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STUDIES IN AUSTRALIAN LAMIACEAE

2. *EICHLERAGO*, A NEW GENUS ALLIED TO *PROSTANTHERA*

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Abstract

Eichlerago, a new genus from Western Australia, is characterized. The single species, *E. tysoniana*, known from only two collections, is described and figured. *Eichlerago* possesses characteristics of both Lamiaceae and Verbenaceae (s. lat.), and an outline of the history of classification in both families is followed by a discussion of the relationships of the new genus, which is placed tentatively in Lamiaceae-Prostantheroideae.

Eichlerago Carrick, gen. nov.

Calyx bilabiatus, labio infero *sursum plicato fructum includenti*; corolla *bilabiata*, labio supero bilobo, lobis aequalibus, labio infero trilobo, lobis aequalibus; stamina quatuor, didynama, *fertilia*, *antheris bilocularibus*, *connectivo appendiculato*; *nectarium disciforme praesens*; ovarium tetraloculare, ovulo unico axillari basin versus in quoque loculo, stylo *terminali*; fructus siccus, ut videtur *indehiscens*, seminibus *albuminatis*.

Species typica: *E. tysoniana* Carrick, sp. nov.

Etymologia: honori Hj. Eichleri, per plures annos custodis Herbarii Australiae Meridionalis, doctoris fautorisque ardentis investigationum taxonomicarum hoc genus dicavi; atque $\alpha\gamma\omega$ sensu duco adhortorque suffixi.

Calyx two-lipped, the lower lip folding upwards and enclosing the fruit; corolla two-lipped, the upper lip two-lobed, the lobes equal, the lower lip three-lobed, the lobes equal; stamens four, didynamous, fertile, anthers bilocular, connective appendaged; nectariferous disc present; ovary four-locular, one axile ovule attached towards the base of each loculus, style terminal; fruit dry, apparently indehiscent, seeds albuminous.

E. tysoniana Carrick, sp. nov.

[“*Prostanthera Tysoni* F.v.M.”, Muell. herb., nom. nud.; “*P. Tysoni* F.v.M.” in Gardner, C. A., Enum. Pl. Austral. Occ. (1931)114, nomen; “*P. sp.*” (“*P. tysonii*” in a bracketed note indicating illegitimacy) in Blackall, W. E. & Grieve, B. J., West. Austral. Wildfl. 3(1965)593, nomen; “*P. tysonii* F. Muell.” in Beard, J. S., West Austral. Pl. ed. 2(1970)116, nomen.]

Typus: *Isaac Tyson 25*, “Mt. Narryer, Murchison River, 1898,” (PERTH), holotypus hic designatus; (K) isotypi (2 specimenes).

Frutex lignosus, ut 1 m altus aut ultra videtur, intricatus, divaricate ramosus, ferrugineus, ramulis lanatis, pilis implexis brunneolis dense vestitis. *Folia* decussata, brevissime petiolata, late elliptica vel suborbicularia vel transverse elliptica, rare ovata, 2-4 mm longa lataque, basi plus minusve truncata, margine integra vel interdum sinuata, plana vel interdum undulata; juvenilia lanata, adulta sparse villosa, utrinque glandulis circularibus sparsis tecta. *Flores* solitariae, axillares, pedicellis villosis, circa 1 mm longis, bracteolis villosis, lineari-lanceolatis, circa 1 mm longis. *Calyx* tubo obconico, circa 3 mm longo, costato, extus sparse villosus, intus glabro; labio supero depresso ovato, concavo, obscure vel evidenter trilobo, lobis plus minusve aequalibus, utrinque sparse villosis et glandulis circularibus sparse tectis, circa 3 mm longo et 5 mm lato, fructifero recurvo atque accrescenti, circa 5 mm longo et 8 mm lato; labio infero late orbiculari, integro aut retuso vel emarginato, extus et margine intus villosus et glandulis circularibus sparse tecto, circa 3 mm longo et 4 mm lato, fructifero accrescenti, circa 3.5 mm longo et 6 mm lato. *Corolla* tubo obconico, circa 5 mm longo, utrinque glabro, purpureo-striato; labio supero recto, circa 6 mm longo latoque, profunde bilobo, lobis oblongis, late obtusis, utrinque villosis; labio infero profunde trilobo, lobis patulis, circa 5 mm longis et 3 mm latis, obtusis, utrinque villosis. *Stamina* filamentis ligulatis, tubi basin versus affixis, superis circa 3.5 mm longis, inferis circa 4.5 mm longis; antheris circa 1 mm longis, loculis subparallelis, connectivi calcare longiore loculum bis superante, apice cristato, breviori loculo aequilongo, adnato, cristato. *Fructus* sphaericus, circa 3 mm diametro, stylo persistenti.

Shrub, intricate, divaricately branched, reddish brown, woody, probably 1 m high or more, branchlets densely clothed in pale brown matted hairs. *Leaves* decussate, very shortly petiolate, broadly elliptic to almost circular to transversely elliptic, seldom ovate, 2-4 mm long and broad, more or less truncate at the base, the margin entire or sometimes slightly sinuate, flat or sometimes undulate; woolly when young, becoming sparsely villous, both surfaces with scattered small circular glands. *Flowers* solitary, axillary, pedicels villous, about 1 mm long, bracteoles villous, linear-lanceolate, about 1 mm long. *Calyx* tube obconic, about 3 mm long, ribbed, sparsely villous outside, glabrous inside; upper lip depressed ovate, concave, obscurely or obviously 3-lobed, the lobes more or less equal, sparsely villous and with circular glands on both sides, about 3 mm long and 5 mm broad, recurved in fruit and enlarging to about 5 mm long and 8 mm broad; lower lip broadly orbicular, entire or retuse or emarginate, villous and with circular glands outside and near the margin inside, about 3 mm long and 4 mm broad, enlarging in fruit to about 3.5 mm long and 6 mm broad. *Corolla* tube obconic, about 5 mm long, glabrous outside and in, streaked with purple; upper lip erect, about 6 mm long and broad, deeply 2-lobed, the lobes oblong, broadly obtuse, villous on both sides; lower lip deeply 3-lobed, the lobes spreading and each about 5 mm long and 3 mm broad, obtuse, villous on both sides. *Stamens* with strap-shaped filaments attached near the base of the tube, the upper about 3.5 mm long, the lower about 4.5 mm long; anthers about 1 mm long, the locules almost parallel, the longer appendage of the connective as long again as the cell, the apex cristate, the shorter appendage about as long as the cell, adnate, cristate. *Fruit* spherical, about 3 mm diameter, style persistent. (Fig. 1).

There are two collections, both of which were made by Isaac Tyson. The first, MEL 41916, is annotated in Mueller's hand: "Prostanthera Tysoni F.v.M. Upper Murchison R. 1892. Isaac Tyson" and, on a separate label: "No 4." The PERTH portion of the second collection is annotated in an unknown hand: "Prostanthera Tysoni Mt. Narryer, Murchison River. Isaac Tyson 25 (1898)". The name was never legitimized but was mentioned by Gardner (1931), Blackall & Grieve (1965) and Beard (1970). Both collections have fragments in envelopes and are adequate for identification. Although the later collection was not seen by Mueller who died in 1896, it is identical with his "Prostanthera Tysoni", and as it is the better of the two, and now contains mounted dissections of the flower, it is designated as the holotype (PERTH). The two isotypes (K) are mounted on one sheet, one obtained through the "Herb. A. Morrison", the other presumably received direct from C. A. Gardner.

Attempts have been made to obtain specimens from the Mt. Narryer area of Western Australia. In 1975, heavy local rains caused severe flooding and the track from Mt. Narryer Homestead was impassable. A search in the neighbourhood of the Homestead was unsuccessful. In 1976, there had been widespread lack of rainfall resulting in poor growth and flowering, and collectors passing through the area did not consider it worth while to visit the mount.

Taxonomic position

Taxonomic studies in the Lamiaceae (Labiatae, nom. alt.) and the Verbenaceae (s. lat.) at the State Herbarium of South Australia were begun under the direction of Dr. H.J. Eichler, now Curator, Herbarium Australiense, C.S.I.R.O., Canberra, and he comments (pers. comm., 1976): "*P. tysonii* F. Muell., ined., seems to be exceedingly interesting, and I think may just represent the link between Prostantheroideae and Chloanthaceae I was hoping could be found to show the close relationship between the groups you and Munir are working on." [See Munir (1976)].

During the past almost three hundred years, systematists have experienced difficulties in arranging the numerous species in both families into appropriate taxonomic units, in the case of the Lamiaceae because of its homogeneity, and in the case of the Verbenaceae (s. lat.) because of its diversity. The following notes on the history of

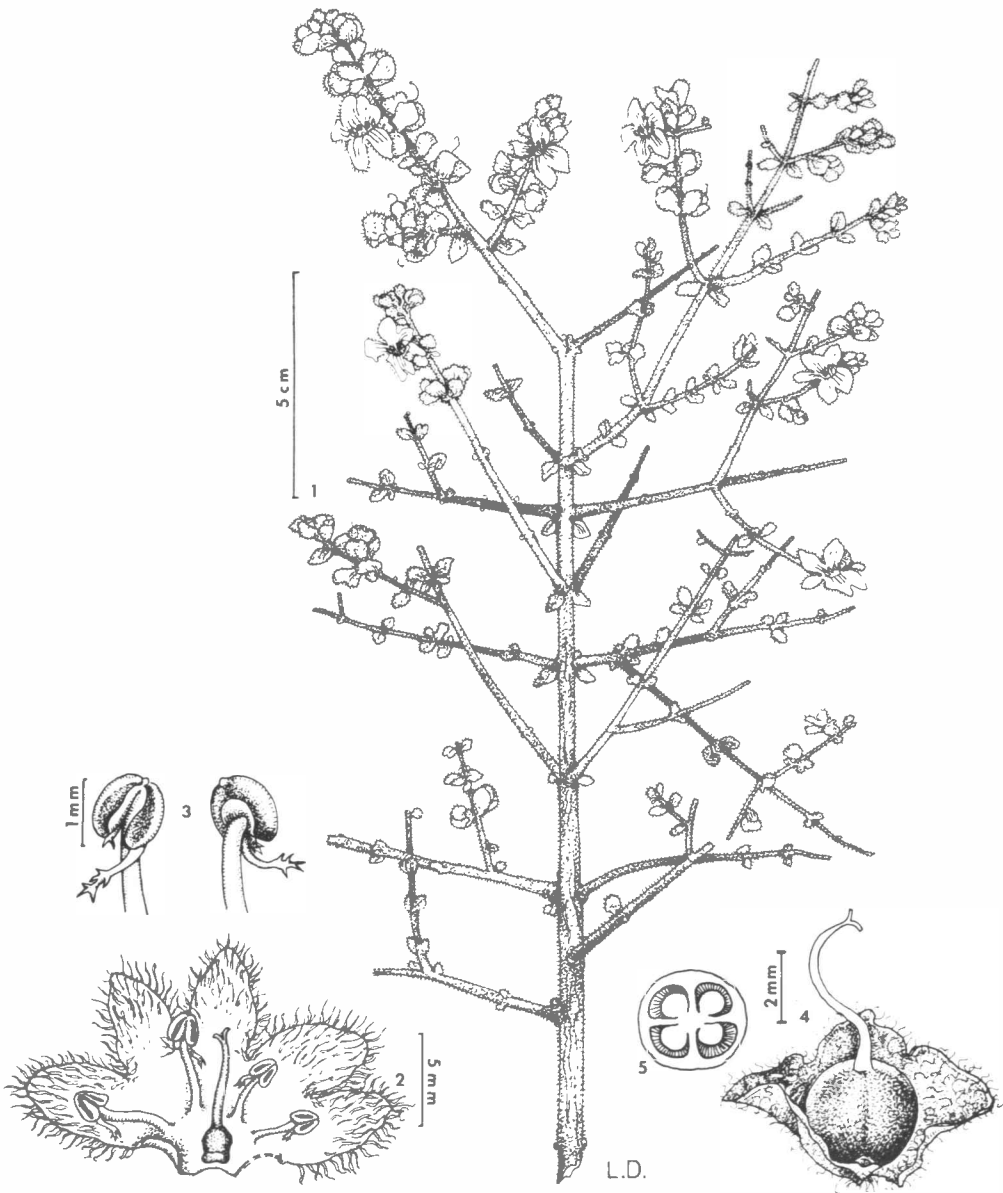


Fig. 1. *Eichlerago tysoniana* Carrick. Based on the Isaac Tyson 25 collection from Mt. Narryer, Murchison River, Western Australia, in 1898.

1, habit; 2, corolla opened out to reveal stamens and ovary; 3, front and back view of anther; 4, calyx upper lip with mature fruit (lower lip removed); 5, diagrammatic transverse section of fruit near base.

classification within these families assist in the placement of the new genus, albeit with some reservation.

Lamiaceae

Linnaeus (1751) adopted the name *Verticillatae*, which had been used previously by Ray (1682) for a group of genera now contained in *Lamiaceae*, and this was accepted by Ruling (1774), Scopoli (1777), Batsch (1802) and others. Tournefort (1694) used the name *Labiati* for a similar subdivision, B. de Jussieu (1759) amended the name to *Labiatae* and Lindley (1836) introduced the new alternative name *Lamiaceae*, which conforms with current usage. Both latter names are conserved.

Adanson (1763) first noted the uniformity of the group, a feature often later commented upon, particularly by A. L. de Jussieu (1789), Jaume St.-Hilaire (1805) and Bentham (1832-36). In consequence, throughout its history, the family has been subjected to various methods of classification based on different criteria. Adanson (1763) found characters of calyx, stamens, stigmas and pistil too little different, and those of corolla so varied even in species of the same genus, that he grouped his genera on the disposition of the flowers, the criteria being the presence or absence of bracts, whether these were similar to the stem leaves or not, and whether the flowers were distinct or several together on common peduncles. However, in his presentation of the genera in tabular form, he distinguished two-lipped and five-partite calyces and sterile stamens.

Scopoli (1777) based his primary division on whether all four stamens are fertile or only two, subdivision being made on the presence of a labiate or non-labiate calyx. Jussieu (1789) used the same criteria with, in addition, features of the corolla, so that *Ajuga* and *Teucrium* were segregated from the rest because the corolla appears "unilabiate". Jaume St.-Hilaire (1805) followed Jussieu closely and commented: "The genera are all the more artificial as the families of which they are part are the more natural." (transl.). Brown (1810) and Bartling (1830) also used characters of calyx and stamens but not corolla, resulting in separation of the Australian genera described by Smith (1797), Labillardière (1806) and Brown (1810), the present *Prostantheroideae*, into two parts.

Bentham, in his revision of the family (1832-36), and in his review for de Candolle's 'Prodromus' (1848), and Walpers (1844-45), had difficulty in arranging the species into genera and tribes. Bentham's exhaustive discussion of the vegetative and reproductive parts of the plants reveals the difficulties encountered in ordering the many genera and species. "The order of the *Labiatae* is one of the most natural and distinctly marked of all. The opposite leaves, monopetalous corolla, 2 or 4 stamina and the free 4-lobed ovarium are characters so easily observed, and so constantly accompanying the general habit of the whole series, that, from the time of Linnaeus to the present day, but two or three genera have been improperly associated with, or separated from, it." (1835). "The genera have very close affinities amongst themselves, and are with difficulty delimited, and the numerous species amongst themselves are exceedingly similar or extremely variable, it is often with great doubt that they are joined together or separated." (1848), (transl.). Bentham placed considerable weight on the features of the stamens associated with those of calyx and corolla for the diagnosis of the tribes. His arrangement was followed by Endlicher (1838) and is well shown by Meisner (1840) who presented the data in the form of an indented dichotomous key.

With Bentham & Hooker (1876), some change in emphasis occurred, and characters of the gynoecium were used to determine the major subdivisions of the family. Lindley (1836) had already commented: "The 4-lobed ovary, with a solitary style arising from the base of the lobes, has no parallel among monopetalous orders except *Nolanaceae*, which have a plaited corolla, and *Boraginaceae*, to which *Labiatae* must be considered as most closely allied." In Bentham & Hooker (1876), Briquet (1895-97) and Melchior (1964), the depth of separation and the attachment of the nutlets differentiated the groups of

subfamilies, and the Ajugoideae and Prostantheroideae became segregated from the others. In these, Briquet considered that the style was not gynobasic, and Melchior that it was terminal or sunken. Bentham (1832-36), Lawrence (1955) and Hutchinson (1973) considered the style gynobasic. Cronquist (1968), in his key to the Lamiales, used as one of the distinguishing features of the Lamiaceae "style mostly gynobasic" as opposed to "style terminal" for Verbenaceae (s. lat.).

In distinguishing the genera of Prostantheroideae, as at present recognized, Bentham (1848, 1870), Briquet (1895-97) and Carrick (1976) have placed considerable emphasis on the fertility of the stamens and the presence of staminal modifications or appendages.

Verbenaceae (s. lat.)

The Asperifoliae of Ray (1682) and the Personatae of Linnaeus (1751) comprised several families, for one of which Jaume St.-Hilaire (1805) introduced the name Verbenaceae, which is conserved. However, Reichenbach (1828) placed the family in Verbenaeae as a section of Labiatae, and Junell (1934), on the basis of anatomical studies of the gynoeceum, placed a large part of the Verbenaceae (s. lat.) in the Labiatae, notably Chloanthoideae close to *Ajuga*, a rearrangement which has not since been supported.

From the outset, the emphasis for classification of the Verbenaceae (s. lat.) has been placed on the fruit. Jussieu (1806) commented: "This last character [fruit] varies in a number of ways which combine to designate the genera. Thus, sometimes it is a stone-fruit [noyau] with four single-seeded cells occupying the centre of a more or less fleshy berry; sometimes it contains two stone-fruits each with two cells, or four single-seeded stone-fruits. Sometimes the seeds exist in the fruit without a bony envelope; sometimes the almost dry fruit takes the form of a capsule which does not open: or, reduced to a simple reticulate tissue around the seeds and serving to unite them prior to maturity, it disappears while the seeds are enclosed, and leaves them almost naked as in the Labiatae. This last character is most remarkable in the Verbenas, which thus establish a transition from one family to the other." (transl.).

Lindley (1836) viewed the Verbenaceae (s. lat.) thus: "The difference between these plants and Labiatae consists in the concrete carpels of the former, their terminal style, and the usual absence of reservoirs of oil from their leaves, as contrasted with the deeply 4-lobed ovary and aromatic leaves of the latter." Bentham & Hooker (1876), Briquet (1895-97) and Melchior (1964), utilised the inflorescence and features of flower and fruit in various ways to group genera into subfamilies and tribes.

As was to be expected, some of these have been separated and raised to family rank: Stilbaceae by Kunth (1831), Avicenniaceae by Endlicher (1841), Phrym[at]aceae by Schauer (1847), Dicrostylidaceae by Drummond & Harvey (1855) nom. illeg., Nyctanthaceae, Durantaceae and Petreaeaceae by Agardh (1855), Symphorem[at]aceae by van Tieghem (1891), Chloanthaceae by Hutchinson (1959). Some of these families are not recognized by some authors; most remain in Verbenaceae (s. lat.) with subfamily rank. The basis of subdivision, as shown in Briquet (1895-97) and Melchior (1964), is mainly on number of locules and their separation at maturity, type and placentation of ovules, presence of albumen.

Discussion

From the outline history of the classification of the Lamiaceae, it is clear that the bilabiate calyx and unique stamens of *Eichlerago* place it in close relation to *Prostanthera* in the Prostantheroideae. *Eichlerago* is similar to *Prostanthera* in having: simple, decussate leaves; simple hairs; surface glands; bracteoles; a two-lipped calyx enclosing the fruit; four fertile didynamous stamens; anther cells mucinous and not confluent; an appendaged connective; a basal disc; axile/basal placentation; albuminous seeds. *Eichlerago* differs in having: lower corolla lip with three equal lobes; a dry, indehiscent

fruit; a terminal style. Note that, of the ninety or so species of *Prostanthera*: only one has branched hairs; many have anther cells which are not muticous; many have connectives which are not appendaged; albumen is usually meagre. The stamens of *Eichlerago tysoniana* are almost identical with those of *Prostanthera lasianthos* Labill. The bilabiate calyx with three more or less distinct lobes on the upper lip and/or two lobes on the lower, are features also found in a number of species of *Prostanthera*.

From a consideration of the development of classification in the Verbenaceae (s. lat.), the entire, four-locular, indehiscent ovary, the terminal style and the presence of endosperm relate *Eichlerago* to the Chloanthaceae (or Chloanthoideae of the Verbenaceae). *Eichlerago* is similar to Chloanthaceae in having: simple decussate leaves; surface glands; bracteoles; persistent calyx; two-lipped corolla; four fertile didynamous stamens; anther cells muticous and not confluent; a basal disc; a four-celled ovary; a terminal style; a dry, indehiscent fruit; albuminous seeds. *Eichlerago* differs in having: simple hairs; a two-lipped calyx enclosing the fruit; lower corolla lip with three equal lobes; appendages on the connective; axile/basal placentation. Note that, in Chloanthaceae: the corolla is two-lipped in Chloantheae only, not so in Physopsidae; anther cells are confluent in *Spartothamnella* only; the fruit is a succulent drupe in *Spartothamnella* only; the ovary is four-celled and placentation axile/apical, contrary to Hutchinson (1973). There are no instances in the Verbenaceae (s. lat.) of stamens with connective appendages as found in *Prostanthera* and *Eichlerago*. [Munir (1976, and verb. comm.)].

The data are shown in Table 1. Many characters are common to *Prostanthera*, *Eichlerago* and Chloanthaceae, completely so or only partially. Those which distinguish *Eichlerago* and *Prostanthera* from Chloanthaceae are features of the gynoeceum, placing *Eichlerago*, on the data at present available, between Prostantheroideae and Chloanthaceae.

While the gynoeceum of Lamiaceae affords but little variation for use as a taxonomic criterion, that of Verbenaceae (s. lat.) provides the primary basis for subdivision. Affinities between the two families are close, many characters being common, even to a superficial similarity in the ovaries. The ovary of Lamiaceae develops as four separate nutlets. In Prostantheroideae and Ajugoideae the ovary is much less lobed than in most other subfamilies of Lamiaceae. The attachment of the nutlets in Lamiaceae is sometimes very oblique or almost lateral, yet I have observed in *Prostanthera* that the receptacle extends upwards between the nutlets, and the point of attachment of the style is at the apex of the receptacle, a condition which, at least, can be considered not terminal. In *Verbena* and Chloanthaceae the ovary is initially slightly lobed, but there is always present an axis between the receptacle and the base of the style, which is always terminal. In *Verbena* and *Spartothamnella*, the ovary always develops as a unit and separates into four fruitlets after it has matured.

Remarking on the relationships between the two families, Bentham (1832-36) wrote: "Amongst the genera in other respects intermediate, *Chloanthes* has been instanced by Mr. Brown as having the habit of Labiatae with the characters of Verbenaceae; and *Hoslundia*, on the contrary, as being Verbenaceous with Labiate characters; to these instances may be added the close resemblance in all but fruit [italics mine] between *Teucrium betonica*, etc. and *Vitex ovata*, etc." Also indicative of close family ties is Bentham & Hooker's (1876) action in referring "*Oxera* Labill., sometimes previously included in Labiatae, to Verbenaceae because of the drupaceous fruit." (transl.).

While it is recognized that the inclusion of a genus in a family, or its rejection from it, on the basis of one or two characters, may be questionable, it is true that one constant character is of more value than several inconstant ones. Here, the constant characters of greatest importance are the gynobasic style and free nutlets of Lamiaceae, the two-lipped calyx enclosing the fruit and the appendaged connective of Prostantheroideae, and the terminal style and dry, indehiscent fruit of Chloanthaceae.

The anomalous nature of *Eichlerago* is shown in its possession of a combination of these characters and places it between Prostantheroideae and Chloanthaceae. Because *E. tysoniana* does not fit readily into either, it is tempting to propose a new family to accommodate it, but although from the information available it is sufficiently distinct, further studies on pollen, chromosomes, anatomy, etc. are necessary before deciding its appropriate taxonomic position. The overall impression of the plant is prostantheroid, the aberrant feature being the fruit, while the bilabiate calyx and appendaged connective appear, in this case, to be more significant. *Eichlerago* is therefore tentatively placed in the Prostantheroideae, but, because of the fruit, in a tribe distinct from the other genera.

In order to accomodate *Wrixonia* and *Eichlerago*, the diagnoses for Prostantheroideae in Bentham (1832-36), Bentham & Hooker (1876), Briquet (1895-97) and Melchior (1964) should be modified in the following particulars: stamens 4, fertile, or only 2 (upper or lower pair sterile); style gynobasic, very rarely terminal; fruit of 4 separate nutlets, very rarely entire, dry and indehiscent.

The two tribes are then distinguished as follows:

Tribus 1. Prostanthereae Benth.

Calyx quinquelobus vel bilabiatus; corolla lobo medio labii inferi magniore; stamina 4 vel 2 fertilia, bilocularia vel abortu unilocularia, connectivo appendiculato vel diverse immutato; stylus gynobasicus; fructus ex 4 nuculis discretis consistens.

Genus typicum: *Prostanthera* Labill.

Tribus 2. Eichleragineae Carrick, trib. nov.

Calyx bilabiatus; corolla lobis labii inferi aequalibus; stamina 4 fertilia, bilocularia, connectivo appendiculato; stylus terminalis; fructus integer, siccus, indehiscens.

Genus typicum: *Eichlerago* Carrick.

Table 1. Comparison of *Eichlerago* with *Prostanthera* and Chloanthaceae.

(For greater ease of comparison, the data are presented so that in each case *Eichlerago* has a + sign.)
(+ = present; - = absent; ± = present in some species.)

Character	<i>Prostanthera</i>	<i>Eichlerago</i>	Chloanthaceae
Leaves simple, decussate	+	+	+
Hairs simple	±	+	-
Surface glands present	+	+	+
Bracteoles present	+	+	+
Calyx two-lipped	+	+	-
persistent	+	+	+
enclosing fruit	+	+	-
Corolla two-lipped	+	+	±
lower lip with three equal lobes	-	+	-
Stamens all fertile	+	+	+
didynamous	+	+	±
cells not confluent	+	+	±
cells muticous	±	+	±
connective appendaged	±	+	-
Basal disc present	+	+	+
Ovary four-celled	+	+	+
Style terminal	-	+	+
Fruit dry, indehiscent, entire	-	+	+
Placentation axile/basal	+	+	-
Seeds albuminous	±	+	+

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