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PALYNOLOGY AND SYSTEMATICS OF CUPHEA (LYTHRACEAE). II. POLLEN MORPHOLOGY AND INFRAGENERIC CLASSIFICATION[1]

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A B S T R A C T

Present taxonomic studies in *Cuphea* (Lythraceae) reveal that a broad spectrum of biosystematic data is required for an understanding of evolutionary relationships among this large and complex group of species. As part of these studies pollen data have proven to be of greater pragmatic value than is frequently true for more stenopalynous taxa. A survey is made of pollen types in 160 species of *Cuphea* with special reference to specific taxonomic problems, and a summary presented of points at which pollen data can profitably contribute to taxonomic revision of the genus.

IN AN EARLIER PAPER (Graham, Graham, and Geer, 1968) the pollen of *Cuphea* was shown to be eurypalynous and of practical importance to taxonomic studies in the genus. The aim of the present investigation is to consider pollen morphology within the framework of the standard taxonomic treatment (Koehne, 1903). Suggestions for altering infrageneric categories are presented, but formal taxonomic changes are deferred until revisions synthesizing all available morphological and biosystematic information are prepared. Table 1 summarizes Koehne's infrageneric classification and includes species referred to in this treatment.[2]

MATERIALS AND METHODS—The study is based on observations of approximately 160 of an estimated 260 valid species. Pollen was obtained from field collections and herbarium material, and vouchers of these are in one of several herbaria (AA, GH, MICH, NY, US). The authors gratefully acknowledge the cooperation of these herbaria in providing pollen material. Slides were prepared by the KOH- acetolysis technique and are deposited in the pollen reference collection at Kent State University with duplicates at the herbaria in which the material is vouchered.

[1] Received for publication 24 March 1971.

[2] The authors are aware that the nomenclature of Koehne's treatment is not completely in accord with the International Code of Botanical Nomenclature. For example, under Art. 22 disposition of the type species in the system calls for Subgenus Lythrocuphea, Section Enantiocuphea, and Subsection Gastrodynamia to bear the generic name unaltered and under Art. 21 for the other subgenus to receive a new name, Subgenus Eucuphea being unacceptable. Such changes will be made formally in another publication where they can be dealt with more extensively. Our concern here is primarily with the relationships of taxa as demonstrated by pollen and for ease of reference Koehne's taxonomic scheme and nomenclature have been adhered to in knowledge of certain shortcomings.

Although our studies are based on permanently prepared slides, routine examination of pollen morphology can be made from temporary lactic acid mounts. By this technique pollen characters are, in fact, more easily examined than some of the more standardly-used features in the genus, such as stamen length or ovule number. Temporary slides are prepared by touching the moistened tip of a dissecting needle to an open anther, then to a drop of lactic acid on a slide. A cover slip is added and the slide is passed through an alcohol flame once or twice to clear the grains, making the features of the exine more visible.

OBSERVATIONS—In the following treatment figures in parentheses after the section names indicate the number of species in that section, followed by the number examined in this study; the latter are listed at the beginning of each description. Figures after the species name refer to publications illustrating pollen of that plant: 1- Graham and Graham, 1967; 2- Graham, Graham, and Geer, 1968; and 3- Coz Campos, 1964.

Section Archocuphea (3-2)

Description: *mimuloides* (Fig. 1), *anagalloides* (1)—oblate, triangular to oval-triangular in polar view; tricolporate, colpi straight, meridionally elongated, equatorially arranged, equidistant, margin entire, tapering to an acute apex, 8–10 μ long, narrow costae colpi present; pores arranged and slightly elongated equatorially, situated at midpoint of the colpus, equidistant, margin entire, faint costae pori present; exine tectate, wall ca. 1.5 μ thick, psilate; size 20–24 μ.

These grains are small compared to most of the other pollen types. They are non-syncolpate, lack protruding pores, and are psilate. Relationship of the species, based on pollen morphology, is with the two following sections.

TABLE 1. *Infrageneric classification of Cuphea according to Koehne* (1903)

Subgenus Lythrocuphea
- Section 1. Archocuphea—*anagalloides, mimuloides*
- Section 2. Enantiocuphea
  - Subsection 1. Notodynamia—*correntina, fruticosa, longiflora, racemosa*
  - Subsection 2. Gastrodynamia—*decandra, denticulata, flavisetula, gaumeri, salicifolia, utriculosa*

Subgenus Eucuphea
- Section 3. Heteranthus—*bombonasae, bonplandii, epilobiifolia, setosa, sordida, tarapotensis, tetrapetala*
- Section 4. Melicyathium
- Section 5. Brachyandra
  - Subsection 1. Microcuphea—*repens*
  - Subsection 2. Melanium—*calophylla, cordifolia, melanium, pseudosilene, pustalata, rotundifolia, serphyllifolia, urens*
  - Subsection 3. Micranthium—*micrantha*
  - Subsection 4. Lophostomopsis—*affinitatum, ferrisiae, michoacana, vesiculigera*
  - Subsection 5. Lythrocupheopsis
  - Subsection 6. Balsamonella—*aperta, carthagenensis, elliptica, parsonsia*
- Section 6. Euandra
  - Subsection 1. Platypterus—*campestris, campylocentra, carunculata, corisperma, fiebrigii, glutinosa, hexasperma, ingrata, strigulosa, thymoides, urbaniana*
  - Subsection 2. Hyssopocuphea—*hyssopifolia, pertenuis, spruceana*
  - Subsection 3. Amazonianae—*cataractarum, kubeorum, philombria*
  - Subsection 4. Pachypterus—*reitzii*
  - Subsection 5. Hilariella—*acinos, linarioides, linifolia*
  - Subsection 6. Oidemation—*aspera, confertiflora, lysimachioides, retrorsicapilla, tuberosa*
- Section 7. Trispermum—*anisoclada, antisyphilitica, ericoides, flava, patula, ramulosa*
- Section 8. Pseudocircaea—*costata, lutescens, persistens, prunellifolia*
- Section 9. Heterodon
  - Subsection 1. Lophostomum—*angustifolia, calcarata, crassiflora, goldmanii, koehneana, lanceolata, llavea, lophostoma, lozani, lutea, palustris, paucipetala, procumbens, purpurascens, quaternata, trochilus, viscosa, viscosissima, wrightii*
  - Subsection 2. Glossostomum—*glossostoma, laminuligera, leptopoda, lobophora*
- Section 10. Melvilla
  - Subsection 1. Eumelvilla—*melvilla*
  - Subsection 2. Pseudolobelia—*lobelioides*
  - Subsection 3. Polyspermum—*micropetala, rasilis*
  - Subsection 4. Paramelvilla
  - Subsection 5. Pachycalyx—*annulata, bracteolosa, gardneri, grandiflora, pulchra*
  - Subsection 6. Erythrocalyx—*caeciliae, heterophylla, ignea, intermedia, jorullensis, retroscabra, subuligera, watsoniana*
- Section 11. Leptocalyx—*aequipetala, appendiculata, boissieriana, bustamanta, calaminthifolia, cristata, graciliflora, infundibulum*
- Section 12. Diploptychia
  - Subsection 1. Trichoptychia—*cyanea, nitidula*
  - Subsection 2. Leioptychia—*cordata, dipetala, empetrifolia, hookeriana, ianthina, ixodes, painteri, pinetorum, scaberrima*
  - Subsection 3. Ornithocuphea—*avigera, hintoni, pulcherrima*

Sections Enantiocuphea (20-10) and Heteranthus (19-7)

Description: Enantiocuphea—*correntina, decandra* (3), *ciliata*), *denticulata, flavisetula, fruticosa, gaumeri, longiflora* (1), *racemosa* (3), *salicifolia, utriculosa* (Fig. 2, 3); Heteranthus—*bombonasae* (Fig. 4), *bonplandii, epilobiifolia* (2), *setosa* (3), *sordida, tarapotensis* (3), *tetrapetala* (1, 3)—oblate, triangular to oval-triangular in polar view; tricolporate, colpi straight, meridionally elongated, equatorially arranged, equidistant, margin frequently diffuse, faint, narrow costae colpi present in some species, tapering to an acute apex, 10–12 μ long; pores equatorially arranged, situated at midpoint of colpus, equidistant, margin entire to frequently diffuse; exine tectate, wall ca. 1.5 μ thick, rugulate to distinctly striate; size (24-) 30–34 μ.

The sections cannot be separated on the basis of pollen characters nor can the two subsections of Enantiocuphea be distinguished. The species within the sections vary in length of the colpi, size of the grain, and distinctiveness of sculpture pattern. They are most similar to Section Archocuphea but are larger and are rugulate to striate in ornamentation.

Koehne divided *Cuphea* into two subgenera, Archocuphea, comprised of Sections Archocuphea and Enantiocuphea, for species lacking pedicellate bracteoles, and Eucuphea comprising the rest of the sections, with most species having bracteoles. There are exceptions, as noted by Koehne, and we have found that within a few species the bracteoles may be present on some plants and absent on others. Pollen morphology more clearly separates Section Archocuphea from the rest of

the genus and unites Enantiocuphea and Heteranthus, which according to Koehne belong to different subgenera. Thus on the basis of pollen data and floral morphology the present subgeneric classification of the genus appears invalid.

Section Melicyathium (1-0)

Section Brachyandra (27-18)

Because of the large number of species in Brachyandra (ca. 27 in 6 subsections) and the accompanying diversity of pollen types, this section is treated at the subsectional level.

Subsection Microcuphea

Description: *repens* (Fig. 5)—oblate, triangular in polar view, trisyncolporate, colpi straight, meridionally elongated, equatorially arranged, equidistant, margin entire, slight costae colpi present; pores equatorially arranged, non-protruding, situated at midpoint of colpus, slight vestibulum present, equidistant; exine tectate, psilate; size 22–26 μ.

The only species in the subsection, *C. repens*, is vegetatively unlike any other in the genus in having a creeping, heath-like habit with narrow, rolled, verticillate leaves. The pollen is unlike other members of Brachyandra, resembling in a general way that of Section Archocuphea and a few types in Section Euandra, but quantitative differences, e.g., thickness of the exine and conspicuousness of the costae colpi coupled with the distinctive external morphology negate close relationships with either of these taxa.

Subsection Melanium

Description: Type I, *calophylla* (Fig. 6, 7), *cordifolia* (1), *melanium*, *rotundifolia*, *serphyllifolia* (1, 3), *urens*—oblate, triangular in polar view; tricolporate, colpi straight, meridionally elongated, equatorially arranged, equidistant, margin entire, tapering to an acute apex, 15 μ long; pores equatorially arranged, non-protruding, situated at midpoint of colpus, oval, equidistant, margin entire; exine tectate, wall relatively thin (ca. 1–1.5 μ), finely rugulate to striate, the striae slightly sinuous, occasionally tending to be parallel to the margin of the grain; size 24–28 μ.

Type II, *pseudosilene* (Fig. 9, 11; 1), *pustalata* (3)—oblate, triangular in polar view with conspicuously protruding pores; trisyncolporate, colpi straight, meridionally elongated, equatorially arranged, equidistant, margin entire, 22 μ long; pores equatorially arranged, protruding 5–6 μ, situated at midpoint of colpus, circular, equidistant, margin entire; exine tectate, wall 2–4 μ thick, coarsely striate, striae extending from periphery to pole, diminishing slightly in height toward the pores; size 30–36 μ.

On the basis of pollen, species of this subsection fall into two very distinct, seemingly unrelated groups. In Type I the pollen lacks protruding pores, is not syncolpate, and has a finely rugulate to striate exine. Pollen differences among the species with this type are minor, suggesting this to be a natural assemblage. The pollen type compares most closely to Type III of Section Euandra. Pollen of Type II has conspicuously protruding pores, is syncolpate, and has a coarsely striate exine. In Koehne's treatment, the subsection is defined only by the perennial or shrubby habit, and further refined into four series, using primarily the position of the floral disc. This character is often inconsistent and difficult to determine on pressed specimens. A secondary character used to define the series is the infrastaminal vesicle. These are found in Series 2 (containing the single species, *C. pustalata*) and Series 4 (with only *C. psuedosilene*). The character has proven elsewhere in *Cuphea* (in Section Heterodon) to be important in suggesting species relationships. Here its appearance correlates with distinctive pollen. The more natural arrangement of species in Subsection Melanium, as shown by pollen, into two, not four, groups is supported by other morphological features. The first group may be distinguished by Type I pollen, no infrastaminal vesicles, and ovules (4-) 5-14; the second group has Type II pollen, infrastaminal vesicles, and ovules 3.

Subsections Micranthium, Lophostomopsis, Lythrocupheopsis, and Balsamonella

Within these four subsections there are four basic pollen types, but these do not correspond to subsectional lines. Consequently the types are described apart from subsection names.

Description: Type I, *micrantha* (1), *aperta* (Fig. 8; 1)—oblate, oval-triangular in polar view; trisyncolporate, colpi straight, meridionally elongated, equatorially arranged, equidistant, margin entire, slight costae colpi present, 12 μ long; pores equatorially arranged, equidistant, slightly protruding (ca. 2–3 μ), situated at the midpoint of colpus; exine tectate, psilate, with interaperturate thickenings; size 28 μ.

Type II, *affinitatum*—prolate varying to spherical, excluding protruding pores, oval-triangular to nearly circular in polar view; diporate, pores circular, ca. 5.5 μ in diam, protruding ca. 3.5 μ beyond margin of grain, endexine extending only partially into protruding pores, margin entire, pores connected by three colpi with equatorial pores, the colpi meridionally elongated, straight, equidistant, broad at equator, 7–9 μ wide and tapering toward poles, 7–8 μ long (pole to equator), margo present, 2–3 μ wide, margo margin straight, entire; exine tectate, striate, striae oriented horizontally between colpi, slightly sinuous, moderately fine (ca. 0.5–1 μ wide); size 27 $\times$ 19 μ, including protruding pores.

Type III, *carthagenensis* (2, 3), *elliptica*, *ferrisiae*

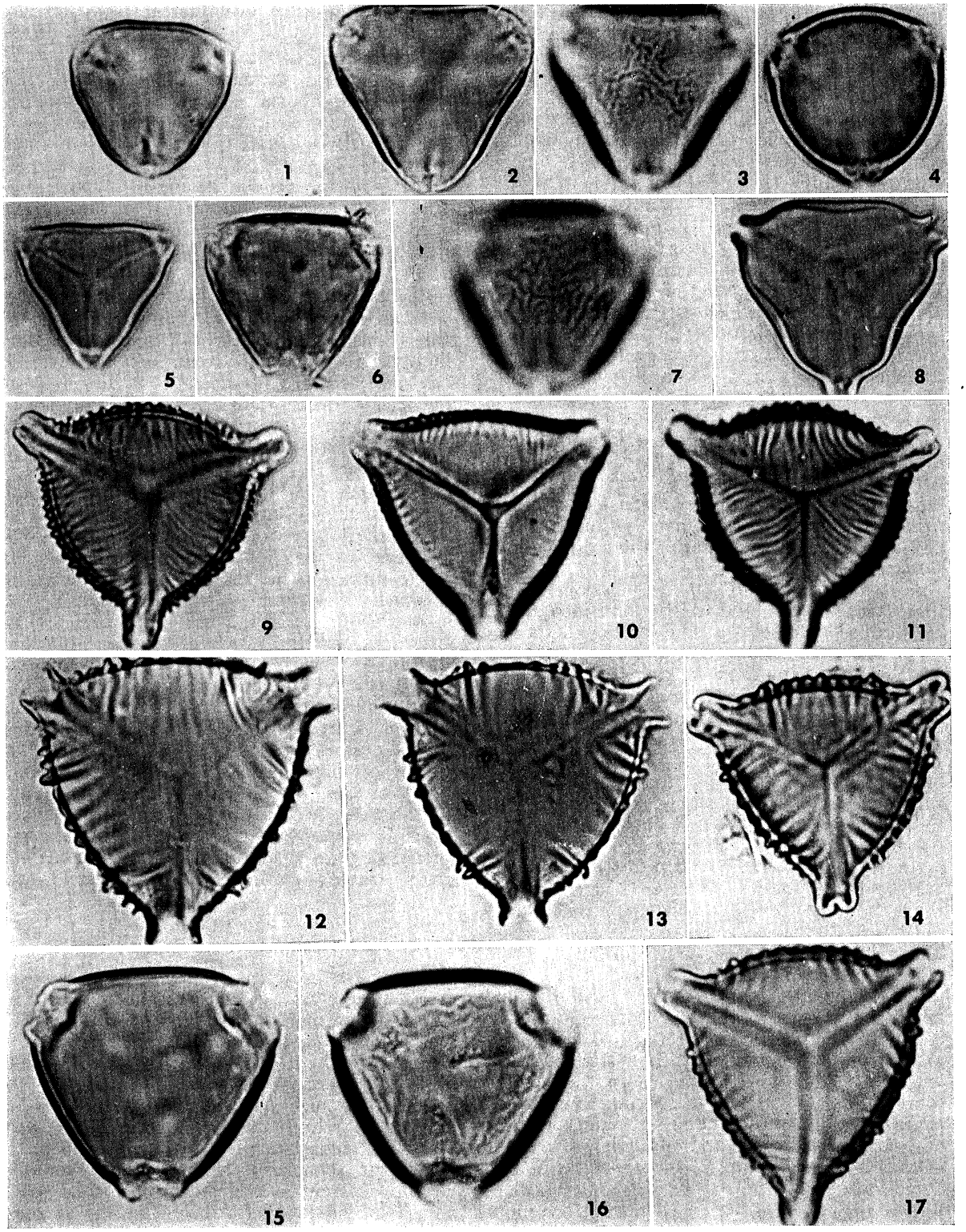

Fig. 1–17. Pollen types in *Cuphea*.—Fig. 1. *C. mimuloides*.—Fig. 2, 3. *C. utriculosa*.—Fig. 4. *C. bombonasae*.—Fig. 5. *C. repens*.—Fig. 6, 7. *C. calophylla*.—Fig. 8. *C. aperta*.—Fig. 9, 11. *C. pseudosilene*.—Fig. 10. *C. confertifolia*.—Fig. 12, 13. *C. hexasperma*.—Fig. 14. *C. corisperma*.—Fig. 15, 16. *C. kubeorum*.—Fig. 17. *C. carunculata*.

(1), *michoacana, vesiculigera* (Fig. 25, 26)—oblate, oval-triangular in polar view with conspicuously protruding pores, tricolporate or trisyncolporate, colpi straight, meridionally elongated, equatorially arranged, equidistant, margin entire, 15–18 μ long; pores equatorially arranged, protruding 2–4 μ, situated at midpoint of colpus, equidistant; exine tectate, striate, 2–4 striae adjacent to pores largest, extending ca. ½ distance to pole; size 34 μ.

Type IV, *parsonsia* (1)—comparable to Subsection Melanium, Type II. Pollen morphology indicates (1) that the species of the remaining subsections of Brachyandra are of diverse origins and (2) that there are relationships suggested by pollen morphology which are not obvious from the standpoint of vegetative or floral morphology, and which differ from those suggested by species arrangement in Koehne's subsections. The subsections are delimited by ovule number (3 vs. 4–11) but this distinction is in practice a poor one. Although a species may in general be said to have a certain number of ovules, the number in an individual flower can vary by one or more and separation on this character alone is of doubtful value. The species share only the annual habit and the definitive character of the section, short stamens.

A clearer picture of species relationships in these last four subsections of Section Brachyandra is obtained from pollen studies. Four types of pollen occur. The major characteristics of Type I (cf. Fig. 8) are interaperturate thickenings and psilate exine. This type is found elsewhere in the genus, characterizing the South American Section Trispermum (cf Fig. 22). Other features of the species (*C. micrantha* and *C. aperta*) are amiable to placement in Section Trispermum with the single exception of the stamens, which are distinctly shorter than the calyx tube, the character which Koehne chose to separate Section Brachyandra from other sections. Their distribution is in part Brazilian; species of Section Trispermum are concentrated in Brazil. The common pollen morphology of these two species and species of Section Trispermum points out a relationship which is otherwise lost because of the large size of the genus. *Cuphea micrantha* and *C. aperta* would better be placed in Section Trispermum. The character distinguishing Sections Brachyandra and Euandra, stamen length in relation to tube length, is an unfortunate choice, associating totally unrelated groups of species. The stamen character appears to have arisen independent of other character groups and does not warrant the emphasis placed on it by Koehne in his section definitions.

The diporate grain of *C. affinitatum* is unique in Section Brachyandra, but characterizes the homogeneous Section Pseudocircaea (cf Fig. 27–29, 31–34). Lourteig (1965) after examination of type material believes *C. affinitatum* to be synonymous with *C. prunellifolia* of Section Pseudocircaea. The pollen morphology supports this synonymy.

Type III grains (Fig. 25, 26) are rather heterogeneous but share common features of protruding pores flanked by coarse striations. *Cuphea elliptica, C. carthagenensis, C. michoacana* are syncolpate; *C. ferrisiae* and *C. vesiculigera* are nonsyncolpate. Type III pollen is also found in part of the following Section Euandra (Type I, Fig. 12, 13), and these two groups are in turn closely allied to Section Heterodon from the standpoint of pollen morphology (cf Fig. 30).

The Type IV pollen of *C. parsonsia* cannot be distinguished from that of *C. pseudosilene* and *C. pustalata* in Subsection Melanium. Beyond the pollen the species shares with *C. pseudosilene* only the unusual 6-staminate condition. We have not seen specimens of *C. pustalata*, but judging from the species description, it is totally unlike *C. parsonia*. This is an instance where pollen seems at variance with the other morphological features of the species.

In summary, when species with Type I and Type II pollen of Subsections Micranthium et al. are removed to Section Trispermum and Pseudocircaea, respectively, there remain in Section Brachyandra four pollen groups, the two largest of which (Subsection Melanium Type I, and Subsection Micranthium et al. Type III) compare closely to the two largest pollen groups of the next Section Euandra. These four in turn are related closely to Section Heterodon. The third group (Subsection Melanium Type II) has no apparent relationships elsewhere in the genus, and the fourth (Subsection Microcuphea), as previously mentioned, has pollen similar to a species of Euandra, but is morphologically unlike it otherwise. Observation of pollen morphology in Section Brachyandra suggests the removal of certain obvious misfits to other sections of the genus, leaving more natural coherent species groups.

Section Euandra (74-26)

Euandra is the largest section in the genus with ca. 74 species arranged in five subsections. The species are primarily Brazilian and are united in the section by having stamens equal to or exceeding the length of the calyx, and distinguished from other sections with this character by the absence of a thick disc with deflexed tip (Section Trispermum) and absence of persistent petals (Section Pseudocircaea). From the standpoint of pollen the section is extremely heterogeneous. Several different arrangements of species based on pollen characters can be made and at some points the disposition of individual species is an arbitrary one. The following arrangement of seven types will facilitate placement of additional species of the section as pollen of them becomes available. As in previous sections the pollen

groups described do not correspond strictly to the subsectional lines.

Description: Type I, *campestris* (2), *carunculata* (Fig. 17), *corisperma* (Fig. 14), *hexasperma* (Fig. 12, 13) *lysimachiodes* (1), *retrorsicapilla*, *strigulosa* (3)—the description of Section Brachyandra, Subsection Micranthium et al., Type III is applicable, with the exceptions that all species here are syncolporate, and *C. campestris* has but one striation on either side of the pore.

The grains of this group are syncolporate with conspicuously protruding pores and most have a few large striae flanking the pores. Although the pollen is comparable to that of one group in Section Brachyandra, there does not appear to be any other parallel character shared by the two. The species of both sections are vegetatively extremely diverse, being annuals or perennials, with small or large flowers, spurred or not, having few to many ovules, sessile or petiolate leaves, erect or deflexed discs, etc. Pollen of *C. corisperma* and *C. carunculata* exhibits many tetraporate grains suggesting infertility and perhaps recent origin of these species through hybridization. The pollen characters of *C. corisperma* (Fig. 14) and *C. carunculata* (Fig. 17) tend to be intermediate between the other species of this type (cf Fig. 12, 13) and the species with Type II pollen (Fig. 10), particularly in the degree of striation.

Type II, *camplyocentra*, *confertiflora* (Fig. 10), *pertenuis*—oblate, oval-triangular in polar view, pores slightly protruding; trisyncolporate, colpi straight, meridionally elongated, equatorially arranged, equidistant, margin entire, 12–14 μ long; pores equatorially arranged, situated at midpoint of colpus, equidistant; exine tectate, uniformly striate, striae extending to the pole; size 32–36 μ.

These species have pollen with the general appearance of Type I, but have a uniformly striate exine. To have included them in Type I seemed to blur the distinctive character of Type I. If they are considered together, however, there is seen a trend, in otherwise generally similar grains, toward an increase in striations from the single striation of *C. campestris*, to two or three striae in *C. lysimachiodes* through *C. carunculata*, to the more frequent uniform striae of *C. camplyocentra*, *C. confertiflora*, and *C. pertenuis*.

Type III, *acinos*, *fiebrigii*, *hyssopifolia*, *kubeorum* (Fig. 15, 16), *linearioides*, *linifolia*, *philombria*, *spruceana* (2, 3)—the description is comparable to that of Section Brachyandra, Subsection Melanium Type I, except for the addition of two grains with more psilate exines (*C. fiebrigii* and *C. hyssopifolia*) and two (*C. linifolia* and *C. linearioides*) tending to be prolate rather than oblate.

The grains are characteristically non-syncolpate, lack protruding pores and have a subdued sculpture pattern which ranges from psilate to scabrate, rugulate or low-striate. The species *C. linifolia* and *C. linearioides*, whose similar vegetative characteristics suggest close relationship, have virtually identical pollen of a prolate form unique to the genus. Comments made for Type I of this section are equally applicable here. The type shares pollen characteristics with a great number of species in Section Brachyandra, but otherwise the diversity in floral and vegetative characters displayed by the species in both sections follows no parallel pattern in the two sections.

Type IV, *ingrata* (2), *glutinosa*, *thymoides* (Fig. 20, 21), *tuberosa* (1)—the description of the diporate grains of Section Brachyandra, Subsection Micranthium et al., Type II is equally applicable here.

Cuphea ingrata, *glutinosa*, and *thymoides* were placed by Koehne, together with several species having typical triporate grains, in Subsection Platypterus of Euandra by virtue of their shrubby habit, narrow seed margin, and lack of tuberous roots. Their placement here is not out of keeping with the vegetative features of the triporate pollen species. On the other hand, neither are they, with one exception, unlike the species of Section Pseudocircaea, a section (to be discussed) characterized by diporate pollen. The exception is their lack of persistent petals, the other feature besides pollen morphology uniting the members of Pseudocircaea.

Cuphea tuberosa, now in Euandra, Subsection Oidemation with other tuberous rooted species, was first placed (Koehne, Fl. Braz. 13(2): 294, 1877) in Section Pseudocircaea, then later removed to its present position where it is the only diporate species in that subsection. There is no apparent character other than the non-persistent petals which prevents this species from being placed in Pseudocircaea near the diporate *C. costata* and *C. persistens*.

We thus have a situation in which there are alternatives to species placement based on equally distinctive characters; persistent petals, tuberous roots, and diporate pollen are all highly unusual features within the genus. The answer to the most workable arrangement of species with one or more of these features from the taxonomist's view should come from a revision of Euandra as a whole. Pollen cannot be the sole character on which species relationships and subsectional lines are determined here, but it should be included in the study along with other traditional features. The several distinct pollen categories should prove highly significant in determining the relationships of the species in this large, poorly known, and confusing section.

Type V, *cataractarum* (Fig. 18, 19)—the pollen is somewhat comparable to that in Section Brachyandra, Subsection Microcuphea. The syncolpate, psilate pollen with non-protruding pores is most like that of *C. repens* (Fig. 5) in Brachyandra, but seems unrelated in any other way.

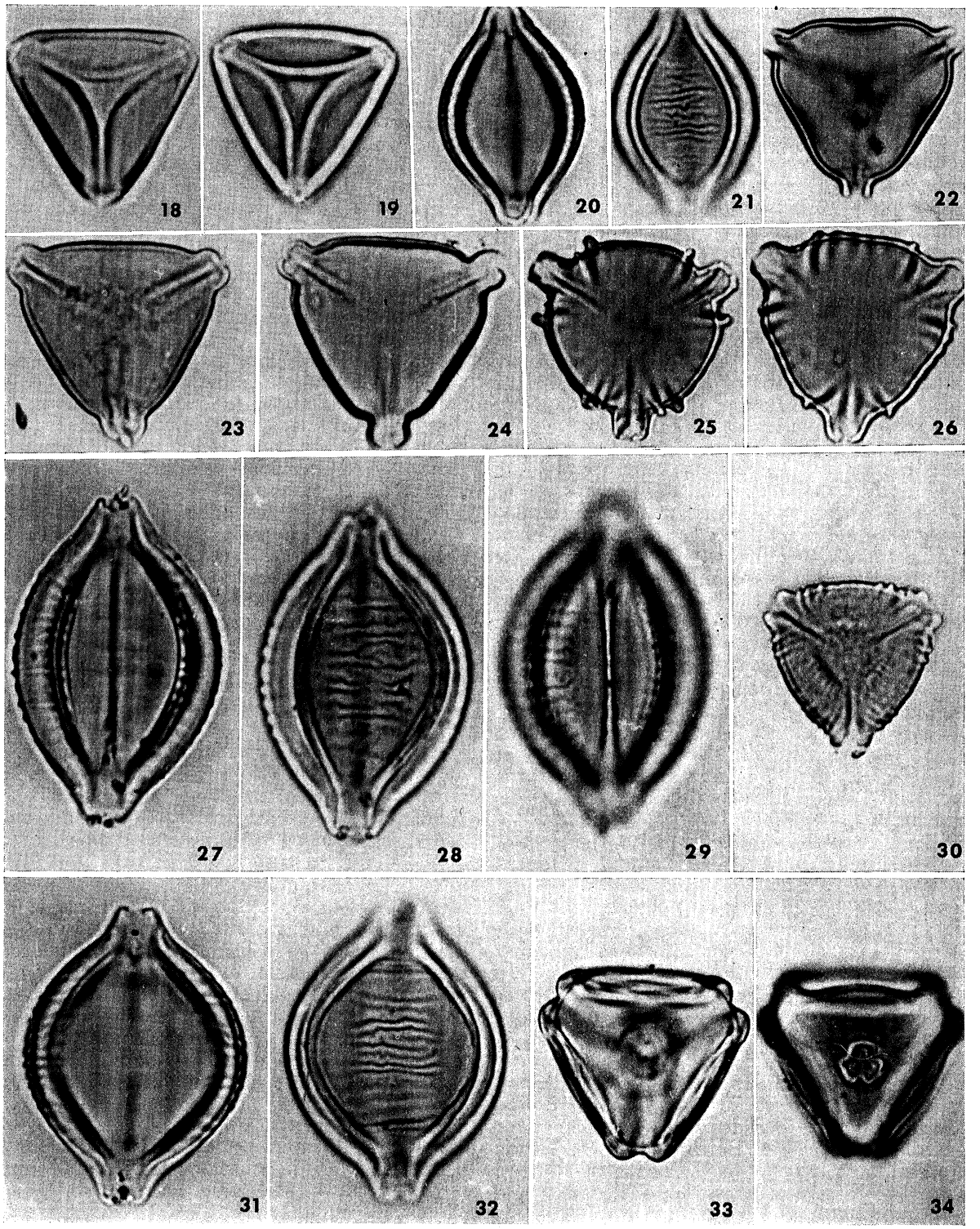

Fig. 18–34. Pollen types in *Cuphea*.—Fig. 18, 19. *C. cataractarum*.—Fig. 20, 21. *C. thymoides*.—Fig. 22. *C. patula*.—Fig. 23. *C. urbaniana*.—Fig. 24. *C. reitzii*.—Fig. 25, 26. *C. vesiculigera*.—Fig. 27–29, 31–34. *C. persistens*.—Fig. 30. *C. angustifolia*.

Type VI, *reitzii* (Fig. 24), *urbaniana* (Fig. 23)—oblate, oval-triangular in polar view; tricolporate, generally syncolpate, occasionally colpi not meeting, colpi straight, meridionally elongated, equatorially arranged, equidistant, margin entire, relatively conspicuous costae colpi present; pores slightly protruding, equatorially arranged, situated at midpoint of colpus, equidistant; exine tectate, psilate; size 24–48 μ.

The pollen is generally but not consistently syncolpate, with pores only moderately protruding and with relatively conspicuous costae colpi. Herbarium specimens of *C. reitzii* examined (at US) appear to differ only slightly from *C. urbaniana* in having smaller leaves and flowers. Since the pollen of the two species is identical as well, in a section with an otherwise heterogeneous pollen assemblage, this supports the author's (S. Graham) contention that the species are synonymous.

Type VII, *aspera* (1, 2)—oblate, oval-triangular in polar view; trisyncolporate, colpi straight, meridionally elongated, equatorially arranged, equidistant, margin entire, slight costae colpi present; pores conspicuously protruding, 3.5 μ long, equatorially arranged, situated at midpoint of colpus, equidistant; exine tectate, psilate; size 30–32 μ.

The pollen of this Florida endemic is singularly distinct, with its combination of conspicuously protruding pores and psilate exine. It shows no relationship to pollen of any particular species elsewhere in the section or the genus. It is likely that the closest relatives of *C. aspera* are to be found among several morphologically similar but rarely collected South American species in Subsection Oidemation, Series 1, for which pollen samples are not presently available.

In summary, the pollen of the large Section Euandra is extremely diverse with no one type characterizing a subsection. Two pollen types, each containing several species, correspond to two like groups in Section Brachyandra, but comparison of other characters of these species seems to indicate no direct or close relationship between the groups. A third group of species has diporate grains characteristic of Section Pseudocircaea and in other respects resembles species of that section except for the lack of persistent petals, the 'key' character of Section Pseudocircaea. The remaining species of Euandra display a range of pollen types each relatively distinct and without obvious relationships to other species either in or outside the section.

Specific suggestions for taxonomic revisions in Brachyandra and Euandra based on pollen data are not advisable at present because of the great array of pollen types and lack of additional kinds of comparative data for the species within the sections. It is evident, however, that morphology of the pollen, generally distinct for individual species, can be used as a significant taxonomic character in revision of these sections.

Section Trispermum (18-5)

Description: As described for Section Brachyandra, Subsections Micranthium et al., Type I, *antisyphilitica* (3), *patula* (Fig. 22), *ramulosa* (1, 2), *ericoides, flava, anisoclada.*

The section palynologically is a homogeneous one characterized by unique interaperturate thickenings. As previously discussed, two species outside the section having pollen with this character, *C. micrantha* and *C. aperta* (Fig. 8), probably should be transferred to Trispermum. It is surprising that the pollen of the section is so distinct from the preceding Section Euandra since the sections are so poorly separated in other ways. Features by which Trispermum is defined actually may not be present (e.g. stamens are shorter than the calyx tube in *C. gracilis* and *C. antisyphilitica*) or may overlap those of Euandra.

Within the Section Trispermum all species studied share the same pollen type and possess a thick disc with deflexed tip. On the basis of other morphological characters there are two species groups: those with thin leaves, small flowers up to 6 mm long, and stamens actually shorter than the calyx tube (Koehne's Series 1); and thick-leaved, shrubby, heath-like plants with long-spurred flowers up to 11 mm long and stamens equal to or exceeding the tube (Koehne's Series 2 and 3). In both groups the species are quite variable and difficult to distinguish from one another. The evidence then indicates the section to be one of closely related, interacting taxa. We suggest Section Trispermum is most succinctly defined by the thick disc with deflexed tip and pollen with interaperturate thickenings.

Section Pseudocircaea (12-4)

Description: As described for Section Brachyandra, Subsections Micranthium et al., Type II, *costata* (1), *lutescens, persistens* (Fig. 27–29; 31–34), *prunellifolia.*

Another homogeneous section from the standpoint of pollen morphology, Pseudocircaea has two distinguishing features: (1) persistent petals, which are known elsewhere in the family only in the genus *Rotala*, and (2) diporate pollen, known here and in a few species of Section Euandra and Section Melvilla (see prior discussion, Euandra, Type IV and Melvilla, Subsection Pachycalyx).

Section Heterodon (25-23)

The section was divided by Koehne into two subsections on the basis of the presence or absence of scales at the base of the upper petals. The character, in the experience of the senior author, is too variable in some of the species to be taxonomically dependable (e.g., in *C. lobophora* and *C. leptopoda*). Further, the pollen characteristics

do not support such a distinction and therefore subsections are not discussed individually in the following treatment.

Description: *angustifolia* (Fig. 30), *calcarata*, *crassiflora* (2), *glossostoma*, *goldmanii*, *koehneana* (2), *laminuligera*, *lanceolata*, *leptopoda*, *llavea*, *lobophora*, *lophostoma*, *lozani*, *lutea*, *palustris*, *paucipetala*, *procumbens*, *purpurascens*, *quaternata*, *trochilus*, *viscosa*, *viscosissima*, *wrightii* (1)—oblate, oval-triangular in polar view; trisyncolporate, polar areas granular in some species, colpi straight, meridionally elongated, equatorially arranged, margin entire, costae colpi present; pores equatorially arranged, equidistant, slightly protruding; exine tectate, striate with 2–4 striae on either side of pore generally largest, occasionally uniformly striate, striae extending from periphery toward poles and in some species fine striae also radiating from poles; size 18–26 μ.

Section Heterodon is relatively stenopalynous, characterized by oval-triangular, syncolporate pollen with slightly protruding pores and a striate exine. The 2–4 striae nearest the pores are generally largest. *Cuphea koehneana*, *paucipetala*, *palustris*, *quaternata*, and *goldmanii* differ slightly in being uniformly striate, and the last two also have thicker, coarser exines than the other species of the section. *Cuphea viscosissima* is also uniformly striate but the striations are faint. In a single species, *C. glossostoma*, the pollen is so distinct that its characteristics have not been included in the general description above. The grains are much larger than the typical Heterodon pollen, are non-syncolpate with a hyaline exine and distinctly shortened colpi. There is nothing in the external morphology of the species which suggests its placement should be anywhere but in Section Heterodon.

The definition of the section relies primarily on the presence of an enlarged dorsal calyx lobe, which unites a large group of species distributed mainly along the western and southern ranges of Mexico. The character also occurs in a few species whose affinities otherwise are found in other sections, i.e., *C. ferrisiae* and *C. vesiculigera* of Section Brachyandra, and *C. calaminthifolia* of Section Leptocalyx. Pollen of the latter is unlike that of Heterodon, but characteristic of Section Leptocalyx. This information was employed in deciding the proper section placement of the species to be Section Leptocalyx, not Heterodon (Graham, 1968). The dorsal calyx lobe of *C. ferrisiae* and *C. vesiculigera* is large on some specimens and small on others. The authors of the species indicated they could have been placed in either Section Heterodon or Section Brachyandra but for ease of keying chose the latter. The pollen points to exactly the same relationships, combining as it does some pollen characteristics of Heterodon (protruding pores and few, coarse striations) and Brachyandra (smaller, non-syncolpate grains).

Pollen of *Cuphea koehneana*, *C. paucipetala*, and *C. palustris* is the most distinctive in the section by virtue of its uniform, fine striations covering the entire grain and the but slightly protruding pores. The pollen type is so characteristic of Sections Diploptychia and Leptocalyx (to follow) that we were led to reexamine the morphology of the species. Both *C. koehneana* and *C. paucipetala*, having the internally winged elongate calyx of Diploptychia and the large calyx lobe of Heterodon, could be placed with equal ease in either section though the pollen would best support their placement in Diploptychia. Flowers of *C. palustris* are not internally winged and the species in all respects except pollen morphology seems well placed in Section Heterodon.

In a third group of species within Heterodon, the pollen displays an unusual granular sculpture pattern at the poles. *Cuphea angustifolia* (Fig. 30), *lophostoma*, *procumbens*, *calcarata*, and *lozani* likewise share similarities in floral morphology (such as bearded stamens) and preference for damp habitats. Unfortunately, at least one other very closely related species, *C. crassiflora*, has striate rather than granular poles.

Outside the exceptions noted above, species in Heterodon have the basic pollen type described for the section, with minor variations in striation pattern distinguishing the individual species.

Pollen morphology in Heterodon indicates there is a large core of closely related taxa with two smaller, more distantly related groups sharing characteristics of both Heterodon and one other section. The 'key' character of Heterodon, the large upper calyx lobe, is a feature shared by all the species, but also is found elsewhere in the genus.

The pollen record suggests that the derivation of the Mexican Section Heterodon should be sought among certain primarily South American complexes in Section Brachyandra (species with Type III pollen) and Section Euandra (species with Type I pollen) for three reasons. First, the pollen of those types is very similar to that of Section Heterodon. Secondly, the species with that pollen type are primarily South American, one center of species concentration. Thirdly, many display the more generalized floral morphology of the genus, having such characters as small, nearly regular, non-spurre flowers with equal petals, and equal calyx lobes.

At the specific and varietal level in Section Heterodon the pollen of *Cuphea* is extremely informative. For example, the documented case of allopolyploidy between two Heterodon taxa (*C. wrightii* subsp. *wrightii* and subsp. *compacta*, Graham and Graham, 1967) was substantiated by the 'hybrid' character of the pollen, its larger size and combination of parental striation patterns, and by the increased number of abnormal tetraporate grains in the allopolyploid.

The high incidence of tetraporate grains in

species with normally triporate pollen is a valuable indicator of recent or active species evolution. *Cuphea ferrisiae* var. *rosea* is a robust, showy, multiflowered taxon tending to have the large calyx lobe of Heterodon, approximately 15–30 cm tall, with a low percentage (10 %) of abnormal pollen. Variety *ferrisiae* is weak, few-flowered, ca. 7–20 cm tall with small calyces and petals, and the nearly equal calyx lobes of Section Brachyandra. It has approximately 40 % abnormal grains. The pollen indicates that var. *rosea* is the stable, presumably parental taxon from which var. *ferrisiae* recently has been derived.

Of the 150 species of *Cuphea* whose pollen we have examined, ca. 30 have a significantly high number of aborted grains; that is, 20 % or greater abnormal pollen, abnormality being indicated by the morphology of the grain, such as tetraporate condition, enlarged, thin-walled or exceedingly small, thick-walled grains. The pollen thus suggests that several groups within the genus are actively speciating. It further points to specific complexes which can be profitably investigated from the biosystematic standpoint. Table 2 lists species in which abnormal grains constitute 20 % or more of the pollen sampled.

Section Melvilla (36-17)

This is a large section of approximately 36 species in six subsections. Five of the six subsections are represented in our pollen collection. Four of these are characterized by distinctive pollen types, consequently the subsections are treated individually.

Subsection Eumelvilla

Description: *melvilla* (2,3)—oblate, triangular in polar view; trisyncolporate, colpi straight, equatorially arranged, meridionally elongate, equidistant, 10–12 μ long, margin entire to finely dentate, narrow costae colpi present, colpus membrane (and especially apocolpus polar region) granular; pores equatorially arranged, situated at apices of triangular grain, meridionally elongate, not protruding; exine tectate, sculpture of low, broad, slightly sinuous elongated elements (rugulate-striate) oriented parallel to the periphery of the grain; size 26–30 μ.

The subsection is comprised of ca. five species, all South American and morphologically unique in the section by virtue of their simple, rather than compound, small-bracted racemes and the distinctive pollen with its unusual parallel rugulate striations.

Subsection Pseudolobelia

Description: *lobelioides* (2)—oblate, oval-triangular in polar view; trisyncolporate, colpi straight, equatorially arranged, meridionally elongated, equidistant, 8–10 μ long, margin entire, narrow costae colpi present; pores equatorially arranged, situated at the apices of a triangular grain, conspicuously protruding (ca. 4–5 μ); exine tectate, striate, striae moderately fine, uniform, extending from the periphery toward the poles, slightly sinuous, occasionally anastomosing; size 34–38 μ.

This is subsection of one Cuban species, small flowered but with as many as 100 or more seeds and with pollen unlike any other in the section, being large, distinctly syncolpate with large protruding pores, and having relatively uniform striae covering most of the exine.

Subsection Polyspermum

Description: *micropetala* (Fig. 35, 36), *rasilis*—oblate, distinctly triangular in polar view; trisyncolporate, colpi straight, equatorially arranged, meridionally elongate, equidistant, 9–10 μ long, margin entire, narrow costae colpi present, pores equatorially arranged, situated at apices of triangular grain, not or only slightly protruding; exine tectate, uniformly fine to moderately coarse striae occasionally anastomosing, extending from the periphery toward the poles; size 28–34 μ.

The subsection is immediately recognizable by

TABLE 2. *Species of Cuphea having 20 % or more abnormal pollen.*

Section Enantiocuphea
C. correntina, decandra var. *vestita*
Section Brachyandra
C. calophylla ssp. *mesostemon, ferrisiae* var. *ferrisiae*[a], *vesiculigera*
Section Euandra
C. campestris, campylocentra[a], *carunculata*[a], *corisperma*[a], *hyssopifolia*[a], *lysimachioides, spruceana, urbaniana*
Section Trispermum
C. flava
Section Heterodon
C. calcarata, glossostoma, goldmanii, laminuligera[a], *leptopoda, lobophora* var. *arnottiana, lophostoma, lozani, trochilus*
Section Melvilla
C. melvilla, retroscabra
Section Leptocalyx
C. cristata var. *endotrichia, graciliflora, infundibulum*[a]

[a] Indicates an unusually high % (40 % or more) abnormal pollen.

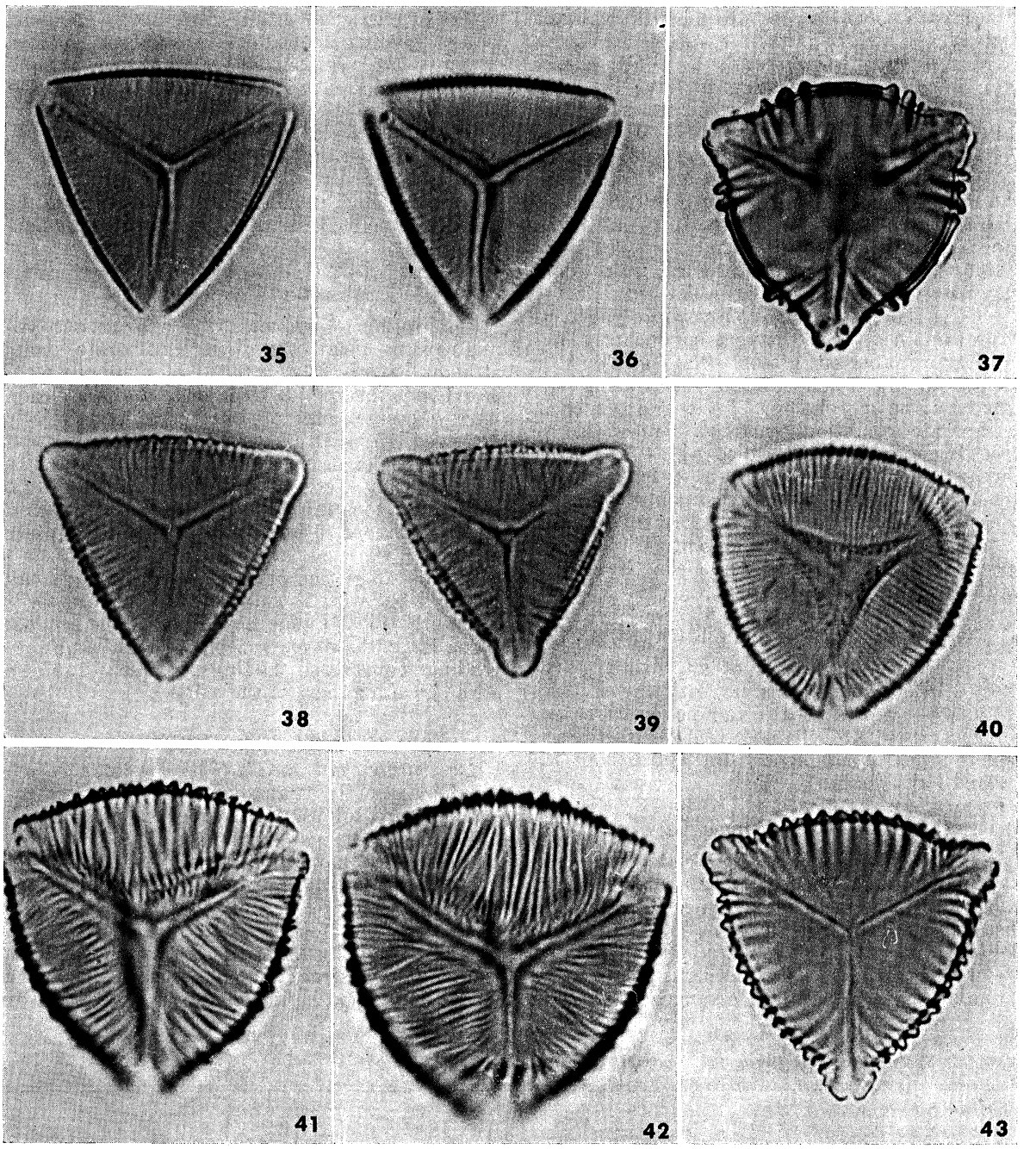

Fig. 35–43. Pollen types in *Cuphea*.—Fig. 35, 36. *C. micropetala*.—Fig. 37. *C. retroscabra*.—Fig. 38, 39, *C. ixodes*.—Fig. 40. *C. cyanea*.—Fig. 41, 42. *C. heterophylla*.—Fig. 43. *C. aequipetala*.

the distinct triangular pollen. Of interest is the fact that virtually identical pollen is found in two other species, *C. bustamanta* of Section Leptocalyx, and *C. ixodes* (Fig. 38, 39) of Section Diploptychia. Certainly one would not predict a close relationship between species of Subsection Polyspermum and these two species, their external appearances being so different. The common occurrence of seemingly identical pollen of a very distinct type is without explanation at this point.

Subsection Paramelvilla (3-0)

Subsection Pachycalyx (10-5)

There are approximately ten species in the subsection, with at least six probably known only

from type material. Kew Herbarium kindly supplied pollen from type material for four of the five species studied. The survey of the subsection provided an astonishing, inexplicable diversity of pollen, as is obvious from the following descriptions.

Description: Type I, *annulata, gardneri*—diporate pollen as first described in Section Brachyandrya, Subsection Micranthium et al., Type II, and as is characteristic of Section Pseudocircaea.

Type II, *pulchra*—the pollen type having psilate exine and interaperturate thickenings, as first described in Section Brachyandra, Subsection Micranthium et al., Type I and as is characteristic of Section Trispermum.

Type III, *grandiflora, bracteolosa*—the pollen is of the type characteristic of the next subsection of Section Melvilla (Subsection Erythrocalyx). It is tricolporate, oval-triangular, syncolpate, and completely and uniformly striate.

The occurrence of species with diporate pollen (Type I) and pollen with interaperturate thickenings (Type II) in this section is entirely unexpected. These species of Subsection Pachycalyx have large, red, long-spurred calyces, small petals and calyx lobes, and large leaves. They seem to share little in common with the small, purple-flowered, small-leaved species of Sections Trispermum and Pseudocircaea beyond the distribution of many of the species within the same states in Brazil. It will be of interest to see how intensive biosystematic investigations elucidate or resolve this intriguing situation of the presence of unique pollen types in seemingly distantly related taxa.

Subsection Erythrocalyx

The species of this subsection have a uniform pollen type with one exception, *C. retroscabra*, in which the pollen is different enough to require a separate description.

Description: Type I, *caeciliae, heterophylla* (Fig. 41, 42), *ignea, intermedia, jorullensis* (2), *subuligera, watsoniana*—oblate, oval-triangular in polar view; trisyncolporate, colpi straight, equatorially arranged, meridionally elongated, equidistant, margin entire, 5–9 μ long; pores equidistant, situated at apices of grain, non- to slightly protruding; exine tectate, striate, striae faint to moderately coarse, occasionally anastomosing, extending from periphery toward poles; size 22–35 μ.

Within Section Melvilla, the greatest number of species endemic to Mexico and Guatemala occurs in Subsection Erythrocalyx (all 12 species), other Mexican and Central American species constituting Subsection Polyspermum (3 species) and Paramelvilla (ca. 3 species), and a part of Subsection Pachycalyx (1 of 10 species). The pollen of the subsection is quite uniform, excepting *C. retroscabra*, being oval-triangular, syncolpate and completely striate, varying only in size and in the number and coarseness of the striae. Pollen suggests the group is a closely related one. Of greater interest, however, is the fact that all the species of the next two sections, Leptocalyx and Diploptychia, with a single exception in each, have the same pollen type as Section Melvilla, Subsection Erythrocalyx. Most of the species of these two sections are also Mexican or Central American in distribution. Evaluation of this situation is presented in the next section.

Type II, *retroscabra* (Fig. 37)—oblate, oval-triangular in polar view; trisyncolporate, colpi straight, equatorially arranged, meridionally elongated, equidistant, narrow costae colpi present; pores equatorially arranged, situated at apices of grain at mid-point of colpi, equidistant, circular to slightly oval, margin entire, protruding ca. 3 μ; exine tectate, striate with 3–4 large striae adjacent to pores, finer striae radiating from the poles; size 28–34 μ.

The external morphology of *C. retroscabra* places it unquestionably in Melvilla, Subsection Erythrocalyx, but its pollen is most similar to the type of Section Heterodon, especially in striation pattern. At present no adequate explanation can be offered for this situation and though one can postulate that *C. retroscabra* might be the product of parents from different sections, the lack of other definitive characters peculiar to any one or more members of Heterodon makes such speculations tenuous.

Section Leptocalyx (14-8)

Description: *aequipetala* (Fig. 43), *appendiculata, boissieriana* (2), *calaminthifolia, cristata, graciliflora, infundibulum* (1)—the pollen is equivalent to that of Section Melvilla, Subsection Erythrocalyx, Type I.

Type II, *bustamanta* (2)—the pollen is equivalent to Section Melvilla, Subsection Polyspermum.

The entire section finds pollen counterparts in the preceding Section Melvilla. The majority of species of Leptocalyx have the same pollen features as Melvilla, Subsection Erythrocalyx. One species, *C. bustamanta*, has pollen of the type in Melvilla, Subsection Polyspermum. In other respects the two sections differ in but a single character. The calyces in Section Melvilla are described as thick (*crassus*), and dorsally convex, while those of Leptocalyx are somewhat slender (*subgraciles*) or usually very slender at the base. The convex appearance of the calyces in Melvilla is not always obvious on young, aestivating flowers but becomes apparent in fruit when the convex lines are accentuated by the developing ovary. This character, although difficult to quantify, does consistently distinguish Melvilla from Leptocalyx. Rearrangement of sectional lines to join Melvilla, Subsection Erythrocalyx and Section Leptocalyx on the basis of a common pollen type would create a different but equally artificial classification. What pollen studies contribute at

this point is further (and quite striking) evidence for the close genetic connections among the large-flowered Mexican species in Melvilla and Leptocalyx, information actually suppressed as a result of their sectional separation. In addition, pollen indicates a more distant relationship between the Mexican and South American species of Melvilla than between the Mexican species of Melvilla and the species of Section Leptocalyx (all Mexican or Central American). The comments on these sections are continued under the following treatment of Section Diploptychia.

Section Diploptychia (20-14)

The section includes ca. 20 species (14 Mexican and Central American and 6 South American) in three subsections. Subsection Ornithocuphea was elevated to sectional status as Ornithocuphea (Koehne) Bullock, but neither treatment seems justifiable in view of the morphological continuity between species of that subsection and the preceding one. The recognition of Subsection Trichoptychia containing two closely related Mexican species is based on their possession of short hairs on the internal wings of the calyx. The separation is otherwise unsupported. In view of the weak subsectional distinctions, the two pollen types of the section, which do not correspond to the subsections, are presented without reference to these categories.

Description: Type I, *avigera, cyanea* (Fig. 40), *cordata* (2, 3), *dipetala* (3), *empetrifolia, hintoni, hookeriana, ianthina* (3), *nitidula, painteri, pinetorum, pulcherrima, scaberrima*—equivalent to the pollen of Section Melvilla, Subsection Erythrocalyx.

Type II, *ixodes* (Fig. 38, 39)—equivalent to Section Melvilla, Subsection Polyspermum.

Pollen of Diploptychia parallels that of the two preceeding sections, with one species having the pollen type common to Section Melvilla, Subsection Polyspermum (as does one species in Section Leptocalyx), and the remainder of the species, as in Leptocalyx, having the pollen type of Section Melvilla, Subsection Erythrocalyx. The only difference lies in the fact that Diploptychia contains species endemic to Mexico and South America while the species of Section Melvilla, Subsection Erythrocalyx and Section Leptocalyx are all restricted to Mexico or Central America, the South American taxa of Section Melvilla representing other subsections which are also distinct palynologically.

Within the Type I pollen group of Diploptychia there is a small subgroup in which the pollen is smaller (ca. 12–16 μ) and more faintly striate. This includes *C. avigera, hintoni, pulcherrima, dipetala,* and *empetrifolia.* Pollen of *C. avigera, hintoni,* and *pulcherrima* is indistinguishable and suggests there is but one taxon represented. A survey of the herbarium material of these three species suggests there is only one species whose disjunct populations might, at best, deserve varietal status.

Two pollen types common to so many species of Sections Melvilla, Leptocalyx, and Diploptychia is not surprising in light of numerous other morphological features shared by species of these sections. The first two sections differ basically in but one character, Section Melvilla having species with thick, convex calyces, while species of Section Leptocalyx have generally slender ones. Distinctive features of Diploptychia are the wings developed below the dorsal stamens within the calyx and the usually sub-ascending calyx spur. In other respects the morphology of the section parallels that of Leptocalyx.

Conclusions—It is apparent from this survey that pollen alone does not provide an adequate basis for subdividing the genus into a more natural series of infrageneric categories in spite of the diversity displayed, a diversity probably exceeded by few genera of comparable size. Such a needed revision will require a broad spectrum of biosystematic data, including hitherto neglected palynological information. The major contribution pollen data, as presented here, can make is to suggest profitable directions for these biosystematic studies. An explanation for the diverse pollen types discovered in Section Melvilla, Subsection Pachycalyx, for example, and the genetic connections between those species and ones with similar pollen in the seemingly distant and distinct Sections Pseudocircaea and Trispermum would ultimately contribute to an understanding of evolutionary mechanisms and relationships within the genus as a whole.

Because of the unusual degree of pollen variation within the genus, however, many specific and more immediate taxonomic contributions can be obtained from pollen studies in *Cuphea,* particularly at the species level (e.g., the relationships of newly described species, documentation of the supposed hybrid nature of particularly difficult species via the degree of pollen sterility, evaluation of suspected synonomies of species belonging to eurypalynous subgeneric taxa, and the natural versus artificial nature of certain sections and subsections as defined in the present taxonomic treatment of Koehne).

This survey of pollen types in *Cuphea* has provided much information useful in an eventual revision of the genus, some of a broad nature, some suggesting very specific changes. Some of the more striking contributions and suggestions are summarized below.

1. Pollen data do not support recognition of subgenera as they are presently defined, but rather suggest that the first three sections are more closely related to one another than to the remainder of the genus.

2. Diversity of pollen types in the large Section Brachyandra suggests it to be highly artificial in

composition and further suggests these specific changes or studies: (a) a more natural arrangement of Subsection Melanium into two rather than four groups, (b) removal of two species to Section Trispermum and one species to Section Pseudocircaea, (c) need for intensive studies of species in Subsection Micranthium, Lophostomposis, Lythrocupheopsis, and Balsamonella, particularly the relationships of *C. parsonsia*, *C. pseudosilene*, and *C. pustalata*.

3. Pollen of Section Euandra reveals a heterogeneous section with at least half the species studied having pollen relationships to Section Brachyandra, and four species related by diporate pollen to Section Pseudocircaea. Of specific interest is the identical pollen displayed by *C. reitzii* and *C. urbaniana*, which suggests the species to be synonymous.

4. On the basis of pollen morphology Sections Trispermum and Pseudocircaea are natural assemblages, the first characterized by grains with interaperturate thickenings, the latter by diporate pollen.

5. Pollen data indicate that Section Heterodon is composed of a large core of closely related taxa with two smaller, more distantly related species groups sharing characteristics of Heterodon and one other section. They further suggest the derivation of the section be sought among certain species groups in Section Brachyandra and Section Euandra.

6. Section Melvilla displays several pollen types corresponding in great degree to present subsectional lines and suggesting the presence of independent evolutionary lines within the section. Two of the types are found also to represent the total pollen diversity of adjacent Sections Leptocalyx and Diploptychia. The three sections morphologically share many other characters as well. Pollen suggests the close relationship of Sections Leptocalyx and Diploptychia and Melvilla, Subsection Erythrocalyx. More specifically within Section Melvilla, (a) the relationship of Subsection Polyspermum to *C. bustamanta* (Leptocalyx) and *C. ixodes* (Diploptychia) should be investigated since all share a distinct pollen type not found elsewhere in the genus, (b) the inexplicable diversity of pollen types in Melvilla, Subsection Pachycalyx, types thought unique to earlier sections of the genus, provides a stimulating problem for biosystematic study, and (c) morphological characters separating *C. avigera*, *C. hintoni*, and *C. pulcherrima* of Section Diploptychia are weak and their identical pollen in an otherwise palynologically diverse section suggests only a single species is represented.

7. Pollen data do not support the recognition of sectional status for Ornithocuphea (Koehne) Bullock.

These contributions and suggestions emphasize the pragmatic nature of pollen studies in taxonomic investigations of *Cuphea*. Changes in taxonomy as a result of pollen data alone are, of course, no better than any other artificial rearrangement. The information pollen morphology adds to an understanding of the internal dynamics of the genus, however, appears to us to be of great value because it suggests relationships presently submerged in the morasse of variable, shared, micromorphological features, and ultimately because it provides yet another character upon which more accurate taxonomic judgments can be made.

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