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A REVISION OF THE ASIATIC GENUS ENKLEIA (THYMELAEACEAE)

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THIS STUDY OF ENKLEIA is the second of three revisions treating the three genera which comprise the subtribe Linostomatinae of the Thymelaeaceae. It completes the revision of the two Asiatic members, *Linostoma* Wall. ex Endl. and *Enkleia* Griff., and prepares the way for a more enlightened appraisal of the Amazonian genus *Lophostoma* Meissn.

The members of the Linostomatinae have been combined taxonomically in various ways in the past so that a taxonomic re-evaluation is of primary importance. The revision of *Linostoma* and *Enkleia* has resulted in the reduction of the number of species and the alignment of several taxa with *Enkleia*, rather than with *Linostoma*. There is little doubt that *Lophostoma* is related to both *Linostoma* and *Enkleia*, as is evidenced by the common possession of a number of diagnostically important morphological and anatomical characteristics. An effort has been made to include, as a secondary study, certain anatomical information which may prove to be taxonomically significant. The large geographic disjunction that now exists between the South American and the Asian genera adds to the fascination of the interrelationships to be found among members of the subtribe.

SPECIAL MORPHOLOGY

Some of the more interesting morphological features found within the genus *Enkleia* are presented in this section. In addition, a deliberate and conscientious attempt has been made to parallel closely the discussion of morphological characteristics of *Linostoma* (Nevling, 1961). This has been done to simplify comparisons between the two genera. Additional morphological information can be found in the description and in the discussion following each species.

Gross and microscopic structure of the leaf was studied by clearing and staining with safranin or with ferric chloride and tannic acid. In addition, it was studied from safranin-fast green-stained cross and longitudinal thin sections, as was the petiole. This material was tested with phloroglucin and

hydrochloric acid, as well as with potassium iodide and sulphuric acid, to estimate chemically the degree of lignification of certain tissues.

The stem and inflorescence axes were studied by means of free-hand sections which were stained with either safranin or phloroglucin and hydrochloric acid. This technique was also employed with inflorescences and young shoots.

Flower structure was studied from material that was cleared and stained with safranin. In this instance, the study was limited to whole mounts and did not include sectioned specimens. The source material was from herbarium specimens in all instances, and the details of the techniques outlined above can be found in a previous paper (Nevling, 1961).

Vegetative Morphology. The vegetative axis is monopodial. Leaf position is opposite or subopposite except in extremely vigorous young shoots. In slow-growing shoots a cycle composed of an elongate internode and an extremely shortened internode accounts for the opposite to subopposite position, the trace for one leaf departing from the stele prior to the initiation of the second trace. In vigorous shoots, all internodes undergo similar elongation, thus accounting for the alternate leaf position. A single trace per node is formed in all cases, and the resultant gap is unilacunar.

Unequal bifurcations and trifurcations of the shoot are not unusual in *Enkleia* but do not occur with the frequency found in *Linostoma*. They are induced more generally by damage to the terminal bud which allows the development of subtending axillary buds in a haphazard manner, but, in some cases, the trichotomies occur without apical damage (see *Put* 2305 and the flowering sheet of *Van Royen* 3592). In the Van Royen collection the opposite axillary branches are gracefully curved (not recurved) and the subtending leaves are borne a considerable distance above the point of external branching. The lowest leaf on these branches is unpaired and is the displaced leaf of the subtending node; the trace for this leaf has its origin below the point of external branching. It seems that the leaf is borne upon the axillary branch which it subtends. In reference to the "misplaced" leaf one should not expect to find a bud in its axil, but an axillary bud is almost invariably present. It is impossible to account for this unless it is a supernumerary bud.

In several specimens of *Enkleia malaccensis* (*Toroës* 4099 and *Ridley* 6427) development of multiple axillary buds has occurred. In the *Toroës* specimen two axillary branches develop from the axil of a single leaf and are positioned one above the other. A specimen of *E. siamensis* ssp. *siamensis* (*Kerr* 16136) has the terminal bud injured, and supernumerary axillary buds have developed (three from one leaf axil, two from another). In the subgenus *Neivira* of the genus *Daphnopsis* supernumerary axillary buds are the rule, rather than the exception, and allow the plants to become cauliflorous. After examining the beautiful photograph of a *Phaleria* in Hou's treatment of the Thymelaeaceae (1960), I suspect that the same phenomenon is acting in that genus.

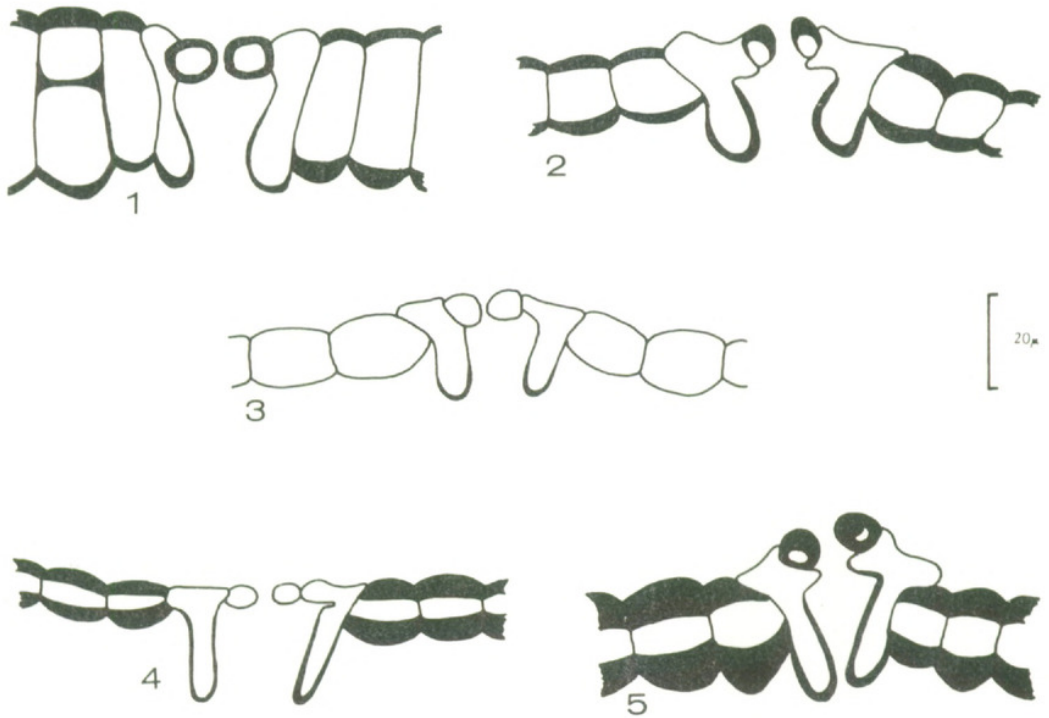
Axillary branches sometimes become gently to strongly uncinatate, facilitating climbing. Such branches are quite thickened towards the base and bear very reduced leaves. The frequency of these modified branches varies rather widely, but some generalizations about their occurrence among the species may be made. *Enkleia thorelii* lacks them altogether; in *E. paniculata* and *E. siamensis* they are found infrequently but may be well developed; and in *E. malaccensis* they are found generally, sometimes very well developed (*Anta 1713*, for example).

The extraxylary fiber sheath surrounding the stele, by which the family is often identified, is well developed in this genus. It becomes well lignified after a number of years. In addition, in the pith are found scattered fibers which also appear to be well lignified. In general, the fibers and xylem of the *Enkleia* species are lignified to a greater extent than the corresponding structures in *Linostoma*.

The leaves are dorsiventral. The upper epidermis is composed of tabular cells, is unbroken by stomata, and is very poorly cutinized. In *Enkleia siamensis* and *E. paniculata* the upper epidermis is a single cell thick, with the periclinal walls much thicker than the anticlinal walls. There is a possibility that these differentially thickened cells may be slime cells. A single epidermal layer is found also in *E. malaccensis*, but the cell walls are not differentially thickened. *Enkleia thorelii* is unusual because the epidermis is one or two cells thick, varying irregularly with neither number predominant. When double, the two cells occupy the same volume as that occupied by the single cell components. The palisade tissue is composed of compact columnar cells and is two or three cells thick, except in *E. paniculata* in which it is only one or two cells thick. In all species, the palisade cells are smaller in diameter than the cells of the upper epidermis. A spongy parenchyma layer underlies the palisade and is composed of loosely knit branched cells interspersed with many large air spaces. This layer is developed to the fullest in *E. paniculata* in which it occupies fully three-quarters of the entire depth of the leaf. The lower epidermis is composed of cells smaller than those of the upper epidermis, and, in addition, it is interrupted frequently by stomata. In *E. siamensis*, *E. paniculata* and *E. malaccensis* it is uniseriate, the individual cells with the outer periclinal wall slightly bullate. The periclinal cell walls are differentially thickened in *E. siamensis* and *E. paniculata* but not in *E. malaccensis*. As might be expected, the lower epidermis in *E. thorelii* occasionally is double, and the individual cells are short-columnar with conspicuously bullate outer periclinal walls.

The stomata of all species of this genus are of the pit-type previously described for *Linostoma decandrum* (Roxb.) Wall. ex Endl. These stomata, when examined microscopically in cleared material stained with ferric chloride, resemble in face view many small doughnuts scattered on the lower leaf surface. A slight shift in focus is necessary to observe the guard cells. As in *L. decandrum*, a rosette of accessory cells surrounds each stoma, the number being rather variable (generally eight, nine, or ten, but as few as six and as many as thirteen). Each accessory cell is

somewhat awl-shaped and extends beyond and slightly over the guard cells, forming an urceolate or campanulate structure. Occasionally an accessory cell can be found being shared by two adjoining stomata. The guard cells are borne at the base of the accessory cells and are situated at most only slightly above the lower epidermis. Differences in the structure of the stomata can be found among the species (Figs. 1-5), but the amount of variation has not been determined, so their taxonomic worth cannot be evaluated.

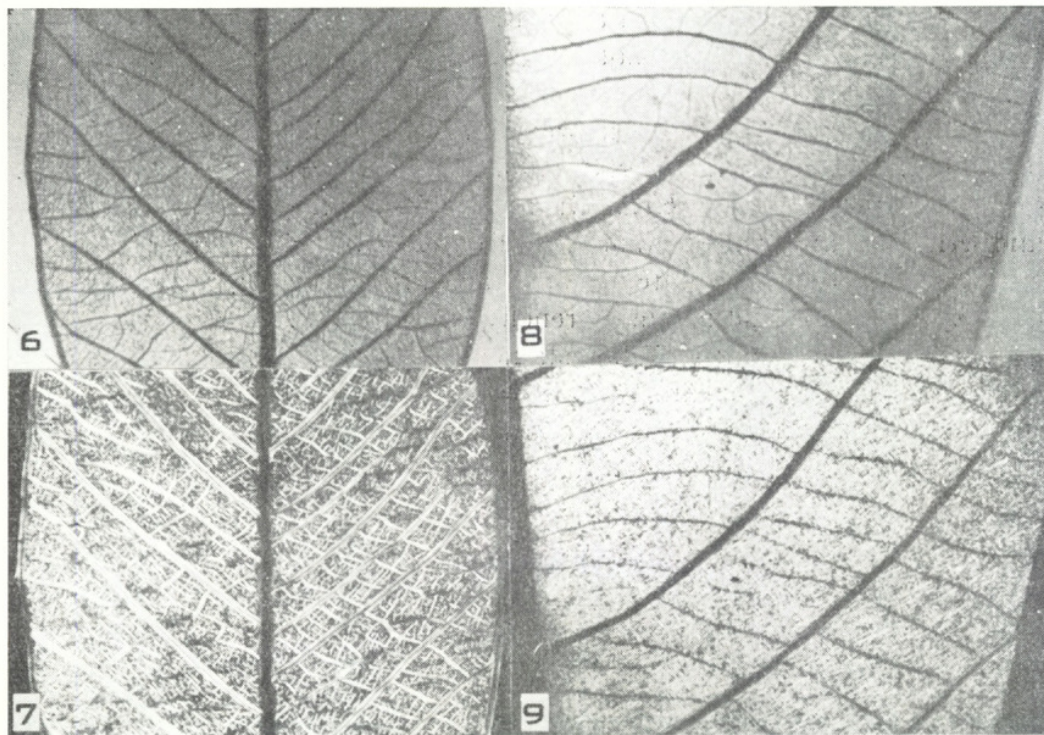


FIGS. 1-5. Cross sections of lower leaf epidermis of species of *Enkleia* including the stomatal apparatus. Guard cells (borne above the lower epidermis) are shown in cross section while the accessory cells (projecting below the lower epidermis) are shown in longitudinal section. Mesophyll and other leaf tissues are not illustrated. Note variation in the differentially thickened walls of epidermal cells. 1, *E. thorelii* (Kerr 19930); 2, *E. paniculata* (Van Royen 3592); 3, *E. malaccensis* (Kostermans 7034); 4, *E. siamensis* ssp. *siamensis* (Poilane 14229); 5, *E. siamensis* ssp. *andamanica* (Parkinson 384).

The pinnate venation is similar throughout the genus. The primary lateral veins number from nine to thirty-five per leaf. They are separated by a distance of several millimeters to a centimeter and a half (the distance between major veins appearing to be determined by leaf size). These veins are somewhat arcuate-ascending and end in a variously developed submarginal vein. Each vein is supported above and below by an extra-xylary fiber sheath which is more extensive than the vein.

The secondary veins are numerous and generally form direct connections between adjacent primary veins. In the larger leaves, at least, these cross-connecting veins are almost at right angles to the costa. The pat-

tern thus formed is quite distinctive (Figs. 6, 8). The secondary veins have a fiber sheath associated with them in the same manner as the larger veins. The xylem is very poorly lignified, and, in *Enkleia malaccensis*, I could perceive no color reaction when testing with phloroglucin and hydrochloric acid. The xylary elements, with the exception of the protoxylem, often have very thickened walls and reduced lumina. This peculiarity is discussed further in the paragraph on petiole structure.



FIGS. 6-9. Photographs of cleared leaves showing veins and associated fibers of two species of *Enkleia*, $\times 3$. FIGS. 6, 7. *E. thorelii* (Thorel 2823); 6, with transmitted light showing venation pattern; 7, with polarized light showing venation pattern as outlined by the associated fibers. FIGS. 8, 9, *E. malaccensis* (Griffith 4375); 8, with transmitted light showing venation pattern; 9, with polarized light showing venation pattern and fibers not associated with the venation.

The extraxylary fibers accompanying the veins have very thick secondary walls. In prepared material, the secondary wall is usually pulled away from the thin primary wall. Concentric lamellations appear to be present in the secondary walls but should be studied further. The secondary walls react quite strongly with potassium iodide and sulphuric acid but give no reaction with phloroglucin and hydrochloric acid, thus indicating their cellulosic nature. These fibers, which appear superficially similar to the primary phloem fibers of *Cannabis* figured by Esau (*Pl.* 24 A), are intimately associated only with the veins in *Enkleia thorelii* (FIG. 7) and *E. siamensis* ssp. *siamensis*. In *E. siamensis* ssp. *andamanica* and *E. paniculata* a few of the fibers wander from the vein and intrude into adjacent tissues. The wandering of fibers reaches its zenith in *E.*

malaccensis where they are found in great profusion (FIG. 9). They apparently grow apically, often striking out vertically until reaching the upper or lower epidermis and then running horizontally. They can be observed readily in leaf sections and appear to be similar to the fibers described by Thoday (1921) in the African *Passerina filiformis* L. Near the veinlet endings in *E. thorelii* and *E. siamensis* ssp. *siamensis* the fibers are replaced by irregularly shaped sclereids. Sclereids also are found associated with the vein endings in *E. siamensis* ssp. *andamanica* and *E. paniculata* but are not as reduced as in the preceding two species. The situation in *E. malaccensis* could not be determined because of the too numerous wandering fibers.

Cross sections of the petiole were studied to check information given by Metcalfe and Chalk (1950) indicating the presence of intraxylary phloem in petioles of *Enkleia*. In all species of the genus the xylem, at midpetiole, is arc shaped. The arc often has strongly recurved ends and appears somewhat involute. The tracheary elements, except for the protoxylem but including the parenchyma, have curiously thickened walls and very reduced lumina. When stained with safranin and fast green, only the middle lamella appears to stain well with safranin but the entire wall can be weakly stained with phloroglucin and hydrochloric acid. No color reaction is formed with potassium iodide and sulphuric acid, probably indicating very weak lignification of the wall. Visually the walls appear to be rather similar to those of the extraxylary fibers. The greatest degree of thickening has taken place in *E. thorelii*. Phloem is found on both sides of the arc, confirming the statement of Metcalfe and Chalk, but the taxonomic significance of this is doubtful. Few to many scattered extraxylary fibers are found surrounding the trace, but the fibers are not nearly as prevalent as in the stem and leaf. The fibers have thick nonlignified cellulose walls.

Reproductive Morphology. The same terminology which I applied to the inflorescence in previous papers concerning the Thymelaeaceae (1959, 1961) is used here. The inflorescence is composed of the primary peduncle with a pair of bracts, a bracteole, a rachis, the secondary peduncles, and the flowers with their pedicels.

The floriferous branches of *Enkleia* are composed of many inflorescences which collectively appear to form a single, large, terminal inflorescence. The species of *Enkleia* (with the exception of *E. malaccensis*) bear their inflorescences in an axillary position on the terminal portions of young shoots. Each axillary inflorescence is simple, with the individual members cymosely arranged, i.e., opposite, except in very vigorous plants in which they become alternate by elongation of the internodes.

The floriferous shoots of *Enkleia malaccensis* are characterized by the development of several to many axillary branches which bear the individual inflorescences. The floriferous branches thus appear to be paniculiform. A few specimens of *E. siamensis* subsp. *siamensis*, such as *Poilane 14229*, also branch in this manner.

The reduced leaves subtending the axillary inflorescences are borne on the primary peduncle which they subtend; the trace initiation is, of course, below the point of external branching. Occasionally, this displacement is quite striking, as in *Zippelius 148a*. On one of the flowering shoots of this specimen the reduced leaves have been "carried out" onto the axillary shoots for about eight millimeters. The mechanics and meaning of this displacement are not entirely clear. It is interesting that the separation layer of the petiole appears to be forming at the point where the petiole and axillary branch fork. The entire pattern is essentially the same as that found in *Linostoma*.

Vegetative growth is resumed by the development of dormant axillary buds subtending the floriferous region of the shoot. The old inflorescences die shortly after fruiting and are soon broken off.

A single bracteole is borne at the apex of the primary peduncle. It is linear, to 8 mm. in length, and almost invariably persistent in fruit.

In addition to the bracteole, the primary peduncle bears a pair of bracts. In this genus the bracts are small and very strongly keeled until anthesis. At anthesis they are opposite or subopposite and are borne near or below the middle of the primary peduncle (*Enkleia paniculata* and *E. siamensis* ssp. *siamensis*), below the middle of the primary peduncle (*E. malaccensis* and *E. thorelii*), or above the middle of the primary peduncle (*E. siamensis* ssp. *andamanica*). Subsequently, they rapidly expand and become plane. A change in orientation generally accompanies the expansion, for the bracts are suberect prior to anthesis and then become deflexed, sometimes strongly so, in fruit. In addition, their position on the primary peduncle is radically shifted sometimes because of differential elongation of the axis. Elongation, during fruit maturation, takes place in all taxa except *E. siamensis* ssp. *siamensis* and is in striking contrast to the situation in *Linostoma* in which elongation is negligible. The function of the bracts is still an open question, as I suggested previously (1961), although Ridley (1930, p. 93) says, "When ripe the fruit on its peduncle, with the 2 bract leaves attached, separates from the plant and, rotating rapidly, drifts away in the wind across the forest to some distance, very much in the same way as the fruit of a Lime tree does." As in *Linostoma*, the separation layer occurs between the secondary peduncle and pedicel so that the chances of the drupe separating with the primary peduncle and its bracts seem slim.

Mature bracts are elliptic to obovate in shape and are quite unlike the foliage leaves. In addition to shape, the bracts are dissimilar in other respects, namely, smaller size, lighter color, thinner texture, and more reticulate venation. The venation pattern is essentially the same as that of the leaf (particularly with respect to the orientation of secondary veins). The individual veins, however, tend to be larger, giving a more thickly veined aspect to the bracts. The submarginal vein is well developed in *Enkleia siamensis* but poorly developed in *E. paniculata* and *E. malaccensis* (*E. thorelii* not determined because of insufficient material).

A study of the anatomical characteristics of the bract, based on cross sec-

tions, was not pursued, except in *Enkleia malaccensis*, because of the difficulty in obtaining satisfactory results. The bracts from herbarium specimens re-expand poorly because of the large number of thin-walled cells. The epidermal cells lack the extreme thickening found in the leaves, but the stomatal distribution is the same (i.e., on the abaxial surface only). The stomatal structure, however, is modified and is discussed below. Since extreme crushing and distortion were found in the mesophyll, no observations could be made on this tissue. The veins have the usual fibers associated with them. In *E. siamensis* and *E. paniculata* the outermost fibers of the fiber sheath are modified into shorter sclereids which have one wall conspicuously enated as in *Linostoma*, but in *E. malaccensis* this does not occur. As might be expected the fibers in the bracts of *E. malaccensis* and *E. paniculata* wander from the veins just as in the leaves of these species. The bract petiole is enervated by a single arc-shaped trace with strongly inrolled margins. All cells with the exception of phloem cells embraced by the arc are heavily sclerified. Extraxylary fibers do not appear to be present.

The stomatal structure is superficially dissimilar in leaf and bract. In the bract, the numerous accessory cells are fewer in number (generally four to eight), and they retain the tabular form which characterizes the surrounding epidermal cells. Thus, the stoma is not borne within a substantial pit. I believe that this indicates the pit-type (as found in leaves of all *Enkleia* species and *Linostoma decandrum*) to be much more closely related to the ranunculaceous type (as in *L. persimile* and *L. pauciflorum*) than might be expected. It indicates also the need for ontogenetic studies of the stomatal differentiation to determine the sequence of divisions in the formation of the pit-type. Unfortunately, small leaves from herbarium specimens are too difficult to handle because of brittleness and pubescence to permit such a study, even if sufficient material was available.

The flowers are arranged on the rachis in an indeterminate manner (the lowermost flower being the first to bloom). The flower clusters are umbelliform to subracemiform, depending on the length of the rachis. The form of the flower cluster is somewhat static within the species, but it is not considered to be a dependable taxonomic character. The number of flowers per inflorescence varies from three to sixteen in *Enkleia siamensis*, with the range of variability of other species falling within this number.

The flowers are bisexual, regular, pentamerous, perigynous and pedicellate. The terminology applied to the parts is the same as used in my previous papers concerning the family (1959, 1961). Further gross morphological information concerning the flower, beyond that presented in the following discussion, may be found in the specific descriptions.

The calyx tube, as in other members of the family, is composed of the fused bases of calyx, corolla, and androecial members. It is tubular in all species except *Enkleia malaccensis* in which it varies to suburceolate. The exterior is variously pubescent; the pubescence in all cases is minute. The interior is glabrous in all species, except *E. malaccensis* in which the tube interior is completely glabrous, or villous above and glabrous below, or

completely villous. The trichomes are exclusively unicellular and unbranched.

The tube is vascularized by ten distinct veins which are marked externally by inconspicuous ridges. Five of the traces are in the antisepalous position (median traces) and five are in the alternisepalous position (each consisting of a fused pair of traces designated as commissural traces). Occasional branching of a main trace occurs, but these branches usually reunite with the parent trace. Approximately half way up the tube the traces to the alternisepalous stamens depart from the commissural traces and shortly thereafter the traces to the antisepalous stamens depart from the median traces. In *Enkleia siamensis* each commissural trace and median trace gives rise to two lateral traces slightly above the insertion of the alternisepalous stamens. These lateral traces fuse (i.e., one of commissural origin with one of median origin) forming an inverted "V" pattern lying between the main traces. At the apex of this inverted "V" a trace is formed which contributes eventually to the vascularization of the calyx lobes. The commissural traces then dichotomize giving rise to the two lateral calyx lobe traces, and the median traces continue undivided as the calyx lobe median traces. In *E. thorelii* and *E. paniculata* a minor deviation from this pattern is found. The median trace gives off a pair of lateral traces in the same position and manner as in *E. siamensis*, but the corresponding lateral traces from the commissural traces are not formed. The laterals (from the median trace only) thus do not form the inverted "V" pattern but fuse directly with the commissural traces. This pattern appears similar to that demonstrated by Heinig (1951, *Fig. 56*) in *Pimelea prostrata*, except that in *Enkleia* the commissural traces are fully developed for the entire length of the tube.

The size and shape of the five calyx lobes vary insignificantly among the species. The lobes are vascularized by three or five main veins which send off numerous branches which anastomose repeatedly. As in *Linostoma*, the aestivation of the lobes is quincuncial.

The petals are inserted at the orifice of the calyx tube in an alternisepalous position and are erect and glabrous in all species. They are divided medially either completely or incompletely. The median division is incomplete in *Enkleia paniculata* and *E. malaccensis* but complete in *E. siamensis*, and *E. thorelii*. The shape of the lobes is ensiform (*E. paniculata*), linguiform (*E. malaccensis*), or liguliform (*E. siamensis* and *E. thorelii*).

The petals can be interpreted in two conflicting ways depending on the supposed origin of these structures. Heinig supports the hypothesis that the structures are stipular in nature (see her 1951 publication for comprehensive discussion), while I support a petalaceous origin (1960, 1961). It is, admittedly, easier to explain the various types found within the family on the basis of her hypothesis but I feel that an attempt to gain information in support of the other view must be made. I interpret the incomplete division of the lobes as primitive and the complete division of the lobes as advanced (Heinig's position would be quite the opposite).

Only the petals of *Enkleia thorelii* have any hint of vascularization. I found one petal lobe which was vascularized for about one-third its length, the vascularization consisting of a single trace at most three tracheids in diameter and with a few accompanying fibers. Several other lobes bore a few fibers in the position that vascularization would be expected. I interpret the presence of these fibers as indicating a degeneration of a previously existing vascular system. The vascular supply of the single lobe and the fibers of several additional lobes appear to arise from the lateral calyx lobe trace.

The androecium consists of ten stamens inserted on the calyx tube. They are in two whorls, the upper whorl in the antisepalous position and the lower whorl in the alternisepalous position. The traces which supply the stamens reflect the external position of the stamens in that they also depart from their parent traces in two distinct whorls.

The filaments are short (to 1 mm. long), stout, and slightly inflated just below the anther. They are glabrous except in some specimens of *Enkleia paniculata* in which a few trichomes may be present at the base of the anther. Vascularization is by a single bundle which either ends at the base of the connective (*E. siamensis* and *E. malaccensis*) or extends to the very distal portion of the connective (*E. paniculata* and *E. thorelii*).

The antisepalous anthers are exserted or subexserted, except in *Enkleia siamensis* ssp. *andamanica* where they are included. Alternisepalous anthers are included except in *E. paniculata* in which they are subexserted. They are 4-lobed and 4-loculed in cross section. Dehiscence is longitudinal. There is some basal inflation of the connective but not nearly so pronounced as in *Linostoma*. The connective is minutely produced beyond the pollen sacs and, on the basis of cell shape and size, may be glandular in function.

The pollen of the four species is, for all practical purposes, uniform. It is polyporate and highly sculptured. It cannot be distinguished from the pollen of *Linostoma*.

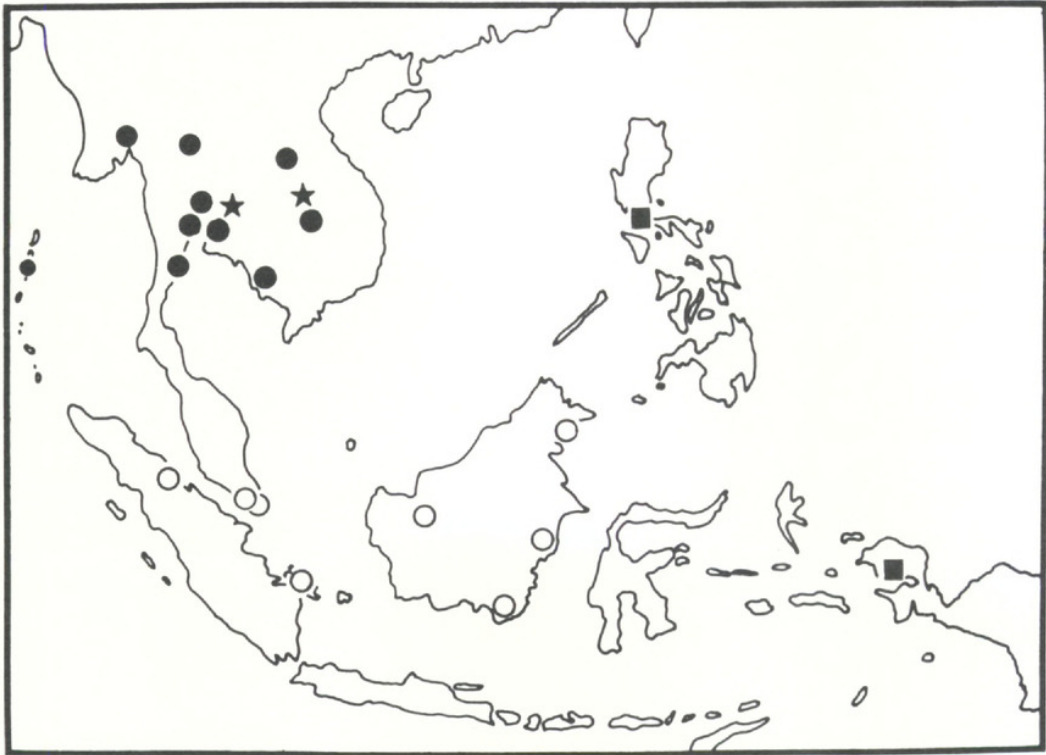
The disc is borne at the base of the calyx tube. It consists of minute free lobes in *Enkleia siamensis* and *E. thorelii*, while in *E. paniculata* it is basally adnate to the calyx tube. No vascularization is present. The disc in *E. malaccensis* is completely adnate and amounts to only a few additional cells in the thickness of the calyx tube wall. It is regularly lobed with the apex of each lobe coinciding with one of the main veins of the tube.

The gynoecium is composed of a single pistil, presumably of the pseudomonomeric type. It is sessile or nearly so. I have found it impossible to clear the gynoecium satisfactorily, even when placed in clearing agents for greatly extended periods of time, so that vascular patterns could not be established.

The style is borne terminally on the ovary. It is filiform, glabrous, and sometimes variable in length. Style length in comparison to ovary length has been used in the past as a character to separate *Enkleia* and *Linostoma*. An evaluation of this character is made in the discussion of *E.*

siamensis. The stigma is subcapitate in *E. paniculata* and *E. siamensis* but clavate in *E. malaccensis* and *E. thorelii*.

As in *Linostoma*, the drupes of *Enkleia* are preserved poorly and I do not feel that I can comment upon them. The calyx tube is persistent but not accrescent. It is longitudinally ruptured by the developing drupe in *E. malaccensis* but transversely ruptured in *E. paniculata* and *E. siamensis* (see also discussion following *E. paniculata*). The fruit of *E. thorelii* is unknown at this writing.



Distribution of the species of *Enkleia*: squares, *E. paniculata*; circles, *E. malaccensis*; large solid dots, *E. siamensis* ssp. *siamensis*; small solid dot, *E. siamensis* ssp. *andamanica*; stars, *E. thorelii*.

GEOGRAPHY

The four species of *Enkleia* have a composite range extending from Burma, Thailand, and Cambodia, on the north, through the Malay Peninsula, Andaman Islands, and Sumatra to Bangka, on the south, eastward through Borneo to western New Guinea and the Philippine island of Luzon. The distribution is strongly correlated with specific delimitation with the exception of *E. paniculata*. The disjunct distribution of the latter species (Luzon and western New Guinea) is puzzling indeed, but the species is represented so poorly in herbaria that additional collections may show this disjunction to be an artifact.

The distribution of each species is shown on the accompanying map. The symbols indicate place of collection only and are in no way indicative of the relative frequency of the plants.

MATERIALS

This revision is based on specimens from the following herbaria, the abbreviations for which are taken from Lanjouw & Stafleu's *Index Herbariorum, Part I*, Ed. 4 (Regnum Vegetabile, 15, 1959).

- A Arnold Arboretum of Harvard University, Cambridge
- BM British Museum (Natural History), London
- C Botanical Museum and Herbarium, Copenhagen
- DD Forest Research Institute & Colleges, Dehra Dun
- F Chicago Natural History Museum, Chicago
- G Conservatoire et Jardin botaniques, Genève
- GH Gray Herbarium of Harvard University, Cambridge
- K Herbarium, Royal Botanic Gardens, Kew
- L Rijksherbarium, Leiden
- P Muséum National d'Histoire Naturelle, Paris
- US U. S. National Museum, Smithsonian Institution, Washington

I wish to take this opportunity to thank the directors and curators of the above institutions for allowing me to examine the specimens in their care. I also wish to thank, in particular, Drs. C. E. Kobuski, C. E. Wood, Jr., and O. T. Solbrig for unfailing interest, constructive advice and technical assistance.

TAXONOMY

Enkleia Griffith, Calcutta Jour. Nat. Hist. 4: 234. 1844 (TYPE: *E. malaccensis* Griffith).

Linostoma subg. *Linostoma* Kurz, Jour. As. Soc. Bengal 39(2): 83. 1870, as to species cited.

Macgregorianthus Merrill, Philippine Jour. Sci. 7: 312. 1912 (TYPE: *M. paniculatus* Merrill).

Erect or scandent shrubs or lianas, the axillary branches sometimes modified for climbing, the bark containing many fibers. Leaves opposite, subopposite, or rarely alternate, simple, pinnately veined, the primary lateral veins arcuate, with numerous oblique secondary veins; entire, petiolate, estipulate. Inflorescences laxly clustered towards the apex of the young shoots, the bracts small and keeled at anthesis, becoming plane and much enlarged in fruit, the primary peduncle generally elongating following anthesis. Flowers bisexual, pentamerous, perigynous; calyx tube tubular, nonarticulated, ribbed, variously pubescent; calyx lobes 5, quincuncial, spreading; petals 5, medially cleft to the base or nearly to the base, inserted alternisepalously at the orifice, the lobes ensiform, linguiform or liguliform, glabrous; stamens 10, inserted in 2 whorls, the upper whorl antisepalous, the lower whorl alternisepalous, the anthers short filamented, basifixed, longitudinally dehiscent, the connective minutely produced beyond the pollen sacs; disc of irregular lobes, minute, free to adnate to the calyx tube; gynoecium single, pseudomonomeric, superior,

unilocular with a single anatropous ovule, the style terminal, the stigma clavate or subcapitate. Fruit drupaceous, the calyx tube variously ruptured by the developing drupe.

KEY TO THE SPECIES

- a. Leaf surface at most minutely puberulent, often glabrescent beneath, the trichomes short, straight, at most suberect; calyx tube becoming spirally twisted in the upper half before being transversely ruptured by the developing drupe; petals cleft nearly to the base; alternisepalous stamens subexserted. 1. *E. paniculata*.
- a. Leaf surface tomentulose, velutinous, glabrescent or glabrous beneath, the trichomes of medium length, curly or at least curved, suberect to erect; calyx tube never twisting before being transversely or longitudinally ruptured by the developing drupe; petals cleft to the base or nearly to the base; alternisepalous stamens included.
 - b. Erect shrubs, scramblers or lianas; leaves tomentulose, velutinous, glabrescent or glabrous beneath; inflorescence umbelliform; calyx tube 5–8 mm. long; ovary densely sericeous.
 - c. Primary lateral veins 10–15 pairs per leaf; calyx tube glabrous, partially or completely villous within, longitudinally ruptured by the developing drupe; petals cleft nearly to the base, about 1 mm. long; antisepalous stamens exserted; disc completely adnate to the calyx tube. 2. *E. malaccensis*.
 - c. Primary lateral veins 20–35 pairs per leaf; calyx tube glabrous within, transversely ruptured by the developing drupe; petals cleft to the base, 2–2.5 mm. long; antisepalous stamens included to subexserted; disc free. 3. *E. siamensis*.
 - b. Erect shrubs, usually low; leaves glabrous beneath; inflorescence subracemiform; calyx tube 6–11 mm. long; ovary sparsely sericeous. 4. *E. thorelii*.

1. *Enkleia paniculata* (Merrill) Hallier f. Med. Rijksherb. 44: 26. 1922.

Macgregorianthus paniculatus Merrill, Philippine Jour. Sci. 7: 312. 1912 (TYPE: *McGregor B.S. 12360!*).

Enkleia zippeliana Hallier f. Med. Rijksherb. 44: 26. 1922 (TYPE: *Zippelius 148a!*).

Climbing shrubs or lianas; young stems minutely ochraceous-velutinous and glabrescent, reddish brown, the lenticels conspicuous, horizontally elongate. Leaves opposite, subopposite or alternate; leaf blades ovate to elliptic or oblong-elliptic, 4–11 cm. long, 2.5–6 cm. broad, acute to obtuse at the apex, obtuse at the base, subcoriaceous, minutely and sparsely puberulent, often glabrescent, slightly darker above than beneath, the costa plane to immersed above, elevated beneath, the primary lateral veins 9–20 pairs, the submarginal vein coinciding with the margin; petiole terete or nearly so, 3–9 mm. long, minutely puberulent or velutinous. Inflorescences borne terminally on the young stems, usually 15–45 cm. long, many nodes involved, minutely velutinous throughout; each inflorescence

5–12-flowered, subumbelliform, the primary peduncle 2–3.5 cm. long, enlarging to 6 cm. in length with most of the elongation above the insertion of the bracts, usually bearing the reduced leaf of the subtending node near the base, the rachis 1–2 mm. long, the secondary peduncles to 2 mm. long, the bracts at anthesis opposite or subopposite, borne near the middle of the primary peduncle or below, keeled, small, minutely velutinous, suberect, the bracts in fruit becoming plane, narrowly elliptic, 5–6.5 cm. long, blunt at the apex, obtuse to subcordate at the base, membranaceous, deflexed, the bracteole borne near the summit of the primary peduncle, linear, 2–5 mm. long, persistent. Calyx tube tubular, 5.5–6.5 mm. long, 1–1.5 mm. in diameter at the orifice, minutely puberulent without, glabrous within; calyx lobes ovate, 2–2.5 mm. long, 1–1.25 mm. broad, minutely but densely puberulent within, erect; petals cleft nearly to the base, the lobes ensiform or when immature erosely truncate, ca. 1 mm. long, glabrous, erect; stamens inserted in two whorls, the antisepalous whorl inserted just below the petals, exserted as far as the petal apices, the alternisepalous whorl inserted about one anther's length below the antisepalous one, subexserted, the anthers oblong, 0.5–1 mm. long, 0.25 mm. broad, the filaments 0.25–0.75 mm. long, thick, glabrous or with a few minute trichomes near the base of the anther; disc of minute, irregular lobes, adnate to the calyx tube; ovary ellipsoid, densely short-sericeous, the style terminal, filiform, ca. 2 mm. long, glabrous, the stigma subcapitate, papillose; pedicel 2.5–5.5 mm. long, greatly thickening in fruit. Only one fruit per inflorescence developing; calyx tube spirally twisting before being ruptured by the developing drupe, torn portions persistent at the base; drupe ovoid to ellipsoid, ca. 1.5 cm. long, 1 cm. in diameter, sericeous, becoming glabrescent.

ILLUSTRATION. Thymelaeaceae. *In*: Flora Malesiana I. 6: 1–48, fig. 10, *h.i.* 1960.

DISTRIBUTION. Collected only three times, once on Luzon and twice in western New Guinea. The McGregor collection from Luzon was found "on forested slopes at low or medium altitudes." This collection was made in December when the plant was beginning to flower. The Van Royen collection from New Guinea was made in December in flower and fruit. Van Royen wrote of the locality, "The area in which the species is found consists of elevated limestone cliffs, alternating with brown muddy swamps."¹ He says, in addition, "I am quite surprised that my collection of this species is only the second one as this species was really common where I found it. I had to scale a relatively steep slope covered with an open forest of *Quercus* sp. and *Pometia* as the dominating trees. This *Enkleia* was climbing on an *Artocarpus vrieseanus* Miquel, but was found climbing also over *Paratrophis* sp., *Cyathocalyx papuanus* Diels and over both *Quercus* and *Pometia*. It is a rather striking species owing to its relatively large flowers."

¹ Personal communication.

Philippine Islands. LUZON: Calauan, Prov. of Laguna, *McGregor B.S. 12360* (K-lectotype, BM, L, US). **Netherlands New Guinea.** Steenkool, road to Temboeni, km. 1.5, hills east of the road, opposite police barracks, *Van Royen 3592* (L); without locality, *Zippelius 148a* (L-holotype and isotypes of *E. zippeliana*).

Presumably, the holotype of this species was destroyed with the Philippine National Herbarium. As lectotype I choose the specimen of *McGregor 12360* deposited in the herbarium at Kew. It is the most complete specimen of this collection and consists of two immature floriferous branches and a packet containing a nearly mature flower.

Merrill allied his new genus *Macgregorianthus* with *Wikstroemia*, a large and wide-ranging genus of the Eastern Hemisphere. He placed it near this genus, undoubtedly, because of his familiarity with it rather than because of any morphological similarities. There is no question that *Macgregorianthus* (= *Enkleia*) is not closely related to *Wikstroemia*, although they are members of the same subfamily.

The calyx tube, immediately following anthesis in the New Guinea specimens, becomes spirally twisted in the upper half. It twists, up to a half dozen times, quite tightly before being ruptured by the developing drupe. The twist is invariably counter clockwise. The significance of this peculiar behavior has not been ascertained.

Enkleia paniculata was first united with *E. zippeliana* shortly after Hallier's description of the latter species. Hou recently (1960) pointed out that the distinguishing features mentioned by Hallier in the original description of *E. zippeliana* are of little taxonomic consequence. These features include leaf pubescence, pubescence color and prominence of leaf venation.

There is, however, a discrepancy in one major floral character which requires explanation. The flowers of the New Guinea specimens collected by Zippelius and Van Royen have petal lobes which are ensiform, whereas, the McGregor collection consisting of immature flowers has petal lobes which are broadly squamelliform with the apices erosely truncate. The petals have not fully developed in the McGregor specimens. Fortunately, the superb Van Royen collection consisting of flowering and fruiting material is available so that immature flowers can be compared with those of the Luzon collection. In buds of comparable size to those of the McGregor collection, the petal lobes have already undergone major elongation and they have assumed the mature form, but in somewhat younger buds the erosely truncated petal apices so characteristic of the Luzon collection can be observed.

Cleared leaves of the New Guinea specimens have a remarkable number of druse-like crystals which can be observed readily under low magnification. The leaf specimen of *McGregor 12360* which I cleared was absolutely devoid of crystals. The applicability of this character is very doubtful as crystal formation may be due to the physiological state of the plant at the time of collection and not directly genetically controlled. Indeed, in *Enkleia malaccensis* crystals can be found in the leaves of most

of the specimens but are entirely lacking in others, *Griffith 4375*, for example. Since all of the leaves were handled in a similar manner there is little chance that crystal formation was induced by the clearing process in some instances and not in others.

2. *Enkleia malaccensis* Griffith, *Calcutta Jour. Nat. Hist.* 4: 234. 1844 (TYPE: *Griffith*?).

Lasiosiphon scandens Endl. *Gen. Suppl.* 4(2): 67. 1847, based on *Enckleia* [*Enkleia*] *malaccensis* Griffith.

Enkleia malayana Griffith, *Notul. As.* 4: 363. 1854.

Linostoma scandens (Endl.) Kurz, *Jour. As. Soc. Bengal* 39(2): 83. 1870.

Enkleia riouwensis Hallier f. *Med. Rijksherb.* 44: 25. 1922 (TYPE: *Teysmann s.n.*!).

Enkleia coriacea Hallier f. *Ibid.* (TYPE: *Hallier B.2264*!).

Climber; young stems terete, densely golden-brown velutinous, gradually glabrescent and conspicuously lenticellate, reddish brown; axillary branches often strongly recurved uncinat, thickening at the base with age. Leaves subopposite, the blade ovate to elliptic (sometimes broadly so), 3.5–14(–15) cm. long, 2–7(–10) cm. broad, acute to obtuse or emarginate or rarely short-acuminate at the apex, cuneate to obtuse at the base, coriaceous, both surfaces golden-brown velutinous and glabrescent, the trichomes slightly curved, the costa immersed above, elevated beneath; the primary lateral veins 10–15 pairs, the submarginal vein coinciding with the margin, conspicuously thickened; petiole terete, densely puberulent although somewhat glabrescent in very old leaves, 6–10(–12) mm. long. Inflorescences borne terminally on the young shoots, involving several nodes, generally compound and forming a paniculate structure often 15 cm. long but sometimes to 30 cm. in length, golden-velutinous throughout; each inflorescence 3–9-flowered, umbelliform, the primary peduncle 3–5 cm. long, enlarging to 9 cm. in fruit with most of the elongation above the insertion of the bracts, usually bearing the very reduced leaf of the subtending node near the base, the rachis to 2 mm. long but sometimes elongating in fruit, the secondary peduncles obsolete to 2 mm. long, the bracts at anthesis subopposite, borne slightly below the middle of the primary peduncle, keeled, 3–5 mm. long, golden-brown velutinous, erect, the bracts in fruit becoming plane, elliptic to obovate 4–7 cm. long, 1–2.5 cm. broad, obtuse at the apex, subtruncate at the base, puberulent, conspicuously veined, strongly deflexed, the bracteole borne at the summit of the primary peduncle, linear, 1–3 mm. long, often persistent. Calyx tube tubular to suburceolate, 5–6 mm. long, green to yellow and densely golden-brown velutinous without, glabrous, villous above and glabrous below or completely villous within; calyx lobes more or less oblong but obtuse at the apex, 1–2 mm. long, 0.75 mm. broad, erect, white puberulent within; petals cleft almost to the base, the lobes somewhat linguiform, ca. 1 mm. long, somewhat carnose, glabrous, exserted; stamens inserted in two whorls, the antisepalous stamens inserted just below the petals, exserted

but not as far as the petals, the alternisepalous stamens inserted one to two anther-lengths below the antisepalous whorl, included, the anthers oblong, 0.5–1 mm. long, 0.25–0.5 mm. broad, the filaments obsolete to 0.5 mm. long, slightly inflated just below the anthers, glabrous; disc completely adnate to the calyx tube, ca. 0.5 mm. tall, somewhat fleshy; stigma included, clavate, papillose; style filiform, 0.5–1 mm. long, the ovary fusiform, ca. 2 mm. long, densely short-sericeous; pedicel 1–3 mm. long. Usually only one or rarely two fruits per inflorescence developing; calyx tube persistent, usually longitudinally ruptured and persistent at the base of the drupe; drupe ovoid, 10–15 mm. long, 6–8 mm. in diameter, glabrescent but usually puberulent at least at the apex, prominently ribbed; pedicel thickening in fruit.

ILLUSTRATIONS. Ridley, H. N., Dispersal of plants throughout the world. *tab. 6, fig. 13*, L. Reeve & Co., Ltd., 1930; Thymelaeaceae. *In: Flora Malesiana I. 6: 1–48. fig. 10, a–g.* 1960.

DISTRIBUTION. Primary forest in Malaya, south to Sumatra and Bangka, east to North Borneo. All specimens which I have seen indicate that this species is never found above 50 meters altitude. It has been collected flowering in April, September and October; fruiting in April, May, August and September. Merrill (1929, p. 212) says, "A woody vine forming tangled masses in forests, the stems a few inches in diameter." Keith reports that the bast fibers can be used for tying purposes, and Burkill (1935, p. 925) says that it yields an inferior aromatic wood.

Malaya. MALACCA: Malacca, Griffith "1845" (K). LOCALITY UNCERTAIN: Sungei Hudacely, Ridley 1764 (BM); Griffith E.I.C. 4375 (GH, K). Singapore. Bukit Temah, Ridley 6427 (BM); Garden Jungle, Ridley 5565 (BM); south side of MacRitchie Reservoir, Sinclair SFN 40694 (K); Maingay 1308/2 (BM, GH, K, L); without collector (possibly Maingay?) 1256 "Sept. 1867" (G). Indonesia. SUMATRA: Laboehan Batoe; Dist. Kota Pinang, Si Mandi Angin (on the Soengei Kanan), *Toroes* 4099 (A). BINTAN: Tandjung-Pinang, *Teysmann s.n.* (L-holotype and isotype of *Enkleia riouwensis*). BANGKA: G. Maroe, *Anta* 1373 (A). BORNEO: Tandjong Bangko region, near mouth of Mahakam river, *Kostermans* 7034 (L); Loa Djanan, west of Samarinda, *Kostermans* 6672 (L); Pleihari [Pelaihari], *N.I.F.S. bb.* 19256 (A, L); zwischen dem Súngai Djëmělá und dem Gûnŭng K(e)lamm, *Hallier B.2264* (L-holotype and isotype of *Enkleia coriacea*). British North Borneo. EAST COAST: Selangan, F.R., Semporna, *Keith N.B.F. D.N.* 9234 (K, L); Tawao [Tawau], Elphinstone Province, *Elmer* 20834 (BM, C, L).

It appears that a type specimen has never been selected for this species, although I have seen several specimens which have been considered by others to be type material. This species was described by Griffith (1844) in an article entitled, "On some remarkable Plants in the H. C. Botanic Gardens, Calcutta." However, immediately preceding the description of *Enkleia* (p. 234) he says, "The other plants of this family that I have met with on the N. E. frontier and Straits of Malacca, localities that, however distant, present remarkable affinities in vegetable forms, are—"

Enkleia malaccensis is the last of nine species in a list and it is marked clearly from "Malacca." The actual description is contained in an extensive footnote in which no specimen was selected as a type. Thus, it would seem that a selection of a type would be restricted to specimens collected by Griffith (or one of his collectors) in Malacca prior to 1844 but, as I intend to show, the selection of a type is relatively complicated.

Griffith first set foot in Malacca in August, 1841 (see Van Steenis-Kruseman, pp. 201, 202. 1950), and served as a civil surgeon until mid-1842. During this period he made collections and trained native collectors. In August of 1842 (see Griffith 1847, introductory notes) he left to assume the directorship of the Botanic Gardens in Calcutta, a post which he occupied until December, 1844. In January of 1845 he returned to Malacca. Of no little consequence is that during his directorship at Calcutta he remained in contact with his native collectors in Malacca and they sent him a steady stream of dried specimens, seeds, and living plants. The living plants were grown in the gardens (see Griffith, 1847, Extract of Letters).

One would assume from the title of Griffith's paper that the plants which he intends to discuss are growing in the botanic garden until he adds the qualification that he has met some of them elsewhere. In the case of the locality of this particular species I believe that it can be interpreted in two ways: one, the description is based on a plant which he collected in Malacca between August, 1841, and August, 1842; or two, the description is based upon a specimen growing in the botanic garden which was sent from Malacca by his collectors, but which may have been a plant with which he had familiarity prior to leaving Malacca. If the description is based upon one of his Malaccan collections there is a possibility that the specimen did not go through his normal channels of distribution, for, in a letter to R. Wight, postmarked Malacca, April 15, 1842 (Griffith 2: xxvii) he says, "I intend adopting an entirely new system of tactics, and when I pounce on any thing interesting, to keep it until it is in print." On the other hand, if the description is based upon a living specimen there is the distinct possibility that no herbarium specimen was made. As an example, in the same letter quoted above, he says, of three new genera, "which I suppose no body will adopt at home without specimens."

I have seen three specimens which have been considered to be authentic collections. Two of these are deposited at Kew. The one bears the stamp of "Herbarium Hookerianum, 1867," and in longhand is written, "Malacca, Griffith, 1845. *Enkleia Malaccensis* Griffith;" the other bears the same stamp of Hooker, plus the printed label of the East India Company with the identification number 4375 (see Hooker, 1865), and is identified as "*Lasiosiphon scandens*, Endl." (a substitute name for *Enkleia malaccensis*), the place of collection is given as "Birma and Malay Peninsula." In addition, it bears the longhand identification "*Enkleia Malayana* Gr." The third sheet, deposited at the Gray Herbarium, bears the identical East India Company label and identification as the Kew specimens but has no other marks. There is little question that all of

these sheets are Griffith collections but the sheet at Kew bearing the date 1845 is automatically eliminated as authentic type material. The remaining two sheets cannot be either confirmed or denied as type material. Griffith's description of the new genus is lengthy, well drawn, and easily interpreted so that I believe that the choice of a type should be left an open matter at this time.

Enkleia coriacea, on first examination, appears to be a distinct species. The aspect of the two Leiden specimens which seem to set them apart from others is due to a decidedly reddish cast to the leaves which is coupled to an almost complete lack of pubescence. It is surprising how this combination of characters is so readily noticeable. On very immature leaves the characteristic pubescence of *E. malaccensis* can be observed but the trichomes are shorter than usual. It is possible that these two specimens show one extreme of the total variation in trichome length of the species. The trichomes of other Bornean specimens in general appear to be shorter than those of peninsular specimens but none reach the extreme attained in Hallier B.2264. It is of interest that these plants were growing in association with *Linostoma pauciflorum* Griffith, a species of the genus most closely related to *Enkleia*.

Enkleia riouwensis was described by Hans Hallier from sterile collections of Teysmann from the Riouw island of Bintan. Hou (1960), in his treatment of Thymelaeaceae for the *Flora Malesiana*, relegated this species to the synonymy of *E. malaccensis*, an action with which I agree. I have examined the holotype and an isotype from the Leiden herbarium and can find no characteristics to distinguish it from *E. malaccensis*, except a more pronounced undulation of the leaf margin which may be due to the method of drying. In the description, Hallier refers to the plants as shrubs but I can find no such information on the two specimens which I examined, so I regard this character as questionable.

3. *Enkleia siamensis* (Kurz) Nevling, comb. nov.

Linostoma siamense Kurz, Jour. As. Soc. Bengal 39(2): 82. 1870 (TYPE: Teysmann 5986!).

Erect to scrambling shrubs or large lianas; young stems terete, puberulent or golden to light-brown velutinous, glabrescent; axillary branches usually normal, only rarely becoming uncinat. Leaves opposite, subopposite or rarely alternate on vigorous young shoots; leaf blade ovate, lanceolate, oblong-elliptic, broadly elliptic or rarely orbicular, 4–13 cm. long, 2–9 cm. broad, acute, attenuate, or obtuse to truncate and minutely mucronulate at the apex, cuneate to obtuse at the base, coriaceous, glabrous or densely to sparsely tomentulose and often glabrescent, the trichomes curly, the costa immersed above, elevated beneath, the primary lateral veins 20–35 pairs, the submarginal vein poorly or well developed, coinciding with the margin; petiole scarcely canaliculate, glabrous or velutinous, 5–8 mm. long. Inflorescences borne on the modified portions of the young shoots, involving several nodes (to as many as 8), the main

axis seemingly leafless, to 15(-30) cm. long, minutely golden-velutinous throughout; each inflorescence 3-16-flowered, umbelliform, the primary peduncle 2.5-5 cm. long, sometimes elongating to 9 cm. in fruit, with the reduced leaf of the subtending node near the base, the rachis to 2 mm. long, the secondary peduncles to 1 mm. long, the bracts opposite to subopposite, keeled at anthesis, becoming plane and more or less oblong, 2-9 cm. long, 1-2.5 cm. broad, obtuse at the apex, obtuse to subcordate at the base, membranaceous, tomentulose, deflexed, the bracteole borne at the summit of the primary peduncle, linear, 1-8 mm. long, often persistent. Calyx tube tubular, 5-8 mm. long, 1-1.5 mm. in diameter at the orifice, golden-tomentulose without, glabrous within; calyx lobes spatulate, 2.5-4.5 mm. long, 1.5-2.5 mm. broad, minutely puberulent within, spreading; petals cleft to the base, the lobes liguliform, ca. 2.5 mm. long, glabrous, fleshy, long-exserted; stamens inserted in two whorls, the antisepalous whorl inserted just below the petals to 1 anther-length below, subexserted or included, the alternisepalous whorl inserted 2-3 anther-lengths below the antisepalous whorl, included, the anthers oblong, 0.5-1 mm. long, ca. 0.25 mm. broad, the filaments 0.25-1 mm. long, somewhat inflated, glabrous; disc of minute free lobes, glabrous; ovary ellipsoid, 1-2.5 mm. long, densely sericeous, the style of varying length, filiform, glabrous, the stigma subcapitate, included to exserted (see discussion); pedicel 3-6.5 mm. long. Only a single fruit per inflorescence developing; calyx tube transversely ruptured but persistent as a short ruffle at the base of the drupe; drupe ovoid to almost ellipsoid, 10-18 mm. long, 6-8 mm. in diameter, puberulent at least at the apex; pedicel thickening in fruit.

The proper taxonomic treatment of this species and the preceding, *Enkleia malaccensis*, is somewhat perplexing but it has been my decision to recognize two species, one with two subspecies. There is little doubt that these taxa are derived from common ancestral stock as indicated by morphological similarities and present day distribution. Each of the taxa is allopatric and the possibility of interbreeding between them seems remote because of distance alone.

Enkleia malaccensis is most certainly distinct from *E. siamensis* ssp. *siamensis* as can be demonstrated with any number of morphological or anatomical characters, many of which are apparent to the unaided eye. It is with the introduction of specimens from the Andaman Islands (originally described as *Linostoma andamanica* and here treated as *E. siamensis* ssp. *andamanica*) that difficulties begin. Unfortunately, only two collections from the Andamans are available, and this seriously impairs knowledge of the variability of these plants; but even with these few it is possible to see that they combine characteristics of *E. malaccensis* and *E. siamensis* ssp. *siamensis*. Further, they entirely lack distinguishing characters of their own; otherwise I would recognize three species. Of the characters which are combined, the great majority are from *E. siamensis* ssp. *siamensis*. It is not surprising to find the Andaman plants most closely related geographically with those of ssp. *siamensis*. Char-

acteristics of *E. malaccensis* which are found in ssp. *andamanica* are habit, enlargement of the fruiting peduncle, bract size, and the presence in the leaf of some fibers which are not associated with the vasculature. Some of the more important features which are shared with ssp. *siamensis* are the large number of primary lateral veins, the degree of clefting of the petals, the calyx tube pubescence, the free disc, the mode of fruit development, and the absence of subepidermal fibers.

The Andaman Island plants may have arisen at a time when the morphological characteristics which now delimit the species were still in a state of flux and not yet geographically segregated, or they may be the result of considerable convergent evolution. The former case seems most probable because of the lack of distinguishing characters not represented in other taxa. Whether *E. malaccensis* or *E. siamensis* is primitive or advanced, generalized or specialized, cannot be determined, for both have elements which I consider primitive and advanced.

KEY TO THE SUBSPECIES

- a. Leaves densely to sparsely tomentulose, often glabrescent, the submarginal vein well developed; primary peduncle to 5 cm. long; bracts at anthesis borne near the middle of the primary peduncle or below, 2-4(-5) cm. long, 1-1.5 cm. broad; calyx tube 6-8 mm. long; antisepalous stamens subexserted. 3a. *E. siamensis* ssp. *siamensis*.
- a. Leaves glabrous, the submarginal vein poorly developed; primary peduncle to 9 cm. long; bracts at anthesis borne above the middle of the primary peduncle, 4-8 cm. long, 1.5-2.5 cm. broad; calyx tube about 5 mm. long; antisepalous stamens included. 3b. *E. siamensis* ssp. *andamanica*.

3a. *Enkleia siamensis* ssp. *siamensis*

Linostoma siamense Kurz, Jour. As. Soc. Bengal 39(2): 82. 1870 (TYPE: *Teysmann 5986*!).

Linostoma scandens var. *cambodianum* Lecomte, Not. Syst. Paris 3: 127. 1915, "*cambodiana*" (TYPE: *Pierre 511*!).

DISTRIBUTION. Open deciduous forest or scrub in Burma, Thailand and Cambodia. Collected from 100 to 1200 meters altitude. Flowering in January, although buds apparently forming as early as November; fruiting in January, February and March.

Burma. PEGU: Pegu Yomak, e. and w. slopes, *Kurz 3122* (K). Thailand. CHAIYAPHUM: Chaeyapuon [Chaiyaphum], *Kerr 19959* (BM). CHIANGMAI: Lampang Mae Saikham, *Wanadorn 1590* (L). CHONBURI: Kanboerie [Chonburi], *Teysmann 5986* (L-isotype of *Linostoma siamense*), *Kerr 10136* (BM), *10620* (BM). NAKON PHANOM: Nawkawn Panom [Nakhon Phanom], *Kerr 8214A* (BM). PHETBURI: Tung Quang, Petchaburi, *Kerr 20601* (BM). PRACHUP: Kan Kradai, Prachuap, *Put 2305* (BM); Hua Hin, *Kerr 16136* (BM). Nang Rawng (?) *Kerr 8214* (BM). Cambodia. In montibus Krewand Prov. Tpong [Thpong], *Pierre 511*^{bis} (A, BM, G, GH, K, P); in prov. Peû Lover (see discussion), *Pierre 511* (isotypes of *Linostoma scandens* var. *cambodianum*: A, BM, F, K, L, P); Stung Treng, *Poilane 14229* (P); without locality, *Jullien s.n.* (P).

In the original description of *Linostoma siamense*, Kurz gave the place of collection as, "Siam, Bookit Kathay near Kanburi." Attempts to locate Bookit Kathay were in vain. Re-examination of the handwritten label on the isotype showed the collector's name and number plus, "Daphnoideae. Boekiet Kethaay, Kanboerie, Siam." Therefore, it appears as though Kurz removed the comma following "Kethaay" and inserted the word "near." Teysmann's account of his travels (1863, p. 201) shows that "Boekiet Kethaay" is not the place of collection but the common name! The place of collection is Kanboerie (= Bang Pla Soi, Chanburi, Choburi, Chonburi, Jolburi or Kanburi) which Teysmann visited for several days toward the end of March, 1862.

Pierre 511 is a collection consisting of two parts. The first, collected in March, 1870, is the more important as it serves as the basis of Lecomte's *Linostoma scandens* var. *cambodianum*. In the original description of this varietas Lecomte gives the location as "Prov. de Pan Louvea." Examination of the numerous sheets of this collection has added these possibilities: Pen Saver, Peû Saver, Peû Sover and Peû Lover. Unfortunately, I have not been able to locate, to my satisfaction, the place of collection. I have the following possibilities: Kompong Svay (ca. 13° N, 195° E), Prey Lovea (ca. 11° N, 105° E) and Lovea (ca. 13° N, 103° E) and therefore have not plotted this collection on the map. The second portion of *Pierre 511* was collected June, 1870, "in montibus Krewand prov. Tpong." The locality is probably Thpong and I have plotted it so. This portion of the collection has been designated as 511^{bis}.

The displacement of the reduced leaves borne near the base of the primary peduncles has been discussed previously (Nevling, 1961). These leaves generally are only several millimeters in length, although in *Kerr 16136* they are fully developed, normal leaves. This evidence helps secure the hypothesis that these reduced leaves are homologous with the leaves of the vegetative shoot.

Only a very small number of the specimens of this subspecies which I examined were in flower. The description and measurements of the flower are, of necessity, based on few specimens and further variability should be expected.

The final position of the stigma with respect to the calyx tube orifice is dependent upon the amount of elongation of the style. The mechanics of stylar elongation in *Pimelea* has been discussed by Burrows (1960) and a similar mechanism is suspected in *Linostoma* (Nevling, 1961). It is almost certainly in operation in this species of *Enkleia*. The elongation ceases at the time of pollination or shortly thereafter, and the length of the style thus is determined by the pollination time. In *Wanadorn 1590* two floral dissections by Dr. Ding Hou show one with a very short style and the other with an extremely long style. Other collections which I have observed have the style of varying length. Unfortunately, the length of style has been used as a key character to separate *Enkleia* from *Linostoma*, and now the character appears to be useless.

- 3b. *Enkleia siamensis* ssp. *andamanica* (Hutchinson ex C. E. Parkinson) Nevling, comb. & stat. nov.

Linostoma andamanicum Hutchinson ex C. E. Parkinson, Fl. Andaman Is. 229. 1923, "*andamanica*" (TYPE: *Parkinson 384!*).

According to Parkinson, the plants are found on Baratang and Have-lock islands. They are dispersed but very uncommon. They flower and fruit during the hot season. The habit is described by Parkinson as "a woody climber as thick as a man's arm and climbing over the tallest trees, stems hooked."

Andaman Islands. Ali Masfid Reserve, *Parkinson 384* (DD-holotype of *Linostoma andamanicum*, κ); without locality, *Parkinson 309* (DD).

See discussion following specific description above.

4. *Enkleia thorelii* (Lecomte) Nevling, comb. nov.

Linostoma thorelii Lecomte, Not. Syst. Paris 3: 127. 1915 (TYPE: *Thorel 2823!*).

Erect shrubs to 0.5 m. tall; young stems terete, strigose and glabrescent, becoming reddish brown, the axillary branches normal. Leaves subopposite to alternate; leaf blades elliptic, 2.5–4.5 cm. long, 1–2 cm. broad, obtuse and mucronate at the apex, cuneate at the base, coriaceous, glabrous, the costa plane above, slightly elevated beneath, the primary lateral veins inconspicuous, ca. 15–20 pairs, the submarginal vein coinciding with the margin, conspicuously thickened; petiole nearly terete, glabrous, 1–3 mm. long. Inflorescences borne from the young shoots, generally simple; each inflorescence 6–12-flowered, subracemiform, the primary peduncle 2–4 cm. long, elongating to 6.5 cm., with most of the elongation above the insertion of the bracts, bearing the reduced leaf of the subtending node near the base, the rachis 1–7 mm. long, the secondary peduncles 1–2 mm. long, the bracts at anthesis opposite to subopposite, borne below the middle of the primary peduncle, keeled to plane, 5–25 mm. long, to 20 mm. broad, minutely strigose, the bracteole borne at the summit of the primary peduncle, linear, to 5 mm. long, minutely strigose, persistent. Calyx tube tubular, 6–11 mm. long, ca. 1.5 mm. in diameter at the orifice, minutely strigose to hirsute without, glabrous within; calyx lobes oblong, ca. 3.5 mm. long, 1.5 mm. broad, spreading, minutely puberulent within; petals cleft to the base, the lobes liguliform, ca. 4.5 mm. long, greatly exserted, erect to spreading, glabrous; stamens inserted in two whorls, the antisepalous ones inserted about 1 anther-length below the petals, subexserted, the alternisepalous whorl inserted about 3 anther-lengths below the antisepalous whorl, included, the anthers oblong, ca. 1 mm. long, 0.5 mm. broad, the filaments thick, 0.25–0.5 mm. long, glabrous; disc of many minute lobes; ovary fusiform, ca. 2 mm. long, very sparsely sericeous, the style filiform, ca. 1 mm. long, glabrous, the stigma clavate; pedicel 2–3 mm. long. Fruit unknown.



Nevling, Lorin I. 1961. "A revision of the Asiatic genus *Enkleia* (Thymelaeaceae)." *Journal of the Arnold Arboretum* 42(4), 373–396.
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