

STUDIES IN THE *LEPIDAPLOA* COMPLEX
(*VERNONIEAE: ASTERACEAE*) IV.
THE NEW GENUS, *LESSINGIANTHUS*

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Abstract.—The genus *Lessingianthus* is described as new for a series of 101 neotropical species typified by *Vernonia buddleiifolia*. The typical subgenus is characterized by pollen with type B areolation and has a few species with type D pollen. A second subgenus, *Oligocephalus*, is established for three species having type C pollen areolation. The genus contains some of the species previously placed in the *Vernonia* series *Buddleiifoliae*, *Brevifoliae*, *Macrolepidiae*, *Remotiflorae*, and *Flexuosae*. The members of the new genus have consistently lophate pollen, as do members of the related genus *Lepidaploa*, but the new genus lacks the rhizomatous condition of the pollen crests, lacks the basal node of the style, lacks glands on the achenes, and often has pedunculate heads. *Lessingianthus myrsinites*, is described as new, using an apparently unpublished species name of Ekman.

The present paper is the fourth in a series of seven devoted to the study of the neotropical *Lepidaploa* complex (Robinson 1987a, b, c, 1988). The element from the broad concept of *Vernonia* treated herein is the largest in the series other than *Lepidaploa* itself. My interest in the group first developed during a study of style bases in the Vernonieae, which demonstrated that the members of the present group lacked a node. Interest was increased by the realization that many species lacking nodes were of a group referred to in prior treatments of *Vernonia* as the section *Lepidaploae Macrocephalae* (Baker 1873). The fact that most species of the group have distinctive, large, lophate pollen (Jones 1979b), and the recent discovery of non-rhizomatous crests on the pollen grains has led to the conclusion that the group should be recognized as a new genus, herein named *Lessingianthus*.

Prior taxonomic treatments of *Vernonia* sensu lato have provided very imperfect approximations of the group treated here as *Lessingianthus*. Furthermore, the species were always included within the also im-

perfectly defined *Lepidaploa* subgroup of *Vernonia*. Both the sections *Lepidaploae Macrocephalae* of Baker (1873) and the series *Buddleiifoliae* of Jones (1982) were recognized on the basis of the relatively large size of the heads in many of the species of the group. Although large heads remained a prime distinction of the group for Jones (1982), the 22 species included in his comparatively refined treatment did not all have large heads. Subsequently, relationships have been traced to species included by Jones in his series *Brevifoliae*, *Macrolepidiae*, *Remotiflorae*, and *Flexuosae*. In most of these taxonomic series, the members of *Lessingianthus* were intermixed with species placed in this series of studies in the related genus *Lepidaploa*. It is the accurate delimitation of *Lessingianthus* from *Lepidaploa* that is the primary aim of the following discussion. Four characters are most instructive in this: the presence or absence of a basal stylar node, the pollen structure, the form of the inflorescence, and the form of the involucre. Each of these will be discussed separately.

Basal Stylar Node

The presence of basal stylar nodes has been noted in various Asteraceae since at least the work of Cassini (1818), and they have been found taxonomically useful in some groups such as the Eupatorieae (Robinson & King 1977, King & Robinson 1987). Nodes seem to have a function in species of the tribe Heliantheae where they expand belatedly and tear the corolla base loose from the achene. In other tribes such as the Eupatorieae and Vernonieae, however, there is no function sufficiently important to prevent variability within the groups.

In the Vernonieae, the stylar node appears basic for the tribe, but seems to differ in commonness in the Eastern and Western Hemispheres. A highly developed node, such as that in the African-Indian Ocean genus *Distephanus* (Robinson & Kahn 1986), is otherwise found in comparatively few members of the tribe in the Eastern Hemisphere, where most Vernonieae lack nodes. In the Western Hemisphere, however, a stylar node is much more widely distributed and its absences appear to be more significant. The distribution of the character has been surveyed and has yielded some interesting results.

In the Western Hemisphere, the stylar node is lacking or poorly differentiated in a few small groups such as *Lepidonia* and *Stramentopappus* (Robinson & Funk 1987) in the *Leiboldia* group, and in *Stenocephalum* and *Chrysolaena* in the *Lepidaploa* group (Robinson 1987a, 1988), but it is well-developed in the genus *Lepidaploa* itself. The node is present in most other elements of *Vernonia* s.l., but is again lacking in a series of species traditionally placed in the genera *Eremanthus* and *Lychnophora* of the Lychnophorinae. In the latter group, the lack of a basal node correlates with the rather unique variation from the common cymose maturation pattern of the heads (Robinson 1980a). All these groups give the impression of many separate losses of a bas-

al stylar node. Each loss seems correlated with other characters that favor recognition of the groups at generic or higher levels.

The essential lack of a basal stylar node in *Lessingianthus* contrasts strongly with the rather marked structure seen in almost all members of the related *Lepidaploa*. In the species of *Lessingianthus*, there is no enlargement whatsoever, and there may or may not be a sclerified ring. The sclerified ring may appear enlarged when the softer upper tissue has collapsed. Some species included here, such as *Vernonia regis* and *V. brevifolia*, seem to have a slight but distinct enlargement at the base of the style, but fully soaked material of styles shows the lower shaft equals the sclerified ring in width. The ring differs from that of *Lepidaploa* by its slight angle and the wide area of attachment that remains inside the ring. In *Lepidaploa* the sclerified surface cuts under the base of the style and leaves a very narrow area of attachment.

Immaturity of style bases may lead to misinterpretation, but mistakes in observation are usually caused by failure to extract the complete style. The typical *Lessingianthus* style base closely resembles a broken *Lepidaploa* style base. It should be noted that *Lessingianthus* style bases may be distinguishable even from broken bases of *Lepidaploa* because they are often larger.

Pollen

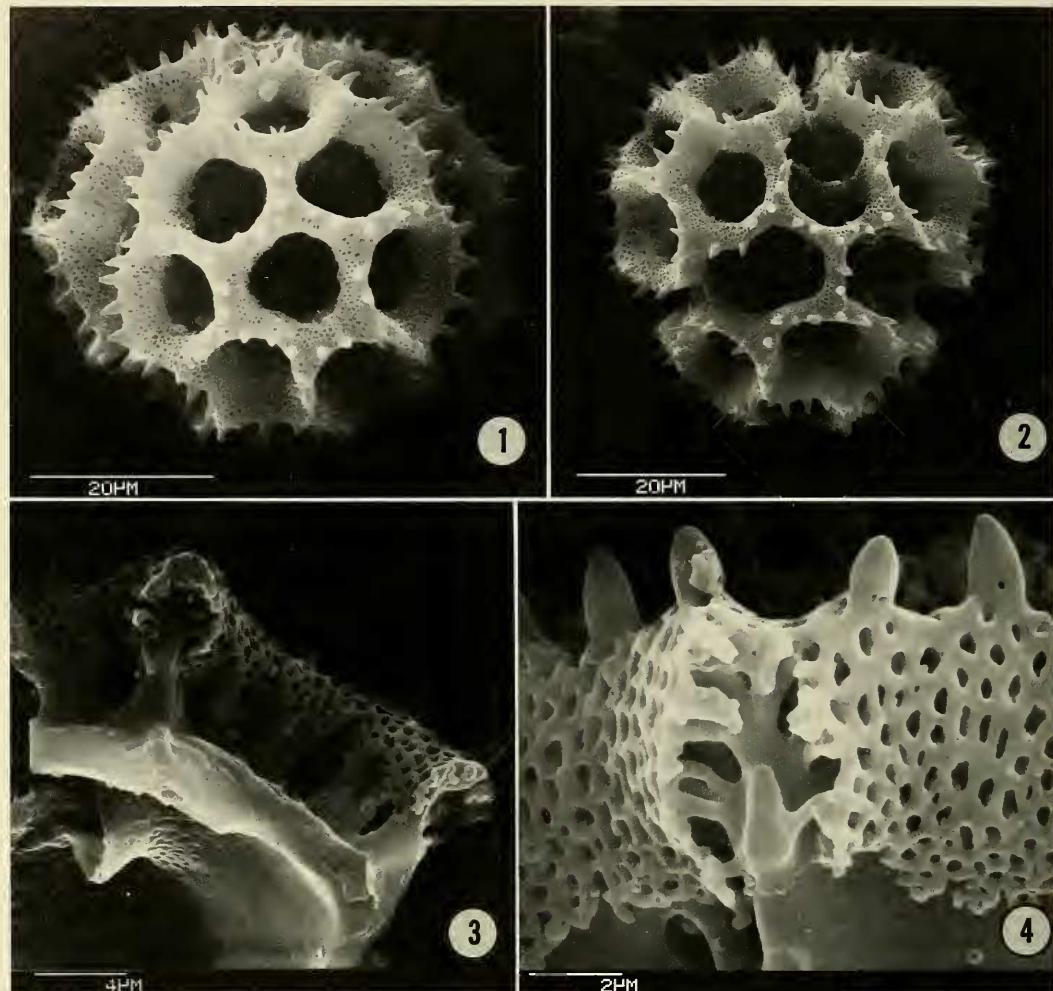
Two aspects of the pollen of *Lessingianthus* are significant for taxonomic discrimination. The pollen in both *Lessingianthus* and *Lepidaploa* is lophate with crests forming regular patterns. Regular patterns occur widely in both Eastern and Western Hemisphere Vernonieae, and they are regarded here as primitive in the tribe. The non-lophate types are regarded as reversions. The lophate types in both hemispheres show the perforated tectum restricted to the crests (Figs. 1-16) or completely lacking. The crests of the pollen of Eastern Hemisphere species

and of genera such as *Stokesia*, *Mattfeldianthus*, and *Lessingianthus* from the Western Hemisphere have stout, high baculae separate from the point of attachment on the footlayer to the point above where they join the ridge of the crest (Figs. 3, 7, 9, 10, 15). This condition appears ancestral. The crests in the related *Lepidaploa* show a condition previously described as "rhizomatous" (Robinson 1987a, b, c), where the baculae under the crests are joined into a transverse basal rhizome and where the attachment of the rhizome to the footlayer is comparatively weak. The drawing by Stix (1960) of her general *Vernonia* type pollen seems to show this rhizomatous structure. If so, her inclusion of the *Vernonia argyrophylla* type pollen under this category was an error. The "rhizomatous" type of crest has a tendency to peel away from the pollen grain rather easily, a trait that can best be seen under SEM but which can also be seen under the light microscope. The *Lepidaploa*-type rhizomatous crest is reviewed more fully in the treatment of *Lepidaploa*. Only a few Brazilian species in *Lepidaploa*, mostly those having type D pollen, have an intermediate development of the rhizomatous character. Pollen with rhizomatous crests must be regarded as a restricted type within the tribe, which probably evolved only once. The precise form is known only in the Neotropical members of the tribe. There is reason to believe that all other genera characterized by such pollen, e.g., *Stenocephalum* (Robinson 1987a), and *Echinocoryne* (Robinson 1987b), are related directly to *Lepidaploa*, and one other occurrence of such pollen in *Eirmocephala* may be derived from an intergeneric hybridization involving *Lepidaploa* (Robinson 1987c). Because of the close relationship among the groups with such pollen, it is possible to conclude that the rather closely related *Lessingianthus* departs phyletically from a point slightly below the origin of the "rhizomatous" apomorphy. The pollen of *Lessingianthus* could be seen as being of a more ancestral type at

the same time the style base is of a more derived type. It is possible that the crest structure has undergone reversals in the evolution of the group, but everything observed could be explained without such reversals.

The precise form of the lophate pattern of the pollen also distinguishes almost all species of *Lessingianthus* from any *Lepidaploa*. The *Vernonia argyrophylla*-type pollen described by Stix (1960), also called type B pollen by Jones (1979b), in its typical form appears to be restricted to *Lessingianthus* and is completely absent from *Lepidaploa*. Such pollen has colpar areolae extending the whole length of the grain and meeting at the poles at the same time that the intercolpi have three areolae across at the equator (Figs. 1, 2, 5, 6, 8). The three areolae across the intercolpar equator may be part of a 1:2:3:2:1 pattern (Fig. 1) or a 1:2:1:2:1 pattern (Fig. 6). The type B grains tend to have diameters greater than the other lophate types in the *Lepidaploa* relationship. They are mostly 50–80 μm in diameter in fluid. Most *Lepidaploa* have pollen grains 40–55 μm in diameter, rarely to 60 μm . The larger grains of *Lessingianthus* tend to occur in the species with the most robust flowers and heads. All neotropical species seen with *Vernonia argyrophylla* or type B grains are recognized here as members of *Lessingianthus*. A number of the species of *Lessingianthus* were included by Jones (1979b) under series *Macrolepidiae* Benth. & Hook. with the pollen type listed as A, but the latter seems to have been a misprint.

The *Vernonia argyrophylla* or type B pollen has been adequately distinguished by both Stix (1960) and Jones (1979b) from other types of lophate grains found in *Vernonia* that have separate areolae at the pollen poles or that have cross-walls across the colpar area above and below the pore. However, distinction has not been ordinarily made between the larger type B pollen with three areolae across the intercolpar region and the generally smaller forms with only

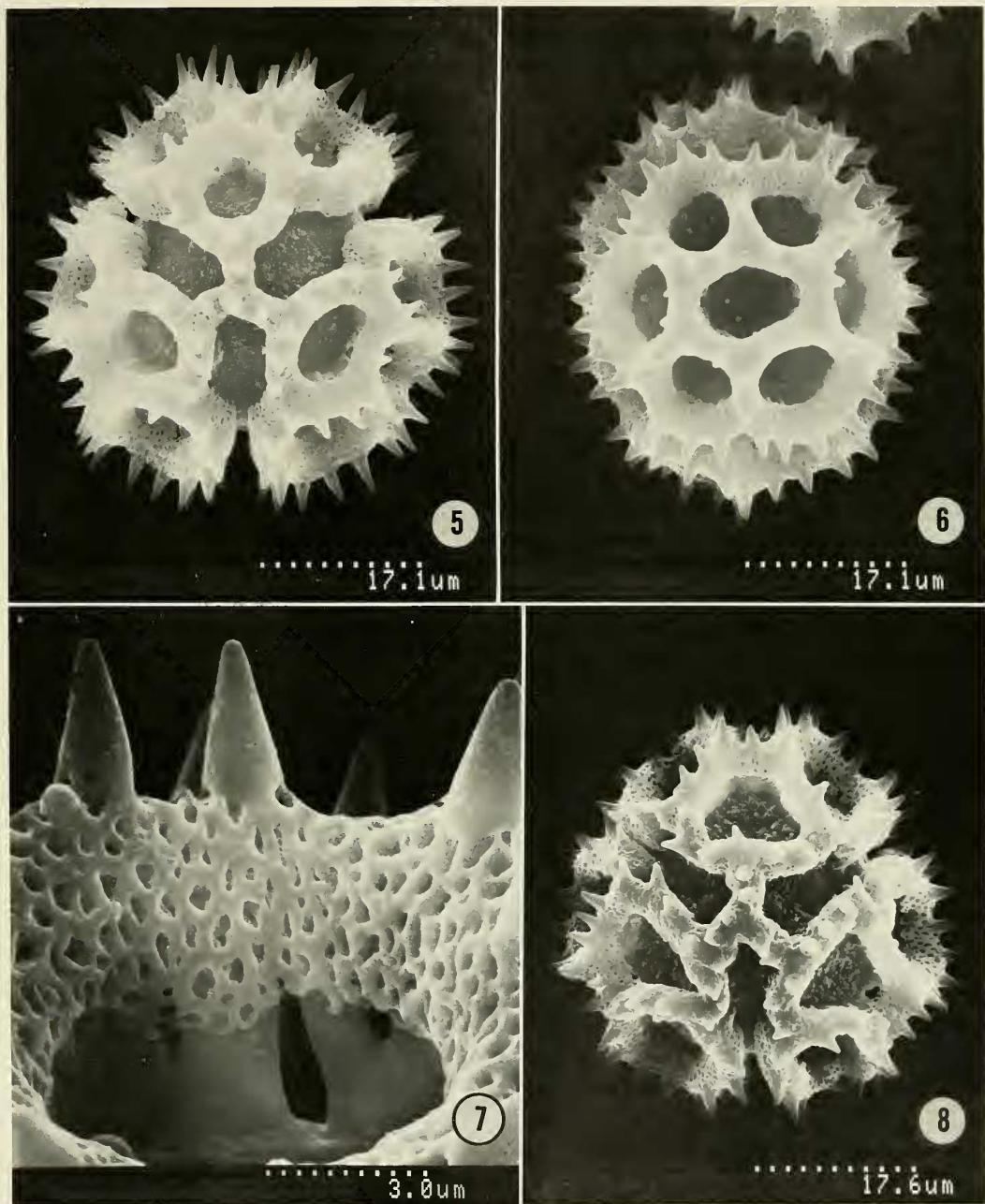


Figs. 1-4. Pollen of *Lessingianthus argyrophyllus* (Less.) H. Robins. 1. Intercolpar view showing 1:2:3:2:1 pattern. 2. Polar view showing the three colpi meeting at the pole. 3. Broken grain showing baculae. 4. Broken grain showing detail under perforated tectum.

two areolae across the intercolpar region. The latter type has been recognized as the *V. geminata*-type by Robinson (1980b). Present observations show that the distinction is more than technical. All species with *V. geminata*-type pollen prove to be members of the genus *Lepidaploa* or *Echinocoryne*. They are more closely related to species with type C and D pollens than to the *Lessingianthus* species with regular type B pollen. The *V. geminata* type grains all have rhizomatous crests, which the typical type B grains do not have. Pollen with three ar-

eolae across in many of its intercolpar regions has been seen in *Lepidaploa* in *V. vio-liceps* H. Robins. from Ecuador and in a specimen of an unnamed *Vernonia* received from Badillo in Venezuela, and in some intercolpar regions of such species as *V. her-bacea*, but the pollen involved is not true type B. The grains have rhizomatous crests and polar areolae that clearly indicate the identity of the species as *Lepidaploa* or *Chrysolaena*.

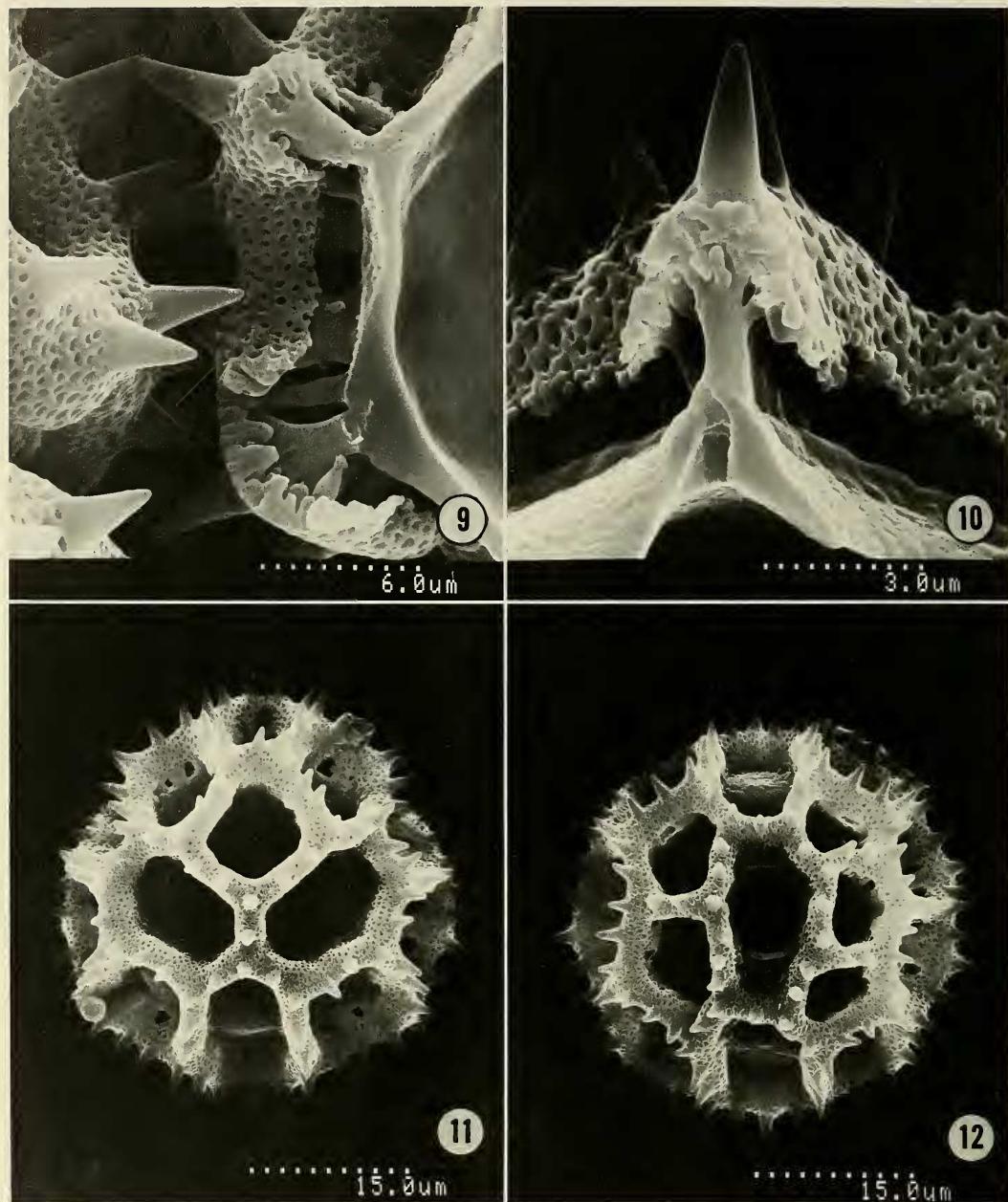
The only pollen in a *Lepidaploa* that might qualify as a true type B is in *V. psilostachya*



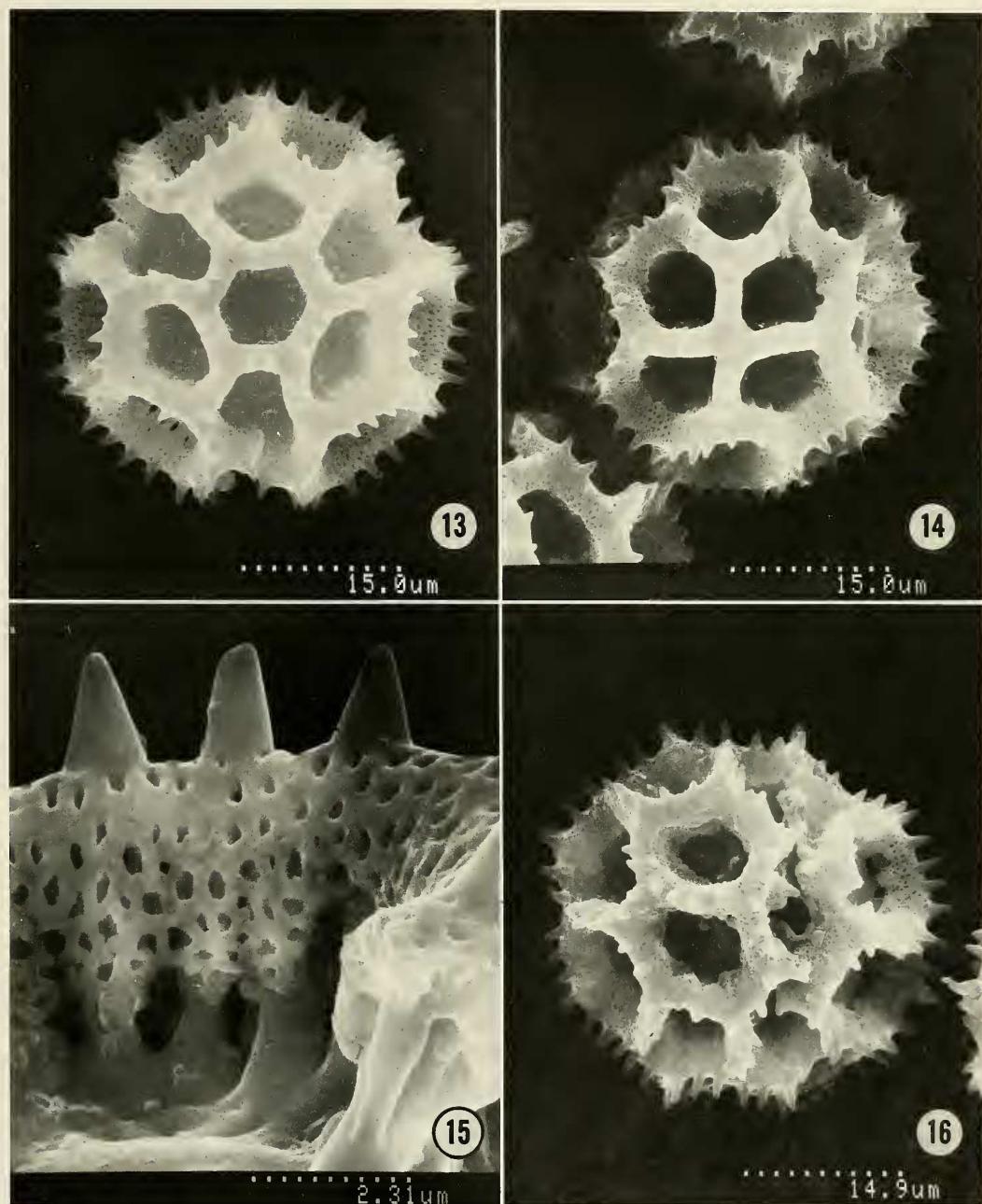
Figs. 5–8. Pollen of *Lessingianthus*. 5–7. *L. tomentellus* (Mart. ex DC.) H. Robins. 5. Polar view showing three colpi meeting at pole. 6. Intercolpar view showing 1:2:1:2:1 pattern. 7. Detail of pollen crest showing baculae. 8. *L. cephalotes* (DC.) H. Robins., polar view showing three colpi meeting at pole.

DC. The latter has colpi reaching the poles and a variable number of 2 or 3 areolae across the intercolpus in 1 or 2 tiers. Careful examination shows that very few of the

grains actually match true type B in all the intercolpi simultaneously. The habit of the plants is small compared to any *Lessingianthus*, and the involucre is a *Lepidaploa*



Figs. 9-12. Pollen of *Lessingianthus*. 9. *L. laurifolius* (DC.) H. Robins., broken grain showing baculae. 10. *L. niederleinii* (Hieron.) H. Robins., broken grain showing baculae. 11, 12. *L. brevifolius* (Less.) H. Robins. 11. View with pole below middle showing three areolae above pores meeting at pole. 12. Colpar view showing crosswalls above and below pore.



Figs. 13–16. Pollen of *Lessingianthus*. 13–15. *L. simplex* (Less.) H. Robins. 13. Polar view showing polar areola. 14. Intercolpar view showing 1:2:2:1 pattern. 15. Detail of pollen crest showing baculae. 16. *L. virgulata* (Mart. ex DC.) H. Robins., near-colpar view showing truncate poles and 1:2:2:1 intercolpar pattern.

type. The approximation of the pollen to type B might incline one to place the species in *Lessingianthus*, but SEM study shows a clearly rhizomatous structure under the crests.

There is one area of overlap in pollen areolation type. *Vernonia simplex* (Figs. 13–15) and *V. virgulata* (Fig. 16) have a type C lophate pattern with polar areolae. The intercolpar region usually is only two areolae wide in a 1:2:2:1 pattern (Figs. 14, 16). In the pattern of the areolae the pollen of these species is like the pollen that occurs in such species as *V. (Chrysolaena) flexuosa*. The pollen in *V. simplex* and *V. virgulata* differs from that of *Lepidaploa* and is like that of *Lessingianthus* in that the baculae attach directly to the foot-layer without a "rhizome." Previous treatments have associated these *Lessingianthus* species with two specialized groups now placed in *Chrysolaena* (Robinson 1988) and *Echinocoryne* (Robinson 1987b). *Vernonia simplex* was included by Jones (1981) in his series *Flexuosae* in his refined concept of the group. In this latter case, the pubescence of the plants and the lophate pattern of the pollen seemed to re-enforce the relationship between species in the series. However, the pollen distinction seems to correlate rather well with the presence of pedunculate heads in the group. The series *Flexuosae*, in spite of initial appearances, actually consists of two totally separate elements, one in *Lessingianthus* and the other, *Chrysolaena*, having rhizomatous crests on the pollen and glanduliferous anther appendages. The latter group is closer to *Lepidaploa*. Although its pollen has not been examined with the SEM, *V. desertorum*, which Jones (1981) also placed in series *Flexuosae* apparently is a *Lessingianthus*. Light microscope observations of the crests indicate that they are not rhizomatous. The three pedunculate species with type C pollen, including the two from the series *Flexuosae*, have grains of ca. 50 μm diameter, in the size range common to both *Lessingianthus* and *Lepidaploa*.

Vernonia virgulata was placed by Jones (1979b) in his series *Subulatae*, which otherwise proves to belong to the genus *Echinocoryne*. The Jones (1979b) citation of type B pollen from *V. virgulata* seemed to correlate with the type cited for the remainder of the series, but none of grains involved were actually type B. As stated above, the pollen of *V. virgulata* is closest to type C; and as indicated by Robinson (1987b), the species of *Echinocoryne* have pollen of the *V. geminata* type with only two rows of intercolpar areoles and no polar areolae.

Two additional pollen variations occur in *Lessingianthus*. The pollen of *V. brevifolia* (Figs. 11, 12) and *V. dura* have crests of exine across the colpi above and below the pores. Such crosswalls were characteristic of the *Vernonia arenaria*-type of Stix (1960) and the type D of Jones (1979b). The *V. brevifolia* and *V. dura* pollen differs from type D and resembles other *Lessingianthus* pollen in the presence of non-rhizomatous crests with high baculae and by the presence of three areolae equatorially across the intercolpus. It should be recognized that these type D grains differ from the type B only in the presence of the crosswalls above and below the pores, and the genetic difference may not be very great.

Although *V. cephalotes* normally shows type B pollen (Fig. 8), some specimens have grains with an irregular surface pattern best classified as type A. Type A pollen has been considered a reversion type in the tribe because of the wider distribution of lophate types, but *V. cephalotes* is the only specific example of such a reversion thus far known in the Western Hemisphere. The grains measure ca. 45 μm in fluid, larger than the common type A. The irregular pattern of colpi and spines suggests the influence of irregular meiosis. Another species in which only large type A pollen has been seen, *V. glazioviana* is included here in the belief it represents a similar reversion from a type A pollen.

The size of pollen in Asteraceae often cor-

relates with chromosome number, but the larger size of pollen in many species of *Lessingianthus* is not particularly correlated with known polyploidy, except to the extent that the $\bar{X} = 17$ basic to Neotropical Vernonieae is a polyploidy. Jones (1979a) provided counts for four members of the genus. Two of the species, *V. bardanioides*, and *V. glabrata* include higher polyploids having $N = 34$, but each also has lower counts of $N = 17$. A similar mixture of lower counts and higher polyploidy is also seen in at least one member of *Chrysolaena* (as *V. cognata* in Jones 1979a).

Inflorescence Form

The general *Lepidaploa* and *Lessingianthus* group is notable for a type of inflorescence that can best be termed seriate-cymose. *Lepidaploa* itself exemplifies the structure where each head is technically terminal with a lateral branch from immediately below the head bearing the rest of the series. The result looks like a series of lateral sessile heads except for the usual slight deflection at each head. This form is seen in every species presently recognized as a true *Lepidaploa*, and it seems to derive from ancestors more like the Brasilian *Vernonia diffusa* Less. that have less regular cymes and are outside of the *Lepidaploa* complex. Such ancestral stocks seem to have produced some other strongly seriate-cymose forms like those of the neotropical *Cyrtocymura* and *Eirmocephala* (Robinson 1987c) and the Colombian *Dipterocypsela* Blake. The latter are considered to be basically outside the *Lepidaploa* complex. All of the other marked examples of such cymes except *V. peculiaris* Verdcourt of Africa seem to be in *Lepidaploa* or its close relatives. These include *Mattfeldanthus* Robins. & King of Brasil that has lophate pollen. The cymes have been retained with smaller, less distinct heads in *Stenocephalum* (Robinson 1987a). In the closely related *Echinocephalum* the inflorescence is drastically altered

by the presence of peduncles, sometimes very long peduncles, under the heads. The latter condition seems derived within the complex.

Lessingianthus has many species that show the same seriate-cymose condition noted for *Lepidaploa*, but includes variations of this form that differ from anything in the latter genus. One variation is the development of pedunculate heads. This character occurs in members of the genus, such as *V. psilophylla* and *V. secunda* that have a closer relationship to species with sessile heads than to each other. Many of the species such as *V. sellowii*, *V. carvalhoi*, *V. santosii*, and *V. scaposa* have scapose inflorescences from abbreviated vegetative plants, but the species do not form a related group within the genus. The pedunculate and scapose characters represent general trends in *Lessingianthus* that are lacking in *Lepidaploa*. The species group with type C pollen, which has been misplaced in the series *Subulatae* and *Flexuosae*, is characterized by pedunculate heads. *Vernonia virgulata* is not distinguishable from *Echinocoryne* on the basis of that character, but differs in other features including its pollen. In both the pedunculate heads and the non-rhizomatous crests of the pollen, the latter species along with *V. simplex* and *V. desertorum* fall easily within *Lessingianthus*.

One other modification in a few species of *Lessingianthus* was discussed by Robinson (1980c) in connection with the description of *V. eitenii*. Although the small group of species involved has inflorescences closely resembling the seriate-cymes of their relatives, the sequence of maturation of the heads is reversed, so that the uppermost head matures first and the progress is downward. This sequence indicates that developmentally the inflorescence has converted to a cyme with the lower heads truly lateral. It is another variation that does not occur in *Lepidaploa*.

The species with seriate cymes in *Lessingianthus* and *Lepidaploa* are often distin-

guishable by an additional feature. In those species having distinct foliose bracts in the cymes, the bracts in *Lessingianthus* never seem to have the abrupt reduction in size from leaves to bracts that is seen at the base of the cyme in many species of *Lepidaploa*.

Involucral Bracts

Lessingianthus is essentially the same as *Lepidaploa* in the ratio of involucral bracts to flowers in the head. The bracts are usually twice to three times as many as the flowers. *Lessingianthus* never has excessive numbers of involucral bracts, as is seen in *Echinocoryne*. In other aspects of the involucre, however, there are characters that help to distinguish the two genera. One of these is the degree of differentiation between the outer and inner bracts.

In *Lessingianthus* and *Lepidaploa*, the involucral bracts are graduated with the inner bracts progressively larger and longer than the outer ones. The bracts in *Lessingianthus* show only the differences to be expected in such graduated structures. In those where the bracts are narrow and pointed, as in *V. bardanioides*, or those where they are short, as is *V. buddleiifolia* and *V. argyrophylla*, the slender or obtuse tips occur throughout the involucre. In *Lepidaploa* the outer bracts are often very different in shape from the inner ones. The innermost bracts may often be rather abruptly wider and the outermost bracts are often very aristate and spreading. Such differences are not found in all *Lepidaploa*, but they are found in almost no species of *Lessingianthus*. The condition is approached in *Vernonia glabrata* and *V. neiderleinii* which are otherwise like *Lessingianthus* in their rather large habit. A number of species of *Lessingianthus*, such as *V. arachnolepis* and *V. pseudosquarrosa*, have outer bracts with spreading, rather foliose tips, a feature not noted in *Lepidaploa*.

The tips of the involucral bracts in *Lessingianthus* are often very short in an almost reptilian scale pattern. Such a pattern is characteristic of the typical element of the genus characterized by larger heads, but it

also occurs in some smaller-headed species such as *V. psilophylla*. The narrowly pointed bracts of *V. bardanioides*, *V. eitenii*, *V. irwini*, and their relatives taper evenly to the tips and have a distinct longitudinal median costa externally of a type not seen in *Lepidaploa*. They do not have the apical mucros or aristae seen in many *Lepidaploa* species. The latter short apical mucros occur in *Lessingianthus* in only a few species such as *V. elegans*.

The involucral bracts of most species of *Lessingianthus* are imbricate in many series, but some species such as *V. carvalhoi* and *V. brevifolia* have involucres that appear less imbricate because of the narrower bracts. The most significant examples of reduced involucres in *Lessingianthus* are in the three species, *V. virgulata*, *V. simplex*, and *V. desertorum* that have been noted above as having type C pollen. These species are treated below as part of a distinct subgenus within *Lessingianthus*.

A number of other characters show variations of interest in *Lessingianthus* although they are not as useful for delimiting the genus. In many species of *Lessingianthus* the tendency for pedunculate heads seems correlated to some extent with the occurrence of distinct petioles. Nevertheless, shortly petiolate and sessile leaves occur in both genera. The corolla lobes of *Lessingianthus* show a broad fusion and enlargement of the vascular strands at the tip, a feature that seems rather characteristic of most of the *Lepidaploa* complex. The vascular strands of the corolla lobes of most other American Vernonieae are only narrowly fused or separated at the tips. The inner pappus in both genera is unfailingly capillary, but in *Lessingianthus* the bristles are comparatively short in a number of species such as *V. eitenii* and *V. bardanioides*. The pappus in these species is shorter in relation to the involucre and corolla, and the corolla throat is mostly exposed. Short pappus bristles of this type do not occur in *Lepidaploa*. The achenes in the genus are normally densely setuliferous, but

a few species such as *V. pseudopiptocarpha* and *V. ixiamensis* have glabrous achenes, whereas *V. glabrata*, *V. saltensis*, and *V. westermanii* have achenes with few setulae. The density of setulae on the achenes of most species allows little space for glands, and unlike many *Lepidaploa* species, no glands have been seen in the genus. A few species such as *V. ammophila* and *V. pycnostachya* have resin cells on the surface of the achene as single cells or small groups of two or three cells. The raphides in the achene wall are usually elongate, but are quadrate in some species such as *V. regis*, *V. pseudopiptocarpha*, and *V. ammophila*.

In one species of *Lessingianthus*, *V. santosii* Robinson (1980b), the flowers in the heads have been noted as opening in two sets, the outer rows first and then the inner disk flowers later as a separate group. The initial phase offers the superficial appearance of a head with ray flowers. The full distribution of the character is not known, but it has been seen again in the comparatively unrelated Vernonian genus *Centratherum*, where the two stages occur on separate days. The character is most obvious in the field, and studies in Brazil might show how common the character is in *Lessingianthus*. The character would obviously not be found in Vernonieae with smaller, fewer-flowered heads such as *Stenocephalum*.

The two generic concepts *Lessingianthus* and *Lepidaploa* represent two elements with basically differing aspects and different geography. The most obvious reason for recognizing two genera is the form of the inflorescence, which in *Lessingianthus* frequently has pedicellate heads and in *Lepidaploa* has all heads essentially sessile in the seriate cymes. It is the form of the pollen that seems to correlate best phyletically with the two groups, the one with many pedunculate heads and mostly undifferentiated involucres, and the second with exclusively sessile heads and mostly differentiated involucres. The generic distinction is therefore placed here technically at the point of the difference between non-rhizomatous

pollen crests with large discrete baculae versus the mostly rhizomatous pollen. Every species of *Lessingianthus* can be assigned either by its pedunculate heads or by its type B or D pollen having no polar areolae in conjunction with 1:2:3:2:1 or 1:2:1:2:1 intercolpar patterns. This distinction creates problems in only a few species. One species falling into *Lessingianthus* on the basis of non-rhizomatous type D pollen having a 1:2:1:2:1 intercolpar pattern seems uncomfortable in the genus on the basis of habit. *Vernonia regis* is most unusual in the genus by the rather prominent ring at the base of the style. Collapse of the softer shaft leaves a more marked enlargement than in any other *Lessingianthus*. Nevertheless, the structure is not truly broader than the shaft and it does not show the narrow attachment commonly seen in *Lepidaploa*. The species is further distinctive in its crowded narrow heads with distinct herbaceous outer bracts. *Vernonia regis* does not look like a *Lepidaploa* but rather like a *Stenocephalum*. The differences from *Stenocephalum* are discussed by Robinson (1987a). This particular species may reflect some area of evolutionary complexity such as hybridization not yet resolved, but for the present the Type D non-rhizomatous pollen character is applied rigorously to include it within *Lessingianthus*.

In the present view, *Lessingianthus* may be circumscribed too broadly in some cases, but the genus is not too narrowly delimited.

The new genus is named in honor of Carl F. Lessing 1809–1862 who was the author of many of the species of the genus.

Lessingianthus, gen. nov.

Plantae herbaceae perennes plerumque erectae ad 1.5–2.0 m altae in caulis foliis pedunculis et bracteis involuci variabiliter pubescentes. Folia alterna breviter petiolata vel sessilia. Inflorescentiae simplices vel cymosae saepe scorpioideo-cymosae vel seriate subcapitulatae proliferatae vel rare stricte cymosae, pedunculis nullis vel variabiliter elongatis. Capitula late plerumque

campanulata; bracteae involucri 2–3-plo plus quam flores in capitulo subimbricatae plerumque multiseriate plerumque late oblongae et obtusae interdum linear-lanceolatae raro leniter imbricatae. Flores in capitulo 15–50; corollae plerumque lavidulae saepe in tubis et faucibus glabris in lobis distaliter plerumque minute glanduliferae vel setuliferae apice in nervis conjunctae et incrassatae; appendices antherarum non glanduliferae; basi stylorum non noduliferi raro distincte annuliferi. Achaenia prismatica plerumque 5-costata plerumque dense sericeo-setulifera non glandulifera raro cellulis resiniferis sparse obtecta; carpodia cylindrica vel obturaculiformia et turbinata, cellulis plerumque oblongis in parietibus striate porulosis; setae pappi interiores capillares longitudinaliter ad corollas subaequales vel multo breviores, seriesbus exterioribus longe squamiformibus. Grana pollinis (45–)50–75(–80) μm in diametro lophata in cristis non rhizomata, colpis ad polos attingentibus, areolaris intercolpis aequatorialiter triplicibus (typus B), raro grana ad polos areolata et in areolaris intercolpis aequatorialiter duplicibus (typus C).

Type. — *Vernonia argyrophylla* Less. The genus is geographically mostly concentrated in Brasil with a comparatively few species occurring westward in Argentina, Paraguay, and Bolivia. The genus has two representatives in Peru, only one, *L. rubricaulis*, as far north as Colombia, and only *L. morilloi* in southern Venezuela.

The following 101 species are recognized in the genus.

Lessingianthus adenophyllus
(Mart. ex DC.)

H. Robinson, comb. nov.

Vernonia adenophylla Mart. ex DC., Prodr. 5:17. 1836. Brasil (Paraná).

Lessingianthus ammophilus (Gardn.)
H. Robinson, comb. nov.

Vernonia ammophila Gardn., Lond. J. Bot. 5:227. 1846. *Cacalia ammophila* (Gardn.)

Kuntze, Rev. Gen. Pl. 2:969. 1891. Brasil (Goiás, Minas Gerais).

Lessingianthus arachnolepis
(Ekman & Dusen) H. Robinson,
comb. nov.

Vernonia arachnolepis Ekman & Dusen in Malme, Kungl. Svenska Vetenskakademiens Handlingar 12(2):17. 1933. Brasil (Paraná, Rio Grande do Sul).

Lessingianthus argenteus (Less.)
H. Robinson, comb. nov.

Vernonia argentea Less., Linnaea 6:672. 1831. *Cacalia argentea* (Less.) Kuntze, Rev. Gen. Pl. 2:969. 1891. Brasil (Paraná, São Paulo).

Lessingianthus argyrophyllus (Less.)
H. Robinson, comb. nov. (Figs. 1–4)

Vernonia argyrophylla Less., Linnaea 6:627. 1831. *Cacalia argyrophylla* (Less.) Kuntze, Rev. Gen. Pl. 2:969. 1891. Brasil (D.F., Goiás, Minas Gerais).

Lessingianthus asteriflorus
(Mart. ex DC.)
H. Robinson, comb. nov.

Vernonia asteriflora Mart. ex DC., Prodr. 5:29. 1836. *Cacalia asteriflora* (Mart. ex DC.) Kuntze, Rev. Gen. Pl. 2:969. 1891. *Vernonia kuntzei* Hieron., Engl. Bot. Jahrb. 22:678. 1897. *Vernonia kuntzei* (Hieron.) Kuntze, Rev. Gen. Pl. 3:138. 1898. Bolivia, Brasil (Paraná, São Paulo, Santa Catarina).

Lessingianthus bardanioides (Less.)
H. Robinson, comb. nov.

Vernonia bardanioides Less., Linnaea 6:669. 1831. *Vernonia reticulata* Gardn., Lond. J. Bot. 5:226. 1846. *Vernonia lappoides* Baker in Mart., Fl. Bras. 6(2):35. 1873. *Vernonia cirsiflora* Mart. ex Baker in Mart., Fl. Bras. 6(2):36. 1873, nomen nudum *Cacalia bardanioides* (Less.) Kuntze, Rev. Gen. Pl. 2:969. 1891. *Cacalia lap-*

poides (Baker) Kuntze, Rev. Gen. Pl. 2: 970. 1891. Brasil (Bahia, D.F., Goiás, Mato Grosso do Sul, Minas Gerais, São Paulo).

Lessingianthus bishopii (H. Robinson)
H. Robinson, comb. nov.

Vernonia bishopii H. Robinson, Phytologia 49:261. 1981. *Vernonia flavescens* Glaz., Bull. Soc. Bot. France Mém. 3, 56:369. 1909, nomen nudum, non *V. flavescens* Less. *Vernonia goiasensis* S. B. Jones, Brittonia 34:107. 1982, nomen nudum Brasil (Goiás, Mato Grosso do Sul).

Lessingianthus brevifolius (Less.)
H. Robinson, comb. nov. (Figs. 11, 12)

Vernonia brevifolia Less., Linnaea 4:285. 1829; 6:659. 1831. *Vernonia ericaefolia* Hook. & Arnott, Comp. Bot. Mag. 1:236. 1835. *Cacalia brevifolia* (Less.) Kuntze, Rev. Gen. Pl. 2:969. 1891. *Vernonia linosyriifolia* Chod., Bull. Herb. Boiss., ser. 2, 2:300. 1902. Argentina, Brasil (Paraná, Rio Grande do Sul, São Paulo, Santa Catarina), Paraguay.

Lessingianthus brevipetiolatus
(Sch.Bip. ex Baker)
H. Robinson, comb. nov.

Vernonia brevipetiolata Sch.Bip. ex Baker in Mart., Fl. Bras. 6(2):85. 1873. *Cacalia brevipetiolata* (Sch. Bip. ex Baker) Kuntze, Rev. Gen. Pl. 2:969. 1891. Brasil (Minas Gerais).

Lessingianthus buddleiiifolius
(Mart. ex DC.)
H. Robinson, comb. nov.

Vernonia buddleiiifolia Mart. ex DC., Prodr. 5:45. 1836, as "Buddleiaefolia." *Vernonia squamosa* Gardner, Lond. J. Bot. 6: 419. 1847. *Cacalia buddleiaefolia* (Mart. ex DC.) Kuntze, Rev. Gen. Pl. 2:969. 1891. Brasil (D.F., Goiás, Mato Grosso, Minas Gerais, São Paulo).

Lessingianthus bupleurifolius (DC.)
H. Robinson, comb. nov.

Vernonia laevigata var. *bupleurifolia* DC., Prodr. 5:56. 1836. *Vernonia pupleurifolia* (DC.) Sch.Bip. ex Malme, Arkiv. Bot. 24A(8):13. 1932. Brasil (Goiás, Mato Grosso).

Near *L. obtusatus*, see Malme (1932).

Lessingianthus caiapoensis
(H. Robinson)
H. Robinson, comb. nov.

Vernonia caiapoensis H. Robinson, Phytologia 45:171. 1980. Brasil (Goiás).

Lessingianthus carduoides (Baker)
H. Robinson, comb. nov.

Vernonia carduoides Baker in Mart., Fl. Bras. 6(2):34. 1873. *Cacalia carduoides* (Baker) Kuntze, Rev. Gen. Pl. 2:969. 1891. Brasil (Minas Gerais).

Lessingianthus carvalhoi (H. Robinson)
H. Robinson, comb. nov.

Vernonia carvalhoi H. Robinson, Phytologia 53:394. 1983. Brasil (Bahia).

Lessingianthus cataractarum (Hieron.)
H. Robinson, comb. nov.

Vernonia cataractarum Hieron., Bot. Jahrb. Syst. 22:681. 1897. Brasil (Santa Catarina).

Lessingianthus cephalotes (DC.)
H. Robinson, comb. nov. (Fig. 8)

Vernonia cephalotes DC., Prodr. 5:57. 1836. Brasil (Goiás, Minas Gerais, São Paulo).

DeCandolle (1836) in his original description cited *Chrysocoma oligophylla* Vell. as a questionable synonym. Kuntze (1891) synonymized the two. The Vellozo description and plate (1825, 1835) indicate a pilose plant with much more pointed, graduated involucral bracts. The Vellozo species is evidently not *L. cephalotes* but the habitually

very similar *V. hypochlora* Malme, which is a *Chrysolaena*.

Lessingianthus chamaepeuceus

(Sch.Bip. ex Baker)

H. Robinson, comb. nov.

Vernonia chamaepeuceus Sch.Bip. ex Baker in Mart., Fl. Bras. 6(2):31. 1873. *Cacalia chamaepeuceus* (Sch.Bip. ex Baker) Kuntze, Rev. Gen. Pl. 2:969. 1891. Brasil (Goiás, Mato Grosso).

Lessingianthus compactiflorus

(Mart. ex Baker) H. Robinson, comb. nov.

Vernonia compactiflora Mart. ex Baker in Mart., Fl. Bras. 6(2):44. 1873. *Cacalia compactiflora* (Mart. ex Baker) Kuntze, Rev. Gen. Pl. 2:969. 1891. Brasil (D.F., Goiás, Minas Gerais).

Lessingianthus cordiger (Mart. ex DC.)

H. Robinson, comb. nov.

Vernonia cordigera Mart. ex DC., Prodr. 5: 58. 1836. *Cacalia cordigera* (Mart. ex DC.) Kuntze, Rev. Gen. Pl. 2:969. 1891. Brasil (Minas Gerais).

Lessingianthus coriaceus (Less.)

H. Robinson, comb. nov.

Vernonia coriacea Less., Linnaea 6:661. 1831. *Vernonia hecatantha* DC., Prodr. 5:53. 1836 (as *hexacantha*, corr. 5:696. 1836). *Cacalia coriacea* (Less.) Kuntze, Rev. Gen. Pl. 2:969. 1891. Bolivia, Brasil (Bahia, D.F., Goiás, Maranhão, Mato Grosso, Minas Gerais, São Paulo). Peru.

Lessingianthus cristalinae (H. Robinson)

H. Robinson, comb. nov.

Vernonia cristalinae H. Robinson, Phytologia 45: 172. 1980. Brasil (Goiás).

Lessingianthus dorsiventralis (Chodat)

H. Robinson, comb. nov.

Vernonia dorsiventralis Chodat, Bull. Herb. Boiss. ser. 2, 1:410. 1901. Paraguay.

Lessingianthus durus (Mart. ex DC.)

H. Robinson, comb. nov.

Vernonia dura Mart. ex DC., Prodr. 5:59. 1836. *Cacalia dura* (Mart. ex DC.)

Kuntze, Rev. Gen. Pl. 2:970. 1891. *Vernonia macedoi* Barroso, Arq. Jard. Bot. Rio de Janeiro 13:9. 1954. Brasil (D.F., Goiás, Mato Grosso, Minas Gerais).

Lessingianthus eitenii (H. Robinson)

H. Robinson, comb. nov.

Vernonia eitenii H. Robinson, Phytologia 46:109. 1980. *Vernonia wasshausenii* S. B. Jones, Brittonia 34:110. 1982. Brasil (D.F., Goiás).

The species concept includes one paratype of *L. cristalinae* (Irwin et al. 32817). Specimens with only a few apical heads can be distinguished from *L. cristalinae* most easily by the less appressed and more yellowish pubescence of the stems.

Lessingianthus elegans (Gardn.)

H. Robinson, comb. nov.

Vernonia elegans Gardn., Lond. J. Bot. 6: 421. 1847. *Cacalia elegans* (Gardn.) Kuntze, Rev. Gen. Pl. 2:970. 1891. Brasil (D.F., Goiás, Mato Grosso, Minas Gerais, São Paulo).

Lessingianthus erythrophilus (DC.)

H. Robinson, comb. nov.

Vernonia erythrophila DC., Prodr. 5:56. 1836. *Cacalia erythrophila* (DC.) Kuntze,

Rev. Gen. Pl. 2:970. 1891. Brasil (D.F., Minas Gerais).

Lessingianthus exiguis (Cabrera)

H. Robinson, comb. nov.

Vernonia exigua Cabrera, Sellowia 13:166.

1961. Brasil (Paraná, Santa Catarina, São Paulo).

Lessingianthus farinosus (Baker)
H. Robinson, comb. nov.

Vernonia farinosa Baker, in Mart., Fl. Bras. 6(2):84. 1873. *Cacalia farinosa* (Baker) Kuntze, Rev. Gen. Pl. 2:970. 1891. Brasil (Bahia).

Lessingianthus floccosus (Gardn.)
H. Robinson, comb. nov.

Vernonia floccosa Gardn., Lond. J. Bot. 5: 225. 1846. *Cacalia floccosa* (Gardn.) Kuntze, Rev. Gen. Pl. 2:970. 1891. *Vernonia robusta* Glaz., Bull. Soc. Bot. France Mém. 3, 56:369. 1909, nomen nudum. Brasil (D.F., Goiás, Minas Gerais).

Lessingianthus fonsecae (H. Robinson)
H. Robinson, comb. nov.

Vernonia fonsecae H. Robinson, Phytologia 45:174. 1980. Brasil (Goiás).

Lessingianthus glabratus (Less.)
H. Robinson, comb. nov.

Vernonia glabrata Less., Linnaea 4:294. 1829; 6:661. 1831. *Vernonia radula* Mart. ex DC., Prodr. 5:52. 1836. *Cacalia glabrata* (Less.) Kuntze, Rev. Gen. Pl. 2:970. 1891. *Cacalia radula* (Mart. ex DC.) Kuntze, Rev. Gen. Pl. 2:971. 1891. *Vernonia oxydonta* Malme, Ark. Bot. 24A(6): 19. 1932. Brasil (D.F., Goiás, Mato Grosso, Minas Gerais, Paraná, Rio Grande do Sul).

Lessingianthus glaziovianus (Baker)
H. Robinson, comb. nov.

Vernonia glazioviana Baker in Mart., Fl. Bras. 6(2):41. 1873. *Cacalia glaziouana* (Baker) Kuntze, Rev. Gen. Pl. 2:970. 1891. Brasil (Rio de Janeiro).

Lessingianthus glomeratus
(Baker ex Warming)
H. Robinson, comb. nov.

Vernonia glomerata Baker ex Warming, Vi-

densk. Medd. Forh. Kjöb. 1890:185.
1890. Brasil (D.F., Minas Gerais).

Lessingianthus grandiflorus (Less.)
H. Robinson, comb. nov.

Vernonia grandiflora Less., Linnaea 6:660. 1831. Brasil (Minas Gerais, Paraná, São Paulo), Paraguay.

Kuntze (1891) equated this species with *Chrysocoma pumilla* of Vellozo (1825), but the plate of the latter (1835) is interpreted here as representing the species commonly known as *Vernonia sessilifolia* Less.

Lessingianthus grearii (H. Robinson)
H. Robinson, comb. nov.

Vernonia grearii H. Robinson, Phytologia 45:175. 1980. Brasil (Goiás).

Lessingianthus heringeri (H. Robinson)
H. Robinson, comb. nov.

Vernonia heringeri H. Robinson, Phytologia 53:395. 1983. Brasil (D.F., Goiás).

Lessingianthus hoveaefolius (Gardn.)
H. Robinson, comb. nov.

Vernonia hoveaefolia Gardn., Lond. J. Bot. 6:423. 1847. *Cacalia hoveaefolia* (Gardn.) Kuntze, Rev. Gen. Pl. 2:970. 1891. Near *L. obtusatus*. Brasil (Goiás, Minas Gerais).

Lessingianthus hypochaeris (DC.)
H. Robinson, comb. nov.

Vernonia hypochaeris DC., Prodr. 5:45. 1836. *Cacalia hypochaeris* (DC.) Kuntze, Rev. Gen. Pl. 2:970. 1891. Brasil (Paraná).

Lessingianthus irwini (Barroso)
H. Robinson, comb. nov.

Vernonia irwini Barroso, Loesgrena 36:2. 1969. Brasil (D.F.).

Lessingianthus ixiamensis (Rusby)
H. Robinson, comb. nov.

Vernonia ixiamensis Rusby, Bull. New York Bot. Gard. 8:125. 1912. Bolivia.

Lessingianthus lacunosus
(Mart. ex DC.)
H. Robinson, comb. nov.

Vernonia lacunosa Mart. ex DC., Prodr. 5: 56. 1836. *Cacalia lacunosa* (Mart. ex DC.) Kuntze, Rev. Gen. Pl. 2:970. 1891. Brasil (D.F., Goiás, Minas Gerais).

Lessingianthus laevigatus
(Mart. ex DC.)
H. Robinson, comb. nov.

Vernonia laevigata Mart. ex DC., Prodr. 5: 56. 1836. Near *L. obtusata*; see Malme (1932). Brasil (D.F., Goiás, Mato Grosso, Minas Gerais, Paraná).

Lessingianthus laurifolius (DC.)
H. Robinson, comb. nov. (Fig. 9)

Vernonia laurifolia DC., Prodr. 5:30. 1836.
Cacalia laurifolia (DC.) Kuntze, Rev. Gen. Pl. 2:970. 1891. Bolivia, Brasil, Peru.

Lessingianthus ligulifolius
(Mart. ex DC.)
H. Robinson, comb. nov.

Vernonia ligulifolia Mart. ex DC., Prodr. 46. 1836. as "ligulaefolia." *Cacalia ligulifolia* (Mart. ex DC.) Kuntze, Rev. Gen. Pl. 2:970. 1891. *Vernonia cotaniensis* Hieron., Bot. Jahrb, Syst. 40:352. 1908. Brasil (D.F., Goiás, São Paulo).

The species is close to *L. coriaceus*.

Lessingianthus linearifolius (Less.)
H. Robinson, comb. nov.

Vernonia linearifolia Less., Linnaea 4:287. 1829. *Cacalia linearifolia* (Less.) Kuntze,

Rev. Gen. Pl. 2:970. 1891. Brasil (Minas Gerais).

Lessingianthus linearis (Spreng.)
H. Robinson, comb. nov.

Vernonia linearis Spreng., Syst. Veg., ed. 16, 3:437. 1826. *Cacalia linearis* (Spreng.) Kuntze, Rev. Gen. Pl. 2:970. 1891. Brasil (Bahia, D.F., Goiás, Minas Gerais).

Lessingianthus lorentzii (Hieron.)
H. Robinson, comb. nov.

Vernonia lorentzii Hieron., Engl. Bot. Jahrb. 22:674. 1898. Argentina, Paraguay.

Lessingianthus macrocephalus (Less.)
H. Robinson, comb. nov.

Vernonia macrocephala Less., Linnaea 4: 298. 1829. *Cacalia macrocephala* (Less.) Kuntze, Rev. Gen. Pl. 2:970. 1891. Brasil (Rio Grande do Sul, São Paulo), Uruguay.

Lessingianthus macrophyllus (Less.)
H. Robinson, comb. nov.

Vernonia macrophylla Less., Linnaea 6:668. 1831. *Cacalia macrophylla* (Less.) Kuntze, Rev. Gen. Pl. 2:970. 1891. Brasil (Bahia, Espírito Santo, Minas Gerais, Rio de Janeiro).

Lessingianthus mansoanus (Baker)
H. Robinson, comb. nov.

Vernonia mansoana Baker in Mart., Fl. Bras. 6(2):84. 1873. *Cacalia mansoana* (Baker) Kuntze, Rev. Gen. Pl. 2:970. 1891. Brasil (Goiás, Mato Grosso).

Lessingianthus mollissimus
(D. Don ex Hook. & Arn.)
H. Robinson, comb. nov.

Vernonia mollissima D. Don ex Hook. & Arn., Comp. Bot. Mag. 1:237. 1835. *Cacalia mollissima* (D. Don ex Hook. & Arn.) Kuntze, Rev. Gen. Pl. 2:970. 1891.

Argentina, Brasil (Mato Grosso, Paraná, Rio Grande do Sul), Paraguay.

Lessingianthus monocephalus (Gardn.)
H. Robinson, comb. nov.

Vernonia monocephala Gardn., Lond. J. Bot. 6:418. 1847. *Cacalia monocephala* (Gardn.) Kuntze, Rev. Gen. Pl. 2:970. 1891. Brasil (Bahia, D.F., Goiás).

Lessingianthus morii (H. Robinson)
H. Robinson, comb. nov.

Vernonia morii H. Robinson, Phytologia 44: 290. 1979. Brasil (Bahia).

Lessingianthus morilloi (Badillo)
H. Robinson, comb. nov.

Vernonia morilloi Badillo, Ernstia 1:2. 1981.
Venezuela (Amazonas).

Lessingianthus myrsinites
H. Robinson, sp. nov.

Vernonia myrsinites Ekman, in herb.

Plantae fruticosae ad 0.5–1.0 m altae superne ramosae dense foliosae. Caules superne lanosi base xylopodiales. Folia sessilia oblonga 2–7 cm longae et 1.0–3.5 cm latae base truncatae vel breviter cordatae margine integrae apice obtusae vel breviter acutae supra subglabrae et sublucidae subtus pilulosae et glandulo-punctatae utrinque in nervulis prominentes, nervis secundariis 3–8 erecto-patentibus. Inflorescentiae in ramis abrupte terminales fasciculatae plerumque ca. 3-capitatae; capitula late cylindrica ca. 12 mm longa et 5 mm lata; squamae involucri subimbricatae appressae 36–40 gradatim ca. 6-seriatae, bracteae extiores late ovatae 2–3 mm longae apice glabrae breviter acutae et minute apiculatae extus plerumque dense pilosulae, bracteae interiores oblongae 4–7 mm longae apice roundatae vel saepe eroso-fimbriatae extus glabrae; corollae lavandulae vel purpureae ca. 11 mm longae plerumque glabrae, tubis

ca. 5 mm longis, faucibus ca. 1 mm longis, lobis ca. 5 mm longis et 0.6 mm latis apice minute scabridulis extus superne paucem glanduliferis; thecae antherarum ca. 3 mm longae, appendices antherarum ca. 0.7 mm longae et base 2.3 mm latae. Achaenia ca. 3 mm longa sericeo-setulifera; setae pappi interiores ca. 30 ca. 7 mm longae apice leniter incrassatae, squamae extiores lineares ca. 1.2 mm longae. Grana pollinis in diametro ca. 60 µm distincte lophata (typus B).

Type.—Brasil: Goiás: Chapada dos Veadeiros. 18–19 km N of Alto Paraiso. Wet campo at 4300 ft. elevation. Coarse suffrutescent herb to 1 m tall. Florets lavender. Local in sandy areas within rocky outcrops. Jan 24 1980. R. M. King and F. Almeda 8281 (Holotype UB; Isotype US).

Paratypes.—Brasil: Goiás: Chapada dos Veadeiros, 14°S, 47°W, ca. 15 km W of Veadeiros. Elev. 1000 m. Much-branched subshrub ca. 60 cm tall. Heads lavender-purple. Frequent. Campo. Feb 8 1966. H. S. Irwin, J. W. Gear, Jr., R. Souza, R. Reis dos Santos 12342 (US); ca. 20 km W of Veadeiros. Elev. 1000 m. Erect subshrub ca. 1 m tall. Heads magenta. Creek margin, among rocks. Feb 9 1966. Irwin et al. 12408 (US); herb ca. 1 m tall. Heads magenta. Frequent. Rocky slopes and wet campo. Feb 11 1966. Irwin et al. 12569 (US); ca. 15 km W of Veadeiros. Shrub to ca. 50 cm tall. Heads cream. Rocky slope and creek margin. Feb 14 1966. Irwin et al. 12839 (US); ca. 10 km S of Alto do Paraiso (formerly Veadeiros). Elev. 1000 m. Subshrub ca. 50 cm tall. Heads in fruit. Rocky slopes. Mar 23 1969. H. S. Irwin, R. Reis dos Santos, R. Souza, & S. F da Fonseca 24953 (US); ca. 19 km N of Alto do Paraiso, elev. ca. 1250 m. Subshrub ca. 1 m tall. Heads in fruit. Outcrops. Cerrado on steep rocky slopes, surrounded by campo. Mar 20 1971. H. S. Irwin, R. M. Harley, G. L. Smith 32812 (US); 18–19 km N of Alto Paraiso. Wet campo at 4300 ft. elev. Shrub 1 m tall. Pappus tawny at maturity. Jan 24 1980. R. M. King & F. Almeda 8282 (US); 20 and 30

km N of Alto Paraiso de Goiás, along road to Monte Alegre de Goiás. Elev. 4200 ft. Subshrub ¾ m tall, flowers lavender or purple. Feb 7 1981. R. M. King & L. E. Bishop 8810 and 8818A (US); West of road to Monte Alegre de Goiás, 12–20 km N of Alto Paraiso de Goiás. Elev. 4000–4400 ft. Shrubs ½–¾ m tall, flowers past anthesis and lavender. Feb 7 1981. King & Bishop 8827 and 8828 (US).

The species is in herbaria under the name *Vernonia myrsinites* Ekman, and a type photograph has been seen of a specimen that was once in the Berlin Herbarium annotated by Ekman in 1912. Unfortunately, no place of publication has been found, and the name does not appear in any of the indices. It is not among the Ekman names validated by Malme (1933). Part of the reason for the oversight is the restricted distribution of the species, with recollections occurring in quantity only comparatively recently. The species is therefore described here as new. Ekman is cited only in synonymy since he proposed the name in a different combination.

There is no evidence that the present species has been confused in the past with the vegetatively similar *Lessingianthus cordigera* of Minas Gerais. The latter has a more branching inflorescence with densely hairy tips on the inner involucral bracts as the most obvious differences.

Lessingianthus niederleinii (Hieron.)
H. Robinson, comb. nov. (Fig. 10)

Vernonia niederleinii Hieron., Bot. Jahrb. Syst. 22:681. 1897. *Vernonia valenzuelae* Chod., Bull. Herb. Boiss. ser. 2, 3:641. 1903. Argentina, Brasil (Paraná), Paraguay.

Lessingianthus obscurus (Less.)
H. Robinson, comb. nov.

Vernonia obscura Lessing, Linnaea 4:296. 1829; 6:663. 1831. *Vernonia davallifolia* Gardn., Lond. J. Bot. 6:422. 1847, as

“*davalliaeefolia*”. *Cacalia obscura* (Less.) Kuntze, Rev. Gen. Pl. 2:970. 1891. Brasil (Goiás, São Paulo).

Lessingianthus obtusatus (Less.)
H. Robinson, comb. nov.

Vernonia obtusata Lessing, Linnaea 6:662. 1831. *Cacalia obtusata* (Less.) Kuntze, Rev. Gen. Pl. 2:970. 1891. *Vernonia subacuminata* Hieron., Bot. Jahrb. Syst. 22: 691. 1897. Bolivia, Brasil (Goiás, Mato Grosso, Minas Gerais, São Paulo).

Lessingianthus octandrus
(Sch.Bip. ex Baker)
H. Robinson, comb. nov.

Vernonia octandra Sch.Bip. ex Baker in Mart., Fl. Bras. 6(2):87. 1873. *Cacalia octandra* (Sch.Bip. ex Baker) Kuntze, Rev. Gen. Pl. 2:970. 1891. Brasil (Goiás?).

Lessingianthus onoporooides (Baker)
H. Robinson, comb. nov.

Vernonia onoporooides Baker in Mart., Fl. Bras. 6(2):36. 1873. *Cacalia onoporooides* (Baker) Kuntze, Rev. Gen. Pl. 2:970. 1891. Brasil (D.F., Goiás, Mato Grosso, Minas Gerais, São Paulo).

Lessingianthus pentacontus (DC.)
H. Robinson, comb. nov.

Vernonia pentaonta DC., Prodr. 5:30. 1836, as *pentacantha*, corr. 5:696. 1836. *Cacalia pentacantha* (DC.) Kuntze, Rev. Gen. Pl. 2:970. 1891. Brasil?

Lessingianthus platyphyllus (Chod.)
H. Robinson, comb. nov.

Vernonia platyphylla Chod., Bull. Herb. Boiss., ser. 2, 2:299. 1902. Brasil (Mato Grosso), Paraguay.

Lessingianthus polyphyllus
(Sch.Bip. ex Baker)
H. Robinson, comb. nov.

Vernonia polyphylla Sch.Bip. ex Baker in Mart., Fl. Bras. 6(2):63. 1873. Brasil (Paraná), Paraguay.

Lessingianthus pseudopiptocarphus
(H. Robinson)
H. Robinson, comb. nov.

Vernonia pseudopiptocarpha H. Robinson, Phytologia 45:180. 1980. Brasil (Goiás, Mato Grosso).

Lessingianthus plantaginodes
(Kuntze)
H. Robinson, comb. nov.

Vernonia rubricaulis var. *squarrosa* Less., Linnaea 4:300. 1829. *Vernonia squarrosa* (Less.) Less., Linnaea 6:678. 1831, non *V. squarrosa* [Don] Less., Linnaea 6:627. 1831 which was given precedence by Kuntze (1891). *Cacalia plantaginodes* Kuntze, Rev. Gen. Pl. 2:969. 1891, non *V. plantaginoides* Hieron. *Vernonia pseudosquarrosa* Hieron., Bot. Jahrb. 22:685. 1897. *Vernonia sancti-pauli* Hieron., Bot. Jahrb. Syst. 22:687. 1897. *Vernonia squarrulosa* Mattfeld ex Malme, Ark. Bot. 24A(6):18. 1931. Argentina, Brasil (Paraná, Rio Grande do Sul, São Paulo), Uruguay.

Lessingianthus psilophyllus (DC.)
H. Robinson, comb. nov.

Vernoniapsilophylla DC., Prodr. 5:28. 1836. *Vernonia graminifolia* Gardn., Lond. J. Bot. 6:421. 1847. *Cacalia graminifolia* (Gardn.) Kuntze, Rev. Gen. Pl. 2:970. 1891. *Cacalia psilophylla* (DC.) Kuntze, Rev. Gen. Pl. 2:971. 1891. Brasil (D.F., Goiás, Minas Gerais, Pará, Paraná).

Lessingianthus pulverulentus (Baker)
H. Robinson, comb. nov.

Vernonia pulverulenta Baker in Mart., Fl. Bras. 6(2):42. 1873. *Cacalia pulverulenta* (Baker) Kuntze, Rev. Gen. Pl. 2:971. 1891. Brasil (D.F., Goiás, Minas Gerais).

Lessingianthus pumilla (Vell.)
H. Robinson, comb. nov.

Chrysocoma pumilla Vell., Fl. Flum. 331. 1825; 8, pl. 32. 1835. *Vernonia sessilifolia* Less., Linnaea 6:659. 1831. *Cacalia pumila* (Vell.) Kuntze, Rev. Gen. Pl. 2:969. 1891. *Cacalia sessilifolia* (Less.) Kuntze, Rev. Gen. Pl. 2:971. 1891. Brasil (Paraná).

Lessingianthus pycnostachyus (DC.)
H. Robinson, comb. nov.

Vernonia pycnostachya DC., Prodr. 5:58. 1836. *Cacalia pycnostachya* (DC.) Kuntze, Rev. Gen. Pl. 2:971. 1891. Brasil (Minas Gerais).

Lessingianthus regis (H. Robinson)
H. Robinson, comb. nov.

Vernonia regis H. Robinson, Phytologia 45: 181. 1980. Brasil (Bahia).

Lessingianthus reitzianus (Cabrera)
H. Robinson, comb. nov.

Vernonia reitziana Cabrera, Sellowia 13: 160. 1961. Brasil (Paraná, Santa Catrina).

Lessingianthus robustus (Rusby)
H. Robinson, comb. nov.

Vernonia robusta Rusby, Mem. Torrey Bot. Club 6:54. 1896, non *V. robusta* Glaz., nomen nudum. Bolivia.

Lessingianthus roseus (Mart. ex DC.)
H. Robinson, comb. nov.

Vernonia rosea Mart. ex DC., Prodr. 5:59. 1836. *Cacalia rosea* (Mart. ex DC.) Kuntze, Rev. Gen. Pl. 2:971. 1891. Brasil (Minas Gerais).

Lessingianthus rosmarinifolius (Less.)
H. Robinson, comb. nov.

Vernonia rosmarinifolia Less., Linnaea 4: 285. 1829. *Cacalia rosmarinifolia* (Less.)

Kuntze, Rev. Gen. Pl. 2:971. 1891. Brasil (Bahia, Minas Gerais).

Lessingianthus rubricaulis
(Humb. & Bonpl.)
H. Robinson, comb. nov.

Vernonia rubricaulis Humb. & Bonpl., Pl. Aequin. 2:66. tab. 99. 1809. *Vernonia intermedia* DC., Prodr. 5:27. 1836. *Cacalia intermedia* (DC.) Kuntze, Rev. Gen. Pl. 2:970. 1891. *Cacalia rubricaulis* (Humb. & Bonpl.) Kuntze, Rev. Gen. Pl. 2:971. 1891. Argentina, Brasil (Mato Grosso, Minas Gerais, Paraná, Santa Catarina), Colombia, Paraguay, Peru.

Lessingianthus rugulosus
(Sch.Bip. ex Baker)
H. Robinson, comb. nov.

Vernonia ruglosa Sch.Bip. ex Baker in Mart., Fl. Bras. 6(2):83. 1873. *Cacalia ruglosa* (Sch. Bip. ex Baker) Kuntze, Rev. Gen. Pl. 2:971. 1891. Brasil (Minas Gerais).

Lessingianthus saltensis (Hieron.)
H. Robinson, comb. nov.

Vernonia saltensis Hieron., Bot. Jahrb. Syst. 22:691. 1897. Argentina, Bolivia.

Lessingianthus santosii (H. Robinson)
H. Robinson, comb. nov.

Vernonia santosii H. Robinson, Phytologia 45:182. 1980. Brasil (Bahia).

Lessingianthus scaposus (Barroso)
H. Robinson, comb. nov.

Vernonia scaposa Barroso, Loefgrenia 36: 2. 1969. Brasil (Minas Gerais).

Lessingianthus secundus
(Sch.Bip. ex Baker)
H. Robinson, comb. nov.

Vernonia secunda Sch.Bip. ex Baker in Mart., Fl. Bras. 6(2):93. 1973. *Cacalia se-*

cunda (Sch.Bip. ex Baker) Kuntze, Rev. Gen. Pl. 2:971. 1891. Brasil (D.F., Goiás).

Lessingianthus sellowii (Less.)
H. Robinson, comb. nov.

Vernonia sellowii Lessing, Linnaea 4:301. 1829. *Cacalia sellowii* (Less.) Kuntze, Rev. Gen. Pl. 2:971. 1891. *Vernonia hasleriana* Chod., Bull. Herb. Boiss., ser. 2, 2:302. 1902. Argentina, Brasil (Paraná, Rio Grande do Sul, Santa Catarina), Uruguay.

Lessingianthus soderstroemii
(H. Robinson) H. Robinson, comb. nov.

Vernonia soderstroemii H. Robinson, Phytologia 45:183. 1980. Brasil (D.F., Goiás).

Lessingianthus souzae (H. Robinson)
H. Robinson, comb. nov.

Vernonia souzae H. Robinson, Phytologia 45:184. 1980. Brasil (Goiás).

Lessingianthus stoechas
(Mart. ex Baker)
H. Robinson, comb. nov.

Vernonia stoechas Mart. ex Baker in Mart., Fl. Bras. 6(2):49. 1873. *Cacalia stoechas* (Mart. ex Baker) Kuntze, Rev. Gen. Pl. 2:971. 1891. Brasil (Goiás, Minas Gerais).

Lessingianthus subcarduoides
(H. Robinson) H. Robinson, comb. nov.

Vernonia subcarduoides H. Robinson, Phytologia 45:185. 1980. Brasil (Minas Gerais).

Lessingianthus subobtusus (Malme)
H. Robinson, comb. nov.

Vernonia subobtusa Malme, Ark. Bot. 24A(8):13. 1932. Brasil (Mato Grosso).

Lessingianthus syncephalus
(Sch.Bip. ex Baker)
H. Robinson, comb. nov.

Vernonia syncephala Sch.Bip. ex Baker in Mart., Fl. Bras. 6(2):64. 1873. *Cacalia syncephala* (Sch.Bip. ex Baker) Kuntze, Rev. Gen. Pl. 2:971. 1891. Brasil (Goiás?).

Lessingianthus tomentellus

(Mart. ex DC.)

H. Robinson, comb. nov. (Figs. 5–7)

Vernonia tomentella Mart. ex DC., Prodr. 5:59. 1836. *Cacalia tomentella* (Mart. ex DC.) Kuntze, Rev. Gen. Pl. 2:971. 1891. Brasil (Minas Gerais, São Paulo).

Lessingianthus ulei (Hieron.)

H. Robinson, comb. nov.

Vernonia ulei Hieron., Bot. Jahrb. 22:686. 1897. Brasil (Minas Gerais).

Lessingianthus varroniifolius (DC.)

H. Robinson, comb. nov.

Vernonia varroniifolia DC., Prodr. 5:56. 1836. *Cacalia varroniifolia* (DC.) Kuntze, Rev. Gen. Pl. 2:971. 1891. Bolivia, Brasil.

Lessingianthus venosissimus

(Sch.Bip. ex Baker)

H. Robinson, comb. nov.

Vernonia venosissima Sch.Bip. ex Baker in Mart., Fl. Bras. 6(2):30. 1873. *Cacalia venosissima* (Sch.Bip. ex Baker) Kuntze, Rev. Gen. Pl. 2:971. 1891. *Vernonia urbaniana* Glaz., Bull. Soc. Bot. France Mém. 3, 57:369. 1909., nomen nudum. Brasil (D.F., Goiás, Mato Grosso).

Lessingianthus veprerorum

(Mart. ex DC.)

H. Robinson, comb. nov.

Vernonia veprerorum Mart. ex DC., Prodr. 5:59. 1836. *Cacalia veprerorum* (Mart. ex DC.) Kuntze, Rev. Gen. Pl. 2:971. 1891. Brasil (Minas Gerais).

Lessingianthus vestitus (Baker)

H. Robinson, comb. nov.

Vernonia vestita Baker in Mart., Fl. Bras. 6(2):83. 1873. *Cacalia vestita* (Baker) Kuntze, Rev. Gen. Pl. 2:971. 1891. Brasil (Minas Gerais).

Lessingianthus warmingianus (Baker)

H. Robinson, comb. nov.

Vernonia warmingiana Baker in Mart., Fl. Bras. 6(2):68. 1873. *Cacalia warmingiana* (Baker) Kuntze, Rev. Gen. Pl. 2:971. 1891. Brasil (Goiás, Minas Gerais).

Lessingianthus westermanii

(Ekman & Dusen)

H. Robinson, comb. nov.

Vernonia westermanii Ekman & Dusen ex Malme, Kungl. Svenska Vetenskapsakad. Handl. 12(2):10. 1933. Brasil (Paraná).

Lessingianthus xanthophyllus

(Mart. ex DC.)

H. Robinson, comb. nov.

Vernonia xanthophylla Mart. ex DC., Prodr. 5:58. 1836. *Cacalia xanthophylla* (Mart. ex DC.) Kuntze, Rev. Gen. Pl. 2:971. 1891. Brasil (Bahia).

Lessingianthus zuccarianus

(Mart. ex DC.)

H. Robinson, comb. nov.

Vernonia zuccariana Mart. ex DC., Prodr. 5:55. 1836. *Cacalia zuccariana* (Mart. ex DC.) Kuntze, Rev. Gen. Pl. 2:971. 1891. Brasil (D.F., Goiás, Mato Grosso, Minas Gerais).

Lessingianthus subg. *Oligocephalus*

H. Robinson, subg. nov.

Vernonia sect. *Lepidaploa* subsect. *Oligocephalae* Baker in Mart., Fl. Bras. 6(2):46. 1873, pro parte.

Lessingianthis subg. Lessingianthis typicus similis sed squamae involucri subaequales et granae pollines polariter areolatae et intercolpe aequatorialiter biareolatae; a

Lepidaplois in capitulis pedunculatis et in cristis pollinis non rhizomatibus differt.

Type.—*Vernonia simplex* Less. (= *Lessingianthus simplex* (Less.) H. Robinson.

Lessingianthus desertorum

(Mart. ex DC.)

H. Robinson, comb. nov.

Vernonia desertorum Mart. ex DC., Prodr. 5:43. 1836. *Vernonia campestris* DC., Prodr. 5:43. 1836. *Vernonia desertorum* var. *campestris* (DC.) Baker in Mart., Fl. Bras. 6(2):48. 1873. *Vernonia desertorum* var. *longipes* Baker in Mart., Fl. Bras. 6(2): 48. 1873. *Cacalia desertorum* (Mart. ex DC.) Kuntze, Rev. Gen. Pl. 2:290. 1981. *Vernonia desertorum* var. *macrocephala* Chod., Bull. Herb. Boissier, ser. 2, 2:300. 1902. Brasil (Bahia, D.F., Goiás, Mato Grosso, Minas Gerais, São Paulo), Paraguay.

Lessingianthus simplex (Lessing)

H. Robinson, comb. nov. (Figs. 13–15)

Vernonia simplex Lessing, Linnaea 4:280. 1829. *Vernonia simplex* var. *angustifolia* Less., Linnaea 4:280. 1829. *Vernonia simplex* var. *latifolia* Less., Linnaea 4:280. 1829. *Vernonia simplex* var. *regnellii* Baker in Mart., Fl. Bras. 6(2):53. 1873. *Vernonia erigerontis* Mart. ex DC., Prod. 5:43. 1836, nomen nudum. Bolivia, Brasil (D.F., Goiás, Mato Grosso, Minas Gerais, Santa Catarina, São Paulo).

Lessingianthus virgulatus

(Mart. ex DC.)

H. Robinson, comb. nov. (Fig. 16)

Vernonia virgulata Mart. ex DC., Prodr. 5: 42. 1836. *Cacalia virgulata* (Mart. ex DC.) Kuntze, Rev. Gen. Pl. 2:971. 1891. Brasil (Goiás, Minas Gerais).

The species is placed in the subgenus because of the polar areolae, but it is probably not closely related to the other two species.

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