Inclusion of Taxaceae in a separate order, Taxales

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Taxus and its related genera, viz. *Torreya*, *Austrotaxus*, *Pseudotaxus* and *Amentotaxus* were unquestionably included in the Pinales (= Coniferales) although they were usually included in a family of their own, the Taxaceae, inclusive of *Cephalotaxus* by Coulter & Chamberlain[1] or exclusive of *Cephalotaxus* by Pilger[2], who placed *Cephalotaxus* in a separate family, the Cephalotaxaceae. However, in 1920, Sahni[3] suggested that *Taxus*, *Torreya* and other closely-related genera and *Cephalotaxus* were so different from other conifers and they should be included in a separate order Taxales. Sahni's suggestion about a wider separation of *Taxus* in a separate order Taxales was supported by Florin[4], but he pointed out that *Cephalotaxus* should continue undisturbed in the Pinales since it did have a female cone, although it was much reduced but *Taxus* alone was radically different from Coniferales because it had no female cone and its female dwarf shoot ended in a terminal ovule (Figures 1 *a*, *b* and 2 *a*). The unique peltate radially organized microsprophylls of *Taxus* (Figure 1 *c*, *d*) seemingly supported the above wider separation of the Taxales. Another point which may have prompted Florin[4] to plead for a wider separation of Taxaceae in the Taxales was the lack of any fossils which showed characters linking Taxaceae with any other conifers. The earliest taxads like *Palaeotaxus redeviva* Florin (Figure 2 *b*) and *Marskea thomasii* Harris (Figure 2 *c*) take us back into the Lower and Middle Jurassic, respectively, but there they leave us in the lurch about their links with any other groups of conifers or other gymnosperms. The only genus of Taxus-like fossil shoots reported from the Palaeozoic Lower Gondwana rocks is *Searsolia opposititifolia* Pant & Bhatnagar[5] but except for some vague carbonless rounded impressions of frutification-like bodies on a shoot, its reproductive parts are unknown (Figure 2 *d*). Thus except for giving overwhelming weight to the evidence of a terminal ovule and the absence of a female cone in the Taxales, neither Sahni[3] nor Florin[4] seems to have taken into consideration the various characters which are common to the Pinales and their new order Taxales. The present article is therefore intended to have a fresh look at the similarities and differences between Taxaceae and other conifers to enable us to decide whether we can continue to keep the Taxaceae as a family within the Pinales or to include them in that family under a separate order, the Taxales.

As Chamberlain[6] had pointed out, 'the grouping into families and sequence of families will depend upon each investigator. If he is an anatomist, anatomy will determine the treatment. If strobili are considered more important, they will determine the grouping and sequence. If gametophytes are emphasized, there will be still another arrangement'. Therefore, in order to eliminate individual bias it seems to be necessary to take diverse characters of the Pinales, exclusive of Taxaceae and of the Taxaceae into consideration in order to decide whether the Taxaceae need to be separated widely under Taxales as suggested by Sahni[3] and Florin[4] or kept within the Pinales (= Coniferales).

In their habitats and habit the Taxaceae are quite like many other Pinales. They are woody pycnoxylic shrubs and trees inhabiting locations like those of the Pinales. Their leafy shoots and simple leaves are similar to those of many conifers. Their secondary xylem no doubt is peculiar in showing tertiary spirals, sometimes called taxinean spirals, but these occur in *Cephalotaxus* as well.

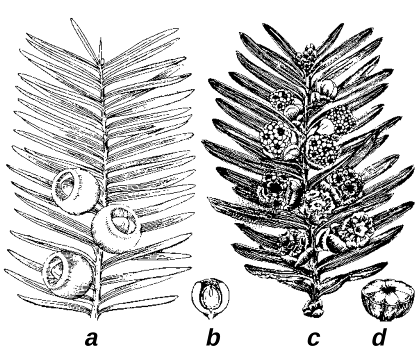

Figure 1. *Taxus baccata*. ***a***, Twig-bearing mature seeds with a surrounding aril; ***b***, Longitudinally split mature seeds inside aril; ***c***, Twig showing mature male 'flowers'; ***d***, A peltate microsporophyll. ***a***, ***b***, after Kerner, 1895; ***c***, ***d***, after Kerner, 1913.

Among characters of *Taxus* which have been mentioned as altogether different from those of all other Pinales, are its radially organized peltate microsporophylls with sporangia attached on the adaxial, inner side. However, other genera of the Taxaceae have dorsiventral microsporophylls with microsporangia attached on the abaxial, underside like those of the Pinales. Thus, if we take the character of peltate microsporophylls into consideration we can widely separate *Taxus* alone into Taxales but the microsporophylls of the other genera conform with those of the Pinales.

The development and structure of the male and the female gametophytes in the Taxaceae are quite comparable with those in the rest of the Pinales. Finally an intricate character of the Pinales like the tiered arrangement of the proembryo, which is characteristic of all conifer proembryos is also found in the Taxaceae as shown by Sterling[7] (see Figure 3).

The basic chromosome number too is $n = 12$ in *Taxus*, but *Torreya* and *Amentotaxus* have $n = 11$ (see Khoshoo[8] and Mehra[9]) and these numbers too are quite in conformity with those prevalent in most of the Pinales.

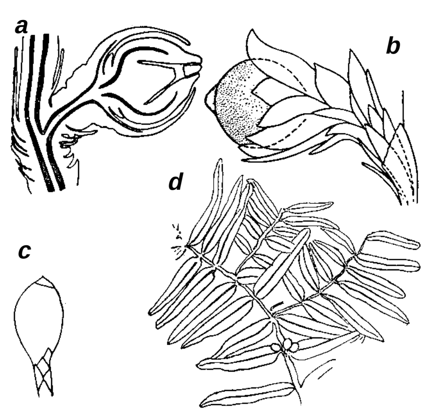

Figure 2. ***a***, *Taxus canadensis* longisection of female dwarf shoot and terminal ovule. ***b***, ***c***, Female flowers of *Palaeotaxus rediviva* and *Marskea thomasii* respectively; ***d***, *Searsolia oppositifolia*, showing a leafy shoot with secondary foliate branches and three shortly stalked globose over the main axis.

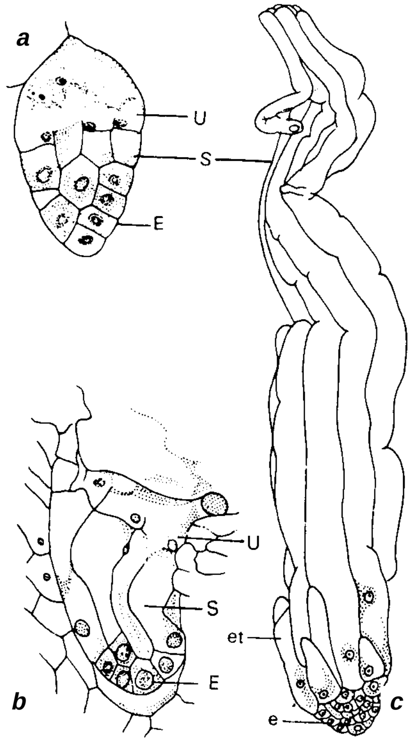

Figure 3. *Taxus*. ***a***, Secondary proembryo with upper (U), suspensor (S) and embryonal (E) tiers; ***b***, Same at a later stage showing a few surrounding gametophytic cells; ***c***, Young proembryo (e) with differentiated embryonal tubes and with one of its cells separated (all after Sterling[7]).

Therefore, taking into consideration all the above characteristics of the Taxaceae we find that the only character which is regarded as categorically supporting their wider separation into Taxales are their terminal ovules in their female dwarf shoots. However, as pointed out by Harris[10,11], a lateral ovule in a fertile dwarf shoot like that of *Lebachia*, can be assumed to have become terminal by the abortion of the dwarf shoot apex and Harris has cited examples from the angiosperms where this actually occurs (Figure 4). Moreover, as mentioned by Miller[12] in his table 10.2 dealing with character states of the OTU used in the CLINCH and PAUP analysis, terminal ovules occur also in *Phyllocladus*, *Microcachrys Saxegothaea* of the Podocarpaceae, *Araucaria* of the Araucariaceae and *Callitris* of the Cupressaceae.

We may thus conclude after taking all the above facts into consideration, that the assignment of *Taxus* and its allied genera to the family Taxaceae appears to be fully justified but their wider separation in a separate order of their own, the Taxales, is supported solely by the terminal position of their ovules in their female dwarf shoots and according to Miller[12] (as mentioned above) this terminal position too is shared by a few members of the Pinales. Moreover, the ovules could have become terminal by the abortion of their dwarf shoot apices as suggested by Harris[10,11]. Further, the cones of Pinales could indeed be derived from the scattered condition of female dwarf shoots like those in *Taxus* to a condition where they become crowded and inserted at each node in pinalean cones as envisaged by Pant & Nautiyal[13] and Pant[14] (see Figure 5). The cumulative evidence of all the diverse characters of *Taxus* and its allied genera, as discussed above, is therefore, adjudged as being strongly against their wider separation in the order Taxales.

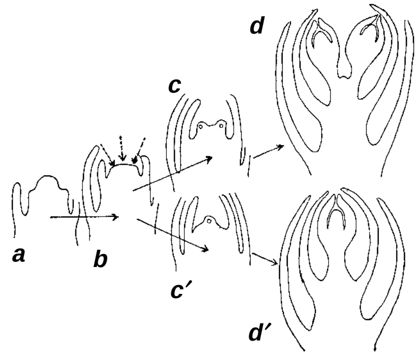

Figure 4. Hypothetical longisections of different onyogenetic stages of apices of an early *Taxus* ancestor. ***a***, Youngest stage with raised apical meristem and shoulders which will form scales; ***b***, as ***a*** but older with apex flattening, ***c***, as ***b*** but older, two ovules marked 'o' are beginning to form; ***c′***, as ***c*** but with one median ovule. ***d′***, as ***c*** but older, the dormant shoot apex bulges between the two integumented ovules; ***d′*** as ***c′*** but older with a terminal ovule (all after Harris[10]).

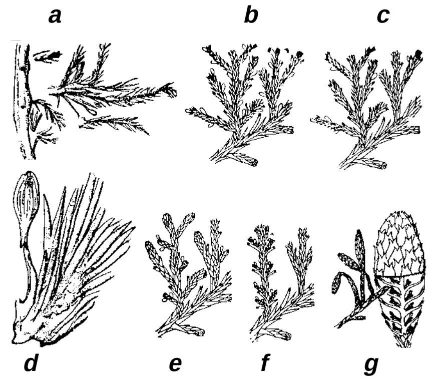

Figure 5. *Buriadia heterophylla*. ***a***, Branched shoot showing attached ovules; ***b***, Portion of shoot showing an attached anatropous ovule among leaves; ***c***, A reconstructed hypothetical shoot showing laterally attached solitary seeds among leaves on branches of all orders; ***d***, Axis of a plant (hypothetical) with seeds as in *Buriadia* but borne only on some unreduced lateral branches; ***e***, Axis of a plant (hypothetical) with reduced lateral branches; ***f***, Hypothetical axis like ***e*** but with fertile short shoots clustered around a specialized lateral branch; ***g***, Reconstructed shoot of *Lebachia piniformis* with terminal cones. Figure on the right side shows a cone with its basal part longitudinally split (after Pant and Nautiyal[13]).

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