The Natural and Taxonomic History Of Chondrorhyncha (Orchidaceae: Zygopetalinae)

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The history of *Chondrorhyncha* began some 50 years before its formal description by Lindley, at the times of José Celestino Mutis' Royal Botanical Expedition of the Nuevo Reyno de Granada (1783-1810). One of the almost seven thousands botanical plates produced by the artists of the expedition depicts in full detail a plant annotate as "Zygophilum" that, according to our actual generic concepts, belongs to the genus *Chondrorhyncha*. The exact origin of this plant was not recorded, but it was likely collected during the residence of the botanical expedition at Mariquita (1783-1791), in northern Colombian Tolima province. Apparently, no description of this orchid was conserved among the descriptions and observations compiled by Mutis and the other botanists of the expedition (Amaya 1999), and no herbarium material of this plant is kept in the Mutis collection at Madrid (MA-MUT) (Pérez Arbeláez, 1995).

In 1846 John Lindley eventually created the genus *Chondrorhyncha* to accommodate a plant originally collected by Schlim at Jaji (Lindley 1846), along the northern slopes of the Sierra Nevada in Venezuela. Among the diagnostic features of the new genus, Lindley (1846) noted "the extremely oblique insertion of the sepals", together with the bristle-like, cartilaginous rostellum (hence the generic name, from the Greek *chondros*, cartilage, and *rhynchos*, beak), and the 4 cereous, dorso-ventrally flattened, overlapped pollinia. At the time of the original description of his new genus, Lindley had already published two genera closely related to *Chondrorhyncha*, namely *Stenia* (based on *S. pallida*, 1837) and *Huntleya* (typified by *H. meleagris*, 1837), and he had also described two other non-pseudobulbous Zygopetalinae as *Zygopetalum cochleare* [1837 = *Cochleanthes flabelliformis* (Sw.) R.E. Schult. & Garay] and *Huntleya violacea* [1839 = *Pescatorea violacea* (Lindl.) Dressler]. Nevertheless, in suggesting a phylogenetic placement of his new genus, Lindley considered *Chondrorhyncha* to be allied to *Helcia* Lindl. and *Trichopilia* Lindl., two distantly related genera of the subtribe Oncidiinae.

It is noteworthy that Lindley could not recognize the affinities of *Chondrorhyncha*. It is true that the narrow, ligular pollinia of *Stenia pallida* are highly anomalous among the species of *Stenia* [and it is interesting that only two years later Rafinesque (1838: 45) published the same taxon with the generic name of *Stenopollen*, alluding to the same diagnostic character], but its rostellum is otherwise very similar to that of *Chondrorhyncha*. *Huntleya meleagris, Cochleanthes flabelliformis* and *Pescatorea violacea,* on the other side, have both a bristle-like rostellum and 4, dorsoventrally superposed, complanate pollinia, coinciding with the characters stated in the protologue of *Chondrorhyncha*.

As by 1846, the only useful character to distinguish *Chondrorhyncha* from its Huntleyoid relatives was the "oblique" insertion of the lateral sepals, which became strongly reflexed with age, a single-feature that gave raise to what has been called the *"Chondrorhyncha"* complex.

In the course of XIX century, Reichenbach (1852) segregated from *Zygopetalum* Hook. other "chondrorhynchous" genera that may be recognized for some diagnostic, morphological characters, among which *Chaubardia, Kefersteinia, Pescatorea, Bollea* (now included in *Pescatorea*, see Whitten *et al.* 2005), and *Warczewiczella*, an interpretation that, with some exceptions (i.e., Allen 1949; Garay 1969), has been followed by most botanists. More genera were split from *Chondrorhyncha* or created for *Chondrorhyncha*-like species in the second half of the XX century [i.e. *Chaubardiella* Garay (1969), *Dodsonia* Ackerman (1979), *Benzingia* Dodson (1989), *Ackermania* Dodson & R. Escobar (1993), and *Chondroscaphe* (Dressler) Senghas & G.Gerlach (1993)]. Nevertheless, by the end of the century the list of *Chondrorhyncha* names had reached the respectful figure of almost 70 binomials.

Although many genera of the Zygopetalinae are well known in horticulture and relatively easy to identify on the basis of their characteristic floral features (i.e., *Pescatorea/Bollea, Huntleya, Kefersteinia*, among others), the nomenclatural inflation of *Chondrorhyncha* well reflects the traditional difficulty in delimitating the remaining genera of the *Huntleya* clade. Fundamental attempts to critically revise the orchid groups belonging to the so-called *Chondrorhyncha* complex were done by Garay (1969), Fowlie (1969) and, more recently, by Dressler (2000). However, it was not until the beginning of the new millennium when a new phylogenetic arrangement of the entire subtribe Zygopetalinae was proposed on the basis of analyses of four DNA regions data sets (Whitten et al. 2005).

According to this study, the subtribe, which includes more than 400 species and ranges from Mexico, through the West Indies, to Brazil, Bolivia and Argentina in South America, is composed by three main clades. The basal grade includes all the genera with homoblastic pseudobulbs and plicate leaves related to *Warrea* Lindl., consecutively sister to the grade mostly composed by the genera related to *Zygopetalum*, with single-node pseudobulbs, convolute leaves, and many-flowered inflorescences; and to the usually pseudobulbless, conduplicate-leaved, one-flowered genera of the *Huntleya* grade (including the two morphologically anomalous genera *Cryptarrhena* R. Br. and *Dichaea* Lindl.) (Whitten *et al.* 2005). Within the better sampled grade of *Huntleya* an the allied genera, the phylogenetic trees clearly showed that *Condrorhyncha* was grossly polyphyletic, its members being scattered in at least 8 different clades. The results of the molecular analyses were not surprising at the light of the pollination mechanisms already known in the group. In most of the documented records (species of *Benzingia* Dodson ex Dodson, *Chaubardia* Rchb. f., *Chaubardiella* Garay, *Cochleanthes* Raf., *Dichaea, Huntleya* Bateman ex Lindl., *Kefersteinia* Rchb. f., *Pescatorea* Rchb. f., *Warczewiczella* Rchb. f., and *Zygosepalum* Rchb. f.), the flowers of Zygopetalinae attract male euglossine bees searching for perfume compounds. However, James Ackerman also recorded the visit of *Cochleanthes* (=*Warczewiczella*) *lipscombiae* in Panama by female euglossine looking for food resources, which extend their tongue into the back-swept lateral sepals in search of nectar (Ackerman, 1983). Species with this deceit morphology, presenting strongly reflexed lateral sepals with the margins infolded at the base, mimicking nectariferous spurs, are scattered in the *Chondrorhyncha* complex among various groups with other floral mechanisms. As it was previously revealed in other advanced orchid groups in which a mix of different pollination syndromes are present among closely related taxa, the resulting genera mainly circumscribed on the basis of gross flower morphology are frequently polyphyletic. In our case, the taxonomic confusion that plagued the history of *Chondrorhyncha* reflects repeated evolutionary changes in pollination mechanisms, with mixtures of reward and deceit pollination.

As a nomenclatural result of the phylogenetic study, many genera in the Zygopetalinae required recircumscription and new genera were created to better reflect the molecular evidence (Whitten *et al.*, 2005). The majority of the newly defined genera are rather intuitive. Neudecker and Gerlach (2000) anticipated the merge of *Dodsonia* into *Stenia* in describing the anomalous *Stenia glatzii*. Dressler (2001) claimed for the inclusion of the *"Chondrorhyncha bicolor"* group into *Chondroscaphe*. The need to distinguish *Warczewiczella* from *Cochleanthes* [so reducing the latter genus to the actual figure of two species (Pupulin 2006)] was already suggested by Fowlie almost 40 years ago (Fowlie, 1969). The merge of *Bollea* into *Pescatorea* easily explains the relative frequency of "intergeneric" natural hybrids among these two supposed genera and points out that the main distinguishing characters among the two groups (i.e., the width of the column wings and of the basal callus of the lip) are taxonomically rather trivial. A special mention deserves the case of *Benzingia*. In the phylogenetic tree (Whitten *et al.*, 2005), the type species of *Benzingia, B. hirtzii* Dodson (Fig. 4), is on a moderately supported clade together with *Chondrorhyncha reichenbachiana* Schltr., species of *Ackermania* and *Benzingia estradae* Dodson. Rather surprisingly, the sister species of *B. hirtzii* is *C. reichenbachiana* (90/100 support), while the only other species transferred to *Benzingia* before the phylogenetic analysis, *B. estradae*, is weakly supported as sister to *Ackermania cornuta* (Garay) Dodson & R. Escobar [described as *Chondrorhyncha* (Garay 1970)]. Eventually, *Ackermania caudata* (Ackerman) Dodson & R. Escobar and *A. hajeckii* D.E. Benn. & Christenson are on strongly supported (96/100) clade. The results of the combined molecular analyses leave some space for taxonomic interpretation, but the recircumscription of *Benzingia* to include *Ackermania* and *Chondrorhyncha reichenbachiana* is by far the most rational, although if the resulting genus is somewhat difficult to define in terms of vegetative and morphological features. The alternative would have been to recognize a *Benzingia s.s.* for *B. hirtzii* and *Chondrorhyncha reichenbachiana* (but excluding *B. estradae*), creating a new genus for *Benzingia estradae* + *Ackermania cornuta*, and another genus (the name *Ackermania* is likely predated by the fungal genus *Ackermannia* Pat.) for *A. caudata* + *A. hajeckii*. With the exception of *Aetherorhyncha* Dressler, which is weakly supported as sister to the genus now treated as *Ixyophora* Dressler, all the other new genera split from *Chondrorhyncha* (namely *Daiotyla* Dressler, *Echynorhyncha* Dressler, *Euryblema* Dressler, *Ixyophora*, and *Stenotyla* Dressler) are on strongly supported branches and rather easy to characterize morphologically.

It is perhaps legitimate to ask in which way the new generic alignments suggested by the use of molecular techniques improve our understanding of the *Chondrorhyncha* complex with respect to previous systematic approaches. I will try to articulate a possible answer to this question into four main points.

1. Morphological characterization is an important requisite to explain the evolutive processes and how they act on certain features of the organisms. However, if morphology has to be maintained as a tool to interpret life's diversity and to propose generic and specific affinities, it is fundamental the accurateness of the observations. A few cases may perhaps illustrate this point. Among the species of the *Chondrorhyncha complex,*

Aetheorhyncha andreettae (Jenny) Dressler is the only one to produce almost erect flowers on short and rather stout inflorescences. The entrance to the lip chamber is ornamented with short, flat and stiff trichomes, and it is unusually narrow, so that we have to presume that only a relatively small bee may gain access to the chamber. Inside the chamber, the column of *A. andreettae* is twisted longitudinally, suggesting that the pollinarium is probably placed on one side behind the head or on the back of the pollinator. It is interesting that these morphological features, which play a substantial role in the pollination biology of this species, were not previously emphasized. The species actually assigned to the genus *Stenotyla* are invariably provided with small but distinct pseudobulbs. The callus of the lip is short and narrow, placed almost in the center of the blade, and it has only 2 to 4 distinct teeth. The pollinarium of *Stenotyla* is very characteristic, with a narrow, triangular stipe that curls after removals and a small, semitubular and almost indistinct viscidium (Pupulin, in press). These features were not constantly described in the past. The genus *Euryblema* is easily characterized by the leaf sheaths that are boldly marked with purple (indigenous people from the region of Bocas del Toro in Panama refer to *E. anatonum* as *"patirroja"*, or red-footed); the broad and laminar callus completely covers the basal half of the lip, and the pollinarium is provided with a very large, broad stipe, and a narrow, thick, ligular viscidium, unlike any other species in the *Chondrorhyncha* complex (Pupulin, 2007). In all the known species currently assigned to the genus *Echynorhyncha*, the ventral surface of the column bears bristly, urchin-like appendages, and the pollinarium present a pandurate stipe, two morphological features that easily characterize the genus if consistently described.

2. The new systematic arrangement of the genera previously included under a broad *Chondrorhyncha* improves the predictability of generic placement in the case of dubious and not yet sampled species. *Chondrorhyncha velastiguii* was originally described and illustrated by Dodson in 1989 on the base of a plant collected along the Río Negro in eastern Ecuador (Dodson & Dodson, 1989). To my knowledge, the species has been collected only five times after the original gathering, always from the eastern Ecuadorian provinces of Morona-Santiago, Pastaza, and Tungurhaua. In realigning *Chondrorhyncha* and the allied genera, Whitten and co-workers had no material to sample *C. velastiguii* and to include the species in the matrix, but they suggested it can likely considered a true species of the genus *Condrorhyncha s. str.* (Whitten *et al.*, 2005: 92). I recently had the opportunity to study living material of *C. velastiguii* from Ecuador, and the vegetative morphology, as well as the shape of the lip callus and the pollinarium agree whit the set of characters now considered diagnostic for the genus *Ixyophora*, so requiring a new nomenclatural combination for *C. velastiguii*.

3. A good taxonomic system improves the recognition of anomalous patterns. Whitten and collaborators were not able to obtain material of *Cochleanthes thienii* Dodson for their study, and they considered this species to be possibly congeneric with the two known species of *Euryblema* (Whitten *et al.*, 2005: 94). However, the recent examination of new living specimens of *C. thienii* revealed several morphological traits that are anomalous with respect to the diagnostic characters of the genus *Euryblema*. The leaf-sheaths of *Euryblema* are heavily spotted and blotched with purple, but this feature is absent in plants of *C. thienii*. The lip of *C. thienii* is deeply cymbiform and provided with a central, narrow callus, contrasting with the open lip of *Euryblema*, provided with a broad, laminar callus. Also, the pollinarium of *Euryblema* presents a large sagittate stipe and a ventrally distinct, ligular, thick stipe (Pupulin, 2007), while in *C. thienii* the stipe is small, shield-shaped, and the viscidium is a large but scarcely distinct gluing pad.

4. The use of molecular techniques has the benefic effect of remembering botanists that "new" species are nothing more that scientific hypotheses, while they provide a revolutionary method to test them. This is true, of course, not only for the complex of genera and species close to *Chondrorhyncha*, and not only because of DNA taxonomy. Although if frequently neglected, the need to compare morphological information with data sets from other disciplines (i.e., biochemistry, cytology, anatomy, ecology, etc.) has been generally recognized among the requisites of a good taxonomic practice. While revising Zygopetalinae specimens during a recent visit to Ecuador, I find a species that apparently does not fit any of the known genera related to *Chondrorhyncha*. The large, yellow flower has a distinctly 3-lobed lip with a laminar callus restricted to the center of the blade, while the pollinarium presents a very large viscidium provided with lateral teeth, and a cuspidate, sigmoid stipe, two features not previously recorded among the Zygopetalinae. On the basis of morphologic comparison, I strongly suspect that this finding not only represents a new species, but a still undescribed genus in the Zygopetalinae. Names into the "*Chondrorhyncha* complex" by far exceed the actual number of species, and it is perhaps advisable to refrain from the urgency to describe new taxa in this group without the necessary evidence. Now, we fortunately have more instruments to check our hypotheses, and as soon as permits to handle genetic material for DNA extraction will be issued by the Ecuadorian authorities, we will sequence this hypothetical new genus to place it into the phylogenetic framework of the Zygopetalinae and its closest relatives of the "*Huntleya* grade".

And what about *Chondrorhyncha*? It is unfortunate that, more than two centuries after the first western botanists discovered a plant of *Chondrorhyncha*, our knowledge of this genus is still very fragmentary due to the lack of available material for many of the taxa. We have now a better picture of what it is not a true *Chondrorhyncha*, and we can, by defect, infer some information about this genus. *Chondrorhyncha s.s.* is strictly South American in distribution, ranging from Venezuela to Bolivia along the western slopes of the Andes, with a probable dispersion center in northwestern South America, where most of the species have been recorded from Colombia and Ecuador. The actual number of *Chondrorhyncha* species is still amply debatable. We saw that *C. velastiguii*, still included into the genus, has to be segregated on the basis of a set of morphological characters. The same is true, in my opinion, for *C. fosterae* Dodson, a taxon likely misplaced in *Chondrorhyncha*. Although Dressler and Dalström (2004), in the first synopsis of *Chondrorhyncha s. str.*, reduced the genus to only five species, I would suggest that a figure of 7 to 9 species is probably close to the actual status of our knowledge. *Chondrorhyncha* species may be mainly characterized morphologically by the presence of a narrow, not fleshy callus near the middle of the lip, wide basally and tapering at apex, and by the pollinarium provided with a narrowly triangular-peltate stipe with the viscidium that becomes scarcely distinct toward the apical portion of the stipe.

The flowers of *Chondrorhyncha* are always resupinate, with the lateral sepals sometimes subfalcate and subuncinate at the apex, spreading-recurved to abruptly reflexed, concave, strongly inrolled-folded toward the base. The petals are obtuse and gentil recurved at apex. The lip, sometimes 3-lobed, is rounded-subsaccate at the base, with the apex obtuse to emarginate or minutely bilobed and the basal margins erect to flank the column.

The species of *Chondrorhyncha* occurs as shady epiphyte, mostly in evergreen premontane wet forests at 500-1800 meters of elevation along the eastern slopes of the Andes. Their flowering has been recorded throughout the year, with a flowering peak from January to July.

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