

**Phylogenetic and biogeography analysis of the species of
the genus *Notidocharis*
(Coleoptera: Leiodidae: Cholevinae: Leptodirini)**

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Abstract

The phylogenetic relationships among the seven species of the litter inhabiting genus *Notidocharis* Jeannel, 1956, endemic to the Cantabrian Range in northwest Spain, were investigated by cladistic analysis and two species groups originated by allopatric speciation were obtained. In view of the inferred phylogenetic tree and present-day distributional patterns, the probable biogeographic history of the genus is discussed in relation to Pleistocene glaciations and allopatric speciation.

Keywords: *Notidocharis*, biogeography, phylogeny, Spain.

Introduction

The classification of the Leptodirinae (= Bathysciinae) proposed by JEANNEL (1911; 1924) has been the subject of a number of recent revisions aimed at more accurately reflecting phylogeny (GUÉORGUIEV, 1976; CASALE *et al.*, 1991; GIACHINO & VAILATI, 1993; GIACHINO *et al.*, 1998; NEWTON, 1998; PECK, 1998a; PERREAU, 2000; SALGADO, 2000).

One recent change has been to join the genera *Notidocharis* Jeannel, 1956 and *Speonomidius* Jeannel, 1924 to form the section *Speonomidius* sensu Salgado 2000, restricted to the Cantabrian Range of northwest Spain and characterized by transverse elytral striae, a high and short mesosternal carina, and various characteristic structures of both the male and female genitalia (SALGADO, 2000).

The genus *Notidocharis* is of fundamental importance for understanding the phylogeny of the Cantabrian Leptodirinae (GIACHINO & SALGADO, 1989), as its distribution, morphological characteristics and habitat indicate that the group ancestor of this genus and of the different genera in the section *Quaestus* sensu Salgado 2000 lived in forest litter feeding as scavengers on yeast or other fungi and on various decay products. The present species of *Notidocharis* colonised moss strata humus and cave entrances, whereas the genera in the section *Quaestus*, undoubtedly their closest relative in the Cantabrian region, colonised the MSS (superficial underground environment) and MSP (deep underground environment). Similar to the the group ancestor of the genus *Bathysciola* and different genera in the section *Speonomus* sensu Jeannel 1924, it carried out the same process in the Pyrenean region as the present species of *Bathysciola* colonised moss strata humus and cave entrances, and the genera in the section *Speonomus* the MSS and MSP (SBORDONI *et al.*, 1982).

Currently, the genus *Notidocharis* is comprised of seven species occurring in detritus-rich microhabitats, largely in humus or under moss, although it is not uncommon to find some individuals close to the entrances of caves in organic substrates of various kinds, or even in caves at depths of up to 200 m. This is in contrast to the principally cavernicolous habitats of the species of the most closely related genera, such as *Speonomidius* Jeannel, 1924, *Leonesiella* Salgado, 1996 and *Quaestus* Schaufuss, 1861.

All the species of the genus *Notidocharis* are restricted to the Cantabrian region, and the collection records to date, though scarce, are sufficient to infer broad distributional patterns (Fig. 1). The degree of dependence of the species of this genus on environmental factors is little known, though they appear generally to occur mostly in ombrophilous vegetation on limestone substrates, and in mossy, subendogean or occasionally endogean habitats. Altitude appears to be an important determinant of the geographical distribution of some species, such as *N. zariquieyi* (Jeannel, 1924) which is widely distributed in the Cantabrian Range above 800 m altitude (TIZADO *et al.*, 1995), or *N. calabrezi* Giachino et Salgado, 1989 which has been found only in coastal-region sites (GIACHINO & SALGADO, 1989).

The present study used morphological, ecological and biogeographic data for two objectives: (1) to investigate the phylogenetic relationships among the species of the genus *Notidocharis*, with a view to future phylogenetic studies of other more complex groups, such as the genus *Quaestus*; and, (2) to infer historical distributional patterns and thus assess the likely role of environmental factors in the diversification of this genus. We have previously reported on the role of environmental factors in the diversification of other related groups in this region (SALGADO & LUIS, 1988; TIZADO *et al.*, 1997; TIZADO & SALGADO, 2000).

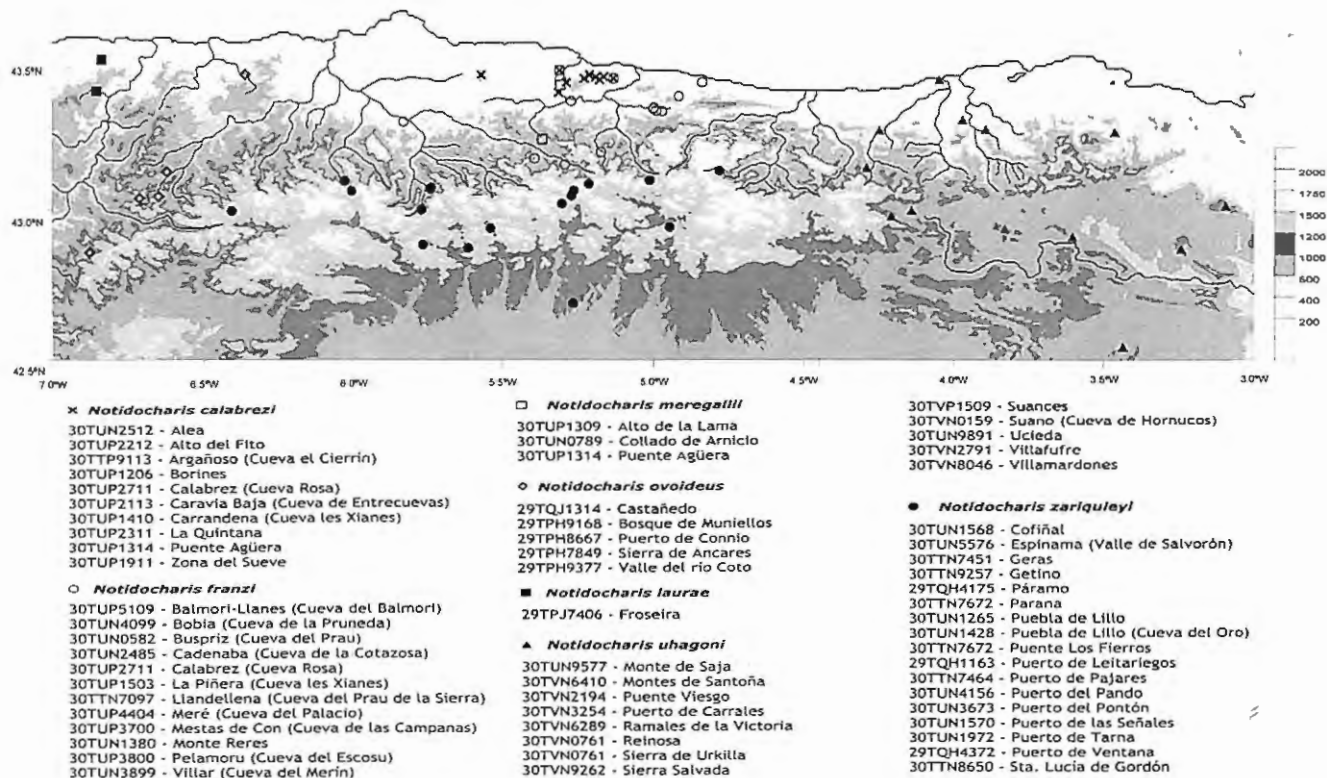


Fig. 1. Map showing distribution records (UTM coordinates and localities) for the species of the genus *Notidocharis*.

Material and methods

The specimen records included in the study were those reported by COMAS (1987), GIACHINO & SALGADO (1989), JEANNEL (1956), SALGADO & GIACHINO (1991), and TIZADO *et al.*, (1995), together with a number of unpublished records. These studies contain full descriptions of the seven known species of the genus *Notidocharis*: *N. calabrezi* Giachino et Salgado, 1989; *N. franzi* Jeannel, 1956; *N. laurae* Salgado et Giachino, 1991; *N. meregallii* Giachino et Salgado, 1989; *N. ovoideus* Jeannel, 1956; *N. uhagoni* (Sharp, 1872); and *N. zariquieyi* (Jeannel, 1924).

1. Morphological study

The morphological characters used for the phylogenetic study (Table 1) were those usually used for leiodids in related groups (JEANNEL, 1924; PECK, 1984, 1986, 1998b; PERREAU, 1989; CASALE *et al.*, 1991; GIACHINO *et al.*, 1998), and were selected after comparison with sister groups such as *Bathysciola*, *Ptomaphagus*, *Quaestus*, *Speonomidius*, *Speonemadus* and *Speonomus*.

Table 1. List of the characters considered in the cladistic analyses.

| Nº | Character | State 0 | State 1 |
|----|---|-----------------|-----------------|
| 1 | Body shape | ovoid | long |
| 2 | Eyes | reduced | absent |
| 3 | Antennae | short | long |
| 4 | Antennomeres II:XI length ratio | < 1 | > 1 |
| 5 | Antennomeres IX and X, shape | transverse | not transverse |
| 6 | Pronotum width:length ratio | = 1.8 | < 1.8 |
| 7 | Protarsus width:tibia ratio | < 1 | > 1 |
| 8 | Sutural striae | marked | indistinct |
| 9 | Mesosternal carina | short | long |
| 10 | Aedeagus, median lobe | straight | curved |
| 11 | Aedeagus, median lobe apex | rounded | truncated |
| 12 | Paramere | short | long |
| 13 | Paramere, all apical zone | undilated | dilated |
| 14 | Paramere, number setae | < 8 | > 8 |
| 15 | Paramere, width | thin | thick |
| 16 | Paramere, setae thickness | absent | present |
| 17 | Internal sac, structures sclerotized position | supraflagellate | infraflagellate |
| 18 | Internal sac, structures sclerotized | simple | complex |
| 19 | Internal sac, stylet | absent | present |
| 20 | Internal sac, piece Y | absent | present |
| 21 | Spermatheca, basal zone | undilated | dilated |

The outgroups chosen were *Bathysciola (B.) ovata* (Kiesenwetter, 1850), in the same biotypes as the species in the genera *Notidocharis* and *Speonomus (S.) longicornis* (Saulcy, 1872) in the troglobite environment. Both species belong to the tribe Leptodirini and are phylogenetically related to *Notidocharis*.

Morphological character states were assessed mainly by examination of male specimens, since they show more marked species differences than females do. A total of 21 characters were used (Table 1). The character illustrations used in this study can be seen in GIACHINO & SALGADO (1989) and SALGADO & GIACHINO (1991).

2. Phylogenetic and biogeographic analysis

The phylogenetic analysis was performed on the basis of the cladistic theory of HENNIG (1966), using Wagner parsimony method (KLUGE & FARRIS, 1969) for the construction of cladograms. The data matrix (Table 2) was analysed using the software Phylogeny Inference package PHYLIP version 3.63 (FELSENSTEIN, 2004).

Table 2. Data matrix used in the cladistic analyses, showing the state (see table 1) of each character in each species. Species codes: NC, *N. calabrezi*; NF, *N. franzi*; NL, *N. laurae*; NM, *N. meregallii*; NO, *N. ovoideus*; NU, *N. uhagoni*; NZ, *N. zariquieyi*; and outgroups (BO, *Bathysciola ovata*; SL, *Speonomus longicornis*).

| Species | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 |
|-------------|---|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|----|
| NC | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| NF | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 |
| NL | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| NM | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 |
| NO | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| NU | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| NZ | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 |
| Outgroup BO | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 |
| Outgroup SL | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 |

In view of the small number of species in the genus *Notidocharis*, we were able to use the branch-and-bound method to find all the most parsimonious trees. This method is implemented in the PHYLIP package in the program PENNY.EXE; in the execution we selected the following options: Mixed method? No; Parsimony method? Wagner; Outgroup root? Yes; branch and bound is simple? yes; how many groups of 100 trees? 1000; use threshold parsimony? no; use ancestral states in input file? no.

Biogeographical reconstruction (WILEY, 1981) of the genus *Notidocharis* was based on the cladistic approach of Hennig (cladistic biogeography), but taking into account the models of allopatric speciation (1) by geographical isolation that are characteristic of temperate continental regions (vicariance biogeography), and (2) capacities for dispersion and adaptation to new environments (dispersal biogeography).

Results and discussion

1. Phylogenetic analysis

Cladistic analysis by the Wagner parsimony method found 9 most parsimonious trees, each of 34 steps. The species of *Notidocharis* from *Bathysciola* and *Speonomus* (concordance 100%) appear independently on all the trees, underlining the monophyletism of this genus. This separation was associated with changes to the state of characters 2, 17 and 20. Also, it is interesting point out that the presence of a stylet in the internal sac (character 19) appears in several lineages of *Notidocharis* and should probably be treated as a convergence.

The extended majority rule consensus tree (Fig. 2) indicates two species groups supported by a concordance of 100%: A) *N. calabrezi* and *N. uhagoni*, and B) *N. zariquieyi*, *N. laurae*, *N. ovoideus*, *N. meregallii* and *N. franzi*. Also, there is 100% of concordance in the line formed by *mergallii* and *franzi* in group B.

The separation of the species of Group A and B is associated with the modification of the median lobe of the aedeagus (character 10): curved in Group A, versus straight in the species of Group B; the paramere setae (characters 14 and 16): few in number, with marked differences in width in Group A, versus more abundant and of more uniform width in Group B; and paramere shape (characters 13 and 15): dilated apical zone and thick width in Group A, versus undilated apical zone and thin width in Group B.

In the phylogenetic analysis of the species of *Notidocharis*, a number of characters are clearly associated, allowing the identification of three principal character groups: (a) the spermatheca of the female genitalia (character 21), internal sac and stylet of male genitalia (characters 17–20), (b) the apical morphology and setae of the parameres (characters 12–16), and (c) the median lobe of the aedeagus (characters 10 and 11). Indeed, these characters are practically sufficient to explain the diversification of the *Notidocharis* species.

2. Biogeographic implications

Our hypothesis of the biogeographical history of the genus *Notidocharis* is based on three assumptions: (1) the biogeographical history of the Iberian Leptodirinae started as part of the east-to-west invasion of Western Europe (SALGADO, 1976); (2) during the glaciations, the snowline in this region was probably located at about 800 m altitude (VALCÁRCEL *et al.*, 1996), suggesting that the wet habitats favored by the ancestors of this genus must have been close to the coast, below 200-300 m altitude (RODRÍGUEZ-GUITIÁN *et al.*, 1995); and (3) the favored habitats of the current species of the genus *Notidocharis* are detritus-rich microhabitats in ombrophilous vegetation on limestone substrates. Thus the original environment of this group may be similar to present-day ombrophilous beechwoods.

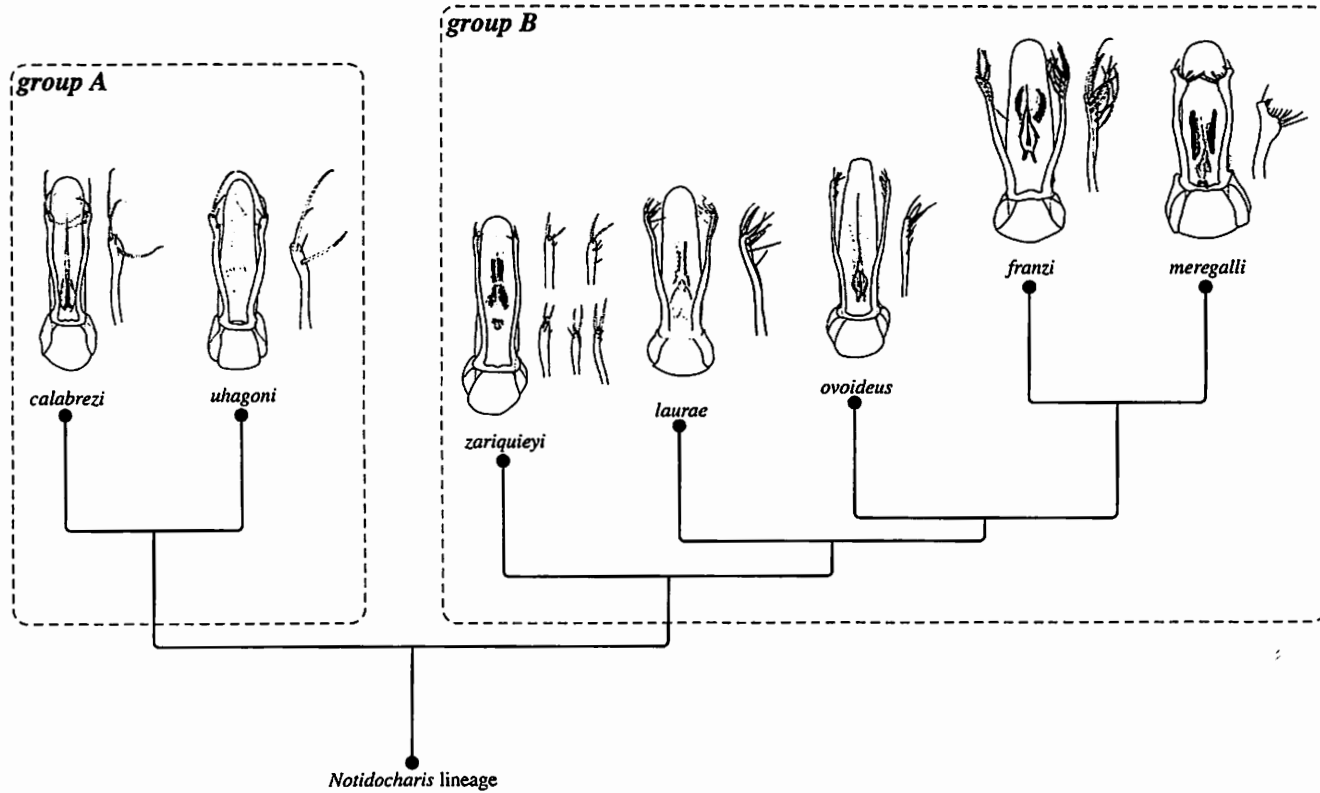


Fig. 2. Phylogenetic tree for the genus *Notidocharis*, inferred on the basis of the consensus tree obtained by Wagner parsimony. Branch lengths is proportional to concordance percent of consensus tree. The two principal groups within the genus (A and B) are delimited with dotted lines.

The range expansions of the ancestral forms probably occurred during various glaciation periods, starting from initial refuge areas such as valley bottoms (BELLÉS, 1987) or transitional wet habitats (PECK, 1998b). At that time, the ancestors of *Notidocharis* occupied the ombrophilous woodlands of the foothills of the Cordillera del Sueve, currently home of three of the seven known species of this genus, and to the west of the Picos de Europa, that is a major geographical barrier, since the snowline in this region would have been very close to the coast during glaciations.

The climatic changes that occurred during the Pleistocene, with the alternation of glacial and interglacial periods, gave rise to cyclic changes in the extent of humus-rich habitats related with ombrophilous vegetation. The populations of various species of *Notidocharis* had distributions which are expected to have varied considerably, including periods of marked fragmentation.

When the snowline rose during interglacial periods, several types of ombrophilous vegetation would have extended their ranges. This geographic increase of favourable litter-layer environments would have encouraged climatic vicariance and speciation of this genus, giving rise to the two main clades of the phylogenetic tree by means of allopatric speciation: the ancestor of Group A would have occupied the drier mesophilous woodlands (*Quercus*, *Corylus*, *Carpinus*, *Acer*, *Castanea*, etc.) at lower altitudes; the ancestor of Group B would have occupied wet ombrophilous woodlands (*Fraxinus*, *Salix*, *Populus*, *Fagus*, etc.) at relatively high altitudes.

During glacial times, ombrophilous vegetation masses retreated to lower altitudes, and *Notidocharis* populations went with them. This can be expected to have enabled dispersion between adjacent watersheds along the coast. During the interglacial periods, on the other hand, ombrophilous vegetation types will have returned to higher altitudes, isolating the different watersheds. This would explain the allopatric speciation processes thought to have occurred within Group B, by isolation of the populations of the *franzi-meregallii* lineage in areas close to River Sella, from the populations of the *ovoideus* and *laurae* lineages in areas close to the confluence of the Rivers Narcea and Navia, and of the populations of the *zariqueyi* lineage with a markedly orophilous distribution.

The drier vegetation masses occupied by the ancestors of Group A would likewise have undergone cycles of expansion and contraction, though the resulting fragmentation would perhaps have been less marked than in the valley bottoms. The dispersion of these was blocked to the south by the presence of wetter habitats and to the north by the sea, so that dispersion from the Cordillera del Sueve would only have occurred to the east and to the west. *N. calabrezi* would have moved towards the west, close to the coast, and currently occurs between the lower Sella watershed and the River España. In contrast, the zones to the east of the northern Picos de Europa would probably have been more favourable for colonization by *Notidocharis*, as a result of large expanses of the drier submediterranean beechwoods, permitting isolation and a rapid expansion of *N. uhagoni* towards the Pyrenean area.

Conclusions

The taxonomy of the extant members of the genus *Notidocharis* can be characterized in terms of specializations of the male genitalia: the median lobe of the aedeagus and the structures of the internal sac and the parameres. Currently, these specializations can be assumed to impede interbreeding, though of course it is unlikely that they were the primary cause of the genetic isolation that promoted the original speciations.

Speciation in many troglobite insect groups appears to have been due to allopatric processes (PECK, 1998b). The principal groups of the genus *Notidocharis* (A and B) appear to have originated as a result of allopatric processes by vicariance on populations living in different habitats without any migration barrier between them; possibly due to the appearance or expansion of new environments in a restricted area with marked altitudinal gradients (the northern slopes of the Cantabrian Range).

Allopatric processes by geographic isolation may have played an important role in the following speciation processes within Groups A and B, as a result of separation of river basins and by mountain ranges, giving rise to fragmentation of humus-rich habitats in karstic limestone areas colonized by the genus *Notidocharis*. This fragmentation provides a plausible explanation for the historical and current biogeography of the extant species of genus *Notidocharis*.

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