, figs. 4, 25, text-fig. 1.

EUGLYPHELLA CROSSICA Peterson

E. crossica Peterson, 1966, p. 5, pl. 1, figs. 25, 32, text-figs. 1, 2.



TEXT-FIG. 2—Composite sketch of *Euglyphella* showing locations of characters coded in this study.

EUGLYPHELLA LISPA Peterson

E. compressa lispa Peterson, 1966, p. 5, pl. 1, figs. 7, 28, 29; pl. 2, figs. 13–15, 18, 22, text-fig. 1.

EUGLYPHELLA MODESTA Peterson

E. compressa modesta Peterson, 1966, p. 4, pl. 1, figs. 14, 15; pl. 2, figs. 24, 27, text-fig. 1.

EUGLYPHELLA NUMISMOIDES Swartz & Oriel

E. numismoides Swartz & Oriel, 1948, p. 562, pl. 81, figs. 1–8. Stover, 1956, p. 1131, pl. 118, figs. 24–27, text-figs. 7, 8. Peterson, 1966, p. 9, pl. 1, figs. 4, 5; pl. 2, figs. 16, 20, 28, 29.

EUGLYPHELLA PARALLELA Peterson

E. parallela Peterson, 1966, p. 6, pl. 1, figs. 30, 31; pl. 2, figs. 1, 5, text-fig. 1.

EUGLYPHELLA PROJECTA Coryell & Malkin

E. projecta Coryell & Malkin, 1936, p. 7, fig. 18. Warthin, 1945, card 77. Stover, 1956, p. 1131, text-fig. 6. Smith, 1956, table 1. Kesling *et al.*, 1959, p. 17, pl. 1, figs. 5–24; pl. 4, figs. 8–19, text-fig. 1. Peterson, 1966, p. 10, pl. 1, figs. 17–20, 37, 38; pl. 2, figs. 8–12.

E. spinosa Stewart, 1950, p. 663, pl. 86, figs. 16, 17.

E. deltella Stover, 1956, p. 1130, pl. 118, figs. 19–23, text-figs. 3–5.

EUGLYPHELLA SIGMOIDALIS (Jones)

Strepula sigmoidalis Jones, 1890a, p. 11, pl. 2, fig. 4. Grabau & Shimer, 1910, p. 350, fig. 1660o.

S. plantaris Jones, 1890b, p. 540, pl. 20, figs. 8a, b.

Octonaria percarinata Van Pelt, 1933, p. 335, pl. 39, figs. 52–54.

Euglyphella sigmoidalis Warthin, 1934, p. 220, pl. 1, fig. 21. Bassler & Kellett, 1934, p. 37, 311, fig. 16 (no. 14). Coryell & Malkin, 1936, p. 7, fig. 17.

Shimer & Shrock, 1944, p. 681, pl. 286, fig. 7. Warthin, 1945, card 78. Kesling & Kilgore, 1952, p. 10, pl. 3, figs. 30–36. Kesling & Weiss, 1953, p. 58, pl. 4, figs. 12–15. Kesling *et al.*, 1959, p. 17, pl. 1, figs. 1–4. Peterson, 1966, p. 7, pl. 1, figs. 13, 21–23; pl. 2, figs. 7, 17, 19, 23, 26.

E. sigmoidalis var. *primitiva* Warthin, 1934, p. 221, pl. 1, fig. 22.

E. primitiva Warthin, 1945, card 76. Smith, 1956, table 1.

EUGLYPHELLA SIMPLEX Kesling & Weiss

E. simplex Kesling & Weiss, 1953, p. 58, pl. 4, figs. 8–11. Peterson, 1966, p. 11, pl. 1, figs. 1, 2, 8–10, 33–35.

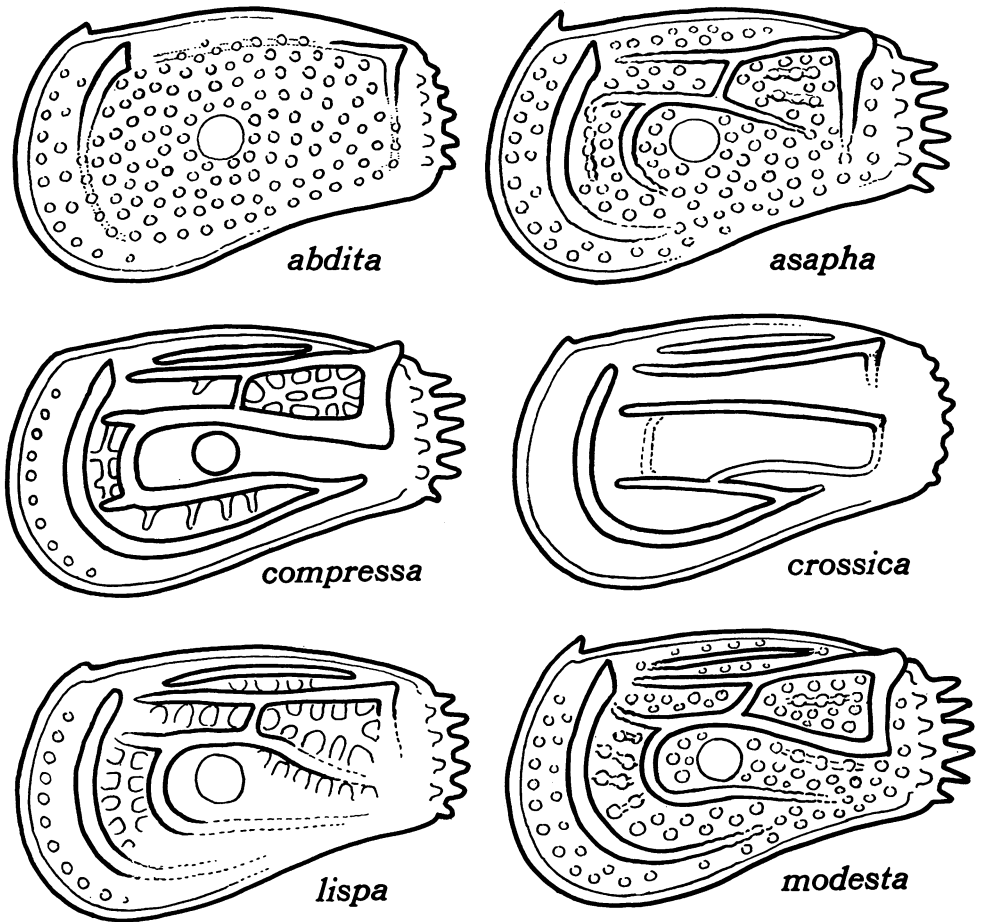
LOCALITIES AND OCCURRENCES

In the course of the investigation, I looked at *Euglyphella* specimens from the following localities:

Northwestern Michigan

Petoskey Formation. (1) Shore of Lake Michigan at low water level, about 1½ miles north of Norwood, Charlevoix County. (2) Kegomic quarry about 1 mile east of Bay View, Emmet County. *Euglyphella abdita*, *sigmoidalis*, and *simplex*.

Gravel Point Formation. (1) Ledges on shore of Little Traverse Bay near end of Encampment Avenue, Bay View, Emmet County. (2) Charlevoix Lime & Stone Company quarry, 2 miles west of Charlevoix, Charlevoix County. *E. compressa*, *parallela*, *sigmoidalis*, and *simplex*.



TEXT-FIG. 3—Simulations of species based on coded characters, differing from sketches of actual species primarily in relative size and proportions.

Northeastern Michigan

Potter Farm Formation. Small shale pit in northwest corner of Evergreen Cemetery, Alpena, Alpena County. *E. compressa*, *sigmoidalis*, and *simplex*.

Norway Point Formation. (1) Southwest bank of Thunder Bay River about 1 mile downstream from Four Mile Dam, Alpena County. (2) South bank of river just below Four Mile Dam. (3) South bank of Thunder Bay River just below Seven Mile Dam. *E. compressa*, *sigmoidalis*, and *simplex*.

Dock Street Clay Member of Four Mile Dam Formation. Abandoned railroad cut leading from Thunder Bay quarry in Alpena, Alpena County. *E. parallela* and *sigmoidalis*.

Alpena Limestone. (1) Shale near middle of formation, quarry of Huron Portland Cement Company in Alpena, Alpena County. (2) Abandoned Griffin or Bolton quarry near Detroit & Mackinac Railroad, about

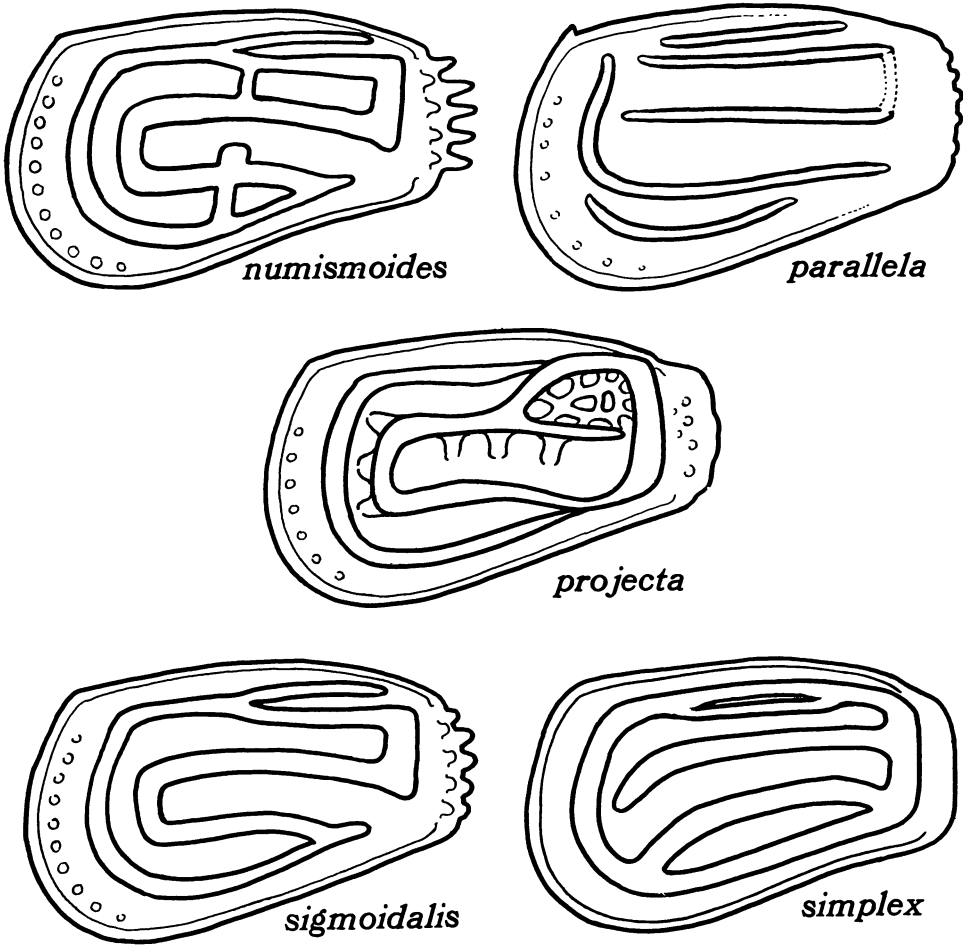
1¼ miles northwest of Bolton, Alpena County. *E. sigmoidalis* and *simplex*.

Genshaw Formation. Ditch on west side of West Long Lake Road, about ⅓ mile north of county line, Presque Isle County. *E. sigmoidalis* and *simplex*.

Ferron Point Formation. Abandoned shale pit of Alpena Portland Cement Company nearly 1 mile east of former site of Genshaw School, 8 miles northeast of Alpena, Alpena County. *E. crossica*, *sigmoidalis*, and *simplex*.

Rockport Quarry Limestone. Road cut on U.S. Highway 23 about ½ mile west of Trout Creek and 10 miles southeast of Rogers City, Presque Isle County. *E. sigmoidalis*.

Bell Shale. (1) Sink fillings in quarry of Michigan Limestone Division of U.S. Steel Corporation, Calcite, ½ mile east of Rogers City, Presque Isle County. (2) Abandoned quarry of Kelley's Island Lime & Transport Company, Rockport, northeast corner



TEXT-FIG. 3 (cont'd).

of Alpena County. *E. projecta*, *sigmoidalis*, and *simplex*.

Northern Ohio

Silica Formation. Quarries of Medusa Portland Cement Company on Centennial Road near Silica, about 2 miles west-southwest of Sylvania, Lucas County. *E. compressa*, *modesta*, *projecta*, and *sigmoidalis*.

Plum Brook Shale. Exposures along tributary of Pipe Creek north of Taylor Road and east of Patton Tract Road in Bloomingville, now a restricted area of National Aeronautics & Space Administration, Erie County. *E. sigmoidalis*.

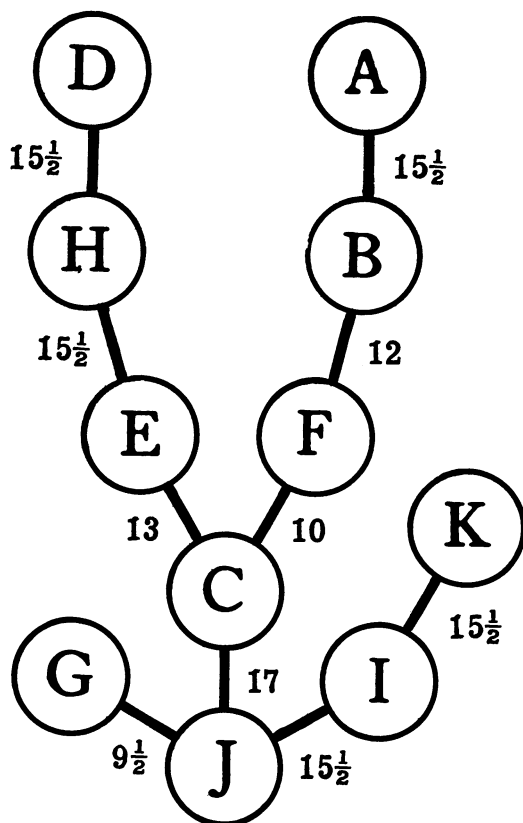
Delaware Limestone. Roadside exposure at junction of McCoy and Scioto River Roads, east side of Scioto River 1 mile north of Fishinger Bridge, Franklin County (Stewart's type locality for *E. spinosa*). *E. projecta*.

Western Ontario

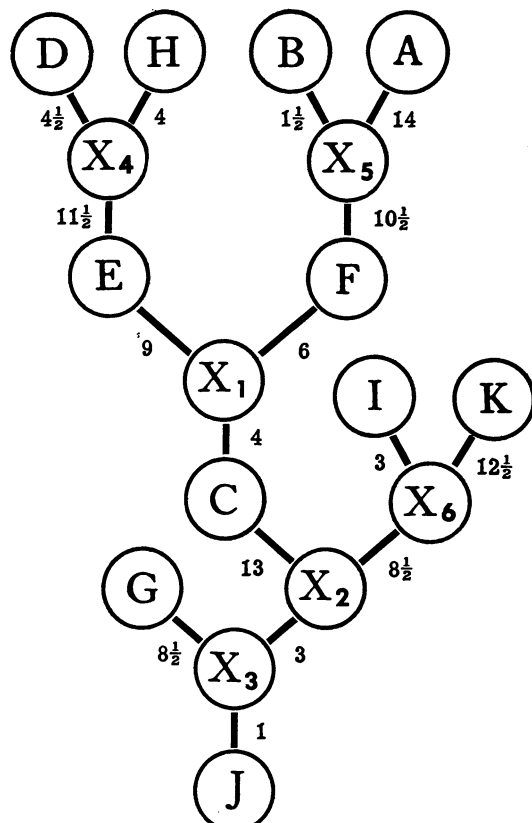
Ipperwash Limestone. Shore of Lake Huron at end of Military Road, Stony Point Provincial Park, Bosanquet Township, Lambton County. *E. sigmoidalis*.

Widder Formation. (1) Roadside exposure at former site of Widder, on west side of King's Highway 82, about 1 mile southeast of Thedford, Lambton County. (2) Abandoned Jim Bell's quarry on Ridge Road, about 1½ miles east-northeast of railroad station in Thedford. (3) Hill Number 4 at base of waterfall ½ mile west of Ausable River and 2 miles north of Arkona, Bosanquet Township, Lambton County. *E. compressa* and *lispa*.

Hungry Hollow Formation. (1) Brick and tile yard just north of Thedford. (2) North bank of Ausable River at Hungry Hollow, West Williams Township, Middlesex County, 2 miles east-northeast of



TEXT-FIG. 4.—Tree I, the preliminary Prim network of species based on the least possible (maximum parsimony) phenetic differences. Total phenetic differences (path) = 139.



TEXT-FIG. 5.—Tree II, cladogram formed by the Prim network with addition of hypothetical intermediates by the Wagner groundplan-divergence method. Total phenetic differences (path) = $114\frac{1}{2}$.

Arkona. *E. compressa*, *lispa*, *projecta*, and *sigmoidalis*.

Arkona Shale. (1) Brick and tile yard just north of Thedford. (2) North bank of Ausable River at Hungry Hollow. (3) East bank of Ausable River at Rock Glen, West Williams Township, about 1 mile northeast of Arkona. (4) Lot 8 on north bank of Ausable River about 4 miles north-northeast of Arkona. *E. sigmoidalis* and *simplex*.

Western New York

Windom Formation. (1) Railroad cut at Highland Acres, Erie County. (2) Banks of Cazenovia Creek, $\frac{1}{2}$ mile west of Spring Brook, Erie County. (3) Exposures on Rush Creek near U.S. Highway 62 between Blasdell and Bayview, Erie County. (4) North bank of small pond $\frac{1}{2}$ mile south of intersection of N.Y. Route 63 and Starr Road, Genesee County. *E. asapha*, *numismoides*, and *projecta*.

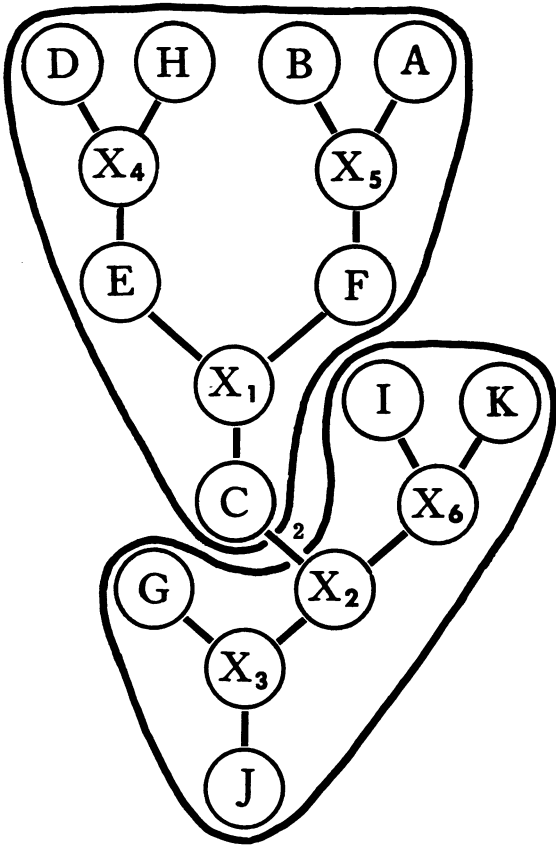
Kashong Shale. (1) Exposures along Black Creek about 1 mile northwest of East

Bethany and $\frac{1}{2}$ mile downstream from Paul Road, Genesee County. (2) Banks of Bowen Brook and road cut north of Walker Road, $2\frac{1}{4}$ miles northwest of Alexander, Genesee County. *E. asapha*, *numismoides*, and *projecta*.

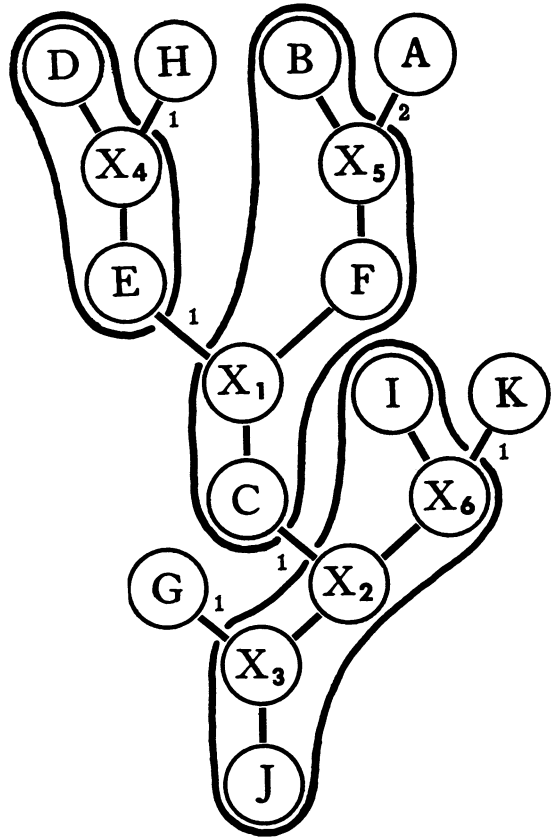
Wanakah Shale. (1) Roadside exposure 2 miles southeast of East Bethany, Genesee County. (2) Abandoned shale pit off Big Tree Road near Lake Shore Highway 5 at Bayview, Erie County. (3) Railroad cut at Highland Acres, Erie County. *E. asapha*, *compressa*, *lispa*, *modesta*, *numismoides*, *projecta*, and *sigmoidalis*.

Ledyard Formation. (1) Cut of Delaware, Lackawanna & Western Railroad $3\frac{1}{2}$ miles west of East Bethany, Genesee County, at overpass of Francis Road. (2) Exposures on west side of Bethany Center Road, just south of railroad cut, $1\frac{1}{2}$ miles west of East Bethany. *E. abdita*, *asapha*, *lispa*, *projecta*, and *sigmoidalis*.

Centerfield Formation. (1) Field exposure



TEXT-FIG. 6—Tree II with the phenetic changes in character 1, the junction of anterior and A ridges. The low total of 2 points indicates a high significance of this character in the evolution of *Euglyphella*.



TEXT-FIG. 7—Tree II with the phenetic changes in character 27, length of left valve, excluding posterior marginal spines. The high total of 7 points indicates a low significance of this character in the evolution of *Euglyphella*.

northwest of intersection of Sumner and Simons Roads, 2 miles northeast of Darien, Genesee County. (2) Cut of Delaware, Lackawanna & Western Railroad 3½ miles west of East Bethany, Genesee County. (3) Cut of D. L. & W. Railroad about 1½ miles west of East Bethany at Bethany Center Road overpass. (4) Exposures along White Creek about 2 miles east of East Bethany and ¼ mile north of D. L. & W. Railroad. *E. compressa*, *lispa*, *projecta*, and *sigmoidalis*.

The relative ages of these formations is indicated in text-figure 9, and the occurrence of species is shown in text-figure 10.

SPECIMENS

The following specimens were examined in my study of the characters in species of *Euglyphella*:

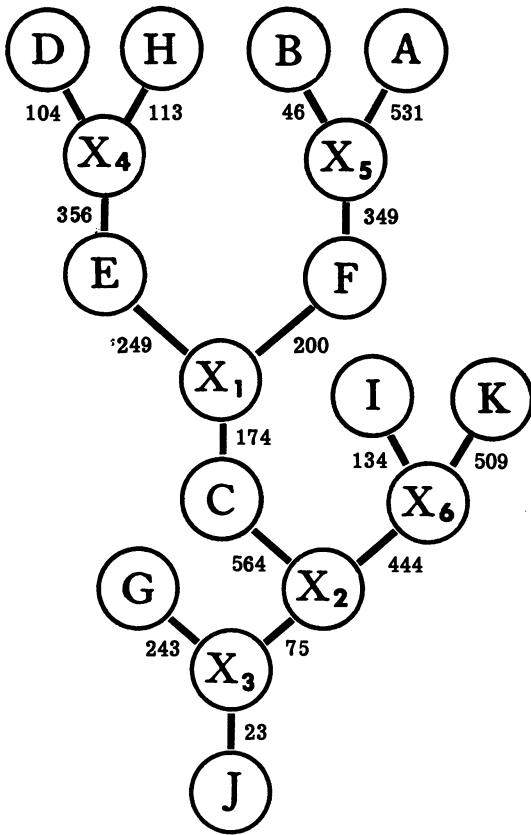
E. abdita—Petoskey Fm., holotype (UMMP

43111) and 4 paratypes (UMMP 43112–43115). Ledyard Fm., 3 specimens.

E. asapha—Ledyard Fm., 5 specimens. Wanakah Sh., 2 hypotypes (UMMP 43105, 43108). Kashong Sh., 2 hypotypes (UMMP 43106, 43107). Windom Fm., 3 hypotypes (UMMP 43104, 43109, 43110).

E. compressa—Gravel Point Fm., hypotype (UMMP 43044). Norway Point Fm., hypotype (UMMP 29850). Potter Farm Fm., hypotype (UMMP 43037). Silica Fm., 8 specimens. Hungry Hollow Fm., 2 hypotypes (UMMP 43045, 43047), 10 other specimens. Widder Fm., 4 specimens. Centerfield Fm., 19 hypotypes (UMMP 35471–35479, 35536–35542, 43040–43042), 6 other specimens. Wanakah Sh., 4 hypotypes (UMMP 43038, 43039, 43043, 43046), 77 other specimens.

E. crossica—Ferron Point Fm., holotype (UMMP 42988).



TEXT-FIG. 8—Tree III, based on weighted phenetic differences.

- E. lispa*—Widder Fm., 5 syntypes (UMMP 43073–43077), 60 other specimens. Centerfield Fm., 6 specimens. Ledyard Fm., 6 syntypes (UMMP 43069–43072, 43117, 43118). Wanakah Sh., 7 specimens.
- E. modesta*—Silica Fm., 13 specimens. Wanakah Sh., 3 syntypes (UMMP 43067, 43068, 43116), 9 other specimens.
- E. numismoides*—Wanakah Sh., 5 hypotypes (UMMP 43095–43098, 43102). Kashong Sh., 2 hypotypes (UMMP 43093, 43094). Windom Fm., 4 hypotypes (UMMP 43099–43101, 43103), 20 other specimens.
- E. parallela*—Gravel Point Fm., holotype (UMMP 42986). Dock Street Clay, paratype (UMMP 42987).
- E. projecta*—Bell Sh., hypotype (UMMP 43004). Silica Fm., 10 specimens. Hungry Hollow Fm., 4 hypotypes (UMMP 42992, 42993, 43001, 43002), 5 other specimens. Ipperwash Ls., hypotype (UMMP 42995). Centerfield Ls., 8 hypotypes (UMMP 35463, 35470, 35531–35535, 42996), 45 other specimens. Ledyard Fm., hypotype (UMMP 42999). Wanakah Sh., 4 hypo-

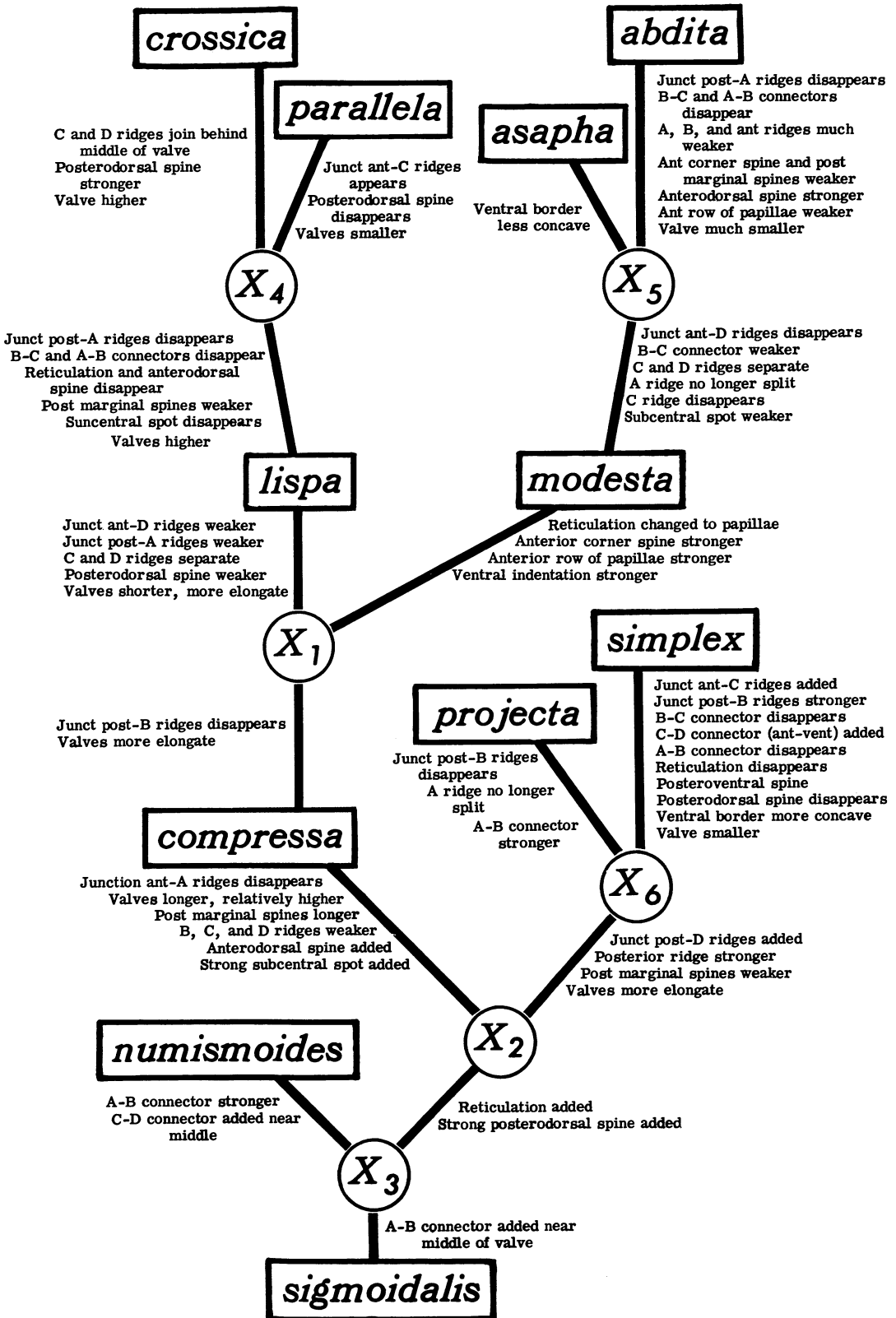
types (UMMP 42990, 42998, 43000, 43005), 83 other specimens. Kashong Sh., hypotype (UMMP 43003). Windom Fm., 4 hypotypes (UMMP 42989, 42991, 42994, 42997), 15 other specimens.

- E. sigmoidalis*—Gravel Point Fm., 2 hypotypes (UMMP 43027, 43028), 8 other specimens. Petoskey Fm., hypotype (UMMP 43031). Bell Sh., 7 hypotypes (UMMP 42832, 43006–43008, 43034–43036), 30 other specimens. Rockport Quarry Ls., hypotype (UMMP 43013). Ferron Point Fm., 4 hypotypes (UMMP 43009, 43018–43020), 40 other specimens. Genshaw Fm., 9 hypotypes (UMMP 28007–28013, 43021, 43022), 7 other specimens. Alpena Ls., 2 hypotypes (UMMP 43029, 43032). Dock Street Clay, 4 specimens. Norway Point Fm., 5 hypotypes (UMMP 29847–29849, 43011, 43030), 20 other specimens. Potter Farm Fm., 2 hypotypes (UMMP 43010, 43023). Plum Brook Sh., 2 hypotypes (UMMP 43012, 43017). Silica Fm., 3 hypotypes (UMMP 43014–43016), 275 other specimens. Arkona Sh., hypotype (43033). Ipperwash Ls., 2 hypotypes (UMMP 43024, 43025). Centerfield Fm., 2 hypotypes (UMMP 35459, 35460). Wanakah Sh., 29 specimens.
- E. simplex*—Uppermost Bell Sh. or basal Rockport Quarry Ls., 4 hypotypes (UMMP 43083–43086). Ferron Point Fm., 2 hypotypes (UMMP 43079, 43081). Genshaw Fm., hypotype (UMMP 43080). Alpena Ls., hypotype (UMMP 43092). Norway Point Fm., holotype (UMMP 29851), 2 paratypes (UMMP 29852, 29853), 3 hypotypes (UMMP 43026, 43087, 43091), 1 other specimen. Potter Farm Fm., 4 hypotypes (UMMP 43082, 43088–43090), 2 other specimens. Arkona Sh., 3 specimens.

In addition, Prof. R. V. Kesling has seen the type specimens described by Stover (1956).

CHARACTERS

The configuration of ridges, grooves, and spines varies so greatly from species to species in *Euglyphella* that it is difficult to formulate a standard pattern against which each species can be compared. The genus encompasses such diverse species as *simplex*, with nearly straight ridges separated by narrow grooves; *sigmoidalis*, with broadly sinuous ridges; *projecta*, with intervening networks of fine ridges between the major ones; and *abdita*, with ridges effaced and supplanted by little spines or papillae. Several models were devised and discarded before I arrived at the one shown in text-figure 1. This composite model of *Eugly-*



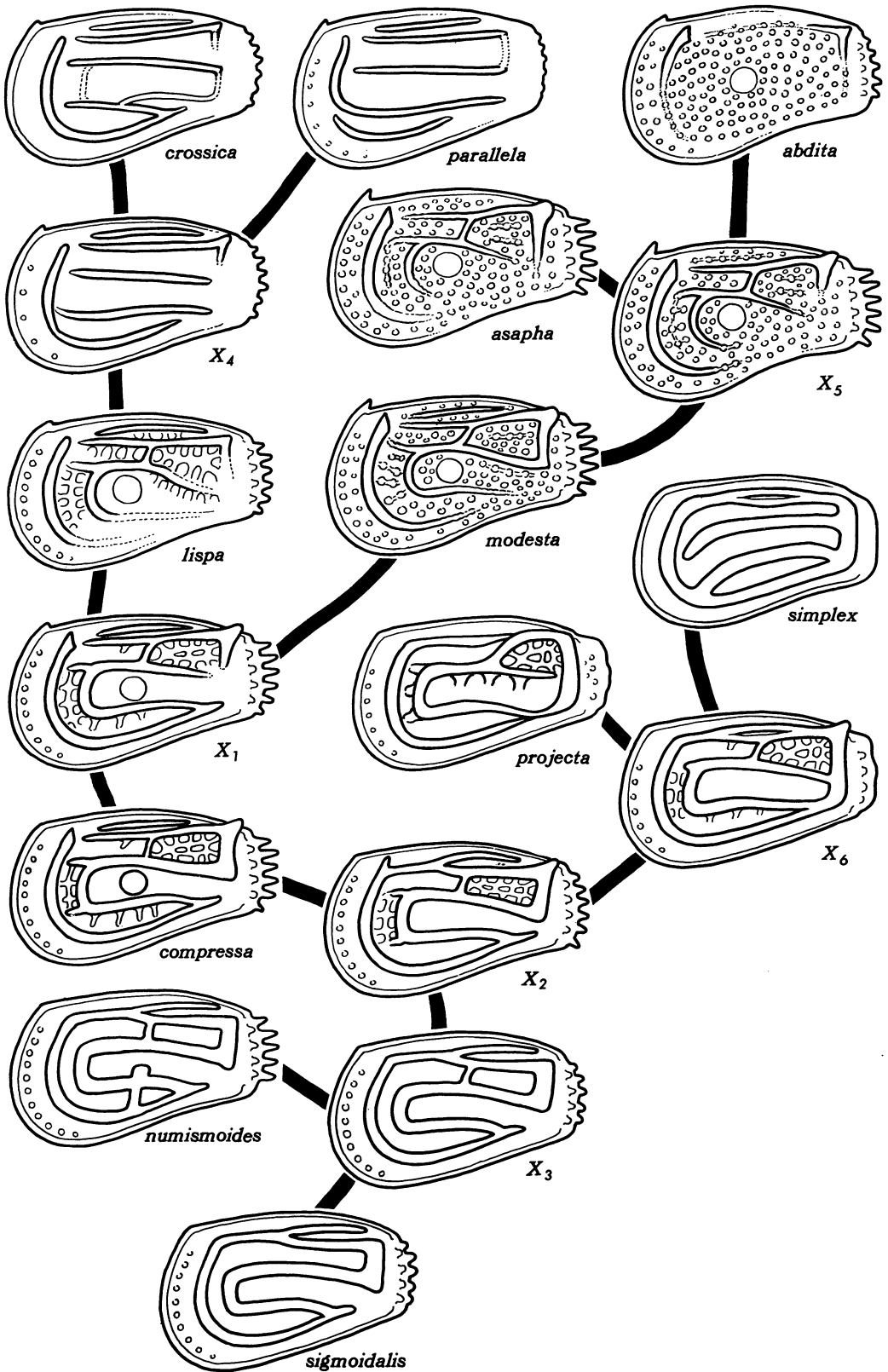
TEXT-FIG. 9—Major character changes (greater than 1/2 in value) in the evolution of *Euglyphella* (see tables 1, 2).

TABLE 1—DATA MATRIX FOR SPECIES OF *EUGLYPHELLA* (OTUs).

Species	OTU	Character																												
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
<i>abdit</i>	A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	2	1	2	1	2	0	1	1/2	
<i>asapha</i>	B	0	0	0	2	0	0	0	1	0	0	1	0	0	1	1	0	0	1	1	2	2	1	2	2	2	1	2	1	1
<i>compressa</i>	C	0	0	2	2	1	0	0	2	0	1 1/2	1	0	2	1 1/2	1	1	1/2	2	1	1	0	1	2	2	1	1/2	2	2	2
<i>crossica</i>	D	0	0	1	0	0	0	0	0	0	1 1/2	0	0	2	1	1	1	1	1	0	0	1/2	0	1/2	2	0	1/2	1	2	0
<i>lispa</i>	E	0	0	1/2	1	0	0	0	1 1/2	0	0	1	0	2	1	1	1/2	1/2	1	1/2	1	1/2	1	1 1/2	1	1	1/2	1	0	2
<i>modesta</i>	F	0	0	2	2	0	0	0	2	0	2	1	1/2	2	1	1	1	1/2	1 1/2	1/2	2	2	1	2	2	2	2	2	1	2
<i>numismoides</i>	G	2	0	2	2	1	0	0	2	0	1 1/2	2	2	1 1/2	2	2	2	2	2	1	0	0	0	2	0	2	1 1/2	2	2	0
<i>parallela</i>	H	0	1	0	0	0	0	0	0	0	0	0	0	2	1	1	1	1	1	0	0	1/2	0	1/2	0	1/2	0	0	1	0
<i>projecta</i>	I	2	0	2	2	0	2	2	2	0	1	2	0	0	2	2	2	2	2	2	1	0	0	0	2	1/2	0	1	0	0
<i>sigmoidalis</i>	J	2	0	2	2	1	0	0	2	0	1 1/2	0	0	1 1/2	2	2	2	2	2	1	0	0	0	1	0	1	0	1	1	0
<i>simplex</i>	K	2	2	2	2	2	2	2	0	1	1	0	0	1	2	2	2	2	2	2	0	0	0	0	0	0	0	1	0	0

TABLE 2—DATA MATRIX FOR HYPOTHETICAL INTERMEDIATES (OTUs).

OTU	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
X ₁	0	0	2	2	0	0	0	2	0	1 1/2	1	0	2	1	1	1	1/2	1 1/2	1/2	1	1/2	1	2	2	1	1/2	2	1	2
X ₂	2	0	2	2	1	0	0	2	0	1 1/2	1	0	1 1/2	2	2	2	2	2	1	1	0	0	1	2	1	0	1	1	0
X ₃	2	0	2	2	1	0	0	2	0	1 1/2	1	0	1 1/2	2	2	2	2	2	1	0	0	0	1	0	1	0	1	1	0
X ₄	0	0	1/2	0	0	0	0	0	0	0	0	0	2	1	1	1	1	1	0	0	1/2	0	1/2	1	1/2	1/2	1	1	0
X ₅	0	0	0	2	0	0	0	1	0	0	1	0	0	1	1	0	0	1	1/2	2	2	1	2	2	2	2	2	1	1
X ₆	2	0	2	2	1	2	2	2	0	1	1	0	1	2	2	2	2	2	2	1	0	0	0	2	1/2	0	1	0	0



TEXT-FIG. 10—Evolution of *Euglyphella* with simulations of species and hypothetical intermediates.

Rel Age	Northwestern MICHIGAN	Northeastern MICHIGAN	Northern OHIO	Western ONTARIO	Western NEW YORK
9	Petoskey Fm	Potter Farm Fm			
8					Windom Fm
7		Norway Point Fm		Ipper-wash Ls	Wanakah Sh
6				Widder Fm	Ledyard Fm
5	Charlevoix Ls	Dock St Clay		Hungry Hollow Fm	Centerfield Fm
4	Gravel Point Fm	Genshaw Fm		Arkona Sh	
3		Ferron Point Fm	Silica Fm, Plum Brook Sh		
2		Bell Shale			
1			Delaware Ls		

TEXT-FIG. 11—Relative ages, insofar as known, of principal Middle Devonian formations yielding *Euglyphella*. Slightly modified from Cooper *et al.*, 1942, pl. 1; Rockport Quarry and Alpena Limestones omitted in northeastern Michigan, Kashong Shale in western New York.

phella contains a pattern of ridges and spines which can serve as a reference for those occurring in any and all species. By omission or slight modification of the features in the composite model, a simulation of the essential configuration in any *Euglyphella* species can be achieved (text-fig. 3); the simulation differs from the actual species only in size and proportions of the valve. To account for the latter, length and height/length ratio are added as characters.

Twenty-nine characters were used in this study (text-fig. 2). Each character was noted and coded for each species. The characters are:

1. Junction of anterior and A ridges.
2. Junction of anterior and C ridges.
3. Junction of anterior and D ridges.
4. Junction of posterior and A ridges.
5. Junction of posterior and B ridges.
6. Junction of posterior and C ridges.
7. Junction of posterior and D ridges.
8. B-C connector ridge in anteroventral region.
9. C-D connector ridge in anteroventral region.
10. Junction of C and D ridges (0 = no junction; 1 = junction near posterior ridge; 2 = junction near middle of valve).
11. A-B connector ridge near middle of valve.
12. C-D connector ridge or bar near middle of valve.
13. Longitudinal division of A ridge (0 = no split; 1 = split but still joined at ends; 1½ = split but joined at one end, bifurcate; 2 = split into separate ridges).
14. Development of A ridge.
15. Development of B ridge.
16. Development of C ridge.
17. Development of D ridge.
18. Development of anterior ridge.
19. Development of posterior ridge.
20. Ornamentation of valve sides (0 = none, smooth; 1 = reticulation of small ridges; 2 = papillae).
21. Anterior corner spine at valve margin.
22. Anterodorsal spine at upper end of anterior ridge.

TABLE 3—PHENETIC DIFFERENCES OF *EUGLYPHELLA* SPECIES (OTUs).

Species	OTU	A	B	C	D	E	F	G	H	I	J	K
		<i>abdita</i>	<i>asapha</i>	<i>compressa</i>	<i>crossica</i>	<i>lispa</i>	<i>modesta</i>	<i>numismoides</i>	<i>parallela</i>	<i>projecta</i>	<i>sigmoidalis</i>	<i>simplex</i>
<i>abdita</i>	A	—	15½	28½	19½	19½	24½	40	18	37	33½	40½
<i>asapha</i>	B	15½	—	17	23	14	12	28½	23½	30½	29	40
<i>compressa</i>	C	28½	17	—	18	13	10	17½	25½	24½	17	33
<i>crossica</i>	D	19½	23	18	—	16	21	26½	8½	27½	20	30
<i>lispa</i>	E	19½	14	13	16	—	15	28½	15½	27½	23	35
<i>modesta</i>	F	24½	12	10	21	15	—	22½	26½	30½	26	34
<i>numismoides</i>	G	40	28½	17½	26½	28½	22½	—	30	21	9½	24½
<i>parallela</i>	H	18	23½	25½	8½	15½	26½	30	—	30	20½	26½
<i>projecta</i>	I	37	30½	24½	27½	27½	30½	21	30	—	15½	15½
<i>sigmoidalis</i>	J	33½	29	17	20	23	26	9½	20½	15½	—	17
<i>simplex</i>	K	40½	40	33	30	35	34	24½	26½	15½	17	—
Totals		276½	233	204	210	207	222	248½	224½	259½	211	296

23. Posterior marginal spines.
24. Posterodorsal spine at junction of posterior and A ridges.
25. Anterior papillae in row parallel to anterior border.
26. Ventral indentation of border (0 = straight; 1 = slightly concave; 2 = distinctly concave).
27. Length of valve, excluding posterior marginal spines (0 = below .80 mm; 1 = .80 to 1.00 mm; 2 = above 1.00 mm).
28. Height/length ratio (0 = below .53; 1 = .53 to .56; 2 = above .56).
29. Subcentral spot, either outlined by furrows or elevated to level of nearby ridges.

PRELIMINARY TREE

Coding.—Most characters appear to vary in progressive degree, so that the coding system is clear and simple. Thus, for most characters I used the following:

- 0 = no development, character absent
 ½ = slight development
 1 = average development
 1½ = above average development
 2 = strong development.

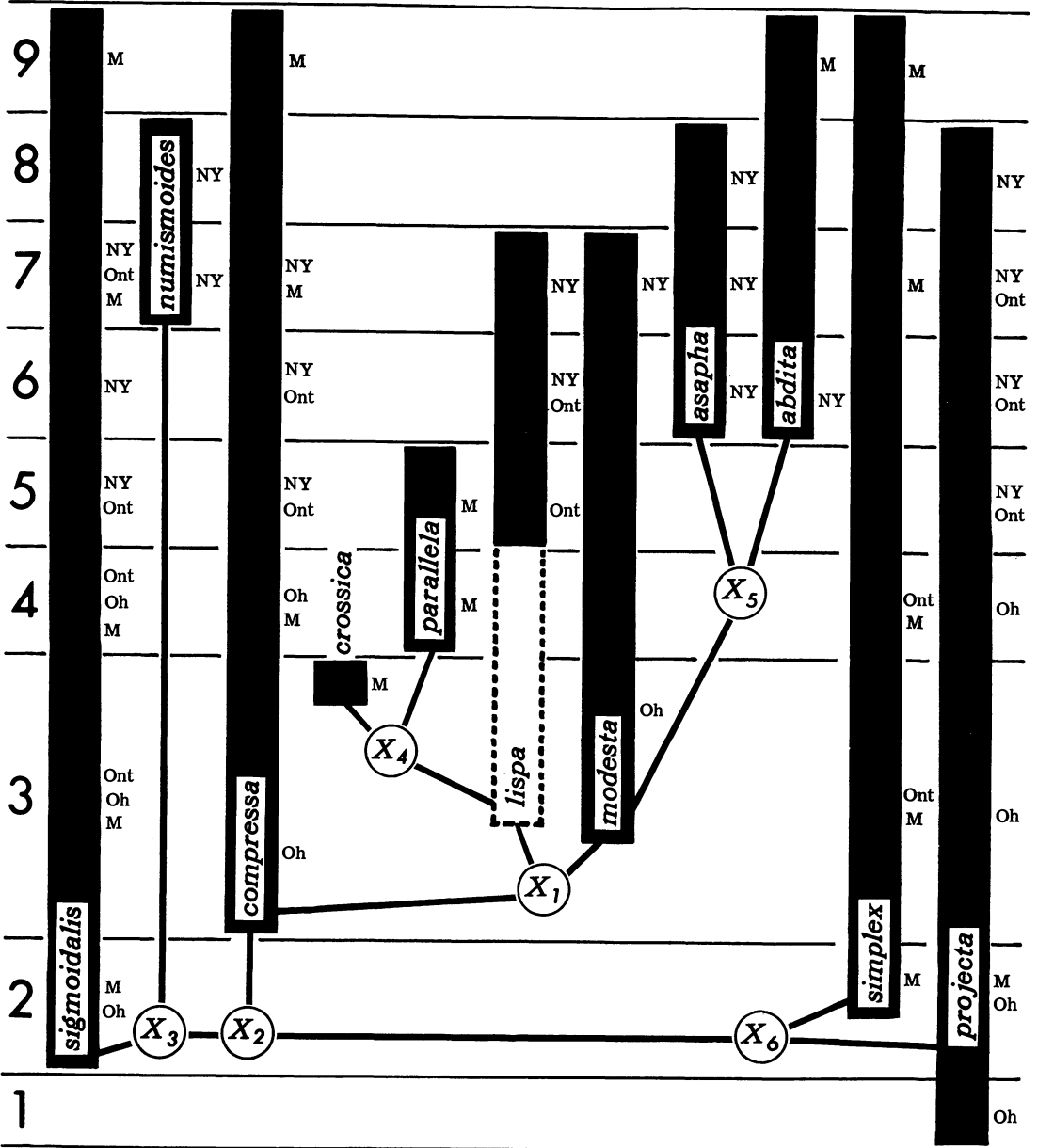
Whereas not all observers might code a character in a particular species the same, their assignments of values would seldom differ by more than one-half.

On the other hand, certain characters do not appear to vary in progressive degree, and a suitable coding system is difficult to devise. Such a character is 13, the longitudinal division of the upper or A ridge; obviously, from an inspection of the different species, one can find examples of the ridge entire (*E. asapha*), split but still joined at both ends (*E. simplex*), split but joined at one end (*E. sigmoidalis*), and separated into two ridges (*E. compressa*, *E. lispa*). The possibility persists that the presence of one ridge could be the result of the disappearance of one of two ridges, rather than one original ridge. In fact, the final linkage of species indicates that *E. sigmoidalis* (split but joined at one end) in one line gave rise to *E. simplex* (split and joined at both ends) and in another line gave rise to *E. compressa* (separate ridges); nevertheless, *E. modesta* (separate ridges) gave rise to *E. asapha* and *E. abdita* (both with single ridges).

Another character which does not vary progressively is 20, ornamentation of the valves other than the main ridges. There can be little doubt that *E. compressa* (with an interridge

TABLE 4—PHENETIC DIFFERENCES OF HYPOTHETICAL INTERMEDIATES (OTUs).

OTU	A	B	C	D	E	F	G	H	I	J	K	X ₁	X ₂	X ₃	X ₄	X ₅
X ₁	24½	14	4	16	9	6	21½	21½	24½	19	35	—	—	—	—	—
X ₂	31½	25	13	20	21	21	11½	24½	11½	4	21	15	—	—	—	—
X ₃	34½	28	16	21	22	24	8½	21½	14½	1	18	18	3	—	—	—
X ₄	17	20½	21½	4½	11½	23½	28	4	28	19½	28½	17½	21½	20½	—	—
X ₅	14	1½	18½	23½	14½	10½	29	24	32	30½	41½	14½	26½	29½	21	—
X ₆	38	31½	21½	26½	26½	29½	20	30	3	12½	12½	23½	8½	11½	27	33



TEXT-FIG. 12—Tree III arranged to show geologic succession and ranges of Middle Devonian species of *Euglyphella*. Based on known occurrences, *Euglyphella projecta* appears to be the ancestral species. Most evolutionary changes took place in the Ohio and Michigan area during the deposition of the Plum Brook, Silica, Bell, Ferron Point, Genshaw, and Gravel Point formations.

reticulation of small ridges) is closely related to *E. modesta* (with interr ridge papillae); the two species have strong resemblance in the development of the subcentral spot, strong posterodorsal spine at junction of posterior and A ridges, large posterior marginal spines, moderate anterodorsal spine at the end of the anterior ridge, weak D ridge, average B and C ridges, A and C ridges separated from anterior ridge, C

ridge separated from posterior ridge, strong B-C connector ridge, and other features. Nor can there be much doubt that *E. compressa* is also closely related to *E. sigmoidalis* (smooth interr ridge areas); these two have many characters in common, including separation of C and anterior ridges, strong junction of posterior and A ridges, separation of C and D ridges from posterior ridge, strong B-C con-

TABLE 5—TOTAL PHENETIC DIFFERENCES IN TREE II FOR EACH CHARACTER.

Character	Phenetic Difference	Character	Phenetic Difference
1	2	16	3
2	3	17	2½
3	4½	18	2½
4	4	19	3
5	3	20	4
6	2	21	3
7	2	22	3
8	6	23	5½
9	1	24	7
10	6	25	5
11	6	26	6
12	3	27	7
13	4	28	7
14	2	29	5½
15	2		

necker ridge, and junction of C and D ridges not far behind the middle of the valve. These resemblances suggest that reticulation evolved on smooth interridge areas and "disintegrated" into papillae; the suggestion gains support by the fact that some of the papillae in *E. modesta* are linked by low ridgelets.

The coding of character 27 (length of valve) and character 28 (height/length ratio) was arbitrarily selected to cover the observed ranges of the characters within the genus.

Based on coded values of characters 1–26 and 29, it is possible to sketch simulations of the species (text-fig. 3). These differ from the actual specimens in relative size, proportions, and minor details.

Data matrix.—The assigned values are shown in table 1. If a character displayed individual variation, the average state in the available specimens was entered.

Phenetic differences.—The summation of differences in coded character values is given in table 3. It can be seen that K (*simplex*) and A (*abdita*) have high total differences; they might be expected to be at the ends of the network. However, C (*compressa*) and E (*lispa*) have the lowest total differences; they might be expected to fit near the middle of the network.

Tree I.—Using the phenetic differences in table 3, we connect all OTUs in a network that involves the least phenetic differences. This preliminary tree of maximum parsimony begins by linking D and H (difference = 8½). In succession E, C, F, B, A, J, G, I, and K are added, producing the tree shown in text-figure 4.

Ancestral species.—Although the linkages

TABLE 6—WEIGHTING FACTOR FOR EACH CHARACTER. Least common denominator = 13860.

Phenetic Change	Weighting Factor	Practical W. Factor
1	13860	140
2	6930	70
2½	5544	55
3	4620	46
4	3465	35
4½	3080	30
5	2772	28
5½	2520	25
6	2310	23
7	1980	20

would remain the same in the network whatever species was selected as the ancestor, most micropaleontologists are concerned with the particular characters of the ancestral species and with the subsequent changes wrought by evolution. The selection would normally be limited to the earliest species, or, in the absence of precise dating, to the species which combines the most primitive forms of the most characters.

In *Euglyphella*, three species may be considered for the position of ancestor: *E. sigmoidalis*, *E. simplex*, and *E. projecta*. *E. sigmoidalis* is widespread and long-lived; it has ridge development that is intermediate between the extremes of *E. simplex* and the lineage leading to *E. abdita*, a development that could also lead to *E. crossica*. *E. simplex* has the most complete set of ridges of any species, which by simplification could be modified to produce the pattern of any other species; it is also long-lived. *E. projecta* is the earliest species of record, being found in the Delaware Limestone of Ohio; yet even after the intensive attention paid to *Euglyphella* by Peterson (1966), we are discovering additional occurrences, so that it is far from certain that the known ranges (and even the known species) comprise an essentially complete record.

In the various refinements of the evolutionary trees (text-figs. 4, 5, 8–10), *Euglyphella sigmoidalis* is shown in the ancestral position. The arrangement in chronological sequence (text-fig. 12) supports the choice of *E. projecta*. Further collecting may extend the ranges of several species; more accurate correlations would also help in the search for precise chronology of *Euglyphella* species.

HYPOTHETICAL INTERMEDIATES

Wagner groundplan-divergence method.—As Wagner proposed (1954), the introduction of hypothetical intermediate OTUs provides for further minimization (or greater parsimony)

TABLE 7—DATA MATRIX OF WEIGHTED FACTORS FOR SPECIES AND HYPOTHETICAL INTERMEDIATES.

OTU	Character														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B	0	0	0	70	0	0	0	23	0	0	23	0	0	70	70
C	0	0	60	70	46	0	0	46	0	35	23	0	70	105	70
D	0	0	30	0	0	0	0	0	0	35	0	0	70	70	70
E	0	0	15	35	0	0	0	35	0	0	23	0	70	70	70
F	0	0	60	70	0	0	0	46	0	46	23	23	70	70	70
G	140	0	60	70	46	0	0	46	0	35	46	92	52	140	140
H	0	46	0	0	0	0	0	0	0	0	0	0	70	70	70
I	140	0	60	70	0	140	140	46	0	23	46	0	0	140	140
J	140	0	60	70	46	0	0	46	0	35	0	0	52	140	140
K	140	92	60	70	92	140	140	0	140	23	0	0	35	140	140
X ₁	0	0	60	70	0	0	0	46	0	35	23	0	70	70	70
X ₂	140	0	60	70	46	0	0	46	0	35	23	0	52	140	140
X ₃	140	0	60	70	46	0	0	46	0	35	23	0	52	140	140
X ₄	0	0	15	0	0	0	0	0	0	0	0	0	70	70	70
X ₅	0	0	0	70	0	0	0	23	0	0	23	0	0	70	70
X ₆	140	0	30	70	46	140	140	46	0	23	23	0	35	140	140

OTU	16	17	18	19	20	21	22	23	24	25	26	27	28	29
A	0	0	0	0	70	46	92	25	40	28	46	0	20	13
B	0	0	55	46	70	92	46	50	40	56	23	40	20	25
C	46	28	110	46	35	0	46	50	40	28	12	40	40	50
D	46	55	55	0	0	23	0	13	40	0	12	20	40	0
E	23	28	55	23	35	23	46	38	20	28	12	20	0	50
F	46	28	83	23	70	92	46	50	40	56	46	40	20	50
G	92	110	110	46	0	0	0	50	0	56	35	40	40	0
H	46	55	55	0	0	23	0	13	0	14	0	0	20	0
I	92	110	110	92	35	0	0	0	40	14	0	20	0	0
J	92	110	110	46	0	0	0	25	0	28	0	20	20	0
K	92	110	110	92	0	0	0	0	0	0	23	0	0	0
X ₁	46	28	83	23	35	23	46	50	40	28	12	40	20	50
X ₂	92	110	110	46	35	0	0	25	40	28	0	20	20	0
X ₃	92	110	110	46	0	0	0	25	0	28	0	20	20	0
X ₄	46	55	55	0	0	23	0	13	20	14	12	20	20	0
X ₅	0	0	55	23	70	92	46	50	40	56	46	40	20	25
X ₆	92	110	110	92	35	0	0	0	40	14	0	20	0	0

of phenetic differences in a cladogram, or evolutionary tree. Each hypothetical species extends the common line of descent from the nearest ancestor, thereby combining parts of two formerly divergent paths, or it links closely related species in a minimized pattern.

Tree II.—To start, the hypothetical X₁ can be introduced at the junction of C, E, and F. Its characters are shown in table 2, and its phenetic differences from actual species are shown in table 4. Comparison of text-figures 4 and 5 indicates a reduction of differences from 23 to 19 by the insertion of X₁ in the tree.

Other triads of species can also be rearranged by introduction of hypothetical intermediates. These include X₂ in the C-I-J branching, X₃ in the G-J-X₂ branching, X₄ in the E-H-D lineage, X₅ in the F-B-A lineage, and X₆ in the X₂-I-K lineage. The total effect of all hypothetical intermediates is the reduction of differences (total path) from 139 in tree I (text-fig. 4) to 114½ in tree II (text-fig.

5). The reduction of 24½ is brought about by X₁ (4), X₂ (4), X₃ (1), X₄ (11), X₅ (1½), and X₆ (3).

Inasmuch as the characters of the hypothetical intermediates are determined, simulations of these hypothetical species can be sketched (text-fig. 10).

WEIGHTING OF CHARACTERS

Procedure.—In the construction of tree II, each character was given equal consideration or weight, no matter to what degree it influenced the arrangement of the tree. Obviously, not all characters entered equally into production of the tree.

The lower the phenetic differences attributable to a character in the linkage, the greater its influence. For example, character 1 (the junction of anterior and A ridges) changes only once in the tree (text-fig. 6), dividing the OTUs into two groups—one in which the ridges are distinctly joined and another in

TABLE 8—PHENETIC DIFFERENCES OF WEIGHTED FACTORS FOR SPECIES AND HYPOTHETICAL INTERMEDIATES (OTUs).

OTU	A	B	C	D	E	F	G	H	I	J	K	X ₁	X ₂	X ₃	X ₄	X ₅	X ₆
A	—	577	1036	741	695	880	1610	722	1660	1414	1973	864	1362	1437	679	531	1668
B	577	—	609	752	375	395	1172	771	1325	1145	1790	481	1047	1122	688	46	1353
C	1036	609	—	617	423	374	718	816	1082	662	1433	174	564	639	693	655	1008
D	741	752	617	—	460	683	1029	217	1219	827	1426	483	845	850	104	752	1177
E	695	375	423	460	—	449	1111	460	1245	941	1626	249	883	918	356	446	1203
F	880	395	374	683	449	—	954	832	1324	996	1653	200	898	973	719	349	1342
G	1610	1172	718	1029	1111	954	—	1138	790	266	1015	902	318	243	1065	1195	762
H	722	771	816	217	460	832	1138	—	1320	872	1367	632	970	895	113	771	1278
I	1660	1325	1082	1219	1245	1324	790	1320	—	616	583	1124	518	593	1231	1391	134
J	1414	1145	662	827	941	996	266	872	616	—	795	696	98	23	823	1191	542
K	1973	1790	1433	1426	1626	1653	1015	1367	583	795	—	1567	893	818	1426	1833	509
X ₁	864	481	174	483	249	200	902	632	1124	696	1567	—	698	773	519	481	1142
X ₂	1362	1047	564	845	883	898	318	970	518	98	893	698	—	75	881	1093	444
X ₃	1437	1122	639	850	918	973	243	895	593	23	818	773	75	—	846	1168	519
X ₄	679	688	693	104	356	719	1065	113	1231	823	1426	519	881	846	—	688	1189
X ₅	531	46	655	752	446	349	1195	771	1391	1191	1833	481	1093	1168	688	—	1419
X ₆	1668	1353	1008	1177	1203	1342	762	1278	134	542	509	1142	444	519	1189	1419	—

which the ridges are separate. Thus, character 1 has great significance in the evolution of *Euglyphella*. In contrast, character 27 (the length of the left valve exclusive of marginal spines) results in no such distinctive grouping (text-fig. 7). The medium-sized J through I lineage is succeeded by the large-size G, the large-size C through B lineage, and the small-size K; similarly, the large-size C through B lineage gives rise to the small-size A and to the medium-size E through D lineage, which in turn leads to the small-size H. The differences total 7, indicating low evolutionary value for this character.

Weighting can be done simply by multiplying the coded character value by the common denominator of all character differences divided by the difference attributable to one character in the tree.

The total difference in tree II attributable to each character is entered in table 5. The common denominator of all is 13860. The weighting factor for each character is therefore 13860 divided by the total phenetic differences caused by the character in tree II (table 6). For practical purposes consistent with the accuracy of the coding, these factors can be divided by approximately 100. Thus, for character 23 (differences of 5½ in tree II), all coded character values (table 1) are multiplied by 25 for weighting.

The new data matrix (table 7) for all OTUs can be used to compute the new phenetic differences between OTUs (table 8).

Tree III.—Using the differences in table 8, a new cladogram or tree can be constructed (text-fig. 8). This tree proves to be identical

with that constructed from unweighted values (text-fig. 5), confirming the cladistic relationships expressed in tree II.

From data in tables 1 and 2, the major evolutionary changes proposed for *Euglyphella* can be listed (text-fig. 9). These can be visualized by substitution of species simulations for OTUs in the tree (text-fig. 10).

CHRONOLOGY

The oldest known species of *Euglyphella* comes from the Bone Beds of the Delaware Limestone in Franklin County, Ohio. This formation is overlain by the Plum Brook Shale, the equivalent of the Silica Formation in Lucas County. Despite the poor preservation, I agree with Peterson (1966) that the ostracod is *E. projecta*.

Correlations of the major Middle Devonian formations yielding *Euglyphella* are indicated in text-figure 11. I frankly admit that the position of some formations is open to question. The Petoskey Formation in the northwestern part of the Lower Peninsula of Michigan has not been conclusively demonstrated to be post-Windom nor even the equivalent of the Potter Farm Formation, at least in its entirety. Whether the Silica Formation of Ohio is equivalent to the combined Bell Shale, Rockport Quarry Limestone, Ferron Point Formation, Genshaw Formation, Newton Creek Limestone, and Alpena Limestone in Michigan, or only to parts of them, is also undecided. There are enough faunal links between the Ferron Point Formation and parts of the Silica Formation and Arkona Shale to indicate contemporaneity.

In text-figure 12, I show the geologic ranges and cladistic linkages of the OTUs. I do not claim that the ranges are complete; in fact, I suspect that future discoveries will necessitate several changes. Hence, the position of *Euglyphella projecta* as the ancestor of all other species needs additional substantiation.

Having reviewed the evolutionary highlights of *Euglyphella* during Middle Devonian time as suggested by cladistic analysis, I looked for other ostracods from which the genus might have descended. *Euglyphella* has so many distinctive features that are lacking or poorly expressed in other ostracods of the family Quasillitidae that I reached no decision.

Insofar as the paleontologic record is known at this time, the last surviving species of *Euglyphella* was *E. subquadrata* Gibson from the Upper Devonian Cerro Gordo Formation of Iowa, undoubtedly a direct descendant of *E. sigmoidalis*, as suggested by Peterson (1966, p. 7). The exact relationship of the *E. ? polonica* described by Přibyl from the Givetian of the St. Croix Mountains in Poland (1953, p. 334, pl. 4, figs. 6-9) is unknown.

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