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A CLASSIFICATION OF ABIES MILLER (PINACEAE)

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ABSTRACT. Previous classifications of the genus *Abies* are reviewed and evaluated. A number of subgeneric names are lectotypified and a list of the validly named subgeneric taxa is given. A new classification scheme is proposed in which *Abies* is divided into ten sections, four of which are further divided into subsections. Three new subsectional names are proposed. A key to the sections and subsections is given and their morphological characteristics and biogeography discussed.

INTRODUCTION

Since the genus was clearly established as a separate entity within the Pinaceae, various attempts at a classification have been made. In the main these have either been limited to restricted geographical areas (e.g. Engelmann, 1878; Mayr, 1890; and Patschke, 1913) or they have used only a limited range of characters as the primary basis for the scheme (e.g. Hickel, 1906–08; Patschke, 1913; Landry, 1984). A result of this is that the classifications proposed are either restricted in their application or produce inconsistent and apparently artificial alliances. The classification we offer here is based on coning and vegetative characters and referenced back to the ecology and geography of the species and is thus, in our opinion, a more natural and complete system than any proposed to date.

HISTORICAL REVIEW

The genus *Abies* was established by Miller in 1754 with *A. alba* [1] as the type species. In addition to *A. alba*, Miller used the genus for *A. balsamea* and for nine other species which are now uniformly treated under either *Picea* or *Tsuga*. Other workers, particularly in the nineteenth century, also included species now treated as belonging to *Pseudotsuga* and *Keteleeria*.

The first attempt at a generic classification was by Spach (1842) who divided the genus *Abies* into five sections:

Section *Picea* (Link) Spach included only species of *Picea* Link.

Section *Piceaster* Spach contained only *A. pinsapo*.

Section *Peuce* Spach included *A. alba, A. nordmanniana, A. procera* (as *A. nobilis*)[2], *A. religiosa, A. sibirica, A. balsamea, A. fraseri, A. grandis, A. spectabilis* and *A. pindrow*.

Section *Peucoides* Spach contained *Pseudotsuga menziesii* (Mirbel) Franco.

Section *Micropeuce* Spach contained *Tsuga canadensis* (L.) Carrière and *T. dumosa* (D. Don) Endl.

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[1]The authorities for species, subspecies and varieties are given in the proposed classification, not where the name is first mentioned in the text.

[2]Throughout, where the original author has used a name which is invalid or at a different level than accepted here we cite the taxon under the name accepted here, with the original name in parenthesis.

Of these sections only *Piceaster* and *Peuce* contained species of *Abies* as presently circumscribed. The name of section *Peuce* Spach is illegitimate under Article 22.1 of I.C.B.N., since it contains the type species of the genus (*A. alba*). The correct name for this section is *Abies* sect. *Abies*.

Carrière (1855) followed Spach in his two sections of true *Abies*, i.e. *Piceaster* and *Peuce*.

Gordon (1858) in '*The Pinetum*' used *Picea* D. Don as the generic name for *Abies*. He divided the genus into two sections:

Section *Bracteata* Gordon was circumscribed by 'the bracteas on the cones not hidden by the scales and either projecting or reflexed'. It included *A. balsamea, A. bracteata, A. cephalonica, A. firma, A. fraseri, A. procera* (as *A. nobilis*), *A. nordmanniana, A. alba* (as *A. pectinata*) and *A. religiosa* (as *A. glaucescens*).

Section *Brevibracteata* Gordon comprised 'those kinds with the bracteas on the cones shorter than the scales, and enclosed'. It included *A. amabilis, A. concolor, A. grandis, A. sibirica* (as *A. pichta*), *A. pindrow, A. pinsapo*, and *A. spectabilis* (as *A. webbiana*).

The names of both of these sections are illegitimate, section *Bracteata* Gordon because it includes the type species of the genus (*A. alba*), and section *Brevibracteata* Gordon because it includes *A. pinsapo* which is the type species of the earlier described section *Piceaster* Spach. The 1875 edition of '*The Pinetum*' lists a few additional species but in the same two groupings.

Engelmann (1878) published an arrangement for the nine species which he recognized as occurring in North America, dividing them into four sections:

Section *Balsamea* Engelm. contained *A. balsamea, A. lasiocarpa* and *A. fraseri* (type *A. balsamea*).

Section *Grandis* Engelm. consisted of *A. grandis, A. concolor* and *A. amabilis* (as *A. grandis* var. *densiflora*) (type *A. grandis*).

Section *Bracteata* Engelm. contained *A. bracteata* and *A. religiosa* (type *A. bracteata*).

Section *Nobilis* Engelm. contained *A. procera* (as *A. nobilis*) and *A. magnifica* (type *A. procera*).

Engelmann was free to use the name *Bracteata* for one of his sections because Gordon's earlier use of the name (in *Picea* D. Don) was illegitimate.

The next proposal was by Mayr (1890) who made three sections:

Section *Momi* Mayr consisted of *A. firma, A. homolepis* var. *umbellata* (as *A. umbellata*), *A. alba* (as *A. pectinata*), *A. nordmanniana, A. bracteata, A. grandis* and *A. magnifica*.

Section *Pindrau* Mayr contained *A. homolepis, A. veitchii, A. mariesii, A. spectabilis* (as *A. webbiana*), *A. pindrow* (as *A. pindrau*), *A. amabilis, A. procera* (as *A. nobilis*), *A. fraseri* and *A. religiosa*.

Section *Pichta* Mayr contained *A. sachalinensis, A. sibirica* (as *A. pichta*), *A. balsamea* and *A. lasiocarpa* (as *A. subalpina*)

All three names of these sections, however, are illegitimate under the current rules of I.C.B.N.; section *Momi* Mayr because it contains the type species of the genus; section *Pindrau* Mayr because it includes the type (*A. procera*) of section *Nobilis* Engelm.; and section *Pichta* for the inclusion of *A. balsamea*, the type species of section *Balsamea* Engelm.

Sargent (1898) amended Engelmann's section *Bracteata*, restricting it to *A. bracteata*.

Kent (1900) divided the genus into three sections:
Section *Abies* (as *Euabies*) with *A. amabilis, A. balsamea, A. cephalonica, A. cilicica, A. concolor, A. firma, A. fraseri, A. grandis, A. homolepis, A. lasiocarpa, A. mariesii, A. nordmanniana, A. numidica, A. alba* (as *A. pectinata*), *A. pindrow, A. pinsapo, A. religiosa, A. sachalinensis, A. sibirica, A. veitchii* and *A. spectabilis* (as *A. webbiana*).
Section *Bracteata* Engelm. emend. Sarg. containing only *A. bracteata.*
Section *Nobilis* Engelm. with *A. procera* (as *A. nobilis*) and *A. magnifica.*

Hickel in a series of papers (1906–08) proposed three sections:
Section *Pseudopicea* Hickel contained *A. homolepis* and *A. spectabilis* (as *A. webbiana*).
Section *Pseudotorreya* Hickel consisted only of *A. bracteata.*
Section *Elate* Hickel contained *A. cephalonica, A. numidica, A. cilicica, A. nordmanniana, A. grandis, A. balsamea, A. religiosa, A. alba* (as *A. pectinata*), *A. amabilis, A. mariesii, A. veitchii, A. fraseri, A. sibirica, A. sachalinensis, A. firma, A. pindrow, A. lasiocarpa* (including var. *arizonica* as *A. arizonica* and with *A. subalpina* as a separate species), *A. pinsapo, A. procera* (as *A. nobilis*), *A. magnifica* and *A. concolor.*
Hickel did not designate a type species for his section *Pseudopicea*, and we propose that the lectotype for this section should be *A. spectabilis.* The name *Pseudotorreya* for the next section is superfluous as it repeats section *Bracteata* Engelm. The name of section *Elate* is illegitimate as it contains the type species of the genus.

Patschke (1913) proposed a scheme dealing with the eastern Asiatic species and gave two sections:
Section *Marginalis* Patschke contained *A. spectabilis* (as *A. webbiana*), *A. pindrow, A. delavayi*, and *A. recurvata.*
Section *Centralis* Patschke included two subsections:
Subsection *Laterales* Patschke consisted of *A. firma, A. fargesii, A. squamata, A. veitchii, A. mariesii, A. kawakamii* and *A. homolepis.*
Subsection *Medianae* Patschke comprised *A. sachalinensis, A. holophylla, A. sibirica* and *A. nephrolepis.*
Section *Marginalis* has by our lectotypification of section *Pseudopicea* Hickel with *A. spectabilis* become a taxonomic synonym. *A. kawakamii* is here proposed as the lectotype for both section *Centralis* and subsection *Laterales.* *A. sachalinensis* is proposed as the lectotype for subsection *Medianae.*

Franco (1950) divided the genus into two subgenera:
Subgenus *Pseudotorreya* Franco consisted of only *A. bracteata.*
Subgenus *Sapinus* (Endl.) Franco was divided into seven sections:
Section *Nobilis* Engelm. with *A. procera* and *A. magnifica.*
Section *Oiamel* Franco with *A. religiosa, A. hickelii, A. hickelii* var. *oaxacana* (as *A. oaxacana*) and *A. vejarii* (lectotype *A. religiosa*, Liu, 1971).

Section *Balsamea* Engelm. emend. Franco with two series:
Series *Grandes* (Engelm.) Franco with (?) *A. mexicana* (*A. vejarii* subsp. *mexicana* in Farjon, in press), *A. guatemalensis, A. durangensis, A. concolor* and *A. grandis.* (type *A. grandis*).
Series *Lasiocarpae* Franco with *A. lasiocarpa, A. balsamea* and *A. fraseri* (type *A. lasiocarpa*).
Section *Pichta* Franco with *A. sibirica* (type), *A. sachalinensis, A. veitchii, A. nephrolepis, A. koreana and A. kawakamii.*
Section *Momi* Franco with three series:
Series *Homolepides* Franco with *A. mariesii, A. homolepis* and *A. holophylla* (type *A. homolepis*).
Series *Firmae* Franco with *A. firma.*
Series *Sinenses* Franco with *A. chensiensis, A. recurvata, A. squamata, A. forrestii* var. *georgei* (as *A. georgei*), *A. fargesii, 4. fargesii* var. *sutchuenensis* (as *A. sutchuenensis*) and *A. delavayi.*
Section *Peuce* Franco containing two series:
Series *Albae* (Franco) Franco with *A. alba, A. nordmanniana, A. nordmanniana* subsp. *equi-trojani* (as *A. bornmuelleriana*), *A.* × *borisii-regis* (as *A. borisii-regis*) and *A. cephalonica.*
Series *Pinsapones* Franco with *A. pinsapo, A. numidica* and *A. cilicica* (type *A. pinsapo*).
Section *Pindrau* Franco containing *A. pindrow* (type) and *A. spectabilis.*

As subgenus *Sapinus* (Endl.) Franco includes the type species of the genus, the name *Sapinus* is illegitimate; if the use of subgenera is considered appropriate, the correct name would be subgenus *Abies.* Although Franco picked up Mayr's names for his sections *Pichta, Momi* and *Pindrau,* he amended these sections in such a way that they became legitimate names, consequently Franco is the authority of these names. The type species of section *Pichta* is *A. sibirica* under the rules of I.C.B.N. (Art. 22.4). We propose *A. firma* as the lectotype for section *Momi,* the type of section *Pindrau* is *A. pindrow,* again under the rules of the Code (Art. 22.4). We propose *A. chensiensis* as the lectotype for series *Sinenses.* The names of section *Peuce* Franco (non Spach) and of series *Albae* (Franco) Franco are illegitimate, as they include the type species of the genus.

Matzenko (1957) published a classification in four sections and thirteen series in the form of a key. His proposal was not valid according to the code (Art. 36.1). In 1963 he modified the names of his four sections and enlarged the number of series to eighteen. The additional series were validly published although without the designation of a type. In 1964 he repeated the latter classification and provided Latin diagnoses for the sections used in 1963 and for the series established in 1957. The descriptions of the series were brought together in one paper in 1968. Lectotypes for the sections were given in the 1964 paper and types for the series in 1968; accordingly, we are taking these dates as the dates when his sections and series were validly published. The amalgamated classification is as follows:

Section *Bracteata* Engelm. emend. Matzenko with four series:
Series *Fargesianae* Matzenko with *A. fargesii* (type), *A. forrestii, A. forrestii* var. *georgei* (as *A. georgei*), *A. delavayi* and *A. squamata.*
Series *Faxonianae* Matzenko with *A. fargesii* var. *faxoniana* (as *A.*

faxoniana: type) and *A. fargesii* var. *sutchuenensis* (as *A. sutchuenensis*).

Series *Fraserianae* Matzenko with *A. fraseri* (type), *A. bracteata, A. hickelii, A. hickelii* var. *oaxacana* (as *A. oaxacana*) and *A. vejarii.*

Series *Religiosae* Matzenko with *A. religiosa* (type), *A. magnifica* var. *shastensis* (as *A. shastensis*) and *A. procera.*

Section *Elate* Matzenko (type: *A. veitchii*) with two series:

Series *Veitchianae* Matzenko with *A. veitchii* var. *veitchii* (type), *A. veitchii* var. *sikokiana* (as *A. sikokiana*), *A. sachalinensis* var. *mayriana* (as *A. mayriana*) and *A. koreana.*

Series *Nephrolepides* Matzenko with *A. nephrolepis* (type) (including *A. gracilis*), *A. sachalinensis* and *A. recurvata.*

Section *Abies* with three series:

Series *Firmae* Franco (as '*Firma*') with *A. firma.*

Series *Nordmannianae* Matzenko with *A. nordmanniana* subsp. *nordmanniana* (type) and *A. nordmanniana* subsp. *equi-trojani* (as *A. equi-trojani* and *A. bornmuelleriana*).

Series *Albae* Matzenko with *A. alba* (type), *A. cephalonica, A.* × *borisii-regis* (as *A. borisii-regis*) and *A. nebrodensis.*

Section *Piceaster* Spach emend. Matzenko with nine series:

Series *Amabiles* Matzenko (as '*Amabilis*') with *A. amabilis* (type), *A. magnifica,* (?) *A. mexicana* (*A. vejarii* subsp. *mexicana* in Farjon, in press) and *A. durangensis.*

Series *Lowianae* Matzenko with *A. concolor* (including *A. lowiana* which he treated as a separate species and as the type), *A. guatemalensis, A. grandis* and *A. lasiocarpa* var. *lasiocarpa* (as *A. subalpina*).

Series *Arizonicae* Matzenko with *A. lasiocarpa* var. *arizonica* (as *A. arizonica* which he made the type) and *A. balsamea.*

Series *Chensienses* Matzenko with *A. chensiensis* subsp. *chensiensis* (type), *A. chensiensis* subsp. *salouenensis* (as *A. salouenensis*) and *A. recurvata* var. *ernestii* (as *A. ernestii*).

Series *Webbianae* Matzenko with *A. spectabilis* (as *A. webbiana:* type) and *A. cilicica.*

Series *Pinsapones* Franco emend. Matzenko (as '*Pinsapo*') with *A. pinsapo* var. *pinsapo* (type), *A. pinsapo* var. *marocana* (as *A. marocana*) and *A. numidica.*

Series *Homolepides* Franco emend. Matzenko with *A. homolepis* (type) and *A. holophylla.*

Series *Mariesianae* Matzenko with *A. mariesii.*

Series *Sibiricae* Matzenko with *A. sibirica* subsp. *sibirica* (type), *A. sibirica* subsp. *semenovii* (as *A. semenovii*) and *A. pindrow.*

Matzenko does not appear to have been aware of the work of Franco (1950), whose authority he should have cited for the names of the series *Firmae* (not amended), *Homolepides* and *Pinsapones* (both amended). His series *Chensienses* has by our lectotypification of Franco's series *Sinenses* become a taxonomic synonym. Like Franco, Matzenko picked up an earlier name for one of his sections (*Elate*) which was illegitimate as used by the original author (see above); consequently Matzenko becomes the authority of this name.

Liu (1971) proposed a system using two subgenera and fifteen sections:
Subgenus *Pseudotorreya* Franco contained:
Section *Bracteata* Engelm. emend. Sarg. with *A. bracteata.*
Subgenus *Abies* contained the remaining sections and species:
Section *Momi* Franco emend. Liu contained only *A. firma.*
Section *Homolepis* (Franco) Liu (as '*Homolepides*') contained *A. homolepis* (type), *A. holophylla, A. mariesii* and *A. kawakamii.*
Section *Chensiensis* (Matzenko) Liu consisted of *A. chensiensis* (type) and *A. recurvata* var. *ernestii* (as *A. chensiensis* var. *ernestii*).
Section *Elateopsis* Liu had within it *A. delavayi* (type), *A. forrestii* (as *A. delavayi* var. *smithii*), *A. forrestii* var. *georgei* (as *A. delavayi* var. *georgei*), *A. fargesii* (with vars *fargesii, faxoniana* and *sutchuenensis*), *A. recurvata* var. *recurvata* and *A. squamata.*
Section *Elate* Matzenko emend. Liu comprised *A. nephrolepis, A. koreana, A. sachalinensis* (with vars *sachalinensis* and *mayriana*) and *A. veitchii* (with vars *veitchii* and *sikokiana*). Liu cites *A. nephrolepis* as the lectotype but Matzenko (1964) had earlier designated *A. veitchii.*
Section *Pichta* Franco emend. Liu contained only *A. sibirica* (with subsp. *sibirica* (type) and subsp. *semenovii*).
Section *Pindrau* Franco comprised *A. pindrow* (type) and *A. spectabilis.*
Section *Abies* emend. Liu included *A. alba* (type), *A. nebrodensis, A. nordmanniana* subsp. *nordmanniana, A. pardei* (here treated as a nomen dubium), *A. cephalonica* (with vars *cephalonica* and *graeca*; the latter including *A. nordmanniana* subsp. *equi-trojani* in part and *A. cephalonica* var. *apollinis*, a taxon not recognized here).
Section *Piceaster* Spach emend. Liu had *A. pinsapo* (with vars *pinsapo* (type), *marocana* and *tazaotana*), *A. numidica* and *A. cilicica.*
Section *Nobilis* Engelm. (cited as emend. Liu but in fact not amended) comprised *A. procera* (type) and *A. magnifica.*
Section *Oiamel* Franco emend. Liu (as '*Oyamel*') included *A. religiosa* (type), and *A. hickelii.*
Section *Vejariana* Liu contained *A. vejarii* (type) (with (?) subsp. *vejarii* and *mexicana*, treated as vars).
Section *Grandis* Engelm. emend. Liu consisted of *A. grandis* (type), *A. guatemalensis, A. amabilis, A. durangensis* (both vars *durangensis* and *coahuilensis*) and *A. concolor* (as vars *concolor* and *lowiana*).
Section *Balsamea* Engelm. included *A. balsamea* (type), *A. fraseri* and *A. lasiocarpa* (with vars *lasiocarpa* and *arizonica*).

Of the sections proposed by Liu, one name picked up from Matzenko, *Elateopsis*, was validated by giving a Latin description and type; consequently Liu becomes the authority of this name. As Franco (1950) used and validated Mayr's names *Pichta* and *Pindrau* for sections, Liu, by incorporating Franco's types, should have cited Franco as the authority of these names.

Murray (1984), in a scheme meant to be a small monograph of the genus, has given a classification which does not in any way consider previous attempts. Totally ignorant of this literature (the author has not seen Liu's monograph and says of it: 'probaliter sine descriptione in Latinis et ergo invalidis'), he introduces completely unnecessary intercalations of additional ranks hitherto unknown in gymnosperm classification. Furthermore, virtually every species

is classified in its own subsection, series and subseries, enumerated in alphabetical order, making the taxonomic objectives of the scheme (if any) almost incomprehensible. It seems better to refer to the original publication (in a home-made 'journal' distributed to botanical institutions at a face-value of '$5/yr. or exchange', but in effect free of charge) for the details. Unfortunately the publication is effective under I.C.B.N. and a number of its names are valid under its rules and have to be dealt with.

Landry (1984) has made the most recent attempt to classify the genus. He followed Franco (1950) in having two subgenera:

Subgenus *Pseudotorreya* Franco (which included only *A. bracteata*) and:

Subgenus *Abies*. In subgenus *Abies* he had five sections:

Section *Liensha* Landry included *A. koreana* (type), *A. sachalinensis* var. *mayriana* (as *A. mayriana*), *A. veitchii* and *A. nephrolepis*.

Section *Abies* emend. Landry included *A. alba* (type), *A. cephalonica*, *A. firma*, *A. nordmanniana* and *A. procera*.

Section *Oiamel* Franco emend. Landry with *A. religiosa* (type), *A. delavayi*, *A. fargesii*, *A. fraseri*, *A. hickelii*, *A. recurvata*, *A. squamata* and *A. vejarii*.

Section *Piceaster* Spach emend. Landry with *A. pinsapo* (type), *A. amabilis*, *A. balsamea*, *A. chensiensis*, *A. concolor*, *A. durangensis*, *A. grandis*, *A. guatemalensis*, *A. kawakamii*, *A. holophylla*, *A. homolepis*, *A. lasiocarpa*, *A. mariesii*, *A. pindrow*, *A. pinsapo*, *A. sibirica* and *A. spectabilis*.

Section *Illeden* Landry contained *A. cilicica* (type), *A. numidica* and *A. magnifica*.

The name of his section *Liensha* is superfluous as it contains the type species of section *Elate* Matzenko (non Hickel): *A. veitchii*.

Besides these classifications, there are several publications dealing with the genus which have grouped the species but are not formalized classifications with nomenclatural implications, of which reference may be made to the following: Endlicher (1847), McNab (1877), Van Tieghem (1891), Viguié & Gaussen (1929), Flous (1936), Gaussen (1964) and Rushforth (1987).

Evaluation of Previous Classifications

The first classifications that dealt only with true *Abies* species and used morphological characters were those of Gordon (1858) (as *Picea* D. Don, non Link), Engelmann (1878) for North American species, and Mayr (1890) who included most species then known to science in a scheme primarily intended for the East Asiatic firs.

Gordon (1858) used the character of whether the bract scales are included or exserted as the basis for his two sections. Using only a single character assists in dividing the species but does not result in a natural classification, particularly as more taxa are discovered.

Engelmann's (1878) classification was of the nine North American species then known to science but made comparison with other species in the genus. He based his classification primarily on the leaf characters but with reference to the bract scales. By this he produced a basically sound system for this limited part of the genus, which can be incorporated in proposed classifications of the genus with few amendments. The most important of these are Sargent's (1898)

restriction of section *Bracteata* to *A. bracteata* and our proposal to separate *A. amabilis* (which he treated as *A. grandis* var. *densifolia*) from section *Grandis* Engelm. and unite it with the very similar *A. mariesii* in a new section.

Mayr (1890) based his classification on the colour of the female cone 'immediately before ripening', which he held to be more consistent than other characters. As Engelmann pointed out (1878: 600) both *A. alba* and *A. concolor* can be very variable in this character and subsequent investigations have shown other species to occur in one or more colour forms (e.g. *A. koreana, A. nephrolepis*). Thus the character is of limited use. Unfortunately Mayr did not consider Engelmann's work and he published two superfluous names for his sections.

Hickel (1906–08) based his classification purely on vegetative characters of the winter buds and branchlets. As *A. bracteata* has very distinctive buds unique in the genus (and sharp, hard pointed foliage like species of *Torreya*) it became the only species in his section *Pseudotorreya,* but this name was superflous when published as it equates directly to section *Bracteata* Engelm. emend. Sargent. The separation of the other two sections on the basis of whether the shoots are grooved and ridged (approaching *Picea*) or with smooth surfaces, created a purely artificial classification which only partly served its apparent function: assisting in the identification of species.

Patschke's scheme (1913) dealt with only a geographically limited group of firs and was based on the position of the resin canals in the leaves. The position of the resin canals can be a useful character but is too variable to be effectively used as a basis for an adequate classification of the genus. Roller (1966), for instance, has demonstrated how the position changed in *A. balsamea, A. fraseri* and *A. lasiocarpa* from peripheral to medial as the tree grew from juvenile to mature, and that within *A. lasiocarpa* the number of resin canals can vary from zero to four.

With Franco (1950) we have arrived at the first classification that deals with the genus as a whole as currently prescribed. His classification is basically geographical, morphological characters being used only to a limited degree although his subdivisions are accompanied by morphological descriptions.

Matzenko (1957–68) primarily used the morphology of the bracts and ovuliferous scales, particularly whether the bract scales of the mature female cone were exserted ('primitive') or included ('advanced') in his classification, although he took account of geographical and ecological arguments, such as 'species of cold regions'.

Liu (1971) followed Franco (1950) not only in the use of subgenera to separate a single species (*A. bracteata*) but also in his application of geographical arguments as the primary basis of his taxonomic classification.

Murray (1984) produced a very confused and poorly researched account, dividing the genus into innumerable parts; as a means of understanding the affinities within the genus it is totally unreliable.

Finally, Landry (1984) used purely morphological arguments, but restricted his diagnostic characters for the subdivision of the genus to the shape of the ovuliferous and bract scales of the mature female cone. His arguments for selecting these are (besides an emphasis on reproductive organs) purely practical (scales of disintegrated cones may be found on the ground beneath the tree) and consequently result in the grouping of species in an artificial manner.

Our opinion is that unrestrained use of geographical and ecological characters, such as that by Franco (1950) and Liu (1971), leads to evolutionary assumptions which can hardly be substantiated by the very incomplete palaeobotanical record currently available, and to the artificial association of species purely because they occur together. However, the use of a very limited range of characters, either of the mature female cone as in Matzenko (1957–68) and Landry (1984), or of shoot characters as in Hickel (1906–08) also results in the grouping of species in an artificial manner. Such schemes may or may not result in reliable keys for the identification of specimens; they are of little value for the phylogenetic understanding of the taxonomic diversity of the genus. We favour a morphological approach but applied to the biology of the whole plant as the primary criterion for a taxonomic classification. (Palaeo-)geography, emphasizing geological events and climatic changes, may be used in an attempt to explain phylogenetic lineages that might appear from the classification scheme (see e.g. Nelson & Platnick, 1981).

From the classifications enumerated above we can list the following names of subgenera, sections, subsections and series which are validly published and available for use in a classification.

SUBGENERA	(LECTO)TYPES
Abies	*A. alba*
Pseudotorreya Franco (1950)	*A. bracteata*
SECTIONS	
Abies	*A. alba*
Piceaster Spach (1842)	*A. pinsapo*
Balsamea Engelm. (1878)	*A. balsamea*
Grandis Engelm. (1878)	*A. grandis*
Bracteata Engelm. (1878)	*A. bracteata*
Nobilis Engelm. (1878)	*A. procera*
Pseudopicea Hickel (1906–08)	*A. spectabilis*
Centralis Patschke (1913)	*A. kawakamii*
Momi Franco (1950)	*A. firma*
Oiamel Franco (1950)	*A. religiosa*
Pichta Franco (1950)	*A. sibirica*
Pindrau Franco (1950)	*A. pindrow*
Elate Matzenko (1964)	*A. veitchii*
Elateopsis Liu (1971)	*A. delavayi*
Homolepis (Franco) Liu (1971)	*A. homolepis*
Vejariana Liu (1971)	*A. vejarii*
Illeden Landry (1984)	*A. cilicica*
SUBSECTIONS	
Laterales Patschke (1913)	*A. kawakamii*
Medianae Patschke (1913)	*A. sachalinensis*
Squamatae E. Murray (1984)	*A. squamata*
SERIES	
Firmae Franco (1950)	*A. firma*

Homolepides Franco (1950)	*A. homolepis*
Lasiocarpae Franco (1950)	*A. lasiocarpa*
Pinsapones Franco (1950)	*A. pinsapo*
Sinenses Franco (1950)	*A. chensiensis*
Amabiles Matzenko (1968)	*A. amabilis*
Arizonicae Matzenko (1968)	*A. lasiocarpa* var. *arizonica*
Fargesianae Matzenko (1968)	*A. fargesii*
Faxonianae Matzenko (1968)	*A. faxoniana*, incl. in *A. fargesii* by Rushforth (1986); as *A. fargesii* var. *faxoniana* in Farjon (in press)
Fraserianae Matzenko (1968)	*A fraseri*
Lowianae Matzenko (1968)	*A. concolor* var. *lowiana*, incl. in *A. concolor* by Farjon (1988)
Mariesianae Matzenko (1968)	*A. mariesii*
Nephrolepides Matzenko (1968)	*A. nephrolepis*
Nordmannianae Matzenko (1968)	*A. nordmanniana*
Religiosae Matzenko (1968)	*A. religiosa*
Sibiricae Matzenko (1968)	*A. sibirica*
Veitchianae Matzenko (1968)	*A. veitchii*
Webbianae Matzenko (1968)	*A. spectabilis*

Of the numerous names proposed by Murray (1984), many are validly published according to the rules of the I.C.B.N. We have listed only one of these here, which we need to adopt in our proposed classification below; it would be a pointless exercise to list the other names here.

In accordance with Recommendation 21.B.1 of I.C.B.N., we have changed epithets of subgenera and sections to (singular) substantives and those of subsections and series to plural adjectives.

Proposed New Classification

In the following classification all accepted species, but only a limited number of accepted infraspecific taxa are listed: in the main they are those treated in the previous works as species. The order of sections given here does not reflect taxonomic inter-relationships; a tentative scheme of affinities of sections is given in the Discussion and Figure 1.

Abies Miller
(Typus: *A. alba* Miller)

Sect. **Abies**

A. alba Miller (type)
A. cephalonica Loud.
A. nordmanniana (Steven) Spach (*A. nordmanniana* subsp. *equi-trojani* (Boiss.) Coode & Cullen)
A. nebrodensis (Lojac.) Mattei
A. cilicica (Ant. & Kotschy) Carrière (*A. cilicica* subsp. *isaurica* Coode & Cullen)
A. × *borisii-regis* Mattfeld emend. Liu

Sect. **Piceaster** Spach **emend.**
A. pinsapo Boiss. (type) (*A. pinsapo* var. *marocana* (Trabut) Ceballos & Bolanos, *A. pinsapo* var. *tazaotana* (H. del Vilar) Pourtet)
A. numidica De Lannoy ex Carrière
Sect. **Bracteata** Engelm. emend. Sarg.
A. bracteata (D. Don) D. Don ex Poit.
Sect. **Momi** Franco **emend.**
(typus *A. firma* Sieb. & Zucc.)
Subsect. **Homolepides** (Franco) **stat. nov.**
(Basionym: *Abies* ser. *Homolepides* Franco, Abetos: 121, 1950)
A. homolepis Sieb. & Zucc. (type) (*A. homolepis* var. *umbellata* (Mayr) Wilson)
A. recurvata Masters (*A. recurvata* var. *ernestii* (Rehder) C. T. Kuan)
Subsect. **Firmae** (Franco) **stat. nov.**
(Basionym: *Abies* ser. *Firmae* Franco, Abetos: 122, 1950)
A. firma Sieb. & Zucc. (type)
A. beshanzuensis M. H. Wu
Subsect. **Holophyllae subsect. nov.**
A. holophylla Maxim. (type)
A. chensiensis Van Tieghem (*A. chensiensis* subsp. *salouenensis* (Bord.-Rey & Gaussen) Rushforth, *A. chensiensis* subsp. *yulong-xueshanensis* Rushforth)
A. pindrow Royle (*A. pindrow* var. *brevifolia* Dallim. & Jackson (= *A. gamblei* Hickel in Rushforth, 1987))
A. ziyuanensis Fu & Mo
Sect. **Amabilis** (Matzenko) **stat. nov.**
(Basionym: *Abies* ser. *Amabiles* Matzenko, Nov. Syst. Plant. Vascul., Ser. Nov. Gen. Abies Miller: 11, 1968)
A. amabilis Dougl. ex Forbes (type)
A. mariesii Masters
Sect. **Pseudopicea** Hickel **emend.**
(lectotype: *A. spectabilis* (D. Don) Spach)
Subsect. **Delavayianae subsect. nov.**
A. delavayi Franch. (type) (*A. delavayi* var. *nukiangensis* (Cheng & Fu) Farjon)
A. fabri (Masters) Craib (*A. fabri* subsp. *minensis* (Bord.-Rey & Gaussen) Rushforth)
A. forrestii C. Coltm. Rogers (*A. forrestii* var. *georgei* (Orr) Farjon)
A. chengii Rushforth
A. densa Griff.
A. spectabilis (D. Don) Spach
A. fargesii Franch. (*A. fargesii* var. *sutchuenensis* Franchet, *A. fargesii* var. *faxoniana* (Rehder & Wilson) Liu)
A. fanjingshanensis Huang, Tu & Fang
A. yuanbaoshanensis Lu & Fu
Subsect. **Squamatae** E. Murray
A. squamata Masters
Sect. **Balsamea** Engelm. **emend.**
(type: *A. balsamea* (L.) Miller)

Subsect. **Laterales** Patschke **emend.**
A. kawakamii (Hayata) Ito (lectotype)
A. sibirica Ledeb. (*A. sibirica* subsp. *semenovii* (B.A. Fedtschenko) Farjon)
A. balsamea (L.) Miller
A. lasiocarpa (Hook.) Nutt. (*A. lasiocarpa* var. *arizonica* (Merriam) Lemmon)
Subsect. **Medianae** Patschke **emend.**
A. sachalinensis (Fr. Schmidt) Masters (lectotype) (*A. sachalinensis* var. *mayriana* Miyabe & Kudo)
A. koreana Wilson
A. fraseri (Pursh) Poir.
A. nephrolepis (Trautv.) Maxim.
A. veitchii Lindley (*A. veitchii* var. *sikokiana* (Nakai) Kusaka)
Sect. **Grandis** Engelm. **emend.**
A. grandis (Dougl. ex D. Don) Lindley (type)
A. concolor (Gordon & Glend.) Lindley ex Hildebr.
A. durangensis Martinez (*A. durangensis* var. *coahuilensis* (I. M. Johnst.) Martinez
A. guatemalensis Rehder
A. flinckii Rushforth (= *A. quatemalensis* var. *jaliscana* Martinez in Farjon, 1989)
Sect. **Oiamel** Franco **emend.**
(lectotype: *A. religiosa* (H.B.K.) Schlecht. & Cham.)
Subsect. **Religiosae** (Matzenko) **stat. nov.**
(Basionym: *Abies* ser. *Religiosae* Matzenko, Nov. Syst. Plant.Vascul., Ser. Nov. Gen. Abies Miller: 9, 1968)
A. religiosa (H.B.K.) Schlecht. & Cham. (type)
A. vejarii Martinez
(?) *A. mexicana* Martinez (= *A. vejarii* subsp. *mexicana* in Farjon, 1989)
A. colimensis Rushforth & Narave (*A. religiosa* alliance, not in Farjon, 1989)
Subsect. **Hickelianae subsect. nov.**
A. hickelii Flous & Gaussen (type) (*A. hickelii* var. *oaxacana* (Martinez) Farjon)
Sect. **Nobilis** Engelm.
A. procera Rehder (type)
A. magnifica Andr. Murray (*A. magnifica* var. *shastensis* Lemmon)

Diagnoses of New Infrageneric Taxa

Abies subsect. **Delavayianae** Farjon & Rushforth, **subsect. nov.**
Rhachis strobili feminii crassa, fusiformis vel cylindro-conica; squamae seminiferae vulgo apice crassiforme; cortex non exfolians in laminis grandibus papyraceis.

Rachis of female cone thick, fusiform or cylindro-conical; seed scales usually apically thickened; bark not exfoliating in large papery flakes.
Typus: *Abies delavayi* Franch.

Abies subsect. **Hickelianae** Farjon & Rushforth, **subsect. nov.**
Foliis emarginatis vel obtusatis; canalibus foliorum resiniferis 4–10 (–12).

Leaf apices emarginate or obtuse; resin canals in the leaves 4–10 (–12).
Typus: *Abies hickelii* Flous & Gaussen

Abies subsect. **Holophyllae** Farjon & Rushforth, **subsect. nov.**
Foliis longa, 2–9cm; strobili feminii cylindrica vel ovoideo-cylindrica, 3.5–6cm lata.

Leaves long, 2–9cm; mature cones cylindrical or ovoid-cylindrical, 3.5–6cm wide.

Typus: *Abies holophylla* Maxim.

Key to Sections and Subsections

1. Bract cusps more than 2.5cm long; vegetative buds fusiform, 1–2 cm long, not resinous ..... Sect. **Bracteata**

\+ Bract cusps much shorter than 1.5cm; buds not fusiform, usually much less than 1cm long, often resinous 2

2. Cones very large (14–30 × 5–10cm); leaves on vegetative shoots usually carinate, imbricate at base, lower leaves curving sideways, upper leaves strongly assurgent ..... Sect. **Nobilis**

\+ Cones smaller, if longer than 15cm then less than 6cm wide; leaves on vegetative shoots usually flattened 3

3. Cones narrowly cylindrical (ratio of length to width greater than 2.5); rachis of cone conical, slender 4

\+ Cones ovoid, conical or broad cylindrical; rachis of cone conical, cylindro-conical or fusiform, stout 8

4. Cones (10–)12–25(–30)cm long, ratio of length to width usually 3 or more 5

\+ Cones 3–12cm long, ratio of length to width usually less than 3 6

5. Bract scales exserted and reflexed (usually included in *A. cilicica*), with elongated cusp; cone apex obtuse or acutish (sometimes papillionate) ..... Sect. **Abies**

\+ Bract scales always included, cusp short; cone apex papillionate ..... Sect. **Piceaster**

6. Cones small, (3–)4–8 × (1.5–)2–3(–4)cm, purplish (rarely greenish); bract scales yellow-brown; leaves emarginate ..... 7 Sect. **Balsamea**

\+ Cones larger, (5–)7–12 × 3–5cm, green, olive-green or rarely bluish during growing season; leaves obtuse, acute or emarginate ..... Sect. **Grandis**

7. Bract scales exserted and reflexed; seed scales reniform ..... Subsect. **Medianae**

\+ Bract scales included; seed scales cuneate-flabellate ..... Subsect. **Laterales**

8. Rachis of cones thick, fusiform or cylindro-conical; seed scales usually apically thickened; shoots usually stout ..... 9 Sect. **Pseudopicea**

\+ Cone rachis less thick, conical; seed scales thickest at or below the middle; shoots usually thin 10

9. Bark exfoliating in large papery flakes ..... Subsect. **Squamatae**

\+ Bark not as above ..... Subsect. **Delavayianae**

10. Bract scales usually exserted with a broad cusp (but not in (?) *A. mexicana* (*A. vejarii* subsp. *mexicana*)); branchlets purplish-brown 11
Sect. **Oiamel**

\+ Bract scales included with a small cusp (which may be slightly exserted) or if exserted, cone oblong-conical and green 12

11. Leaves emarginate or obtuse at apex; resin canals in the leaves 4–10(–12)
Subsect. **Hickelianae**

\+ Leaves acute at apex; resin canals in the leaves 2 .....Subsect. **Religiosae**

12. Young shoots uniformly pubescent; leaves densely crowded above the shoot, directed forward; cones dark purple, rarely lighter
Sect. **Amabilis**

\+ Young shoots glabrous or weakly pubescent in grooves; leaves more pectinate, not dense; cones (yellowish-)green to violet-blue, not dark purple 13
Sect. **Momi**

13. Cones oblong-conical; bract scales strongly exserted; resin canals in leaves 2–4 .....Subsect. **Firmae**

\+ Cones ovoid-oblong to cylindrical; bract scales included or cusps just exserted near the base of the cone; resin canals 2 14

14. Leaves relatively short, 1.5–3(–3.5)cm; cones violet-blue, oblong-cylindrical to ovoid-oblong, 2.5–3.5(–4)cm wide ...Subsect. **Homolepides**

\+ Leaves longer, 2–5(–9)cm; cones yellowish-green to violet-blue, cylindrical or ovoid-cylindrical, 3.5–6cm wide.....Subsect. **Holophyllae**

Discussion

Although our classification is based on the morphology of fruiting and vegetative components of the species, the resulting system puts species with similar ecological preferences from adjoining regions together. Generally the species in any one section or subsection are vicariants with only one species occurring in one locality. Species from two or more sections may occur together, particularly at their ecological borderlines.

Section Abies

This section, containing the type species of the genus, consists of five closely allied species, connected by intermediate forms in a cline from the western and central European *A. alba* to *A. cilicica* and *A. nordmanniana* in Turkey and SW Russia. All have relatively large and narrow female cones, with an acutish to papillionate apex, which are greenish or yellowish-green when immature and ripen to light brown; the bracts are mostly well exserted (mostly included in *A. cilicica*) and reflexed, with an elongated cusp. The leaves are distinctly hypostomatic and usually emarginate at apex. Its species are distributed in a wide arc around the northern shore of the Mediterranean, from the Pyrenees in the west to the Caucasus and Taurus Mountains in the east. They make their best development in cool and moist submontane to montane situations, forming either mixed forests, particularly with *Fagus*, or pure stands. The soils are frequently derived from limestone and thus base-rich.

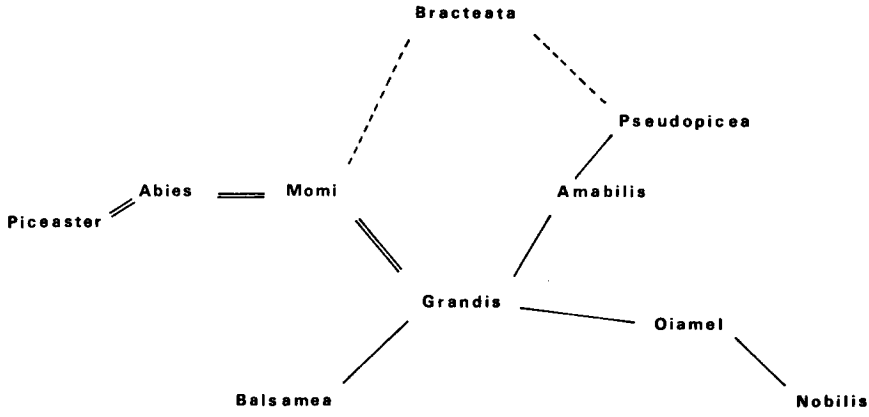

FIG. 1. Tentative relationships between sections in the genus Abies Miller (Pinaceae). ═ closest relationships; — apparent relationships; - - - more distant relationships.

SECTION PICEASTER

This is a small section of closely allied species (and somewhat doubtful varieties), characterized by likewise narrowly cylindrical cones, almost invariably papillionate at apex, which are also mostly green when immature, though sometimes with a purplish hue, but have short cusped, invariably included bracts. The leaves are short and thick, rigid, more or less amphistomatic and radially spreading around the shoot. The species have a limited, relict distribution, restricted to the western Mediterranean region; it is likely that man has had a great influence in this. They occur in the cold temperate zone of summer-dry mountains in SE Spain, N Morocco and N Algeria, usually on slopes with a north aspect. The soils are mainly derived from limestone. This section is allied to section *Abies*.

SECTION BRACTEATA

Although we do not consider that the genus can logically be divided into two or more subgenera, sect. *Bracteata* is not closely related to the other sections. It is distinguished by its unusually long bract cusps, its fusiform, resinless buds, and to a lesser degree by its almost globular female cones and its large, very acute leaves with callous, entire tips. It is endemic to California between 36°N and 37°N, where it occurs in a very summer-dry mediterranean region; growing either in canyon bottoms where moisture collects or on the side of low hills where fog condenses. It appears to be one of the several Californian endemic conifers (e.g. *Pinus radiata* and *P. muricata*) which are relicts whose natural ranges have been restricted by the erosion of the Coast Ranges and, like them, flourishes in cultivation outside its natural territory, growing well as far north as 57°N in Scotland.

SECTION MOMI

The species of this section have ovoid, conical or broad-cylindrical cones of medium size, greenish to violet-blue (but not purple) before ripening, with a stout, conical rachis. The seed scales are thickest at or below the middle; the bract scales are included in the species of subsections *Holophyllae* and *Homolepides* and (slightly) exserted in subsection *Firmae,* which has green, conical cones. The young shoots are mostly glabrous and yellowish to buff; the leaves are pectinate on vegetative shoots, often quite large, especially in species of subsection *Holophyllae,* and commonly emarginate to bifid at apex. This section has a wide distribution from the Himalaya to Japan. The species occur mainly in mixed forests, rarely forming extensive pure stands and never extending near the tree line. In subsection *Firmae* the two species occur in warm temperate and generally rather mesic conditions with Fagaceae, as well as with other conifers. This subsection is restricted to southern Japan and Zhejiang province in eastern China. Subsection *Homolepides* occurs in western China and in southern Japan. In Japan *A. homolepis* occupies an intermediate zone between those of subsections *Firmae* at lower elevation and *Medianae* above, overlapping somewhat with both, and is associated with several other conifers and broad-leaved trees. *A. homolepis* var. *umbellata* is the product of introgression of genes from *A. firma* where the two occur together with a similar flowering time. In China, the subsection occurs in valley bottoms below species of section *Pseudopicea,* in rather drier situations. The species of subsection *Holophyllae* occur in a zone extending from the western Himalaya across China to Korea, characterized by warm summer temperatures. Associated species are mainly broad-leaved trees.

SECTION AMABILIS

This section comprises two species with great similarity, both characterized by ovoid-oblong, purple cones with included bracts, cyathiform to flabellate, puberulent seed scales and light brown, pubescent young shoots covered above by densely crowded, incurved, lustrous dark green, slightly emarginate leaves. One occurs in Japan, the other in western North America. In Japan, *A. mariesii* is a subalpine species of central and northern Honshu. It grows in mixed coniferous forests, and associated broad-leaved trees are never dominant, the most common species is *Betula ermanii*; in the southern part of its range it is frequently mixed with *A. veitchii* of section *Balsamea,* subsection *Medianae. A. amabilis* is restricted to the moister Pacific coast of North America, where it occurs from sea-level to 300m a.s.l. in Alaska and from 250–1800m in Oregon. It may occur in small pure stands, but more often is a constituent of the mixed coniferous forest. This section is allied to section *Pseudopicea.*

SECTION PSEUDOPICEA

This section comprises two subsections: *Delavayianae* and *Squamatae.* The species of the section are characterized by their ovoid-oblong, purple cones, with blue, often exserted bracts and a very thick, fusiform to cylindro-conical rachis. The seed scales are usually apically thickened. The shoots are usually stout, glabrous or pubescent in high altitude forms (varieties) and in most

species in various shades of reddish to purplish-brown. The leaves of some species in subsection *Delavayianae* are strongly revolute, with niveous-white stomatal bands not found to this extent in any other group of species, all leaves on vegetative shoots are emarginate at apex. The single species of subsection *Squamatae* has different leaf characters and a peculiar bark, exfoliating in large, papery flakes similar to some species of *Betula*. This section is made up of a series of vicariant species ranging along the Himalayan axis from Afghanistan to China and across the higher mountains of SW and central China. All species are subalpine, extending to the tree line and forming dense, often pure, forests there. They are found in regions with cool moist summers and frequently deep snow cover in a long winter. At lower elevations, the range of several species may overlap with taxa in section *Momi*. The species of subsection *Delavayianae* occur in regions with a more pronounced monsoon climate than the single species in subsection *Squamatae*.

Section Balsamea

The species of section *Balsamea* have small cylindrical or oblong cones, mostly with a purplish (sometimes greenish) colour and a slender, conical rachis. The bracts, included or exserted, are yellowish-brown, conspicuously lighter than the seed scales. The leaves have emarginate apices. In subsection *Medianae* the bract scales are exserted and reflexed and the seed scales reniform; in subsection *Laterales* the bracts become included in the developed cone, while the seed scales are cuneate-flabellate. The species of this section are either boreal or subalpine, associated with other conifers and *Betula* or *Populus* in the boreal zone. Most species occur to the tree line. Subsection *Laterales* contains the two most widespread firs, with *A. balsamea* and *A. sibirica* covering vast areas of boreal forest across North America and Eurasia. The other two taxa in this subsection are more restricted, occupying subalpine habitats along the Rocky Mountains in North America (*A. lasiocarpa*) and in Taiwan (*A. kawakamii*). Species in subsection *Medianae* occur in east Asia in subalpine regions of Japan, Korea, Pacific Siberia and northeast China and scattered along the highest peaks of the Appalachian Mountains in the eastern U.S.A.

Section Grandis

The cones of the species in this section are narrowly cylindrical, mostly obtuse at apex, with a green or olive-green (rarely bluish) colour during the growing season. The bracts are included or barely exserted in one taxon; *A. flinckii* has most characters which may be rudimentary. The leaves are variable, but narrow and relatively long in all taxa. This section occurs along the Rocky Mountain chain and ranges to the west, from the Canadian border to Guatemala and Honduras. Most species are montane to subalpine and occupy a similar ecological position to those of sections *Abies* and *Momi* in Eurasia. *A. flinckii* is restricted to mesic warm temperate sites in southern Mexico around 20°N and has been found as low as 1300m a.s.l., whereas the other Mexican taxa occur at significantly higher altitudes. At lower elevations the species of this section grow mostly in moist but well-drained sites, usually mixed with other conifers or with broad-leaved trees such as *Acer* (mostly in the North) and *Quercus*.

SECTION OIAMEL

The cones of this section are ovoid-oblong to broad-cylindrical, of medium size, purple to violet-blue, with broad-cusped and mostly exserted bracts and a slender, conical rachis. The slender, olive-green (later purplish-red) young shoots are glabrous or with minute pubescence in the grooves. The leaves of subsection *Religiosae* are acute at apex and have the common number of two resin canals; those of subsection *Hickelianae* are emarginate or sometimes obtuse and have a variable, but uncommonly high number of resin canals, not less than 4 and as many as 12. The species of this section occur in Mexico, from the northeastern states south to Oaxaca. The species in subsection *Religiosae* dominate a zone of vegetation near the summits of the highest mountains, with only *Pinus hartwegii* or *P. rudis* growing above them to the tree line. At lower elevation they mix with species of section *Grandis* and with other conifers. Subsection *Hickelianae* is found at slightly lower elevation in central and southern Mexico.

SECTION NOBILIS

Two vicariant species and a possible product of introgression (*A. magnifica* var. *shastensis*) make up this section. It is distinct in its very large, massive cones, with large but thin, cuneate-flabellate and puberulent seed scales and a slender rachis, and in its foliage, with carinate, densely set leaves which are imbricate at base, curved sideways on the underside of the shoots and assurgent above. The slender shoots, though almost hidden by the adpressed leaves, are densely pubescent when young. This section occurs in the Cascade Range and the Sierra Nevada, from Washington to California. Both species are major constituents of the mixed, varied and magnificent coniferous forests in the upper Transition and Canadian Zones, above the species of section *Grandis* and below the subalpine conifers (e.g. *A. lasiocarpa*) of the Hudsonian Zone. These zones are climatically characterized by warm dry summers and cool snowy winters.

Although we do not consider that we have sufficient evidence to present more than a tentative phylogenetic arrangement of the genus, we offer the scheme shown in Figure 1 as indicating possible relationships between the sections.

We consider sections *Piceaster, Abies, Momi* and *Grandis* most closely related to each other and thus have shown them joined by double lines. These sections are allopatric and together have a similar distribution to the genus as a whole; they are absent only from eastern North America, Taiwan and across northern Eurasia in the areas where species of *Abies* occur. They share a number of characters, e.g. relatively long and cylindrical cones with a slender conical rachis (less so in section *Momi*); the cones are usually green or bluish-green during the growing season; the seed scales are soon deciduous once ripe. Ecologically, they tend to occupy mesic sites and only a few species rarely reach the tree line. The North African taxa of section *Piceaster* may be an exception, but it is probable that the special conditions in which they occur explain reports of their reaching the tree line (Nicholson, 1986).

Section *Grandis* appears to provide the link between these four sections and the remainder of the genus (except section *Bracteata* as discussed below). There

is a link between section *Grandis* and section *Pseudopicea* through section *Amabilis*, with the slender conical rachis of section *Grandis* progressing to the thick cylindro-conical or fusiform rachis of *Pseudopicea*. The link between section *Amabilis* and section *Pseudopicea* is through *A. mariesii* and possibly *A. fanjingshanensis*, which in its turn is allied to *A. fargesii*. At the other end of this line, *A. amabilis* may show some introgression of genes from section *Grandis*, giving it characters such as the lighter coloured hairs, longer leaves and sometimes greenish cones. Ecologically, it is less subalpine than its Japanese counterpart (*A. mariesii*) or the species of section *Pseudopicea*, while more so than the species of section *Grandis*.

Section *Grandis* also shows some relationship to section *Oiamel*, mainly through vegetative characters in the buds and foliage. The link may be through subsection *Hickelianae* as cultivated *A. hickelii* from the Cofre de Perote (Vera Cruz, Mexico) is similar to cultivated *A. durangensis* of the same age. There is also a possible relationship through this subsection to *A. firma* of section *Momi* which is the only other species which regularly has more than two resin canals in the leaves, while the bract scales of the cones of both species are also similar. Section *Oiamel* is related to section *Nobilis* as discussed by Rushforth (1989).

Section *Balsamea* also seems to relate better to section *Grandis* than to any other group. It agrees in the slender conical rachis and the cylindrical cones, which are however much smaller in most species. Its species mainly occur in areas where sections *Abies*, *Piceaster*, *Momi* and *Grandis* are absent.

All these relationships, however, seem to us less obvious than the relationships between sections *Abies*, *Piceaster*, *Momi* and *Grandis* and thus we have connected them in Figure 1 with only a single line.

The more distant (and only monotypic) section seems to be *Bracteata*. It shows affinity with section *Pseudopicea* in the distinctly stalked cones with a fusiform rachis and the long cusps on the bracts (as also found in some specimens of *A. forrestii*), while its male strobili are likewise longer than in any third section. (*A. recurvata* var. *recurvata* of section *Momi*, subsection *Homolepides* is the only other species which sometimes has a stout, fusiform cone rachis, e.g. in plants cultivated from *E. H. Wilson* numbers 4451 or 4457.) The long leaves with a sharp callous apex indicate a relationship with *A. holophylla* of section *Momi*. On the other hand it is difficult to see how the buds of *A. bracteata* relate to the remainder of the genus. We are not certain that the similarities constitute evidence of close relationship and have accordingly shown these links as broken lines in Figure 1.

As to a suggestion for the most 'primitive' section, there is quite strong evidence supporting both section *Grandis* and section *Momi*. Both show considerable variation in some characters, which are more constant in the other sections. Colour of cones varies from yellow-green to pale blue (*A. concolor* of section *Grandis* being very polymorphic in this respect). Both sections exhibit hidden as well as exserted bracts in the mature cones. Length of leaves is variable as well, with extremely long foliage in some taxa (7–9cm). From the evidence presented above, section *Grandis* appears to be most widely linked to other sections. It is perhaps relevant in this respect to note that six of the sections here proposed occur in North America, only four in East Asia and two in Europe, with two sections occurring in both North America and East Asia.

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