

CHROMOSOME NUMBERS IN COMPOSITAE VII: ASTEREAEE III¹

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A B S T R A C T

Reports of 129 new chromosome counts are made for the tribe Astereae of Compositae. They are mostly based on determinations of meiotic material, including first counts for one genus and 43 species or subspecies. Counts are now available for more than 63 of the 100-120 genera and 564 of the approximately 2,000 species in the tribe. Three of every four genera with more than one species counted show more than one chromosome number; 15 genera have species with populations with different numbers. Such variation is very high and indicates the need for more detailed cytotaxonomical study in the group.

THIS IS THE SEVENTH of a series of papers dealing with chromosome numbers in Compositae (Raven et al., 1960; Raven and Kyhos, 1961; Ornduff et al., 1963, 1967; Payne, Raven, and Kyhos, 1964; Solbrig et al., 1964) and the third devoted to the tribe Astereae. Since our last work on the tribe, several papers reporting new chromosome numbers for species of Astereae have been published. These reports have tended to confirm the general conclusions and predictions made regarding chromosome number and phylogeny in the tribe Astereae (Solbrig et al., 1964). The reader interested in these topics is referred to that work.

As in previous reports the present combined effort has been arrived at by the authors working largely independently. Unless otherwise indicated the counts have been made from acetocarmine or acetoorceine squashes of microsporocytes in meiosis. Voucher specimens are available for all counts and are deposited at either the Herbarium of the University of California or the Jepson Herbarium, Berkeley, or the Gray Herbarium of Harvard University, unless otherwise indicated.

COMPARISON WITH EARLIER REPORTS—New reports are presented for one genus and 43 species and subspecies indicated in Table 1 by asterisks. The new genus is *Archibaccharis* from Central America.

Our counts of $n = 13$, $n = 18$, and $n = 36$ for *Aster chilensis* subsp. *adscendens* do not correspond with the previous report of $n = 32$

for that taxon (Huziwara, 1958). The count of $n = 12$ for *Haplopappus racemosus* subsp. *glomeratus* represents a new ploidy level for that taxon as does the count of $n = 8$ for *H. spinulosus* subsp. *spinulosus*. The previous report for *Leucelene ericoides* was $n = 8$ (De Jong and Longpre, 1963; Turner and Flyr, 1966); we found $n = 16$ in three different populations. A previous count for *Machaeranthera leucanthemifolia* was $n = 5$ (Raven et al., 1960); we found $n = 4$ in two collections, and believe that the plant we examined earlier probably had a supernumerary pair of chromosomes. Our count of $n = 8$ for *Gymnosperma glutinosum* differs from previous reports of $n = 7$ for the same species (Solbrig, 1961).

CHROMOSOME NUMBERS IN THE TRIBE ASTEREAEE—There is now a fairly good understanding of chromosome numbers in the tribe Astereae, particularly in North America. Several medium-sized genera, such as *Astranthium* (De Jong, 1965), *Chrysothamnus* (Anderson, 1966) and *Gutierrezia* (Rüdenberg and Solbrig, 1964), have now been surveyed extensively. More information is needed, however, about the chromosome numbers of the species in the rich assemblages of Astereae of South America, Africa, Australia and New Zealand.

Table 2 lists in synoptical fashion the chromosome numbers in all genera of the tribe for which at least one count is available. The preeminence of $x = 9$ as a modal number in the tribe, both at the specific and generic level reported by us previously (Raven et al., 1960; Solbrig et al., 1964) remains unchanged. Likewise, the additional reports since our last paper have tended to confirm the correlation between $x = 9$ and certain characteristics such as the woody habit and more mesic environments, correlations that were inter-

¹ Received for publication 19 September 1968.
The authors are grateful to Denis Breedlove, Angel L. Cabrera, Elias De la Sota, Paul Hutchinson, and Duncan Porter for seeds and fixed materials and to Lee Snyder for technical assistance.
Supported in part by a grant of The National Science Foundation to O. T. S.

TABLE 1. *Original counts of chromosomes in Astereae*^a

<i>Aphanostephus arizonicus</i> A. Gray	4	Lincoln Co., N. M., R 19139
	4	Terrell Co., Texas, R 19197
<i>Aphanostephus ramosissimus</i> DC.	4	Menard Co., Texas, R 19261
<i>Aphanostephus riddellii</i> T. & G.	5	Coke Co., Texas, R 19280
<i>Aphanostephus skirrobasis</i> (DC.) Trel.		
var. <i>skirrobasis</i>	3	Coke Co., Texas R 19282
	3	Mitchell Co., Texas, R 19285
<i>Aphanostephus skirrobasis</i> (DC.) Trel.		
var. <i>thalassius</i> Shinnery	3	Galveston Co., Texas, R 19419
* <i>Archibaccharis asperifolia</i> (Benth.) Blake	9	Mexico, Mun. of Tenejapa, Chiapas, Br 6893
* <i>Archibaccharis torquis</i> Blake	9	Mexico, Mun. of Chamula, Chiapas, Br 7151
* <i>Aster calendulaceus</i> (Griseb.) Ktze	9	Uruguay, Riachuelo, Cabrera, 1963 (progeny)
<i>Aster chilensis</i> Nees subsp. <i>adscendens</i> (Lindl.) Cronq.	13	Uinta Co., Wyo., K 5842
	36	Grand Co., Colo., A 2662
	18	White Pine Co., Nev., K 5796
<i>Aster exilis</i> Ell.	5	Mexico, Mun. of Pueblo Nuevo, Solistahuacán Chiapas, R 19927
* <i>Aster eatonii</i> (A. Gray) Howell	9	White Pine Co., Nev., Br 5797
* <i>Aster foliaceus</i> Lindl. var. <i>parryi</i> (D. C. Eat.) A. Gray	25	Sublette Co., Wyo., Br 5855
* <i>Aster greatai</i> Parish	8	Los Angeles Co., Calif., R 16842
* <i>Aster marginatus</i> H. B. K.	9	Argentina, Prov. Bs. As., La Plata, De la Sota, s.n. (progeny)
	9	Colombia, Bogotá, páramo near Bogotá, Soejarto s.n. (progeny)
<i>Aster montevidensis</i> Griseb.	9	Uruguay, Riachuelo, Cabrera s.n. (progeny)
<i>Aster occidentalis</i> (Nutt.) T. & G.	8	White Pine Co., Nev., Br 5813
<i>Aster pauciflorus</i> (Nutt.)	9	Kern Co., Calif., Twisselmann 8450
* <i>Aster scopulorum</i> A. Gray	9	Harney Co., Ore., R 18436
	18	Elko Co., Nev., R 18527
<i>Aster squamatus</i> (Spr.) Hier.	10	Brazil, Est. Paraná, Curitiba S 62-44 (progeny)
	10	Argentina, Prov. Jujuy, Dept. Tumbaya Cabrera & Solbrig 16886 (GH-LP)
* <i>Baccharis salicifolia</i> (R. et P.) Pers.	18	Argentina, Prov. La Rioja, Dept. Chilecito, Cabrera & Solbrig 16679 (GH-LP)
<i>Baccharis trinervis</i> (Lam.) Pers.	9	Mexico, Mun. of Jitotol, Chiapas, R 19809
<i>Baccharis</i> sp.	9	Argentina, Prov. Entre Rios, Colón, Burkart 23547 (progeny)
* <i>Chaetopappa lyoni</i> (Gray) Keck	9	Los Angeles Co., Calif., R 19017
<i>Chrysopsis pilosa</i> Nutt.	4	Guadalupe Co., Texas, R 19379
	4	Montgomery Co., Texas, R 19441
<i>Chrysopsis villosa</i> (Pursh) Nutt.	9	Grand Co., Colo., A 2651
	9	Coconino Co., Ariz., A 2148
<i>Conyza bonariensis</i> (L.) Cronq.	27	Mexico, Mun. of Pueblo Nuevo, Chiapas, R 19870
	27	Colombia, Dept. Nariño, Porter 1045
	27	Argentina, Prov. Bs. As., Llavallol, S 62-15 (progeny)
<i>Conyza canadensis</i> (L.) Cronq.	9	Jamaica, Portland, Porter 1001
	9	Frio Co., Texas, R 19356
* <i>Conyza coulteri</i> Gray	9	Kings Co., Calif., Twisselmann 9097
<i>Conyza</i> sp.	18	Costa Rica, Prov. Guanacaste, D. M. Porter 1162
<i>Erigeron annuus</i> (L.) Pers.	27	Pottawatomie Co., Kan., R 19484
<i>Erigeron aphanactis</i> (A. Gray) Greene var. <i>aphanactis</i> Cronq.	9	Washoe Co., Nev., R 18413
* <i>Erigeron barbellulatus</i> Greene	ca. 40	Alpine Co., Calif., K 5612
<i>Erigeron bellidiastrum</i> Nutt.	9	Apache Co., Ariz., A 2672
	9	Major Co., Okla., R 19470
<i>Erigeron breweri</i> A. Gray	9	Alpine Co., Calif., Br 5626
* <i>Erigeron chrysopsidis</i> A. Gray	9	Grant Co., Ore., R 18466
* <i>Erigeron chrysopsidis</i> A. Gray var. <i>austinae</i> (Greene) Cronq.	9	Owyhee Co., Idaho, R 18464
	9	Malheur Co., Ore., R 19589

TABLE 1. Continued

<i>Erigeron compositus</i> Pursh var. <i>discoideus</i> A. Gray	2n = 58-9	Tuolumne Co., Calif., Br 5694
<i>Erigeron compositus</i> Pursh var. <i>glabratus</i> Macoun	18	Tuolumne Co., Calif., Br 5693.
* <i>Erigeron coulteri</i> Porter	9	Grand Co., Colo., A 2647
<i>Erigeron divergens</i> T. & G. var. <i>cinereus</i> A. Gray	27 I (12 cells) 25 I + 1 II (2 cells) (23 I + 2 II 1(cell)	Lincoln Co., N. M., R 19134.
<i>Erigeron divergens</i> T. & G. var. <i>divergens</i>	2n = 27 2n = 36	Mohave Co., Ariz., R 18971 Mono Co., Calif., R 18555
	18	Lassen Co., Calif., R 18424
* <i>Erigeron eatonii</i> A. Gray var. <i>eatonii</i>	18	White Pine Co., Nev., Br 5815
* <i>Erigeron eatonii</i> A. Gray var. <i>villosus</i> Cronq.	9	Adams Co., Idaho, K 18505
* <i>Erigeron elatior</i> (A. Gray) Greene	9	Grand Co. Colo., A 2648
* <i>Erigeron fernandezianus</i> (Colla) Solbrig	27	Chile, Masatierra, Juan Fernandez Isl., S 3510
	27	Chile, Masafuera, Juan Fernandez Isl., S 3645
* <i>Erigeron filifolius</i> Nutt. var. <i>filifolius</i> Cronq.	18	Grant Co., Ore., R 18481
	9	Sherman Co., Ore., R 18387
<i>Erigeron flagellaris</i> A. Gray	18	Grand Co., Colo., A 2654
<i>Erigeron glabellus</i> Nutt. var. <i>glabellus</i>	18	Weld Co., Colo., R 19524
* <i>Erigeron linearis</i> (Hook.) Piper	9	Yakima Co., Wash., R 18484
	2n = 27	Harney Co., Ore., R 18435
* <i>Erigeron lonchophyllus</i> Hook.	9	Tuolumne Co., Calif., Br 5775
* <i>Erigeron modestus</i> Gray	27	Sutton Co., Texas, R 19252
	27	Menard Co., Texas, K 19262
<i>Erigeron philadelphicus</i> L.	9	Canyon Co., Idaho, R 19572
* <i>Erigeron poliospermus</i> Gray var. <i>poliospermus</i>	9	Harney Co., Ore., R 18433
* <i>Erigeron pumilus</i> Nutt. subsp. <i>concinnoides</i>		
Cronq. var. <i>concinnoides</i>	9	Clark Co., Nev., R 18917
	9	Mohave Co., Ariz., R 19102
* <i>Erigeron pumilus</i> Nutt. ssp. <i>intermedius</i> Cronq.		
var. <i>gracilior</i> Cronq.	9	Owyhee Co., Idaho, R 18465
	18	Fremont Co., Idaho, R 19559
* <i>Erigeron pumilus</i> Nutt. ssp. <i>intermedius</i> Cronq.		
var. <i>intermedius</i>	9	Grant Co., Ore., R 18482
* <i>Erigeron pumilus</i> Nutt. subsp. <i>pumilus</i>	9	Weld Co., Colo., R 19519
	9	Laramie Co., Wyo., R 19528
* <i>Erigeron pumilus</i> Nutt. (atypical, nearest subsp. <i>intermedius</i> Cronq.)		
<i>Erigeron strigosus</i> Muhl. var. <i>beyrichii</i> (F. & M.) T. & G.	2n = 27 (triploid)	Storey Co., Nev., R 18545
<i>Erigeron strigosus</i> Muhl. var. <i>strigosus</i>	27	Riley Co., Kan., R 19480
	27	Montgomery Co., Texas, R 19439
	27	Hunt Co., Texas, R 19446
* <i>Erigeron ursinus</i> D.C. Eat.	9	Grand Co., Colo., A 2664
<i>Erigeron</i> sp.	27	Brewster Co., Texas, S 3194
* <i>Grindelia decumbens</i> Greene	6	Montezuma Co., Colo., A 2678
* <i>Grindelia nana</i> Nutt.	6	Grant Co., Wash., R 18488
<i>Grindelia discoidea</i> H. & A.	12	Argentina, Prov. Cordoba, Dept. Santa Maria, Cabrera & Solbrig 16551. (GH-LP)
<i>Grindelia pulchella</i> Dun.	6	Argentina, Prov. Catamarca, Dept. Tinogasta, Cabrera & Solbrig 16748. (GH-LP)
<i>Grindelia</i> sp.	6	Terrell Co., Texas, R 19196
<i>Gutierrezia sarothrae</i> (Pursh) Britt. & Rusby	4	Menard Co., Texas, K 19274
<i>Gymnosperma glutinosum</i> Less.	8	Mexico, Mun. of Comitán, Chiapas, Br 8329
* <i>Haplopappus acaulis</i> (Nutt.) Gray	18	Elko Co., Nev., R 18530
	18	Alpine Co., Calif., Br 5614
	18	Park Co., Wyo., S 3116
* <i>Haplopappus</i> aff. <i>clementis</i> Blake		
<i>Haplopappus ericoides</i> (Less.) H. & A. subsp. <i>blakei</i> C. B. Wolf	9	Los Angeles Co., Calif., Thompson 1819
* <i>Haplopappus lanuginosus</i> A. Gray ssp. <i>andersonii</i> (Rydb.) Hall	9	Valley Co., Idaho, R 18514
<i>Haplopappus racemosus</i> (Nutt.) Torr. subsp. <i>glomeratus</i> (Nutt.) Hall	12	Kern Co., Calif., Twisselmann 10169
<i>Haplopappus spinulosus</i> (Pursh) DC. subsp. <i>spinulosus</i>	8	Weld Co., Colo., R 19521
* <i>Haplopappus suffruticosus</i> (Nutt.) A. Gray	9	White Pine Co., Nev., Br 5817
<i>Haplopappus validus</i> (Rydb.) Cory subsp. <i>validus</i>	5	Garza Co., Texas, R 19298
	5	Tarrant Co., Texas, R 19449

TABLE 1. *Continued*

<i>*Haplopappus whitneyi</i> A. Gray	8	Kern Co., Calif., Twisselmann 10178
<i>Heterotheca latifolia</i> Buckl. var. <i>macgregoris</i> Wagenknecht	9	Gillespie Co., Texas, R 19337
<i>*Lessingia lemmonii</i> A. Gray var. <i>ramulosissima</i> (A. Nels.) Ferris	5	Inyo Co., Calif., Hill 47937
<i>Leucelene ericoides</i> (Torr.) Greene	16	Mohave Co., Ariz., R 19101
	16	Yavapai Co., Ariz., R 19108
	16	Torrance Co., N. M., R 19131
<i>*Machaeranthera bigelovii</i> (Gray) Greene	4	Yavapai Co., Ariz., R 19105
<i>*Machaeranthera commixta</i> Greene	4	Fremont Co., Idaho, R 19556
	4	White Pine Co., Nev., Br 5795
	4	Uinta Co., Wyo., Br 5843
<i>Machaeranthera grindelioides</i> (Nutt.) Shinnars	8	Sweetwater Co., Wyo., R 19542.
<i>Machaeranthera leucanthemifolia</i> (Greene) Greene	4	Nye Co., Nev., Br 5665
	4	Clark Co., Nev., K 18908
<i>*Machaeranthera shastensis</i> Gray var. <i>montana</i> (Greene) Cronq.	4	Alpine Co., Calif., Br 5613
<i>Machaeranthera tanacetifolia</i> (Kunth) Nees	4	Weld Co., Colo., R 19518
	4	Midland Co., Texas, R 19216
<i>Monoptilon bellidifforme</i> T. & G. ex Gray	8	Clark Co., Nev., R 18891
	8	Nye Co., Nev., K 18954
<i>Psila</i> sp.	9	Argentina, Prov. Jujuy, Cabrera & Solbrig 17030. (GH-LP)
<i>*Solidago ciliosa</i> Greene	9	Grand Co., Colo., A 2646
<i>*Solidago spectabilis</i> (D. C. Eat.) Gray	9	Owyhee Co., Idaho, R 19575
<i>Xanthisma texanum</i> DC.	4	Midland Co., Texas, R. 19217
	4	Gillespie Co., Texas, R 19338
	4	Garza Co., Texas, R 19299
<i>Xylorhiza glabriuscula</i> Nutt.	6	Albany Co., Wyo., R 19536
	6	Sweetwater Co., Wyo., R 19546

^a Collection numbers preceded by A are Anderson; Br, Breedlove; K, Kyhos; R, Raven; S, Solbrig.

TABLE 2. *Chromosome numbers in genera of Compositae*

Genus	Approx. # sp.	# sp. counted	Geog. distrib.	Habit	Chrom. #'s	Type of var. ^a	Intraspec. variation
<i>Acamptopappus</i>	2	2	N. America	S	9		no
<i>Achaetogeron</i>	7	3	N. America	P	9, 27	P	no
<i>Amellus</i>	10	1	S. Africa	A, P	8		no
<i>Amphiachyris</i>	2	1	N. America	A	5		no
<i>Amphipappus</i>	1	1	N. America	S	9		no
<i>Archibaccharis</i>	18	2	N. America	S	9		no
<i>Aphanostephus</i>	5	5	N. America	A, P	3, 4, 5	A	no
<i>Aster</i>	250 ⁺	102	cosm.	A, P, S	5, 7, 8, 9, 10, 16, 18, 19, 23, 24, 27, 32, 33, 36	A, P	yes
<i>Asteromea</i>	2	2	Asia	P	9		no
<i>Astranthium</i>	12	12	N. America	A, P	3, 4, 5, 6, 8, 9, 10, 12, 18	A, P	no
<i>Baccharis</i>	350 ⁺	18	N., S. America	P, S	9, 18	P	no
<i>Bellidiastrum</i>	1	1	Europe	P	9		no
<i>Bellis</i>	5	3	Europe	A, P	9		no
<i>Bellium</i>	5	1	Europe	A, P	9		no
<i>Benitoea</i>	1	1	N. America	A	5		no
<i>Boltonia</i>	3	3	N. America	P	9, 18, 27	P	yes
<i>Brachycome</i>	50	3	Australia	A, P	9, 18, 27	P	no
<i>Bradburia</i>	1	1	N. America	A	3		no
<i>Calotis</i>	30	2	Australia	P	7, 8	A	no
<i>Celmisia</i>	35	2	N. Z., S. America	P	9		no
<i>Chaetopappa</i>	15	2	N. America	A, P	8, 9, 16	A, P	yes
<i>Charieis</i>	1	1	S. Africa	A	5		no

TABLE 2. *Continued*

Genus	Approx. # sp.	# sp. counted	Geog. distrib.	Habit	Chrom. #'s	Type of var. ^a	Intraspec. variation
<i>Chrysopsis</i>	20	9	N. America	A, P, S	4, 5, 9, 12, 18	A, P	yes
<i>Chrysothamnus</i>	14	14	N. America	S	9, 18, 36	P	yes
<i>Conyza</i>	50	15	cosm.	A, P	9, 27	P	no
<i>Corethrogyne</i>	3	2	N. America	P	5		no
<i>Darwiniothamnus</i>	2	2	Galápagos	S	9		no
<i>Dichaetophora</i>	1	1	N. America	A	3		no
<i>Dichrocephala</i>	5	1	Africa, Asia	A	9		no
<i>Erigeron</i>	200 ⁺	81	cosm.	A, P, S	9, 18, 27, 32, 36	A, P	yes
<i>Eastwoodia</i>	1	1	N. America	S	9		no
<i>Erodiophyllum</i>	1	1	Australia	S	8		no
<i>Felicia</i>	50	7	S. Africa	A, P	6, 8, 9	A	yes
<i>Grangea</i>	2	1	Africa, Asia	P	9		no
<i>Greenella</i>	3	1	N. America	A, P	4		no
<i>Grindelia</i>	50	22	N., S. America	P, S	6, 12	P	yes
<i>Gutierrezia</i>	19	13	N., S. America	A, P, S	4, 8, 12, 16, 20, 28	P	yes
<i>Gymnosperma</i>	1	1	N. America	S	7, 8	A	yes
<i>Haplopappus</i>	180	38	N., S. America	A, P, S	2, 3, 4, 5, 6, 7, 8, 9, 12, 45	A, P	yes
<i>Heteropappus</i>	5	3	Asia	A, P	18		no
<i>Heterotheca</i>	8	8	N. America	A, P	9, 18	P	no
<i>Lagenophora</i>	17	1	S. America, S. Pacific	P	9		no
<i>Lessingia</i>	7	7	N. America	A	5		no
<i>Leucelene</i>	1	1	N. America	P	8, 16	P	no
<i>Machaeranthera</i>	30 ⁺	17	N. America	A, P	4, 5, 6, 9	A	yes
<i>Microglossa</i>	9	3	Africa, Asia	S	9	P	no
<i>Monoptilon</i>	2	2	N. America	A	8, 27	A, P	no
<i>Myriactis</i>	5	2	Asia, Africa	A	18		no
<i>Nidorella</i>	18	4	Africa	S, P	9		no
<i>Olearia</i>	90	3	S. Pacific	T, S	9, 54	P	no
<i>Olivaea</i>	2	2	N. America	A	6		no
<i>Petradoria</i>	2	2	N. America	S	9, 18	P	no
<i>Psadia</i>	30	1	Africa	S	9		no
<i>Psila</i>	10	2	S. America	S	9		no
<i>Rhynchosperma</i>	1	1	Asia	S	9		no
<i>Solidago</i>	100	80	N., S. America	S	9, 18, 27	P	yes
<i>Tetramolopium</i>	7	1	S. Pacific	P	7, 9	A	yes
<i>Townsendia</i>	21	20	N. America	A, P	9, 10, 15, 18, 27	A, P	yes
<i>Vanclevea</i>	1	1	N. America	P	9		no
<i>Vittadinia</i>	6	1	S. America, Australia	P, S	9		no
<i>Xanthisma</i>	1	1	N. America	A	4		no
<i>Xanthocephalum</i>	8	5	N. America	A, P, S	4, 6	A	no

^a Type of variation: A, aneuploidy; P, polyploidy.

puted by us as an indication that $x = 9$ is probably the ancestral basic number in the tribe Asteraeae.

Of the 63 genera that have been counted in the tribe, almost half (30) show variation in the chromosome number. Disregarding the 21 genera for which only a single species has been counted, three out of every four genera remaining show variation in chromosome number. This is a very high degree of variation.

The source of this variation is either polyploidy or aneuploidy. Judging from the chromosome numbers and from observations in those cases where the situation was more carefully investigated, the chromosome variation is due to polyploidy in 14 genera, to aneuploidy in 8 and to a

combination of polyploidy and aneuploidy in another 8. More remarkable still is the fact that in 15 genera, more than one chromosome number has been associated with the same species. Although some of these reports may reflect errors in the reporting of the chromosome number or identification of the species, in most cases the chromosomal variation has been confirmed repeatedly. In certain cases some of the chromosomal variation has been associated with sub-specific taxa as in *Chrysothamnus* (Anderson, 1966). In other cases it has not. However in most instances the situation has not been investigated beyond the reporting of the different chromosome number. As the investigations with the *Haplopappus gracilis*-*Haplopappus ravenii* species pair

have shown (Jackson, 1962), careful study of infraspecific variation can be very rewarding in providing detailed records of the process of evolution.

Certain large and taxonomically difficult genera, such as *Aster* and *Erigeron*, are particularly notable for the chromosome number variation they exhibit. Other genera such as *Chrysothamnus* and the genera of the subtribe Baccharidineae are remarkably uniform. The reason for this discrepancy is as yet unknown.

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