

# Phylogeny of the neotropical rove beetle genus *Nordus* (Coleoptera: Staphylinidae) with a special reference to the evolution of coloration and secondary sexual characters

STYLIANOS CHATZIMANOLIS

Natural History Museum and Biodiversity Research Center, The University of Kansas, Lawrence, U.S.A.

**Abstract.** A phylogenetic analysis for *Nordus* is provided; the monophyly of the genus is established and the phylogenetic relationships of its thirty-eight species are resolved. Analysis of eighty-seven morphological characters, including two coloration characters, produced four equally most-parsimonious trees (tree length = 365, consistency index = 0.38, retention index = 0.66). The coloration of the head and thorax is examined in the context of the reconstructed phylogeny and the evolution of heterochromy is discussed. Golden-orange coloration of the head and thorax evolved in the ancestor of *Nordus*. Black coloration of the head evolved at least five times, and black coloration of the thorax at least six times within the genus. The evolution of secondary sexual structures in *Nordus* is also examined in the context of the phylogeny. In males, a medial emarginate abdominal sternum VIII is the ancestral condition. The presence of a single large median lobe on sternum VIII or the presence of two elongate median lobes with a medial emargination on sternum VIII each represent independent evolution of modifications to the male sternum VIII in different lineages. In females, an unmodified abdominal sternum VIII is the ancestral condition. Evolution of an emargination, small lobe or pointed lobe on the margin of sternum VIII in females occurred in different lineages.

## Introduction

The evolution of coloration in insects has been studied primarily among populations of the same species or among sympatric individuals of the same species (e.g. Harris, 1991; Forsman & Appelqvist, 1999; Merilaita, 2001; Andrés *et al.*, 2002; Sword, 2002). Fewer studies have investigated the interspecific evolution of colour patterns. These studies have focused primarily on butterflies (e.g. Descimon, 1986; Brower, 1996; Jiggins *et al.*, 2001; McMillan *et al.*, 2002) and *Drosophila* (Hollocher *et al.*, 2000a, b; Wittkopp *et al.*, 2002), although there are some investigations for other orders such as true bugs (Zrzavý, 1990; Zrzavý &

Nedvěd, 1997, 1999) and Phasmatodea (Crespi & Sandoval, 2000). Despite the fact that beetles exhibit dramatic colour variations (Evans *et al.*, 2000), there have been few studies about the evolution of the coloration in a phylogenetic context (Okamoto *et al.*, 2001; Robertson *et al.*, 2004).

The genus *Nordus* Blackwelder, 1952 (Fig. 1A, B) contains thirty-eight species and was recently revised by Chatzimanolis (2004). *Nordus* is distributed from southern Mexico to northern Argentina, with the highest species diversity in South America, especially in Ecuador, Peru and Bolivia. The genus belongs to the subtribe Xanthopygina (of the staphylinine tribe Staphylinini), a group of colourful and rather large (up to 2.5 cm) rove beetles. Among all genera in the subtribe, *Nordus* exhibits probably the most dramatic structural modifications in secondary sexual characters (on abdominal sterna VII, VIII and IX) and in the coloration of different species. The colour of the abdomen is always black (except in *N. portokalis*, where it is orange) with a bright yellow apex (part of segment VII and segment VIII). There are several different colour patterns in

Correspondence: Stylianos Chatzimanolis, Division of Entomology, Natural History Museum and Biodiversity Research Center, and Department of Ecology and Evolutionary Biology, The University of Kansas, Lawrence, KS 66045-7523, U.S.A. E-mail: chatzimanolis@yahoo.com

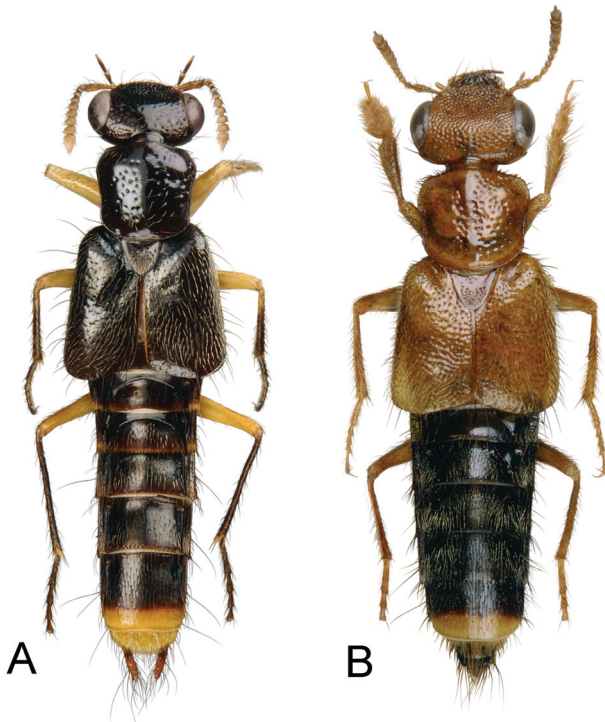


Fig. 1. A, *Nordus cherylae*; B, *N. elytisi*

*Nordus*; most species have (probably aposematic) golden-orange coloration on the head, pronotum and elytra (Fig. 1B). Other species have the pronotum and elytra golden-orange, and the head anteriorly black and posteriorly orange, or head, pronotum and elytra are black (Fig. 1A), whereas one species, *N. speciosus*, has the head, pronotum and elytra metallic green.

The purpose of this paper is to provide a phylogenetic analysis including all species of *Nordus*, and discuss the evolution of coloration and secondary sexual structures in the context of a phylogenetic analysis.

## Materials and methods

### Species selection

All species of *Nordus* currently recognized, based on the revision of the genus (Chatzimanolis, 2004), were included in the phylogenetic analysis. For most species, a large series of specimens was available; in most cases more than thirty specimens were examined for each species. Specimens for study were loaned from the following institutions: American Museum of Natural History, New York (L. Herman) (AMNH); The Natural History Museum, London (M. Brendell) (BMNH); California Academy of Sciences, San Francisco (D. Kavanaugh) (CASC); Canadian National Collection, Ottawa (A. Davies) (CNCI); Centro de Estudios en Zoología CUCBA, Universidad de Guadalajara, Zapopan, Mexico (J. Navarrete Heredia) (CZUG); Deutsches

Entomologisches Institut, Eberswalde, Germany (L. Zerche) (DEIC); Field Museum of Natural History, Chicago (A. Newton, Jr., M. Thayer) (FMNH); INBio, Santo Domingo de Heredia, Costa Rica (INBC); Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium (D. Drugmand) (ISNB); Museum of Comparative Zoology, Harvard University, Cambridge (P. Perkins) (MCZC); Naturhistorisches Museum Wien, Vienna, Austria (H. Schilhammer) (NMW); Snow Entomological Collection, Natural History Museum/Biodiversity Research Center, University of Kansas, Lawrence (J. S. Ashe) (SEM); Museo de Historia Natural, Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá (UNCB); University of Nebraska State Museum, Lincoln (B. Ratcliffe) (UNSM); National Museum of Natural History, Washington, DC (T. Erwin) (USNM); Zoological Museum, University of Copenhagen, Copenhagen (O. Martin) (ZMUC); Museum für Naturkunde der Humboldt-Universität, Berlin (M. Uhlig, J. Frisch) (ZMHB).

The selection of outgroup taxa was not straightforward because phylogenetic relationships of genera in the subtribe Xanthopygina are not known. Sharp (1876) hypothesized that *Nordus* may be related to the genera *Plociopterus* and *Elmas*. Exemplar species from the genera *Allosthenopsis*, *Elmas*, *Plociopterus*, *Xanthopygus* and *Xenopygus* (all currently included in the subtribe Xanthopygina) were used as outgroups, selected because of the hypothesized close relationship with *Nordus* and because this cluster of genera has been used as outgroups in the species-level phylogenies of *Elmas* (Ashe & Chatzimanolis, 2003) and *Philothalpus* (Chatzimanolis & Ashe, unpublished data).

### Character selection

In total, eighty-seven characters (eighty-five characters from adult morphology, including two from coloration) and 227 character states were recorded (Appendix 1). Detailed illustrations of most characters can be found in the revision of this genus (Chatzimanolis, 2004). Larval characters were not considered because the larva is only known for *N. fungicola* (Chatzimanolis, in press). Reductive coding (Strong & Lipscomb, 1999) was used to access the primary homology of characters in the secondary sexual structures (characters 62–74) and genitalia (characters 75–85), but multistate characters were also coded 1. All multistate characters were treated as unordered (nonadditive) and all characters given equal weight. Characters were recorded from both sexes except those concerning genitalia and secondary sexual features. No males are known for *N. longipes* and *N. stomachoponos*, whereas no females are known for *N. aeneiceps*, *N. periergos*, *N. picticornis*, and *N. testaceus*. All characters were observed from dead dried specimens. Thorax colour (character 87) was treated as one rather than two characters (coloration of pronotum and elytra) because a preliminary analysis showed no effect on the tree topology. Dried specimens were relaxed first in warm soapy water, then apical abdominal segments

containing the aedeagus were dissected. Mouthparts of selected individuals were also dissected for study and scanning electron micrography. The apical abdominal segments were cleared using 10% KOH, and the aedeagus removed for study. Body structure, mouthparts and aedeagi were studied using an Olympus SZ-60 dissecting microscope. Scanning electron micrographs were taken using a LEO 1550 field scanning electron emission microscope. Photographs were prepared using a Microptics ML-1000 digital imaging system. The relative size and density of punctures on the head, pronotum and elytra were expressed in terms of the average number of punctures in a transverse linear distance of 0.3 mm measured in the middle of the upper right quadrant of the appropriate body part (frons of head, pronotum or right elytron). Terms for structural features follow Blackwelder (1936), Smetana & Davies (2000) and Ashe & Chatzimanolis (2003).

### Phylogenetic analysis

The data matrix (Appendix 2; WINCLADA file available as Supplementary Material) was created in WINCLADA (Nixon, 1999–2002) and analysed with the parsimony ratchet (Nixon, 1999) as implemented in NONA (Goloboff, 1999). The parsimony ratchet was executed with the following commands '200 iterations per replication', '2 trees to hold per replication' and '9 characters to sample'. The commands *max\**, *unique* and *best* in NONA produced the same results as the parsimony ratchet. Bremer support values were calculated in NONA using the commands *hold 15000*, *suboptimal 20*, *bsupport 10*. Bootstrap values were calculated using NONA executed from WINCLADA, using 1000 replications.

### Results

The analysis resulted in four equally most-parsimonious trees, lengths 365 steps, consistency index (CI)=0.38 and retention index (RI)=0.66. The strict consensus of these trees is shown in Fig. 2 and one of the four most-parsimonious trees with DELTRAN (slow) character optimization is shown in Fig. 3. The four trees differ only in the placement of (*P. fetialis* + *E. hanleyi*) and in the placement of *N. velitaris*. In two trees (*P. fetialis* + *E. hanleyi*) is placed as the sister group to *Nordus*, whereas in the other two (*P. fetialis* + *E. hanleyi*) is placed as the sister group of (*Xen. analis* + *Nordus*). *Nordus velitaris* is the sister group to the clade ((*N. diversiventris* + (*N. styloceros* + (*N. amazonicus* + *N. batesi*))) + ((*N. solitarius* + *N. testaceus*) + ((*N. omios* + *N. terminalis*) + (*N. maculiceps* + *N. xanthocerus*))) in two trees, whereas it is the sister group of ((*N. solitarius* + *N. testaceus*) + ((*N. omios* + *N. terminalis*) + (*N. maculiceps* + *N. xanthocerus*))) in the other two.

The monophyly of *Nordus* is supported by seventeen unambiguous synapomorphies and high Bremer support (10) and bootstrap values (100%). These synapomorphies

are: 3-2, antennal article 1 gradually clublike thickened, but becoming smaller at distal end; 9-1, antennal article 5 longer than article 6 (becoming 9-2 in the ((*N. maculiceps* + *N. xanthocerus*) + (*N. omios* + *N. terminalis*)) and (*N. aeneipennis* + (*N. zischkai* + (*N. portokalis* + (*N. elegans* + (*N. cherylae* + *N. speciosus*)))) clades and in *N. stomachoponos*, *N. facialis*, *N. championi* and *N. fungicola*); 13-1, antennal article 11 with one row of macrosetae except those on tip; 15-1, microtrichiae on antennal article 5 absent; 20-1, punctures on anterior part of epicranium confluent; 24-2, punctures on posterior part of epicranium less dense than those on anterior part; 25-1, punctures on posterior part of epicranium larger than those on anterior part; 33-1, distinctive shape of labrum; 46-2, punctures on scutellum cover posterior three-quarters of surface (becoming 46-3 in *N. championi*, *N. fungicola*, *N. facialis*, *N. omios*, *N. portokalis* and *N. terminalis*); 47-1, micropunctures on metepimeron absent; 51-1, tarsomeres 2–4 of middle and hind tarsi lobed; 53-1, setae on third abdominal tergum absent or less than five; 59-2, shape of distal margin of sternum VII in males with well-defined emargination (becoming 59-3 in *N. styloceros*); 73-1, shape of distal margin of sternum IX in males with two apical processes (becoming 73-2 in the clades (*N. densiventris* + (*N. semelius* + *N. periergos*)) and (*N. elegans* + (*N. cherylae* + *N. speciosus*)) and in *N. cribricollis*, *N. velitaris*, *N. amazonicus* and *N. batesi*); 81-2, paramere in lateral view slightly convex (character state modified in many species, see Fig. 3 for details); 86-1; colour of head orange (modified in some species; see Fig. 4 for details) and 87-1, colour of thorax orange (modified in some species; see Fig. 5 for details).

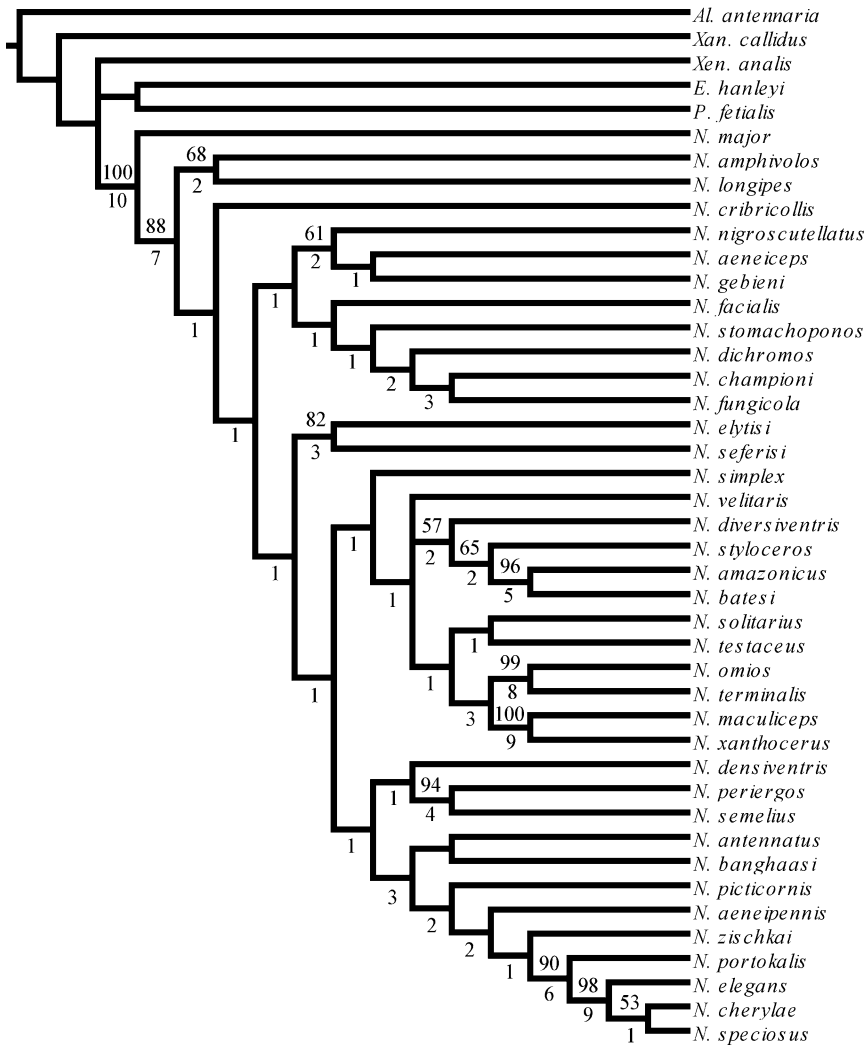
The performance of different character suites (characters from antennae, head, thorax, abdomen, genitalia and coloration) based on CI and RI measures is shown in Table 1. The CI and RI shown in Table 1 for each suite of characters are the arithmetic means of the individual CI and RI of each character constituting a specific suite.

### Discussion

#### Systematics

The sister-group relationships of most species are supported by multiple synapomorphies and high Bremer support values (Fig. 2). *Nordus major* is sister to all remaining *Nordus* species. The overall shape of the head, which exhibits great allometric variation in proportion to the size of the pronotum, resembles the overall shape of the head in species of the genus *Xanthopygus*. This species, of course, is clearly a member of *Nordus* because it has all the above-mentioned synapomorphies, but it has probably retained the plesiomorphic general shape of the head.

The phylogenetic results support the hypothesis that *Nordus* originated in South America; and most species are distributed in South America. Few species are found in Central America (Appendix 3 and Chatzimanolis, 2004) with *N. championi* and *N. terminalis* restricted to that area.



**Fig. 2.** The strict consensus tree of the four equally most-parsimonious trees. The numbers above the branches are bootstrap values (only bootstrap values >50 are shown) and the numbers below the branches are Bremer support values

*Nordus fungicola* and *N. solitarius* occur in both Central America and northern South America. *Nordus diversiventris*, *N. stomachoponos* and *N. omios* are distributed marginally in southernmost Central America (Darién, Panama). A detailed discussion on the biogeography of *Nordus* and other xanthopygine genera will be presented elsewhere (Chatzimanolis, in preparation).

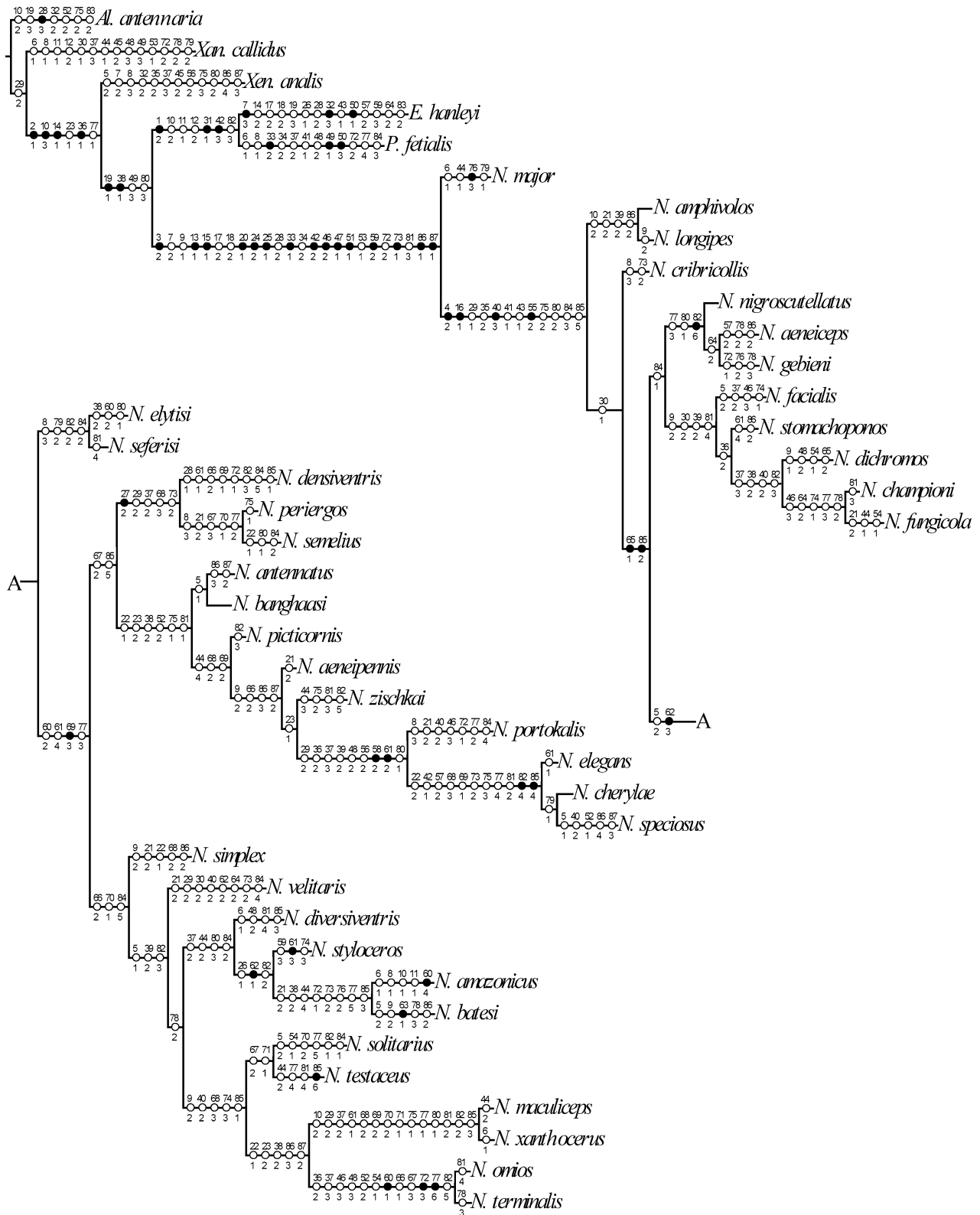
#### Evolution of abdominal sternum VIII

The abdominal sternum VIII in males can have three basic forms (character 62): the hind margin of the sternum can be medially emarginate; it can have a single large median lobe; or it can have two medial lobes that have an emargination between them. These three basic forms have a plethora of variants, as is obvious from the subsequent characters in Appendix 1. The medial emargination appears to be the ancestral form because it is found in the outgroups and in the following taxa or clades of

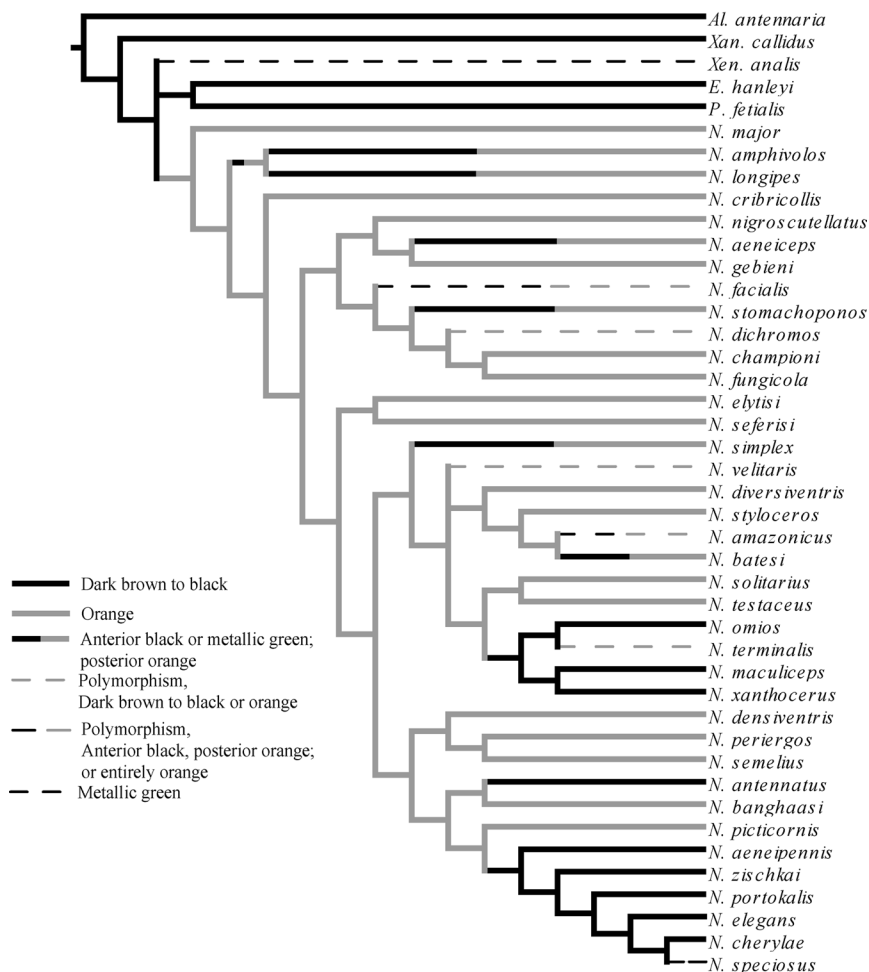
*Nordus*: *N. major*, *N. amphivolos* (no males are known for *N. longipes*), *N. velitaris*, and in the clade ((*N. cribricollis* + (*N. nigroscutellatus* + (*N. aeneiceps* + *N. gebieni*))) + (*N. facialis* + (*N. stomachoponos* + (*N. dichromos* + (*N. championi* + *N. fungicola*))))).

The form with the single large median lobe is found only in the clade (*N. styloceros* + (*N. amazonicus* + *N. batesi*)). The rest of the species have variations of the form with the two median lobes that have an emargination between them.

In females, there are four possible forms for the hind margin of sternum VIII. It can be either unmodified (i.e. not particularly produced and evenly convex), sinuate, strongly pointed, or have a small lobe. The basal form is unmodified, as found in the outgroups; the species mentioned above for sternum VIII with emargination in males (except *N. stomachoponos* and *N. velitaris* that have the small lobe), in *N. densiventris*, in (*N. elytisi* + *N. seferisi*), in *N. elegans* and in (*N. maculiceps* + *N. xanthocerus*). The sinuate form is found in *N. portokalis* and in (*N. speciosus* + *N. cherylae*); the strongly pointed form is



**Fig. 3.** One of the four most-parsimonious trees. The numbers above the hatchmarks refer to characters. The numbers below the hatchmarks indicate state transformation (to the state indicated). Homoplasious characters are indicated with open hatchmarks. Tree length = 365, consistency index = 0.38, retention index = 0.66



**Fig. 4.** The strict consensus tree with character 86 (coloration of the head) mapped on the tree. See text for more details

found only in *N. styloceros*. The remainder of the species have the form with the small lobe.

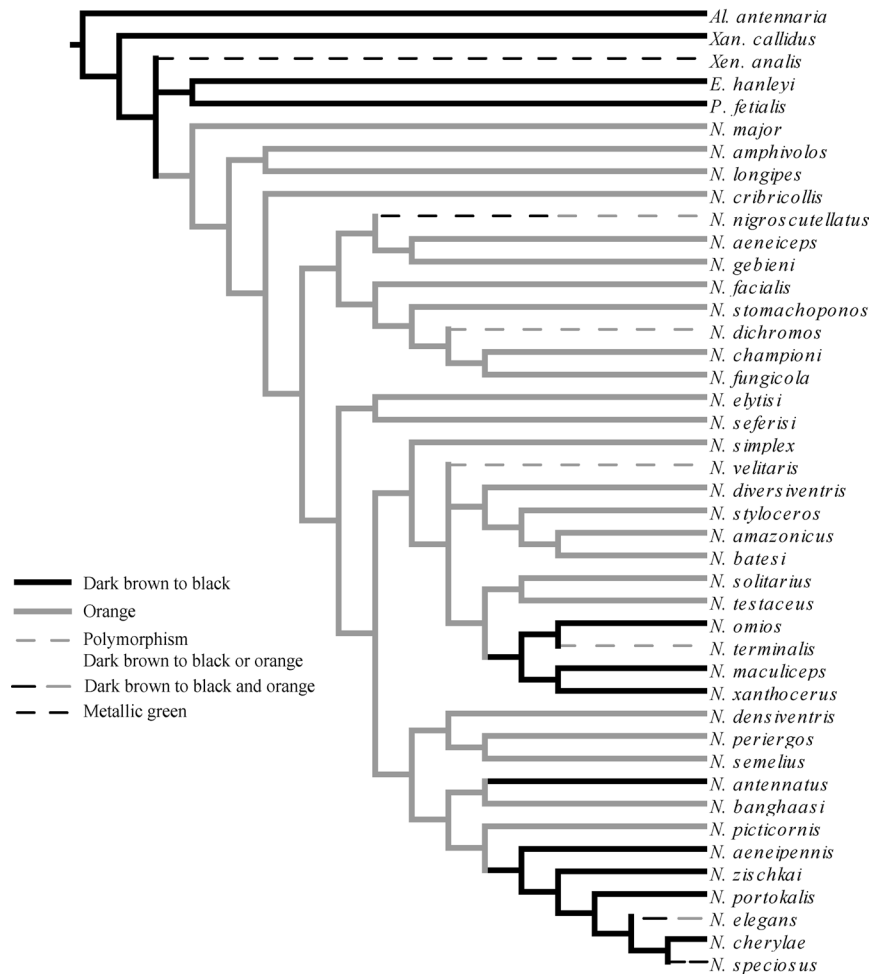
It appears that when the hind margin of sternum VIII in males is emarginate, the hind margin of sternum VIII in females is usually unmodified. This is true for most species with these kinds of structures, but not for all. Similarly, it appears that when the hind margin of sternum VIII in males has two lobes with an emargination between them, the hind margin of sternum VIII in females has a small lobe, but again, this is not true for all species with these structures. In *N. styloceros*, the hind margin of sternum VIII in males (Chatzimanolis, 2004: fig. 91) is modified to the extreme and the large lobe has been modified to a long forklike structure that extends almost as long as one-half the length of sternum VIII beyond the apex of the hind margin. In females, the hind margin of sternum VIII as described above is also strongly pointed (Chatzimanolis, 2004: fig. 120).

These modifications of sternum VIII are probably linked to mating behaviour. During mating, males bend sterna VI–VIII downwards and the shape of sternum VIII in both sexes is probably correlated. Needless to say, no real conclusions about the function of sternum VIII can be made

without detailed behavioural observations. Mating observations exist only for *N. fungicola* (Chatzimanolis, 2003); it has sternum VIII emarginate in males and unmodified in females, but observations are needed in species with different forms of sternum VIII.

#### *Evolution of coloration*

There is a debate about whether characters under investigation (such as the coloration of particular structures) should be included in a phylogenetic analysis (reviewed in de Queiroz, 2000). I chose to include two coloration characters in this phylogenetic analysis because the best conclusions about character evolution must be based on the best estimate of phylogeny, which must be based on all available data (de Queiroz, 2000). De Queiroz (2000) also mentioned that it is logical to include the characters of interest, because they 'provide evidence about the phylogenetic relationships of the taxa in which they occur and thus also about their own evolution'.



**Fig. 5.** The strict consensus tree with character 87 (coloration of the thorax) mapped on the tree. See text for more details

On the other hand, ‘total evidence’ approaches have often been criticized as circular and inappropriately influencing the analysis. It is stated that including the characters of interest will influence the decision (under a maximum parsimony algorithm), as under parsimony, total homoplasy is minimized, including the characters of interest. For *Nordus*, however, such criticisms are not valid; a preliminary phylogenetic analysis without the two colour characters yielded exactly the same information about the evolution of these characters. The presence of colour char-

acters in the analysis does not change the sister-group relationships among species of *Nordus*; inclusion of colour characters improves the resolution of the tree in some clades. In addition, there are multiple origins (instead of one) of the black or golden-orange coloration, both on the head and thorax (Figs 4, 5).

Three species have multiple colour morphs: *N. dichromos*, *N. terminalis* and *N. velitaris*. *Nordus terminalis* has three morphs: a morph with a golden-orange head, pronotum and elytra, a morph with a black head, pronotum and

**Table 1.** Homoplasy levels among different suites of characters.

Character suite	Character number	Consistency index	Retention index
Antennae	1–15	0.60	0.64
Head	16–30, 32	0.57	0.63
Thorax	35–48	0.42	0.67
Abdomen	52–74	0.43	0.63
Genitalia	75–85	0.39	0.53
Coloration	86–87	0.30	0.61

elytra and a morph with a golden-orange head and pronotum and a black elytra. *Nordus dichromos* has two morphs with either a golden-orange or black head, pronotum and elytra. *Nordus velitaris* also has two morphs: one with a black head, pronotum and elytra, and one with a golden-orange head and pronotum and a black elytra. The different colour morphs are allopatric for each species. It is not clear why these species include heterochromatic individuals; Chatzimanolis (in press) mentioned some differences in elevation for different colour morphs: the golden-orange morphs tend to be in the lowlands, whereas the darker-coloured morphs are usually found at elevations above 900 m. Furthermore, there might be differences in habitat preferences, but only detailed field observations can illuminate the reasons for these multiple colour morphs. Field observations of *N. fungicola* (Chatzimanolis, 2000,2003) reveal that these brightly coloured insects, unlike most staphylinid beetles, are very visible and active on rotting fruits and mushrooms, instead of being hidden in the substrate.

The phylogeny in Figs 4 and 5 shows that the probably aposematic golden-orange coloration evolved in the ancestor of *Nordus*, although it is not clear whether this happened in the immediate ancestor of *Nordus*, or is shared with other genera, because the phylogenetic relationships among xanthopygines are unknown.

The coloration of the head (Fig. 4) can be entirely golden-orange, entirely black, anteriorly black (or metallic green) and posteriorly golden-orange, or metallic green. The black coloration has evolved at least five times: in (1) *N. dichromos*, (2) *N. velitaris*, (3) the clade of ((*N. omios* + *N. terminalis*) + (*N. maculiceps* + *N. xanthocerus*)), (4) *N. antennatus*, and (5) in the clade of (*N. aeneipennis* + (*N. zischkai* + (*N. portokalis* + (*N. elegans* + (*N. cherylae*))))). *Nordus speciosus*, the sister group of *N. cherylae*, has metallic green coloration, both on the head and the thorax. In addition, there are multiple species (see Fig. 4) that have a head with the anterior part black and the posterior part golden-orange. The golden-orange coloration has evolved at least twice, in the ancestor of *Nordus* and in *N. terminalis*.

On the thorax (Fig. 5), black coloration has evolved at least six times, in the species mentioned above for the black coloration of the head and in *N. nigroscutellatus*. Golden-orange coloration has evolved at least three times, in the ancestor of *Nordus*, in *N. terminalis* and in *N. elegans*. This discussion about the evolution of coloration will be more meaningful when detailed behavioural observations are available for a number of species, including those that exhibit heterochromy. It will be interesting to know if colour change correlates with behaviour, habitat, or the presence/absence of other species.

In other studies on the evolution of coloration in Coleoptera, Okamoto *et al.* (2001) found no link between coloration and phylogeny in the genus *Ceroglossus* (Carabidae); instead they found a link between coloration and geography. More recently, Robertson *et al.* (2004) examined the evolution of colour patterns in Erotylidae. They did not specifically study the evolution of different colours, but rather the evolution of

different colour patterns on the elytra and pronotum. They claim that according to their data, no general trends can be found between colour patterns across higher-level Erotylidae lineages and feeding habitats or host preferences.

*Nordus* is an excellent organism to study the evolution of pigmentation patterns and sexually selected traits in the last abdominal segments. The phylogeny presented here can provide historical context to future behavioural experiments, even though, as yet, the function of the traits is unknown. Furthermore, work in progress on the phylogeny of Xanthopygina and species-level phylogenies on related genera (e.g. *Plociopterus*) with similar interspecific variations in coloration will greatly improve our understanding of the evolution of coloration in these beetles.

### Supplementary material

The Winclada file is available at: <http://www.blackwellpublishing.com/products/journals/suppmat/SEN/SEN274sm.htm>

### Acknowledgements

I thank J. S. Ashe, C. D. Michener, M. S. Engel and C. A. Murphy for comments and support throughout this project. I thank A. Solodovnikov and an anonymous reviewer for helpful comments. I am also grateful to the curators of the museums listed in the Materials and methods section for the loan of specimens. Darci Kampschroeder took the habitus photographs and did the artwork for Fig. 1. Financial support was provided by an Ernst Mayr Travel Grant from the Museum of Comparative Zoology, Harvard University; a Panorama Grant, Natural History Museum/BRC, University of Kansas; numerous H. B. Hungerford Grants from the program of Entomology, Department of Ecology and Evolutionary Biology, University of Kansas; the Snow Entomological Development Fund from the Division of Entomology, Natural History Museum/BRC, University of Kansas; a 10 week graduate fellowship from the Smithsonian Institution; a Collection Study Grant from the American Museum of Natural History; a Sigma-Xi Grant In Aid of Research; and by NSF PEET Grants (DEB-9521755 and DEB-9978110) awarded to J. S. Ashe. This is contribution number 3388 from the Snow Entomological Collection, Division of Entomology, Natural History Museum, University of Kansas.

### References

- Andrés, J.A., Sánchez-Guillén, R.A. & Cordero Rivera, A. (2002) Evolution of female colour polymorphism in damselflies: testing the hypotheses. *Animal Behaviour*, **63**, 677–685.
- Ashe, J.S. & Chatzimanolis, S. (2003) A revision of the genus *Elmas* Blackwelder, 1952 (Coleoptera: Staphylinidae: Staphylininae: Xanthopygina), with a preliminary reconstructed phylogeny of the species. *Scientific Papers, Natural History Museum, University of Kansas*, **28**, 1–41.

- Blackwelder, M. (1936) Morphology of the coleopterous family Staphylinidae. *Smithsonian Miscellaneous Collections*, **94**, 1–102.
- Blackwelder, M. (1952) The generic names of the beetle family Staphylinidae, with an essay on genotypy. *United States National Museum Bulletin*, **200**, 1–483.
- Brower, A.V.Z. (1996) Parallel race formation and the evolution of mimicry in *Heliconius* butterflies: a phylogenetic hypothesis from mitochondrial DNA sequences. *Evolution*, **50**, 195–221.
- Chatzimanolis, S. (2000) An association between *Ptecticus nigrifrons* (Diptera: Stratiomyidae) and *Nordus fungicola* (Coleoptera: Staphylinidae). *Journal of the Kansas Entomological Society*, **73**, 232–234.
- Chatzimanolis, S. (2003) Natural history and behavior of *Nordus fungicola* (Coleoptera: Staphylinidae). *Annals of the Entomological Society of America*, **96**, 225–230.
- Chatzimanolis, S. (2004) A revision of the neotropical genus *Nordus* Blackwelder (Coleoptera: Staphylinidae: Xanthopygina). *Entomologische Abhandlungen*, **62**, 3–64.
- Chatzimanolis, S. (in press) The larva of *Nordus fungicola* (Sharp) (Coleoptera: Staphylinidae) with notes on natural history. *Deutsche Entomologische Zeitschrift*.
- Crespi, B.J. & Sandoval, C.P. (2000) Phylogenetic evidence for the evolution of ecological specialization in *Timema* walking sticks. *Journal of Evolutionary Biology*, **13**, 249–262.
- de Queiroz, K. (2000) Logical problems associated with including and excluding characters during tree reconstruction and their implications for the study of morphological character evolution. *Phylogenetic Analysis of Morphological Data* (ed. by J. J. Wiens), pp. 192–212. Smithsonian Institution Press, Washington.
- Descimon, H. (1986) L'évolution de la colouration chez les Charaxidae néotropicaux: stratégies adaptatives et cladogenèse. (Lepidoptera: Rhopalocera). *Bulletin de la Société Zoologique de France*, **111**, 261–296.
- Evans, A.V., Bellamy, C.L. & Watson, L.C. (2000) *An Inordinate Fondness for Beetles*. University of California Press, Los Angeles.
- Forsman, A. & Appelqvist, S. (1999) Experimental manipulation reveals differential effects of colour pattern on survival in male and female pygmy grasshoppers. *Journal of Evolutionary Biology*, **12**, 391–401.
- Goloboff, P. (1999) *NONA (NO NAME)*, Version 2. Published by the author, Tucuman.
- Harris, A.C. (1991) Geographic variation for colour in the sand-burrowing beetle *Chaerodes trachyscelides* White (Coleoptera: Tenebrionidae) on New Zealand beaches analyzed using CIELAB L\* values. *Biological Journal of the Linnean Society*, **44**, 93–104.
- Hollocher, H., Hatcher, J.L. & Dyreson, E.G. (2000a) Evolution of abdominal pigmentation differences across species in the *Drosophila dumni* subgroup. *Evolution*, **54**, 2046–2056.
- Hollocher, H., Hatcher, J.L. & Dyreson, E.G. (2000b) Genetic and developmental analysis of abdominal pigmentation differences across species in the *Drosophila dumni* subgroup. *Evolution*, **54**, 2057–2071.
- Jiggins, C.D., Naisbit, R.E., Coe, R.L. & Mallet, J. (2001) Reproductive isolation caused by colour pattern mimicry. *Nature*, **411**, 302–305.
- McMillan, W.O., Monteiro, A. & Kapan, D.D. (2002) Development and evolution on the wing. *Trends in Ecology and Evolution*, **17**, 125–133.
- Merilaita, S. (2001) Habitat heterogeneity, predation and gene flow: colour polymorphism in the isopod, *Idotea baltica*. *Evolutionary Ecology*, **15**, 103–116.
- Nixon, K.C. (1999) The parsimony ratchet, a new method for rapid parsimony analysis. *Cladistics*, **15**, 407–414.
- Nixon, K.C. (1999–2002) *Winclada*, Version 1.0000. Published by the author, Ithaca, New York.
- Okamoto, M., Kashiwai, N., Su, Z.H. & Osawa, S. (2001) Sympatric convergence of the colour pattern in the Chilean *Ceroglossus* ground beetles inferred from sequence comparisons of the mitochondrial ND5 gene. *Journal of Molecular Evolution*, **53**, 530–538.
- Robertson, J.A., McHugh, J.V. & Whiting, M.F. (2004) A molecular phylogenetic analysis of the pleasing fungus beetles (Coleoptera: Erotylidae): evolution of colour pattern, gregariousness, and mycophagy. *Systematic Entomology*, **29**, 173–187.
- Sharp, D. (1876) Contribution to an insect fauna of the Amazon Valley (Col. Staph.). *Transactions of the Entomological Society of London*, **1876**, 27–424.
- Smetana, A. & Davies, A. (2000) Reclassification of the north temperate taxa associated with *Staphylinus* sensu lato, including comments on relevant subtribes of Staphylinini (Coleoptera: Staphylinidae). *American Museum Novitates*, **3287**, 1–88.
- Strong, E.E. & Lipscomb, D. (1999) Character coding and inapplicable data. *Cladistics*, **15**, 363–371.
- Sword, G.A. (2002) A role for phenotypic plasticity in the evolution of aposematism. *Proceedings of the Royal Society of London, Series B*, **269**, 1639–1644.
- Wittkopp, P.J., True, J.R. & Carroll, S.B. (2002) Reciprocal functions of the *Drosophila* yellow and ebony proteins in the development and evolution of pigment patterns. *Development*, **129**, 1849–1858.
- Zrzavý, J. (1990) Evolution of the aposematic colour pattern in some Coreoidea s. lat. (Heteroptera): a point of view. *Acta Entomologica Bohemoslovaca*, **87**, 470–474.
- Zrzavý, J. & Nedvěd, O. (1997) Phylogeny of the new world *Dysderus* (Insecta: Hemiptera: Pyrrhocoridae) and evolution of their colour patterns. *Cladistics*, **13**, 109–123.
- Zrzavý, J. & Nedvěd, O. (1999) Evolution of mimicry in the new world *Dysderus* (Hemiptera: Pyrrhocoridae). *Journal of Evolutionary Biology*, **12**, 956–969.

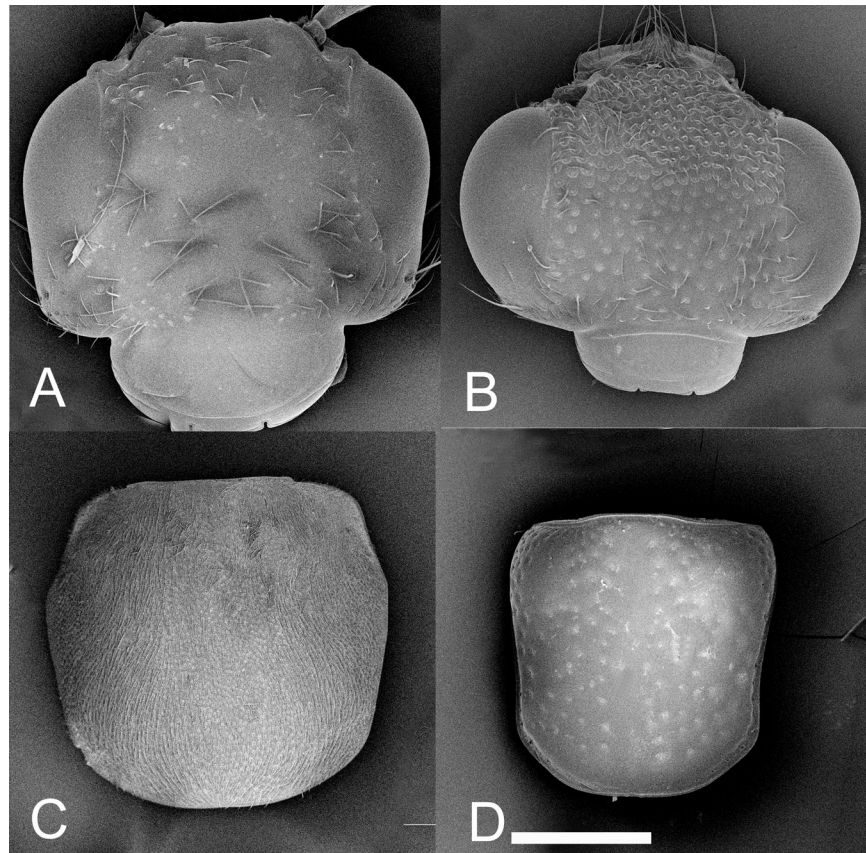
Accepted 14 June 2004

First published 9 December 2004

**Appendix 1**

Characters and character states used to infer the phylogenetic relationships of *Nordus*. Where relevant, figures in Chatzimanolis (2004) are referred to, to illustrate character states.

1. *Antennal articles 5–10*: (1) round; (2) distinctly and strongly flattened.
2. *Antennal article 1*: (1) greatly thickened in relation to article 2; (2) not greatly thickened in relation to article 2.
3. *Antennal article 1*: (1) gradually, clublike thickened; (2) gradually, clublike thickened, but becoming smaller at distal end.
4. *Antennal article 2*: (1) shorter than article 3; (2) subequal to article 3.
5. *Shape of antennal article 4*: (1) longer than wide (Chatzimanolis, 2004: fig. 23); (2) subquadrate (Chatzimanolis, 2004: fig. 27).
6. *Shape of antennal article 5*: (1) longer than wide (Chatzimanolis, 2004: fig. 23); (2) subquadrate (Chatzimanolis, 2004: fig. 27).
7. *Antennal article 4*: (1) longer than article 5; (2) subequal to article 5 (Chatzimanolis, 2004: fig. 23); (3) shorter than article 5.
8. *Shape of antennal article 6*: (1) longer than wide (Chatzimanolis, 2004: fig. 23); (2) subquadrate (Chatzimanolis, 2004: fig. 22); (3) wider than long (Chatzimanolis, 2004: fig. 54).
9. *Antennal article 5*: (1) longer than article 6 (Chatzimanolis, 2004: fig. 22); (2) subequal to article 6 (Chatzimanolis, 2004: fig. 27).
10. *Shape of antennal article 7*: (1) longer than wide (Chatzimanolis, 2004: fig. 23); (2) subquadrate (Chatzimanolis, 2004: fig. 24); (3) wider than long (Chatzimanolis, 2004: fig. 25).
11. *Shape of antennal article 8*: (1) subquadrate (Chatzimanolis, 2004: fig. 23); (2) wider than long (Chatzimanolis, 2004: fig. 24).
12. *Shape of antennal article 9*: (1) wider than long (Chatzimanolis, 2004: fig. 22); (2) subquadrate.
13. *Antennal article 11*: (1) with one row of macrosetae except those on tip; (2) multiple rows of long setae except those on tip.
14. *Microtrichae on antennal article 4*: (1) absent (Chatzimanolis, 2004: fig. 16); (2) present.
15. *Microtrichae on antennal article 5*: (1) absent (Chatzimanolis, 2004: fig. 16); (2) present.
16. *Anteclypeus*: (1) reduced (Fig. 6B); (2) greatly extended.
17. *Punctures on anterior margin of epicranium*: (1) absent (Fig. 6A); (2) present (Fig. 6B).
18. *Punctures on middle of epicranium*: (1) absent (Fig. 6B); (2) present (Fig. 6A).
19. *Size of punctures on epicranium*: (1) large (Fig. 6B); (2) medium (Fig. 6A); (3) small.
20. *Punctures on anterior part of epicranium*: (1) confluent (Fig. 6B); (2) not confluent (Fig. 6A).
21. *Confluent punctures on anterior part of epicranium*: (1) dense (as in *N. longipes*, or Fig. 6B); (2) very dense (as in *N. solitarius*).
22. *Confluent punctures on anterior part of epicranium*: (1) longitudinally elongate; (2) not longitudinally elongate (Fig. 6B).
23. *Punctures on posterior part of epicranium*: (1) deep (Fig. 6B); (2) shallow.
24. *Punctures on posterior part of epicranium*: (1) as dense as puncture on anterior part of epicranium; (2) less dense (Fig. 6B).
25. *Punctures on posterior part of epicranium*: (1) larger than punctures on anterior part (Fig. 6B); (2) same size as punctures on anterior part.
26. *Micropunctures on epicranium*: (1) absent; (2) present.
27. *Microsculpture of transverse microlines on epicranium*: (1) absent; (2) present.
28. *Distance between eyes*: (1) 2× length of eye; (2) 1.5× length of eye; (3) 1× length of eye.
29. *Temporal area on epicranium*: (1) not expanded (Fig. 6B); (2) expanded (Fig. 6A).
30. *Epicranium*: (1) more or less flat (Fig. 6B); (2) convex.
31. *Submentum and mentum*: (1) very wide (as in *P. fetialis* or *E. hanleyi*); (2) not very wide (as in *X. callidus* or *Nordus*).
32. *Surface between postmandibular ridge and eye*: (1) with few large punctures along the ridge; (2) with few large punctures and multiple smaller ones along the ridge; (3) with many large punctures.
33. *Shape of labrum*: (1) as in *Nordus* (Chatzimanolis, 2004: fig. 12); (2) as in *P. fetialis*; (3) as in *X. callidus*.
34. *Punctures on the neck*: (1) multiple; (2) very few (less than four) (Fig. 6B).
35. *Punctuation pattern in pronotum*: (1) uniform (Fig. 6C); (2) not uniform (Fig. 6D).
36. *Punctures on pronotum*: (1) deep (Fig. 6D); (2) shallow.
37. *Impunctate area midlength on pronotum*: (1) as wide as half (or less) puncture; (2) as wide as one to one and a half punctures (Fig. 6D); (3) as wide as two to three punctures.
38. *Punctures on pronotum near impunctate are medially*: (1) dense (as in *N. cribricollis*); (2) less dense (as in *N. diversiventris*, or Fig. 6D).
39. *Pronotum posterolaterally*: (1) with punctures (Fig. 6C); (2) without punctures (Fig. 6D).
40. *Pronotum anterolateral corners*: (1) without any raised impunctate areas (Fig. 6C); (2) with moderately raised impunctate areas; (3) with strongly raised impunctate areas (Fig. 6D).
41. *Pronotum*: (1) shorter than elytra; (2) subequal to elytra.
42. *Shape of pronotum*: (1) longer than wide; (2) subquadrate (Fig. 6D); (3) trapezoid (Fig. 6C).
43. *Pronotum, lateral borders*: (1) flat; (2) curved downwards.
44. *Pronotum, lateral borders*: (1) convex; (2) almost parallel to each other; (3) concave; (4) strongly concave (Fig. 6D).



**Fig. 6.** A, Head of *Xanthopygus callidus*, scale 0.3 mm; B, head of *Nordus cribricollis*, scale 0.3 mm; C, pronotum of *Elmas hanleyi*, scale 0.6 mm; D, pronotum of *Nordus amazonicus*, scale 0.6 mm

45. *Pronotum, basisternum*: (1) with pair of prominent setae; (2) without pair of prominent setae.
46. *Punctures on scutellum*: (1) cover entire surface; (2) cover posterior three-quarters of surface; (3) cover posterior half of surface.
47. *Micropunctures on metepimeron*: (1) absent; (2) present.
48. *Punctures on elytra*: (1) very dense (confluent); (2) dense (punctures with a space of half to one puncture between them); (3) sparse (punctures with a space of more than one puncture between them).
49. *Protarsus, tarsomeres*: (1) as elongate as in meso- and metatarsus; (2) elongate, but not as in meso- and metatarsus; (3) not elongate.
50. *Probasitarsus*: (1) enlarged, wider than second tarsomere; (2) enlarged, as wide as second tarsomere; (3) not enlarged.
51. *Two to four tarsomeres in middle and hind tarsi*: (1) lobed; (2) not lobed.
52. *Punctures on the anterolateral corners of sixth and seventh abdominal sterna*: (1) as dense as rest of sternum; (2) less dense than rest of sternum.
53. *Setae on third abdominal tergum*: (1) absent or less than five setae medially; (2) many setae.
54. *Setae on fourth abdominal tergum*: (1) absent or less than five setae medially; (2) many setae.
55. *Punctuation pattern on terga V–VII*: (1) uniform; (2) not uniform.
56. *Subbasal carinae on tergum V*: (1) absent; (2) present.
57. *Cerci*: (1) slightly curved; (2) straight.
58. *Cerci*: (1) robust (thick); (2) thin.
59. *Shape of distal margin of sternum VII in males*: (1) not modified; (2) with well-defined emargination (Chatzimanolis, 2004: figs 62–64); (3) with deep notch (Chatzimanolis, 2004: fig. 65).
60. *Emargination of distal margin of sternum VII in males*: (1) very deep (as in *N. terminalis*; Chatzimanolis, 2004: fig. 64); (2) deep (as in *N. densiventris*; Chatzimanolis, 2004: fig. 62); (3) shallow (as in *N. dichromos*; Chatzimanolis, 2004: fig. 63); (4) with a small lobe extending medially (as in *N. amazonicus*; Chatzimanolis, 2004: fig. 61).
61. *Shape of distal margin of sternum VIII in females*: (1) not modified (Chatzimanolis, 2004: fig. 114); (2) sinuate (Chatzimanolis, 2004: fig. 118); (3) pointed (Chatzimanolis, 2004: fig. 120); (4) with a rounded lobe (Chatzimanolis, 2004: fig. 115).
62. *Shape of distal margin of sternum VIII in males*: (1) with a single lobe (Chatzimanolis, 2004: fig. 70); (2) emarginate (Chatzimanolis, 2004: fig. 71); (3) with two medially emarginated triangular lobes (Chatzimanolis, 2004: fig. 69).
63. *Shape of lobe of sternum VIII in males*: (1) simple, without any process (Chatzimanolis, 2004: fig. 74); (2) with a process extending beyond the plate (Chatzimanolis, 2004: figs 70, 91).

64. *Shape of emargination of distal margin of sternum VIII in males*: (1) shallow (as in *N. facialis*; Chatzimanolis, 2004: fig. 81); (2) deep (as in *N. fungicola*; Chatzimanolis, 2004: fig. 82).
65. *Shape of emargination of distal margin of sternum VIII in males*: (1) V-shaped (Chatzimanolis, 2004: fig. 75); (2) U-shaped (Chatzimanolis, 2004: fig. 81).
66. *Shape of medially emarginated triangular lobes of distal margin of sternum VIII in males*: (1) tips of lobes pointed (Chatzimanolis, 2004: fig. 72); (2) tips of lobes rounded (Chatzimanolis, 2004: fig. 69).
67. *Shape of medially emarginated triangular lobes of distal margin of sternum VIII in males*: (1) lobes small (Chatzimanolis, 2004: fig. 84); (2) lobes medium (Chatzimanolis, 2004: fig. 69); (3) lobes large (Chatzimanolis, 2004: fig. 87).
68. *Shape of medially emarginated triangular lobes of distal margin of sternum VIII in males*: (1) emargination very shallow (Chatzimanolis, 2004: fig. 72); (2) emargination medium (Chatzimanolis, 2004: fig. 69); (3) emargination very deep (Chatzimanolis, 2004: fig. 94).
69. *Shape of medially emarginated triangular lobes of distal margin of sternum VIII in males*: (1) emargination broad (Chatzimanolis, 2004: fig. 76); (2) emargination moderate (Chatzimanolis, 2004: fig. 69); (3) emargination narrow (Chatzimanolis, 2004: fig. 72).
70. *Shape of medially emarginated triangular lobes of distal margin of sternum VIII in males*: (1) emargination V-shaped (Chatzimanolis, 2004: fig. 80); (2) emargination U-shaped (Chatzimanolis, 2004: fig. 69).
71. *Shape of distal margin of sternum IX in males*: (1) without emargination (Chatzimanolis, 2004: fig. 107); (2) with emargination (Chatzimanolis, 2004: fig. 108).
72. *Shape of emargination of distal margin of sternum IX in males*: (1) shallow (Chatzimanolis, 2004: fig. 105); (2) moderate (Chatzimanolis, 2004: fig. 104); (3) deep (Chatzimanolis, 2004: fig. 108).
73. *Shape of distal margin of sternum IX in males*: (1) with two apical processes (Chatzimanolis, 2004: fig. 104); (2) without apical processes (Chatzimanolis, 2004: fig. 111).
74. *Shape of apical processes of distal margin of sternum IX in males*: (1) small (Chatzimanolis, 2004: fig. 104); (2) medium (Chatzimanolis, 2004: fig. 106); (3) large (Chatzimanolis, 2004: fig. 107).
75. *Shape of paramere, lateral aspect*: (1) straight (Chatzimanolis, 2004: fig. 135); (2) concave (Chatzimanolis, 2004: fig. 127); (3) convex (Chatzimanolis, 2004: fig. 151).
76. *Shape of paramere, lateral aspect*: (1) parallel-sided from base to apex (Chatzimanolis, 2004: fig. 131); (2) distinctly broadened at base (Chatzimanolis, 2004: fig. 127); (3) distinctly broadened at apex (Chatzimanolis, 2004: fig. 195).
77. *Shape of paramere, dorsal aspect*: (1) parallel-sided (Chatzimanolis, 2004: fig. 130); (2) parallel-sided but becoming narrower at middle (Chatzimanolis, 2004: fig. 222); (3) converging to apex (Chatzimanolis, 2004: fig. 122); (4) expanded from base to apex (Chatzimanolis, 2004: fig. 150); (5) expanded from middle to apex (Chatzimanolis, 2004: fig. 126); (6) with expansion at middle (Chatzimanolis, 2004: fig. 202).
78. *Paramere, dorsal aspect*: (1) shorter than median lobe (Chatzimanolis, 2004: fig. 134); (2) subequal to median lobe (Chatzimanolis, 2004: fig. 122); (3) longer than median lobe (Chatzimanolis, 2004: fig. 142).
79. *Paramere, dorsal aspect*: (1) wider than median lobe (Chatzimanolis, 2004: fig. 150); (2) subequal to median lobe (Chatzimanolis, 2004: fig. 174); (3) narrower than median lobe (Chatzimanolis, 2004: fig. 122).
80. *Paramere, condition of apex in dorsal aspect*: (1) pointed (Chatzimanolis, 2004: fig. 125); (2) rounded (Chatzimanolis, 2004: fig. 133); (3) broadly rounded (Chatzimanolis, 2004: fig. 129).
81. *Paramere, condition of apex in lateral aspect*: (1) straight (Chatzimanolis, 2004: fig. 136); (2) slightly convex (Chatzimanolis, 2004: fig. 152); (3) slightly concave (Chatzimanolis, 2004: fig. 148); (4) strongly concave (Chatzimanolis, 2004: fig. 164).
82. *Paramere, distribution of sensory spinules*: (1) in a longitudinal row on each side (Chatzimanolis, 2004: fig. 133); (2) in two longitudinal rows medially (Chatzimanolis, 2004: fig. 129); (3) in a band around apical margin (Chatzimanolis, 2004: fig. 149); (4) uniformly distributed on two disks (Chatzimanolis, 2004: fig. 153); (5) in a band along apical margin and in longitudinal rows (Chatzimanolis, 2004: fig. 205); (6) with no or very few sensory spinules (Chatzimanolis, 2004: fig. 125).
83. *Median lobe, lateral aspect*: (1) more or less tubular; (2) very thin, platelike.
84. *Median lobe, distal margin of apex, dorsal aspect*: (1) slightly emarginate or subtruncate (Chatzimanolis, 2004: fig. 125); (2) emarginate (Chatzimanolis, 2004: fig. 129); (3) broad subacute (Chatzimanolis, 2004: fig. 133); (4) acute (Chatzimanolis, 2004: fig. 197); (5) broadly rounded (Chatzimanolis, 2004: fig. 161).
85. *Median lobe, dorsal tooth/carina at apex*: (1) present as a united medially U- or V-shaped carina (Chatzimanolis, 2004: fig. 160); (2) present as a medial toothlike carina separated at apex into two small lobes (Chatzimanolis, 2004: fig. 124); (3) present as two widely separated apical teeth (Chatzimanolis, 2004: fig. 128); (4) present as two widely separated cariniform teeth (Chatzimanolis, 2004: fig. 154); (5) present as two elongate carina separated at apex into two short lobes (Chatzimanolis, 2004: fig. 132); (6) present as two short lobes and a medial tooth (Chatzimanolis, 2004: fig. 247).
86. *Colour of head*: (1) entirely orange; (2) anteriorly black (or metallic green), posteriorly orange; (3) entirely dark brown to black; (4) entirely metallic green.
87. *Colour of thorax*: (1) orange; (2) dark brown to black; (3) metallic green.

**Appendix 2.** Data matrix of character states for *Nordus* and outgroup taxa. Missing states are shown as '?', inapplicable states as '-', polymorphism of states 1 and 3 as '\$' and polymorphism of states 1 and 2 as '\*\*'.

	1	2	3	4	5	6	7	8
	123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789
<i>A. antennaria</i>	121112122	2212222113	2223112121	1212311212	2222211111	-12-12----	-212-21313	11124-32
<i>E. hanleyi</i>	211112322	2122222223	213311-11	1231311213	12122211213	-12-22----	-212-11113	31324-32
<i>P. fetalis</i>	211111112	2122122111	2112211211	1132311221	3212221111	-12-12----	-222-11413	31313-32
<i>Xan. callidus</i>	121111112	1122222112	1213112321	1212121233	2211211111	-12-12----	-222-11322	11114132
<i>Xen. analis</i>	111122232	3212122112	2223121321	1212321212	2212221211	-12-12----	-212-31113	21114-43
<i>N. aeneiceps</i>	11222***	??***1221	1211221121	3121312113	2111221212	3?2-21----	-2212221323	13611221
<i>N. aeneipennis</i>	122222222	3111111221	1211221121	3121412113	2121412113	243-- --2222	2221211313	21113532
<i>N. amazonicus</i>	112211211	1222111221	1211221121	3121412113	2111221112	4412-----	-212-22523	332123*1
<i>N. amphivolos</i>	112212221	2211111221	2211221112	3121312113	2111221112	312-12----	-2212221113	23113521
<i>N. antennatus</i>	112212221	3211111221	1211221121	3121312113	2121221112	243-- --1213	2221211313	21113532
<i>N. banghaasi</i>	112212221	3211111221	1211221121	3121312113	2121221112	243-- --1213	2221211313	21113511
<i>N. batesi</i>	112222222	3211111221	1211221121	3121412113	2111221112	2411-----	-212-22533	33212321
<i>N. championi</i>	112212222	3211111221	1211221121	3121313113	2111221112	312-21----	-221121323	23311211
<i>N. cherylae</i>	112222222	3211111221	1211221122	3111412123	2121222222	223-- --2231	2222-31411	12413432
<i>N. cribricollis</i>	112212231	3211111221	1211221111	3121312113	2111221112	312-12----	-222-21113	23113511
<i>N. densiventris</i>	112222221	3211111221	1211221121	3121312113	2111221112	213-- --2231	2212-21313	23315111
<i>N. dichromos</i>	112212221	3211111221	1211221121	3121312113	2111221112	312-12----	-2212221113	2431125*
<i>N. diversiventris</i>	112211221	3211111221	1211221121	3121212123	2111221112	243-- --2113	12212221323	34312311
<i>N. elegans</i>	112222222	3211111221	1211221122	3111412123	2121222222	213-- --2231	2222-31413	1241343*
<i>N. elytsi</i>	112222231	3211111221	1211221111	3121312113	2111221112	213-- --1111	2221221112	13212211
<i>N. facialis</i>	112222222	3211111221	1211221121	3121313113	2111221112	312-11----	-221121113	241112*1
<i>N. fungicola</i>	112212222	3211111221	1221221121	2211222322	2111221112	312-21----	-221121323	24311211
<i>N. gebieni</i>	112212221	3211111221	1211221121	3121312113	2111221112	312-21----	-2211222333	13611211
<i>N. longipes</i>	112212222	2211111221	1221221112	3121312113	2111221112	??***??*??	??***??*??	??***??*??
<i>N. maculiceps</i>	112212222	2211111221	1211221122	2211221112	2111221112	213-- --2122	21-1311123	12215332
<i>N. major</i>	112111221	3211112221	1211221111	122212113	2111221112	312-12----	-221213111	33114-11
<i>N. nigroscutellatus</i>	112212221	3211111221	1211221121	3121312113	2111221112	312-11----	-2212221313	1361121*
<i>N. omios</i>	112212222	3211111221	1211221121	3121313133	2121211112	143-- --1333	12313221623	24515132
<i>N. periergos</i>	112222231	3211111221	1221221222	3121312113	2111221112	2?3-- --1333	1222-11213	23113511
<i>N. picticornis</i>	112222221	3211111221	1211221121	3121412113	2121221112	2?3-- --1222	2221211313	21313511
<i>N. portokalis</i>	112222232	3211111221	1211221122	2121413123	2121221122	223-- --2222	2211211213	11114532
<i>N. seferisi</i>	112222231	3211111221	1211221111	3121312113	2111221112	313-- --1111	2221222112	24212211
<i>N. semelus</i>	112222231	3211111221	1211221222	3121312113	2111221112	243-- --1333	1222-21213	13112511
<i>N. simplex</i>	112222222	3211111221	1211221121	3121312113	2111221112	243-- --2123	12212221313	23115221
<i>N. solitarius</i>	112222222	3211111221	1211221121	2121312113	2111221112	243-- --2233	21-1321523	23111111
<i>N. spectosus</i>	112212222	3211111221	1211221122	2111412123	2111222222	223-- --2231	2222-31411	12413-43
<i>N. stomachopomos</i>	112212222	3211111221	1211221121	3121312113	2111221112	?4?***??*??	??***??*??	??***??*??
<i>N. styloceros</i>	112212221	3211111221	1211221121	3121212113	2111221113	-312-----	-221321323	33212211
<i>N. terminalis</i>	112212222	3211111221	1211221121	3121313133	2121211112	143-- --1333	12313221633	2351515*
<i>N. testaceus</i>	?122122??	??*111221	1211221121	2121212113	2111221112	2?3-- --2233	11-1321423	24315611
<i>N. velitaris</i>	112212221	3211111221	1221221122	2121312113	2111221112	242-21----	-222-21313	23314-5*
<i>N. xanthocerus</i>	112211222	2211111221	1211221122	2121312113	2111221112	213-- --2122	21-1311123	12215332
<i>N. zischkai</i>	112222222	3211111221	1211221121	3121312113	2121221112	243-- --2222	22212221313	23513532

**Appendix 3.** Taxa included in the analysis and their distribution.

Taxa	Distribution
<i>N. aeneiceps</i> (Sharp, 1876)	Brazil
<i>N. aeneipennis</i> (Bernhauer, 1917)	Bolivia and Peru
<i>N. amazonicus</i> (Sharp, 1876)	Bolivia, Brazil, Colombia, Ecuador and Peru
<i>N. amphivolos</i> Chatzimanolis, 2004	Brazil and Venezuela
<i>N. antennatus</i> (Sharp, 1876)	Bolivia, Brazil, Colombia, Ecuador and Peru
<i>N. banghaasi</i> (Bernhauer, 1905)	Bolivia
<i>N. batesi</i> (Sharp, 1876)	Bolivia, Brazil, French Guyana and Peru
<i>N. championi</i> (Sharp, 1884)	Costa Rica, El Salvador, Guatemala, Mexico and Nicaragua
<i>N. cherylae</i> Chatzimanolis, 2004	Bolivia
<i>N. cribricollis</i> (Sharp, 1876)	Bolivia, Brazil, Colombia, French Guyana, Guyana, Peru and Suriname
<i>N. densiventris</i> (Bernhauer, 1917)	Colombia and Ecuador
<i>N. dichromos</i> Chatzimanolis, 2004	Ecuador
<i>N. diversiventris</i> (Bernhauer, 1917)	Colombia, Panama and Peru
<i>N. elegans</i> Chatzimanolis, 2004	Peru
<i>N. elytisi</i> Chatzimanolis, 2004	Argentina and Bolivia
<i>N. facialis</i> (Erichson, 1839)	Brazil, French Guyana, Guyana, Suriname and Venezuela
<i>N. fungicola</i> (Sharp, 1884)	Colombia, Costa Rica, Ecuador, Panama and Venezuela
<i>N. gebieni</i> (Bernhauer, 1917)	Bolivia, Brazil, Ecuador and Peru
<i>N. longipes</i> (Sharp, 1876)	Brazil
<i>N. maculiceps</i> (Sharp, 1876)	Bolivia, Brazil, Colombia, Ecuador, Guyana, Peru and Suriname
<i>N. major</i> (Bernhauer, 1905)	Bolivia, Brazil, Ecuador and Peru
<i>N. nigroscutellatus</i> (Bernhauer, 1905)	Bolivia and Peru
<i>N. omios</i> Chatzimanolis, 2004	Panama
<i>N. periergos</i> Chatzimanolis, 2004	Peru
<i>N. picticornis</i> (Solsky, 1872)	Peru
<i>N. portokalis</i> Chatzimanolis, 2004	Peru
<i>N. seferisi</i> Chatzimanolis, 2004	Peru
<i>N. semelius</i> Chatzimanolis, 2004	Bolivia
<i>N. simplex</i> (Sharp, 1876)	Brazil, Colombia, Ecuador and Peru
<i>N. solitarius</i> (Sharp, 1884)	Colombia, Costa Rica, Ecuador, Nicaragua, Panama and Venezuela
<i>N. speciosus</i> (Bernhauer, 1905)	Bolivia and Peru
<i>N. stomachoponos</i> Chatzimanolis, 2004	Colombia and Panama
<i>N. styloceros</i> (Sharp, 1876)	Brazil, Colombia, French Guyana, Guyana and Peru
<i>N. terminalis</i> (Sharp, 1884)	Costa Rica, Guatemala, Nicaragua and Panama
<i>N. testaceus</i> (Fabricius, 1801)	Not known
<i>N. velitarius</i> (Erichson, 1839)	Argentina, Brazil and Paraguay
<i>N. xanthocerus</i> (Nordmann, 1837)	Brazil and Ecuador
<i>N. zischkai</i> (Scheerpeltz, 1971)	Bolivia