9 Conclusion

Molecular phylogenetic analyses of Heliotropiaceae have not previously been available. The most recent study of Heliotropiaceae is that of FÖRTHER (1998). That study was based on both extensive morphological-anatomical investigations of herbarium material and on extensive field collections, especially within the genus *Heliotropium*. FÖRTHER (1998) proposed a schema with eight genera, and a intrageneric subdivision of the genus *Heliotropium* into 19 sections within the Heliotropiaceae. This model constitutes the basis of these present investigations.

In this study, the plastidal *trn*L_{UAA} intron of 66 species and the nuclear ITS1 of 88 species of the Heliotropiaceae were sequenced and systematically analysed. Further, extensive investigations of leaf and seed morphology and anatomy of 65 species of Heliotropiaceae facilitated examination of the phylogenetic hypotheses based on molecular data. Special care was exercised to ensure inclusion of the complete spectrum of Heliotropiaceae within the study. Species representing all genera and subsections in FÖRTHER'S (1998) classification were selected for investigation.

Figure **6-10** (HILGER & DIANE submitted) summarises the principal findings of this thesis. Selected morphological / anatomical apomorphies are shown with bootstrap support values from the molecular phylogenetic hypotheses.

The results of the molecular analyses (DIANE et al. 2002a, HILGER & DIANE submitted) challenge and contradict the traditional taxonomic circumscription of *Heliotropium* and *Tournefortia* (DECANDOLLE 1845, GÜRKE 1893, JOHNSTON 1928, 1930, 1935, FÖRTHER 1998) and suggest that generic limits warrant adjustment. Neither *Heliotropium* nor *Tournefortia* are monophyletic.

According to molecular analyses the Heliotropiaceae fall into two large clades. The first clade includes, in basal position, the monotypic genus *Ixorhea*. *Tournefortia* section *Cyphocyema* is monophyletic and sister to a clade comprising the species of *Hilgeria*, *Schleidenia* and *Heliotropium* section *Orthostachys*. Species of the remaining sections of *Heliotropium*, the *Tournefortia* section *Tournefortia* and the small genera *Argusia*, *Ceballosia* and *Nogalia* constitute the second large clade.

This second large clade has three subclades. In basal position are the species of *Heliotropium* section *Heliothamnus* occuring only in the Andes. The *Heliotropium* species of the NewWorld,

including *Tournefortia* section *Tournefortia*, and the *Heliotropium* species of the Old World, including *Argusia*, *Ceballosia* and *Nogalia*, are sister groups.

Alongside these molecular analyses, leaf anatomy and distribution of foliar trichome types have been investigated within Heliotropiaceae (DIANE *et al*. submitted). The results show that leaf anatomy strongly supports molecular phylogenetic hypotheses, as well as investigations of flower morphology and seed anatomy and morphology (DIANE *et al.* 2002a, DIANE *et al.* 2002b).

By way of conclusion, nomenclature changes within Helitropiaceae are proposed. These suggested revisions reflect phylogeny. Five genera are proposed and described (DIANE *et al*. in press a, HILGER & DIANE submitted):

1. ***Ixorhea***: According to molecular results *I. tschudiana* is in basal position of the first clade. This aberrant species is mainly characterized by apomorphic morphological and anatomical traits. With regards to nomenclature no changes are suggested.
2. ***Myriopus***: This genus comprises the species of *Tournefortia* section *Cyphocyema* following JOHNSTON (1930). Molecular analyses shown that *Myriopus* is in the first clade sister to the genus *Euploca*. With respect to leaf, seed, and flower morphology and anatomy this genus is distinct from *Tournefortia* section *Tournefortia*. Many apomorphies are common with *Euploca* and thus support a close relationship.
3. ***Euploca***: This genus comprises species of former *Heliotropium* section *Orthostachys*, *Schleidenia*, and *Hilgeria*. According to the evidence of molecular analyses they form the sister group of the genus *Myriopus* within the first clade. Their morphology and anatomy differ clearly from *Heliotropium*, and *Euploca* is not related to this genus.
4. ***Heliotropium***: According molecular results this genus comprises all species of the second clade, with the exception of *Tournefortia* section *Tournefortia*. Three genera formerly separated from *Heliotropium* are now reclassified in the synonymy of *Heliotropium*. These genera are *Argusia*, *Ceballosia* and *Nogalia*. *Heliotropium* is well characterized by morphological-anatomical traits. Under this definition the genus *Heliotropium* is still paraphyletic, because the species of *Tournefortia* section *Tournefortia* are not included.
5. ***Tournefortia***: The genus *Tournefortia* comprises the species of *Tournefortia* section *Tournefortia* according to JOHNSTON (1930). The species of *Tournefortia* cluster with *Heliotropium* species of the New World. Both are, according to molecular analyses and morphological anatomical traits, very close related. Thus, the species of section *Tournefortia* have to integrate into the genus *Heliotropium*. Currently, in this thesis the

exact phylogenetic relationships within "*Heliotropium*" are not satisfactorily resolved. A revision of the tropic species is much needed, and this study advocates that the genus *Tournefortia* be maintained.

Furthermore, this thesis shows that the investigation of the secondary structure of sequences provide both phylogenetic important structural traits and a tool to improve the alignment. Since the secondary is more conserved as the primary structure, it is possible to receive with the ITS1 marker, phylogenetic trees on a higher systematic level. This was shown within the Boraginales (GOTTSCHLING *et al.* 2002).

In the context of the investigation of the seed anatomy of the Boraginales (DIANE *et al*. 2002b) it is shown, that the presence of transfer cells in the seed coat and the structure of the endocarp are important common derived traits of the Heliotropiaceae, Cordiaceae, Ehretiaceae, and also Lennoaceae, and supports strongly molecular hypotheses of the phylogeny of Boraginales.

The function of the transfer cells in the testa was experimental demonstrated for the Heliotropaceae (DIANE *et al*. 2002b).

In summary, therefore, this research offers a novel approach to systematic-taxonomic issues within the Heliotropiaceae, and underlines the importance of molecular phylogenetic analyses used in conjunction with morphological and anatomical investigations.