Phylogenetic analysis of the *Niphargus orcinus* species-aggregate (Crustacea: Amphipoda: Niphargidae) with description of new taxa

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**Abstract**

The *Niphargus orcinus* aggregate, also “subgenus *Orniphargus*” of the genus *Niphargus*, is a widely distributed assemblage of large-bodied amphipods. Although it comprises the most prominent European groundwater animals, its phylogeny has not yet been scrutinized and its monophyly has never been tested. In this study, 30 putative “*Orniphargus*” taxa and 14 other *Niphargus* and outgroup species were examined cladistically using a matrix of 71 morphological characters. The strict consensus tree constructed of 34 equally parsimonious trees demonstrated that “*Orniphargus*” does not constitute a monophylum. Most of the species were divided into two large clades. Both clades contain species from the western Balkans (mainly the Dinaric Karst) with partly overlapping ranges. *Niphargus croaticus pachytelson* and *N. orcinus redenseki* are elevated to species rank. Four new species are described: *N. dolichopus* sp. n., *N. polymorphus* sp. n., *N. dabarensis* sp. n. (all Bosnia and Herzegovina) and *N. lourensis* sp. n. (Greece).

**Keywords:** Cladistics, Dinaric karst, Amphipoda, Niphargus, Orniphargus, troglomorphism

**Introduction**

With over 300 described species and subspecies, the genus *Niphargus* Schiödte, 1947 (Amphipoda: Niphargidae) is the largest genus of European freshwater amphipods (Pinkster 1978; G. Karaman and Ruffo 1986; Fišer et al. 2002). Most of the species inhabit subterranean waters and constitute a substantial part of the European groundwater biodiversity (Sket 1999a, 1999b). The genus is distributed across most of Europe, mainly – but not exclusively – south of the Pleistocene ice sheet boundary (Ruffo 1953; G. Karaman and Ruffo 1986; Proudlove et al. 2003). Few species are known from the Arabian Peninsula, Turkey and Iran (G. Karaman 1986, 1998, 2003; Bat et al. 2001). By contrast, over most of the Iberian Peninsula, only its presumed relative *Haploginglymus* Mateus and Mateus, 1958 can be found (G. Karaman and Ruffo, 1986).
Niphargus shows an extremely diverse morphology (G. Karaman and Ruffo 1986; Sket 1999a) with some distinct morphotypes. Not surprisingly, several classifications assigning these morphotypes to subgenera or species groups have been proposed (a brief summary in G. Karaman and Ruffo [1986]; details in S. Karaman [1950a,c, 1952a, 1960]; S. Karaman and G. Karaman [1959]; Sket [1958a, 1972]; Straškraba [1972]; Sket and Notenboom [1993]). However, none of these proposals were supported by results of a phylogenetic analysis. Furthermore, most of the groups had never been morphologically defined and several species could not be assigned to any of the proposed groups (notes in Straškraba [1972]; critics in G. Karaman and Ruffo [1986]). Until now, none of these groupings has been widely accepted, even though some of the names have often been used for convenience.

The “orcinus-group”, or “subgenus Orniphargus S. Karaman, 1950” comprises the largest and the most massive European amphipods. Later the group was even treated as if it was a valid genus (e.g. S. Karaman 1952c). This group of species is named after the species N. orcinus Joseph, 1869. Stanko Karaman (1950c) delimited the “subgenus” with a diagnosis, which ended with the comment “... all the characters are not present in all species; it appears that species may have one or the other character different”. Stanko Karaman (1950b, 1950c) listed 11 taxa. Subsequently another 27 taxa were added to the list (S. Karaman 1953, 1956; Sket 1958a, 1958b, 1959, 1960; Ruffo and Vigna-Taglianti 1968; Alouf 1972, 1973; G. Karaman 1984, 1985a, 1985b, 1986, 1988a, 1988b, 1989; Sket and G. Karaman 1990; Iannilli and Vigna-Taglianti 2004). The list of “Orniphargus” taxa was changing so quickly that a revision of the group (G. Karaman 1984) could not be finished. Even though not discussed in detail, some authors obviously recognized several lineages within the subgenus (G. Karaman 1984, 1986; Straškraba 1972). Here, we use the name “Orniphargus” to embrace all taxa whenever considered as belonging to the “orcinus” morphotype. By keeping the name in quotation marks we emphasize that we do not attribute any taxonomic meaning to it. One has to note that the genus Niphargus has never been entirely divided into subgenera and, thus, no subgenus could attain formal validity. A list of these taxa is provided in Tables C-I and C-III (Appendix C).

As stated by Ruffo and Vigna-Taglianti (1968), the highest diversity of “Orniphargus” species was recorded in the territories of central Italy and the north-western Balkan Peninsula. A significant decrease in diversity elsewhere is illustrated by the presence of only three species in Iraq and Lebanon, which is the second most important area for “Orniphargus” species (Alouf 1972, 1973; G. Karaman 1986).

The “subgenus Orniphargus” cannot be distinguished from the rest of the Niphargus species unambiguously. Authors disagreed whether the species N. virei Chevreux, 1896 (France), N. miljeticus Straškraba, 1959 (Mljet island, Adriatic Sea), N. stefanellii Ruffo and Vigna-Taglianti, 1968 (Italy), N. ictus G. Karaman, 1985 (Italy) and N. carcerarius G. Karaman, 1989 (Montenegro) should be included into the subgenus or not. An overview of congruent and non-congruent classifications is presented in the Tables C-I and C-III in Appendix C.

Apart from the morphological uncertainties, an allozyme analysis of six Niphargus species distinguished N. (“Orniphargus”) parenzani Ruffo and Vigna-Taglianti, 1968 as a taxon, which appeared to be more closely related to the genus Gammarus than to the rest of Niphargus species (Bullini and Sbordoni 1980).

A significant number of niphargids collected during the past years enabled us to conduct a partial revision of the “subgenus Orniphargus”. The present paper is based on a cladistic analysis of morphological characters. Our results show that: (1) the monophyly of
“Orniphargus” is doubtful, since several distinct paraphyletic lineages can be recognized among the listed taxa; (2) the taxonomic rank of some taxa has to be corrected; and (3) four new species were recognized.

**Materials and methods**

The specimens used for this study are deposited in the collection of the Oddelek za biologijo, Biotehniška fakulteta, Univerza v Ljubljani (Department of Biology, Biotechnical Faculty, University of Ljubljana), or they were borrowed from the following institutions: Zoologisch Museum Amsterdam, Museo Civico di Storia Naturale in Verona, and The Natural History Museum in London.

**Preparation techniques**

Specimens were heated in a 10% KOH solution, briefly rinsed with diluted HCl and washed in distilled water. Cleared exoskeletons were stained with chlorazol black in glycerol, partly dissected in glycerol and mounted on slides in a glycerol–gelatine medium. Digital photos were taken with an Olympus DP10 camera mounted on an Olympus SZX9 stereomicroscope. Measurements and counts were made using the computer program Olympus DP–soft. Finer details were examined using a Zeiss microscope with magnifications 100–400 × .

**Taxonomic sampling**

The selection of taxa included approximately two thirds of the taxa considered as members of the “subgenus Orniphargus” (Table C-I, Appendix C), further supplemented by taxa whose affiliation to “Orniphargus” is ambiguous. The position of the latter was tested by inclusion of their alternatively hypothesized relatives (Table C-II, Appendix C). “Orniphargus” species that were not included in the present study are listed in Table C-III (Appendix C).

Because it was not possible to obtain sufficient information on characters from published descriptions, all morphological analyses were based on preserved specimens. If available, several specimens of various lengths and of both sexes as well as from different localities were examined to embrace as much variability as possible. Type or topotype specimens were studied when they were available to us.

The monophyly of the group “Orniphargus” was tested by inclusion of 13 species of Niphargus that do not belong to “Orniphargus” complex (Table C-II); thus 46 taxa in total were analyzed. Gammarus fossarum (Koch, 1935) was defined as the outgroup in all analyses. Even though Crangonyctidae are considered as the most probable sister group to niphargids (Englisch and Koenemann 2001; Englisch et al. 2003), Synurella ambulans Müller, 1846 (the only crangonyctid available) was found to be an inappropriate outgroup due to its rather specialized morphology.

**Character coding**

Size-dependent variability of body shape frequently detected in certain Niphargus species is less pronounced in the “subgenus Orniphargus” than in other species. Nevertheless, to avoid the “semaphoront problem” (sensu Henning 1966) only adult specimens were used.
The analysis includes all the features that vary between the taxa and that can be distinctly split into character states. The shape of some body parts has provided a substantial number of characters used in this study. The main character coding challenges were (1) describing the shapes of certain variable body parts in the form of indices, and (2) finding gaps that defined character states. Gap searching was constrained by a limited number of individuals available (these species rarely appear in high numbers), thus methods based on variability (e.g. Thorpe 1984; Archie 1985) failed. Gaps were searched for as follows. Index values of the appendage article under consideration were treated as intervals for every species. Partially overlapping intervals were joined into larger intervals until non-overlapping intervals, considered as character states, were found. Some problems occurred when only one or two specimens of a species available showed a boundary value. In such cases, characters were coded as polymorphic (Wiens 1995). The highest possible number of character states was chosen as suggested by Pogue and Mickevitch (1990). A commented list of coded characters and the character–taxon matrix can be found in Appendices A and B. The illustrations of the character states (in preparation) shall be published elsewhere.

**Phylogenetic analysis**

Parsimony analysis was performed using NONA 2.0 (Goloboff 1998), run within WinClada (Beta) 1.00 (Nixon 1999a). The heuristic tree search options HOLD 10000, HOLD/100, MULT*1000, and a multiple TBR+TBR branch-swapping search strategy were used. Additionally, the ratchet search (Nixon 1999b), as implemented in WinClada, was run using default settings. All characters were treated as unweighted and unordered. Polymorphic characters were treated as "polymorphic" sensu Wiens (1995). Bremer support indices (Bremer 1988) were calculated using a ratchet algorithm and PAUP 4.beta10 (Swofford 2003). A command file for PAUP was written in PRAP (Parsimony Ratchet Analyses using PAUP) (Müller 2004). Default settings, 200 iterations, 25 characters of weight 2 were used.

**Character analysis**

Hypotheses of character evolution were evaluated to (1) examine sources of disagreement between our results and previous classifications and (2) review character support of the clades. Character distributions were studied in WinClada under “fast” (ACCTRAN) optimization (for rationale see Discussion). The only diagnosis designated (S. Karaman 1950c) was used as a reference for comparison of our results with previous classifications. In particular, the following parameters were evaluated for selected clades: (1) number of characters transformed at the basal node, (2) number of consistent characters, (3) number of reversals, and (4) number of parallelisms. For a character to be consistent it had to remain untransformed within a clade. We regarded reversals as transformations of the type $a \rightarrow b \rightarrow a$ that occurred at least once within a clade. Character states attained independently within a clade at least twice were treated as parallelism. The character support for all major clades and subclades was compared.

**General notes and abbreviations**

We call “spines” strong, rigid structures and “setae” thin, flexible structures. “Spines” and “setae” often cannot be clearly distinguished. Sometimes the same group of spines/setae can contain setae, spines and various intermediate structures. We also observed that strong “spines”
Figure 1. A strict consensus tree of 34 most parsimonious trees (length=472; CI=0.26, RI=0.60). Values of Bremer support index (decay index) are indicated below branches. Taxa traditionally assigned to the ‘‘Orniphargus’’ species aggregate, as well as clades for which character analysis was performed, are encircled in boxes. Note 1: Despite of its position on the cladogram N. pectinicauda has never been considered as an ‘‘Orniphargus’’ taxon. Note 2: Taxa are named according to their lowest rank. For full names, see Tables I and II.
of young specimens become thinner and more flexible ("setae") in adults. For these reasons, when dealing with number of structures in a group, we simply count the number of structures in a group as "number of spines/setae" and do not distinguish between spines and setae.

To make descriptions clearer for the reader, some shapes of some characters expressed as ratios in phylogenetic analysis were replaced here by descriptive means. The numbers can be obtained from the corresponding author, see also Appendices A and B. See also comments of characters and note in Appendix A.

We used the following abbreviations: aI, II (antenna I, II); r/l/p-md (right/left/palpus of mandible); mxI, II (maxilla I, II); mxp (maxilliped); gpI, II (gnathopod I,II), ppIII–VII (pereopods III–VII); upI–III (uropods I–III); r (retinacle); t (telson).

Results

Phylogenetic analysis

The heuristic search found 12 equally parsimonious trees 462 steps long, with a consistency index (CI) of 0.27 and a retention index (RI) of 0.61. The ratchet search found another 22 trees of the same length and similar topology. Following Nixon and Carpenter (1996), the strict consensus method was used to summarize the topological agreement among cladograms. The cladograms differed at six nodes. Collapsing them led to a tree 472 steps long (CI = 0.26, RI = 0.59) (Figure 1). Most of the nodes had low Bremer support values, ranging from one to seven.

Rooting *Niphargus* on *Gammarus fossarum* split the *Niphargus* taxa in two lineages (Figure 1). One was represented by the tiny interstitial species [*N. skopljensis* and *N. longidactylus*], whereas the rest of the analyzed species represented a series of paraphyletic terminal taxa and three distinct clades. All "*Orniphargus*" species were nested within other *Niphargus* species, none of them showing affinities to *Gammarus*. The "*Orniphargus*" group itself emerged as a paraphyletic group. Most of its members were subdivided into two large, non-sister clades, referred to as clades A and B (Figure 1). Species considered transitional by morphology (*N. stefanellii*, *N. virei* and *N. polymorphus*) occupied basal positions in all cladograms, except for *N. miljeticus*, which was positioned among so-called "*stygius sensu lato*" species.

Character analysis

The notorious morphological variability of niphargids was reflected through the analysis of character transformation. It can be summarized in three general aspects. (1) Shape and

| Clade     | Number of taxa | Decay index | No. of parallelisms | No. of reversals | No. of character changes at basal node | No. of consistent characters |
|-----------|----------------|-------------|---------------------|------------------|---------------------------------------|----------------------------|
| A         | 16             | 1           | 31                  | 18               | 4                                     | 12                         |
| a-1       | 5              | 2           | 2                   | 2                | 9                                     | 40                         |
| a-2       | 8              | 1           | 3                   | 6                | 6                                     | 29                         |
| a-2.1     | 2              | 7           | 0                   | 0                | 7                                     | 66                         |
| a-2.2     | 4              | 1           | 2                   | 3                | 4                                     | 51                         |
| B excl. *N. zavalanus* | 8              | 2           | 10                  | 3                | 6                                     | 31                         |
| b-1       | 4              | 5           | 0                   | 1                | 3                                     | 44                         |
| b-2       | 4              | 2           | 3                   | 0                | 11                                    | 53                         |
Table II. Analysis of characters used in S. Karaman’s (1950c) diagnosis of *Orniphargus*.

| “Diagnostic character”                                      | CI  | RI  | Remarks on character                                                                 |
|-------------------------------------------------------------|-----|-----|--------------------------------------------------------------------------------------|
| Large, up to 30 mm long.                                     | 0.28| 0.37| Convergent character. *Troglomorphism?*                                               |
| Body stout.                                                  | 1   | 1   | Plesiomorphic character.                                                               |
| Posterior margin of pleonites with a row of spines.          | 0.2 | 0.5 | Character does not include all possible character states. Convergent character.        |
| Epimeral plates pointed.                                     | 0.5 | 0.71| Plesiomorphic character.                                                               |
| Antennae I up to ¼ of body length.                           | 0.2 | 0.57| Character does not include all possible character states. Assuming character states 0 and 1 together as “long antennae” the character is convergent. In some species reversed. *Troglomorphism?* |
| Flagellum may consist of over 30 articles.                   | –   | –   | Not used in our study to avoid non-independence. We presume, that the same information is enclosed in length of antenna I. *Troglomorphism?* |
| 2–5 aesthetasks per article.                                 | 0.1 | 0.5 | Convergent character, reversions occur. *Troglomorphism?*                              |
| Gnathopod dactylus with several single setae.                | 0.28| 0.64| Mainly plesiomorphic character. Derived states occur parallelly and convergently.     |
| Propodus of gnathopods strong and large.                     | 0.33| 0.7 | Only gnathopod II was examined. Character does not include all possible character states. Apomorphic character of clade A, but reversion occurs. Not present in clade B. |
| Propodus of gnathopod II much larger than I.                 | 0.5 | 0.71| Derived feature of clade A, but reversion occurs. Not present in clade B.              |
| Coxal plates deeper than long.                               | –   | –   | A single character does not describe the observed variability sufficiently. We argue that two characters are needed. Either plesiomorphic or synapomorphic, shared by most of Niphargus species in our study, and thus uninformative. In some species reversed. |
| Our definition of characters: Character 30                   | 0.5 | 0.86| Either plesiomorphic or synapomorphic, shared by most of Niphargus species in our study, and thus uninformative. In some species reversed. |
| Character 40                                                 | 0.33| 0.78| Plesiomorphic and convergent character, reversals occur.                              |
| Bases narrow (in adults) or wide (in young).                 | 0.22| 0.65| Character does not include all possible character states. Convergent character, in some species reversed. |
| Pereopod dactyls long and slender.                           | –   | –   | Not tested due to difficult delimitation of character states. Probably homoplastic. Plesiomorphic character. |
| Telson generally longer than wide, sometimes with long plumose setae. | 0.25| 0.25| Plesiomorphic character.                                                               |
| Uropod rami I straight, endopodite slightly longer than exopodite | 0.42| 0.69| Character does not include all possible character states. Plesiomorphic character.    |
| Uropod rami II straight endopodite slightly or distinctly longer than exopodite | 0.28| 0.72| Character does not include all possible character states. Convergent character.       |
| Uropods I–II with numerous plumose setae along inner side.   | 0.33| 0.68| Convergent character. Interestingly, S. Karaman overlooked the “*arbiter*-type” of spination (see Appendix A), present in several species which he described. A single character does not describe the observed variability sufficiently. We argue that two characters are needed. |
| Uropod III exopodite short and wide.                         | –   | –   |                                                                                       |

*Phylogeny of Niphargus orcinus species–aggregate* 2271
proportions of several appendages had to be coded as multistate characters with three or more character states (14 characters had four or more states, 25 characters had three states). (2) Most of the characters were homoplastic, i.e. they had homoplastic character states. Among all 71 characters only four had a CI and RI value of one. (3) Finally, polymorphic characters were found in almost all taxa.

Table I shows a summary of the quantitative character analysis. The difference in structure of clades A and B is noteworthy. Clade B is rather robust, and its constituent subclades are well supported by numerous character transformations. It encompasses fewer
reversals and parallelisms than clade A. Conversely, clade A is characterized by lower Bremer support values and lower character consistency.

The character transformation analysis identified some fundamental problems with previous diagnosis of the group (S. Karaman 1950c). Most of the proposed diagnostic characters are either plesiomorphic or homoplastic (Table II and Figures 2–5). Furthermore, some characters (e.g. length of antenna, length of uropod I–II rami) may have more states or need to be subdivided into several characters (e.g. depth of coxal plates, shape and length of uropod III). Illustrative is the case of coxal plates I–IV, which are supposed to be “more deep than wide” (S. Karaman (1950c)). If all coxal plates in all species exhibited congruent patterns of shapes, they should be regarded as serial homologues and coded as a single character. In fact, however, they transform independently from each other. Coding them as a single character with character state “more deep than wide” represents an oversimplification and loss of phylogenetic information.

Figure 3. Distribution of characters “antenna I-length” (character 19, CI=0.18, RI=0.53; left) and “gnathopod II article 6 size” (character 39, CI=0.33, RI=0.7; right). Long antennae are considered as troglomorphic, whereas a large-sized gnathopod II is supposed to be a synapomorphy of “Orniphargus” (S. Karaman (1950c)).
Changes of taxonomic rank

The analysis revealed two nomenclature errors, which originated from an earlier work (S. Karaman 1950c). *Niphargus croaticus* and *N. arbiter* occur syntopically. In the course of redescription, S. Karaman misinterpreted the identity of Jurinac’s *N. croaticus*, and in his redescription of what he believed to be *N. croaticus*, criticized the original description as inaccurate. Gordan Karaman (1984), who described S. Karaman’s “*N. croaticus*” as a new species, *N. arbiter*, and redescribed the true *N. croaticus*, later corrected the mismatch. Sket (1959, 1960) erroneously named *N. orcinus redenseki* and *N. croaticus pachytelson* based on S. Karaman’s nomenclature and drawings. *Niphargus o. redenseki* resembles *N. croaticus*, the description of which was at that time rejected, whereas *N. c. pachytelson* resembles *N. arbiter* that was at that time designated as *N. croaticus*.

*Niphargus o. redenseki* is in fact very similar to the true *N. croaticus*, but has a shorter (i.e. less troglomorphic, see Discussion) antenna I and pereopod VII, and partially reduced pleonal spinosity (which might point to more advanced troglomorphy). Different patterns
of troglomorphic features of two sympatric taxa suggest an independent history, thus \textit{N. redenseki} should be raised to species level.

According to the results of the cladistic analysis (Figure 1), \textit{N. croaticus pachytelson} belongs to a different lineage than \textit{N. croaticus}. Its distinct position in the cladogram, as well as marked morphological differences (presence of dorsal telsonic spines, shallower telsonic cleft, several setae on ventro-posterior margin of pereomera VII, lack of pleonal spines, single aesthetasc per article of flagellum I, single distal row of setae on gnathopod I/3, inner-side positioned denticulated spines on propodus II, setae on dactyla I–II in groups), allow us to elevate the taxon to species rank.

\textbf{New species}

\textit{Niphargus dolichopus} n. sp. (Figures 6, 8–11)

\textbf{Type locality.} Cave Suvaja pećina, Lušći polje, Sanski most, Bosnia and Herzegovina
Figure 6. *N. dolichopus* sp. n. (above) and *N. dabarensis* sp. n. (below). Holotypes, lateral view.
Material examined. Suvaja pećina, Lušći polje, Sanski most, Bosnia and Herzegovina, 26 July 2004; coll. P. Trontelj; male and female.

Holotype: female, 17.1 mm; two slides labeled “B”.

Paratypes: male, 16.7 mm, two slides labeled “A”; 5 specimens (males and females) not dissected.

Figure 7. *N. lourensis* sp. n. (above) and *N. polymorphus* sp. n. (below). Holotypes, lateral view.
Holotype and paratypes deposited in the collection of Oddelek za biologijo, Biotehniška fakulteta, Univerza v Ljubljani (Department of Biology, Biotechnical Faculty, University of Ljubljana).

**Etymology.** The species was named after its remarkably long pereopods VI–VII.

**Diagnosis**

Pereonites I–V without spines, pereonite VII with strong spines dorso-posteriorly; posterior margin of urosomite III dorso-laterally with spines; telson cleft shallow. Antenna I very long (1.3–1.35 of body length). Antenna II lengths of peduncle articles 4:5 is 1:1.3; flagellum short consists of 6–8 articles. Pereopods VI–VII extremely elongated, pereopod VII length 0.97–1 of body length.

**Description**

**Head and trunk** (Figures 6, 11). Body length up to 17.5 mm. Head length 10–11% of body length; rostrum absent. Pereonites I–V without setae; pereonite VII with 1–2 postero-ventral setae and up to 12 strong spines dorso-posteriorly. Dorsal spines may be present also on pereonite VI.

Pleonites I–III with 14–16 dorso-posterior spines. Epimeral plate II: angle of postero-ventral corner approximately rectangular; posterior margin sinusoidal; ventral margin convex. Along ventral margin 2 spines, along posterior margin 7–10 setae. Epimeral plate III: angle of postero-ventral corner acute; posterior margin sinusoidal; ventral margin convex. Along ventral margin 3 spines, along posterior margin 7–10 setae.

Urosomite I postero-dorso-laterally with 3–4 spines; urosomite II postero-dorso-laterally with 3 spines and/or setae; urosomite III postero-dorso-laterally with 2 spines. At the base of uropod I 1 spine.

Telson length: width ratio is 1:0.85–0.9; cleft 0.4–0.6 of length. Only 3 apical spines per lobe present, these are 0.4–0.5 of telson length. Plumose setae inserted laterally, in the middle part of telson.

**Antennae** (Figure 8). Antenna I 1.3–1.4 of body length. Flagellum with up to 67 articles; each article with 1–2 aesthetascs. Peduncle articles in ratio 1:1–1.05: 0.6. Proximal article of peduncle dorso-distally slightly produced. Accessory flagellum biarticulated; distal article shorter than half of proximal article length.

Length ratio antenna I:II as 1:0.2–0.25. Flagellum of antenna II with 6–8 articles; aesthetascs absent. Peduncle articles lengths 4:5 is 1:1.3; flagellum 0.2–0.25 of peduncle length (articles 4+5). Peduncular article 4 of antenna II with a row of fine setae ventro-proximally.

**Mouth parts** (Figure 8). Inner lobes of labium longer than half of the outer lobes.

Left mandible: incisor with 5 teeth, lacinia mobilis with 4 teeth; between lacinia and molar row of serrated spines, long seta at the base of molar. Right mandible: incisor process with 4 teeth, lacinia mobilis with several small denticles, between lacinia and molar a row of serrated spines; molar process with a long basal seta. Ratio of mandibular palp article 2:article 3 (distal) is 1:1.1–1.2. Proximal palp article without setae; the second article with 9–10 setae groups and single setae; distal article with 1 A group of 7 setae; 3–4 B groups; 37–38 D single setae; 6–7 E single setae.
Maxilla I distal palp article with 8 apical setae. Outer lobe of maxilla I with 7 uni-, bi- or pluri-toothed spines; inner lobe with 2 setae.

Maxilla II inner lobe slightly smaller than outer lobe; both of them apically setose.

Maxilliped palp article 2 with 8–10 rows of setae along inner margin; distal article with a dorsal seta, a group of small setae at the base of the nail. Maxilliped outer lobe with 13 flattened spines and 4 serrated setae; inner lobe with 3–4 flattened apical spines and 8–9 serrated setae.

Coxal plates, gills (Figures 5, 9, 10, 11). Coxal plate I of rhomboid shape, antero-ventral corner pointed; anterior and ventral margin of coxa I with 8 setae. Coxal plate II width:depth is 1:0.9–1; anterior and ventral margin with 8 setae. Coxal plate III width:depth is 1:0.8; along antero-ventral margin 10–12 setae. Coxal plate IV width:depth is 1:0.9–1; posteriorly slightly concave (0.1–0.2 of coxa width); along antero-ventral margin 11–12 setae. Coxal plates V–VI: only anterior lobe developed; along posterior margin 3 setae or spines. Coxal plate VII semicircular, along posterior margin 2 setae and/or spines. Gills II–VI large, irregularly ovoid.

Gnathopod I (Figure 9). Ischium with postero-distal row of setae. Carpus 0.6–0.65 of basis length and 0.8–0.85 of propodus length. Anterior margin of carpus with the distal and 1 additional group of setae; carpus posteriorly with transverse rows of setae proximally, a row of lateral setae and rows of submarginal setae; postero-proximal bulge large (1/3 of carpus length), positioned medially. Propodus rectangular, palm short, convex and slightly...
inclined. Along posterior margin 7 rows of denticulated setae. Anterior margin with 34–37 setae in 7 groups, antero-distal group with 11–12 setae. Group of 3 facial setae proximally of palmar spine; small groups of surface setae present. Palmar corner with strong palmar spine, single supporting spine on inner surface and 3 denticulated spines on outer side. Nail

Figure 9. *N. dolichopus* sp. n., holotype. Gnathopod I (above) and gnathopod II (below).
length 0.2–0.25 of total dactylus length; along anterior margin 10 single setae; short setae along inner margin present.

**Gnathopod II** (Figure 9). Basis width:length is 1:0.3. Ischium with postero-distal row of setae. Carpus 0.6 of basis length and 1–1.05 of propodus length. Anterior margin of carpus with distal and 2 additional groups of setae; carpus posteriorly with transverse rows of setae proximally, a row of lateral setae and submarginal setae groups; postero-proximal bulge large (1/3 of carpus length), positioned medially. Propodus small (compared to the body) and equal to propodus of gnathopod I. Propodus rectangular, palm short, convex and more inclined than palm of gnathopod I. Posterior margin with 9–10 rows of denticulated setae. Anterior margin with 18–20 setae in 5 groups; antero-distal group with 9–10 setae. Group of 3 facial setae proximally of palmar spine; small groups of surface setae present. Palmar corner with strong palmar spine, single supporting spine on inner surface and 2–4 denticulated spines on outer side. Nail length 0.2–0.25 of total dactylus length. Along anterior margin 10–11 single setae; short setae along inner margin present.

**Pereopods III–IV** (Figure 10). Lengths of pereopods III–IV equal. Dactylus IV 0.5 of propodus IV; nail length 0.35–0.4 of total dactylus length. Dactyli III–IV with dorsal plumose seta; at the base of nail a spine and a seta.

**Pereopods V–VII** (Figure 11). Lengths of pereopods V:VI:VII is 1:1.4–1.45:1.4–1.45. Pereopod VII length 0.97–1 of body length.

Bases V–VII narrow, length:width is 1:0.5; posterior margin straight, without distal lobes; posteriorly 12–19 strong hook-like spines; anteriorly 5–6 single/groups of spines and/
or setae. Dactylus VII length 0.2 of propodus VII length. Dactyli V–VII with dorsal plumose seta; at the base of nail a spine and a seta.

Pleopods and uropods (Figure 10). Pleopods I–III each with 2-hooked retinacles and few setae. Pleopod II rami of 23–24 articles each.

Uropod I protopodit with 10 dorso-lateral spines; 4–5 dorso-medial spines. Exopodite:endopodite length is 1:1–1.05; rami straight. Uropod I rami with groups of spines and/or setae along inner and outer margins. Endopodite with up to 8–10 setae and/or spines in 7–8 groups of spines and/or setae; apically 5 spines. Exopodite with up to 19–21 setae and/or spines in 10 groups; apically 5 spines.

Uropod II exopodite:endopodite length is 1:1.2–1.25.

Uropod III 0.4 of body length. Protopodite with 2 small lateral setae and 6–7 apical spines and setae. Endopodite 0.4 of protopodite length, apically with a single spine and single seta; laterally 1 spine. Exopodite of uropod III rod-shaped, distal article 0.07–0.08 of
the proximal article length. Proximal article with 8–9 groups of setae, plumose setae and spines along inner margin; 7–9 groups of spines and setae along outer margin. Distal article with 1–2 lateral setae groups; setae set along both margins; apically 3–4 setae.

Variability. The studied specimens do not differ in spination and shape; minor differences in number of setae and spines may be a consequence of different body lengths.

Remarks and affinities. In general appearance, *N. dolichopus* with small gnathopods, extremely long pereopods V–VII without distal lobes on narrow bases and extremely long antenna I, as well as with well-developed spination of pleonites and pereopods, resembles both *N. croaticus* and *N. balcanicus*. However, it represents a unique combination of characters that can be found in both species. Short flagellum of antenna II, approximately equal size of propods of gnathopods I and II, shallow telson cleft and spines on urosomite III are characters shared by *N. croaticus*, from which it can be distinguished by the presence of strong dorsal spines on pereonites VI–VII. These spines are also characteristic of *N. balcanicus*. However, *N. balcanicus* has dorsal spination much better developed, also on pereonites I–V; it has a much longer flagellum of antenna II, posteriorly produced coxae V–VI, proxi-posterior lobe on pereopod VII, strong spines on dactyls III–VII, and well developed plumose setae on uropods I–II. On the other hand *N. balcanicus* lacks spines on urosomite III and additional anterior setae on the carpus of gnathopods I–II.

*Niphargus dabarensis* n. sp. (Figures 6, 12–15)

Type locality. Dabarska pećina, Bosnia and Herzegovina.

Material examined. Cave Dabarska pećina, Bosnia and Herzegovina; July 2004; coll. P. Trontelj; 1 female.

Holotype: female, 25.5 mm (two slides).

Holotype deposited in the collection of Oddelek za biologijo, Biotehniška fakulteta, Univerza v Ljubljani (Department of Biology, Biotechnical Faculty, University of Ljubljana).

Etymology. The epithet dabarensis is derived from the type locality.

Diagnosis

Telson with 5 apical spines per lobe, 1 spine on dorsal surface and without lateral and medial spines. Antenna I 0.95 of body length. Carpus I–II with proximal bulge large (1/3 of carpus length), gnathopod II propodus large ([length+width+diagonal] 0.25 of body length;) gnathopod propodi I:II (length+width+diagonal) is 1:0.75. Denticulated spines in palmar corner of gnathopod II on inner side. Coxal plates V–VI disto-posteriorly produced; bases V–VI posteriorly with setae and spines; basis VII with slightly developed proxi-posterior lobe; all bases narrow, without disto-posterior lobe; dactyls V–VII with 2–3 dorsal plumose setae. Uropod I–II with plumose setae.

Description

Head and trunk (Figures 6, 14). Body length up to 25.5 mm. Head length 9% of body length; rostrum absent. Pereonites I–VI without setae; pereonite VII with 3 postero-ventral setae.
Pleonites I–III with 17–19 dorso-posterior spines. Epimeral plate II: angle of postero-ventral corner sub-rectangular; posterior margin sinusoidal; ventral margin convex; along ventral margin 2 spines, along posterior margin 7 setae. Epimeral plate III: angle of postero-ventral corner acute; posterior margin straight to concave; ventral margin convex to straight; along ventral margin 3 spines; along posterior margin 10 setae.

Urosomite I postero-dorso-laterally with 4 spines; urosomite II postero-dorso-laterally with 5 spines; urosomite III postero-dorso-laterally without setae and/or spines. At the base of uropod I 1 spine.

Telson length:width is 1:0.85; cleft 0.6 of length; apical spines 0.35 of length. Plumose setae inserted laterally in the middle part of telson. Telson only with 5 apical spines and 1 dorsal surface spines per lobe.

Antennae (Figure 12). Antenna I 0.93 of body length. Flagellum of antenna I with 65 articles; each article with 1–2 aesthetascs. Peduncle articles in ratio 1:1.1:0.6. Proximal
article of peduncle dorso-distally slightly produced. Accessory flagellum biarticulated; distal article shorter than half of proximal article length.

Length ratio antenna I:II as 1:0.33. Flagellum of antenna II with 19 articles; aesthetasc absent. Peduncle articles lengths 4:5 is 1:1.05; flagellum 0.6 of peduncle length (articles 4+5). Article 4 of antenna II peduncle proximally with ventral row of fine setae.

**Mouth parts** (Figure 12). Inner lobes of labium longer than half of the outer lobes.

Left mandible: incisor with 5 teeth, lacinia mobilis with 4 teeth; between lacinia and molar row of serrated spines, long seta at the base of molar. Right mandible: incisor process with 4 teeth, lacinia mobilis with several small denticles, a row of serrated setae and molar process with a long basal seta. Mandibular palp articles 2:article 3 (distal) is 1:1.25. Proximal palp article without setae; the second article with 9 setae groups and single setae; distal article with 1 A group of 14 setae; 5 B groups; 37 D single setae; 5 E single setae.
Maxilla I distal palp article with 8 apical setae. Outer lobe of maxilla I with 7 uni-, bi- or pluri-toothed spines; inner lobe with 10 setae.

Maxilla II inner lobe slightly smaller than outer lobe; both of them with numerous apical setae.

Maxilliped palp article 2 with 11 rows of setae along inner margin; distal article with a dorsal seta and a group of small setae at the base of the nail. Outer lobe with 15 flattened spines and 10 serrated setae; inner lobe with 4 flattened apical spines and 6 serrated setae.

Coxal plates, gills (Figures 6, 13–15). Coxal plate I of rhomboid shape, antero-ventral corner pointed; anterior and ventral margin of coxa I with 11 setae. Coxal plate II width:depth is 1:0.8; anterior and ventral margin with 12 setae. Coxal plate III width:depth is 1:0.75; antero-ventral margin with 10 setae. Coxal plate IV width:depth is 1:0.85; posteriorly slightly concave (0.1–0.2 coxa width); antero-ventral margin with up to 14 setae. Coxal plates V–VI: anterior lobe developed, coxae disto-posteriorly produced; on posterior margin 1 seta. Coxal plate VII half-elliptic, ventral margin slightly concave; posterior margin with 1 seta. Gills II–VI large, irregularly ovoid.

Gnathopod I (Figure 13). Ischium with postero-distal row of setae. Carpus 0.5 of basis length and 0.7 of propodus length. Anterior margin of carpus only with distal group of setae; carpus posteriorly with transverse rows of setae proximally, a row of lateral setae and
rows of submarginal setae; postero-proximal bulge large (1/3 of carpus length), positioned proximally. Propodus large “hoof” shaped, palm long, convex and oblique. Posterior margin with 14 rows of denticulated setae. Anterior margin with 32 setae in 4 groups; antero-distal group with 11 setae. Group of 4 facial setae proximally of palmar spine; small groups of surface setae present. Palmar corner with strong palmar spine, single supporting spine on inner surface and 3 denticulated spines on outer side. Nail length 0.2 of total dactylus length; along anterior margin 11 single setae; short setae along inner margin present.

Gnathopod II (Figure 13). Basis width:length is 1:0.3. Ischium with postero-distal row of setae. Carpus 0.5 of basis length and 0.75 of propodus length. Anterior margin of carpus with distal group of setae; carpus posteriorly with transverse rows of setae proximally, a row of lateral setae and rows of submarginal setae; postero-proximal bulge large (1/3 of carpus length), positioned proximally. Propodus large (compared to the body), much larger than propodus of gnathopod I. Propodus large “hoof”-shaped, palm long, convex and oblique. Posterior margin with 17 rows of denticulated setae. Anterior margin with 13 setae in 4 groups; antero-distal group with 12 setae. Group of 4 facial setae proximally of palmar spine; small groups of surface setae present. Palmar corner with strong palmar spine, single
supporting spine and 2 denticulated spines on inner surface. Nail length 0.2 of total dactylus length. Along anterior margin 7 single and a pair of setae (totally 9 setae); short setae along inner margin present.

_Pereopods III–IV_ (Figure 14). Lengths of pereopods III–IV equal (1:1). Dactylus IV 0.45 of propodus IV length; nail length 0.45 of total dactylus length. Dactyla III–IV with dorsal plumose seta; at the base of nail a weak spine.

_Pereopods V–VII_ (Figure 15). Lengths of pereopods V:VI:VII is 1:1.25:1.25. Pereopod VII length 0.7 of body length.

- Bases V–VII length:width is 1:0.5–0.55; posterior margin straight or slightly convex; distal lobes absent; posteriorly with 24 (basis V), 13 (basis VI) or 11 (basis VII) setae and spines; anteriorly with 7–8 single slender spines and/or groups of slender spines and/or setae. Postero-proximal lobe on basis VII slightly developed. Lengths relation of propodus:dactylus is 1:0.25. Dactyli V–VII with 2–3 plumose setae; at the base of nail a spine and a seta.

_Pleopods and uropods_ (Figure 14). Pleopods I–III with 2-hooked retinacles each and few setae. Pleopod II rami of 25–28 articles each.

- Uropod I protopodite with 7 dorso-lateral spines and 5 dorso-medial spines. Exopodite:endopodite length is 1:1.05; rami straight. Uropod I rami with groups of spines and/or setae along lateral and medial side. Endopodite with 8 setae and/or spines in 4 groups of spines and/or setae; apically 5 spines. Exopodite with 21 setae and/or spines in 6 groups of spines and/or setae; apically 5 spines.

- Uropod II exopodite:endopodite length is 1:1.05.

- Uropod III length 0.2 of body length. Protopodite with 2 lateral spines and 8 apical spines and setae. Endopodite 0.5 of protopodite length; apically with 1 spine and 1 plumose seta; laterally 2 setae. Exopodite of uropod III slightly flattened; distal article 0.12 of proximal article length. Proximal article with 6 groups consisting of setae, plumose setae and spines along inner margin and 3 groups of spines and setae along outer margin. Distal article of exopodite without lateral setae; apically 3 spines and 3 setae.

_Variability_. Only one female was studied. Another specimen found is preserved in 96% ethanol for molecular analyses.

_Remarks and affinities_. Size and shape of propodus of gnathopods I–II as well as position of palmar spines on gnathopod II are characteristic for species _N. arbiter_, _N. salonitanus_, _N. rejici_ and _N. lourensis_. From these taxa, _N. dabarensis_ can be distinguished by features that are shared with _N. vjetrenicensis_, _N. bilecanus_, _N. hercegovinensis_ and _N. trullipes_: large bulge on carpus I–II, disto-posteriorly produced coxal plates V–VI, by the presence of proximo-posterior lobe of basis VII, dactyls V–VII with 2–3 dorsal plumose setae as well as uropods I–II with plumose setae. Finally, narrow bases without distal lobes of pereopods V–VII and such a long antenna I (similar as in _N. croaticus_ and _N. balcanicus_) are not present in any of the above listed species.

_Niphargus lourensis_ n. sp. (Figures 7, 16–19)

_Type locality_. Spring of Louros River, Vouliasta, Ionannina, Greece.
Material examined. Spring of Louros River, Vouliasta, Ionannina, Greece; 25 April 2004; coll. C. Fišer and R. Verovnik.

Holotype: female, 15 mm; slide no. 4.

Another specimen found is preserved in 96% ethanol for molecular analyses and is deposited in the collection of Oddelek za biologijo, Biotehniška fakulteta, Univerza v Ljubljani (Department of Biology, Biotechnical Faculty, University of Ljubljana).

Etymology. The epithet lourensis is derived from the type locality.

Diagnosis

Pleonites I–III with setae along dorso-posterior margin. Telson with apical spines only; these are very long (0.61 telson length). Carpus I–II with postero-proximal bulge large (1/3 of carpus length); gnathopod II propodus large ([length+width+diagonal] 0.29 body length); much larger than propodus of gnathopod I (1:0.75). Denticulated spines in palmar corner of gnathopod II hidden behind the palmar spine. Coxae V–VII with single posterior setae. Pereopods V–VII with numerous strong spines. Uropod III very spiny and very short (0.19 of body length); exopodite flattened, distal article with setae along one margin only.

Description

Head and trunk (Figures 7, 18). Body length up to 15 mm. Head length 11% of body length; rostrum absent. Pereonites I–VI without setae; pereonite VII with 2 postero-ventral setae.

Pleonites I–III with 6 setae along dorso-posterior margin. Epimeral plate II: angle of postero-ventral corner sub-rectangular; posterior margin concave; ventral margin convex; at the ventral margin 1 spine, along posterior margin 6 setae. Epimeral plate III: angle of postero-ventral corner acute; posterior margin concave; ventral margin convex. Along ventral margin 2 spines; along posterior margin 6 setae.

Urosomite I postero-dorso-laterally with 2 spines; urosomite II postero-dorso-laterally with 4 spines; urosomite III postero-dorso-laterally without setae and/or spines. At the base of uropod I 1 spine.

Telson length:width is 1:0.85; cleft 0.65 of length. Only 3–4 apical telson spines per lobe, they are very long, 0.6 of telson length. Plumose setae inserted laterally in the middle part of telson.

Antennae (Figure 16). Antenna I 0.5–0.55 of body length. Flagellum with 33 articles; each article with 1 aesthetasc. Peduncle articles lengths in ratio 1:0.85:0.55. Proximal article of peduncle dorso-distally slightly produced. Accessory flagellum biarticulated; distal article shorter than half of proximal article length.

Length ratio antenna I:II as 1:0.55. Flagellum of antenna II with 12 articles; aesthetasc absent. Peduncle articles lengths 4:5 is 1:1.05; flagellum 0.65–0.7 of peduncle length (articles 4+5). Article 4 of antenna II peduncle proximally with ventral row of fine setae.

Mouth parts (Figure 16). Inner lobes of labium longer than half of the outer lobes.

Left mandible: incisor with 5 teeth, lacinia mobilis with 4 teeth; a row of serrated spines between lacinia and molar and a long seta at the base of molar. Right mandible: incisor
process with 4 teeth, lacinia mobilis with several small denticles, a row of serrated setae and molar process with a long basal seta. Mandibular palp article 2:article 3 (distal) is 1:1.4. Proximal palp article without setae; the second article with 8 setae groups and single setae; distal article with 2 A groups of 1+7 setae; 4 B groups; 41 D single setae; 6 E single setae.

Maxilla I distal palp article with 4 setae apically. Outer lobe of maxilla I with 7 uni-, bi- or pluri-toothed spines; inner lobe with 4 setae.

Maxilla II inner lobe slightly smaller than outer lobe; both of them with numerous apical setae.

Maxilliped palp article 2 with 9 rows of setae along inner margin; distal article with a dorsal seta and a group of small setae at the base of the nail. Outer lobe with 10 flattened spines and 7 serrated setae. Inner lobe with 4 flattened spines and 10 serrated setae apically.

Coxal plates, gills (Figures 7, 17–19). Coxal plate I of irregularly trapezoid shape; anterior and ventral margin of coxa I with 6 setae. Coxal plate II width:depth is 1:0.88; anterior and ventral margin with 9 setae. Coxal plate III width:depth is 1:0.8; antero-ventral margin with 10 setae. Coxal plate IV width:depth is 1:0.9; posterior concavity slightly developed (concavity depth between 0.1–0.2 coxa width); antero-ventral margin with 10 setae. Coxal
plates V–VI with anterior lobe; posterior margin with 1 spine. Coxal plate VII “half-egg” shaped; posterior margin with 1 seta. Gills II–VI large, irregularly ovoid.

**Gnathopod I** (Figure 17). Ischium with single postero-distal row of setae. Carpus 0.5 of basis length and 0.65 of propodus length. Anterior margin of carpus with distal group of setae only; carpus posteriorly with transverse rows of setae proximally and a row of lateral setae; postero-proximal bulge large (1/3 of carpus length), positioned proximally. Propodus “hoof”-shaped, palm long, oblique and convex. Posterior margin with 10 rows of denticulated setae. Anterior margin with 25 setae in 6 groups; antero-distal group with 10 setae. Group of 3 facial setae proximally of palmar spine; small groups of surface setae present. Palmar corner with strong palmar spine, single supporting spine on inner surface and 4 denticulated spines on outer side. Nail length 0.3 of total dactylus length; along anterior margin 3 single setae and a group of 2 setae; short setae along inner margin present.

**Gnathopod II** (Figure 17). Basis width:length is 1:0.3. Ischium with single postero-distal row of setae. Carpus 0.5 of basis length and 0.6 of propodus length. Anterior margin of carpus with distal group of setae; carpus posteriorly with transverse rows of setae
proximally, a row of lateral setae, and a short row of setae at the base medially; postero-proximal bulge large (1/3 of carpus length), positioned proximally. Propodus much larger than propodus I, “hoof”-shaped, palm long, oblique and convex. Posterior margin with 12 rows of denticulated setae. Anterior margin with 10 setae in 5 groups; antero-distal group with 12 setae. Group of 3 facial setae proximally of palmar spine; small groups of surface setae present. Palmar corner with strong palmar spine, single supporting spine and 2 denticulated spines on inner surface. Nail length 0.25 of total dactylus length. Along anterior margin 6 single setae; short setae along inner margin present.

Pereopods III–IV (Figure 18). Lengths of pereopods III:IV is 1:0.95. Dactylus IV 0.3 of propodus IV length; nail length 0.5 of total dactylus length. Dactyli III–IV with dorsal plumose seta; at the base of nail a spine and a seta.

Pereopods V–VII (Figure 19). Lengths of pereopods V:VI:VII is 1:1.25:1.25. Pereopod VII length 0.55 of body length.

Bases V–VII length:width is 1:0.65–0.7; posterior margin convex to straight; posterodistal lobe small; posteriorly 13 (basis V), 12 (basis VI) or 9 (basis VII) setae; anteriorly 8–9 single and/or groups of slender spines and/or setae. Spines on articles 4–6 of pereopods V–VII, numerous, long and strong. Propodus VII:dactylus of pereopod VII is 1:0.2. Dactylus VII with dorsal plumose seta; at the base of nail a strong spine and a seta.

Pleopods and uropods (Figure 18). Pleopods I–III with 2-hooked retinacles each and few setae. Pleopod II rami of 12–14 articles each.
Uropod I protopodite with 7 dorso-lateral spines and 4 dorso-medial spines. Exopodite:endopodite lengths is 1:1; rami straight. Uropod I rami with groups of spines and/or setae along medial and lateral surfaces. Endopodite with 7 setae and/or spines in 5 groups; apically 5 spines. Exopodite with 7 setae and/or spines in 6 groups; apically 5 spines.

Uropod II exopodite:endopodite length is 1:1.1.

Uropod III length is 0.2 of body length. Protopodite with 2 lateral spines and 8 apical spines and/or setae. Endopodite 0.4 of protopodite length; apically with 1 spine and 1 plumose seta; laterally 1 seta. Exopodite of uropod III flattened; distal article 0.15 of proximal article length. Proximal article with 6 groups of setae, plumose setae and very long and strong spines along inner margin; 5 groups of very long and strong spines and setae along outer margin. Distal article of exopodite with 3 lateral groups of setae; groups set along one margin; apically 3 setae.

Figure 19. *Niphargus lourensis* sp. n., holotype. Pereopods V–VII. Details of pereopod VII.
Variability. Only one female was studied.

Remarks and affinities. The most remarkable features of the species are extremely strong and long spines on telson and appendages as well as setae along the dorso-posterior margins of the pleonites. These characters can be found also in *N. podgoricensis*, which can be distinguished by the presence of spines on urosomite III and plumose setae on uropod I. Another important distinguishing feature between *N. podgoricensis* and *N. lourensis* are proportions of gnathopods and the position of spines on the palmar corner of gnathopod II, which in the new species resembles *N. arbiter, N. salonitanus, N. rejici* and *N. dabarensis*. However, none of these taxa has such long telson spines or setae along the dorso-posterior margins of the pleonites.

*Niphargus polymorphus* n. sp. (Figures 7, 20–23)

Type locality. Bileća, Bosnia and Herzegovina

Material examined. Bileća, Bosnia and Herzegovina; September 1956; coll. B. Sket; 2 females.
- Holotype: female, 16.1 mm; slide no. 3.
- Paratypes: female, 1 specimen dissected, slide no. 2; 5 specimens, not dissected.
- Holotype and paratypes deposited in the collection of Oddelek za biologijo, Biotehniška fakulteta, Univerza v Ljubljani (Department of Biology, Biotechnical Faculty, University of Ljubljana).

Etymology. The name was given on the basis of the mosaic appearance of certain features characteristic of various other species (coxae, bases and number of hooks in retinacles) as well as for the polymorphism of some characters (dorsal setae on carpus of gnathopods I–II, additional spine on dactyl VII), which are usually stable in other species.

Diagnosis
Pleonites I–III with spines and some setae along dorso-posterior margin. Telson with 8–9 apical spines per lobe. Coxal plate of gnathopod I antero-ventrally produced; coxal plates II–IV narrow (width:depth is 1:0.5–0.75); coxal plate IV with well developed posterior lobe. Coxal plates V–VI with posterior lobe much larger than anterior lobe. Bases V–VI with disto-anterior lobe equally developed as disto-posterior lobe; basis VII with extremely large disto-posterior lobe. Pleopods I–III with 3 hooks in retinacula.

Description
Head and trunk (Figures 7, 22). Body length up to 21.5 mm. Head length 11–13% of body length; rostrum absent. Pereonites I–VI without setae; pereonite VII with 3–4 postero-ventral setae.
- Pleonites I–III with up to 29 spines and setae along dorso-posterior margin. Epimeral plate II: angle of postero-ventral corner acute; posterior margin straight to concave; ventral margin convex; along ventral margin 3–4 spines; along posterior margin 11–15 setae.
- Epimeral plate III: angle of postero-ventral corner acute; posterior margin concave; ventral margin convex; along ventral margin 4 spines; along posterior margin 11–15 setae.
Urosomites I–II postero-dorso-laterally with 5 spines; urosomite III without setae and/or spines. At the base of uropod I 1 spine.

Telson length:width is 1:0.75–0.85; cleft 0.7–0.75 of length; apical telson spines 0.3–0.35 of the length. Plumose setae inserted laterally in the middle part of telson. Only apical spines, 8–9 per lobe, present.

**Antennae** (Figure 20). Antenna I 0.9 of body length. Flagellum with 50–62 articles; each article with 1–2 aesthetascs. Peduncle articles in ratio 1:0.8–0.9:0.7. Proximal article of peduncle dorso-distally slightly produced. Accessory flagellum biarticulated; distal article shorter than half of proximal article length.

Length ratio antenna I:II is 1:0.25–0.3. Flagellum of antenna II with 13 articles; aesthetascs absent. Antenna II peduncle articles 4 and 5 equally long (1:1); flagellum 0.6–0.65 of peduncle length (articles 4+5). Article 4 of antenna II peduncle proximally with ventral row of fine setae.

**Mouth parts** (Figure 20). Inner lobe of labium longer than half of the outer lobe.

Left mandible: incisor with 5 teeth, lacinia mobilis with 4 teeth; between lacinia and molar row of serrated spines, long seta at the base of molar. Right mandible: incisor process with 4 teeth, lacinia mobilis with several small denticles, a row of serrated setae and molar process with a long basal seta. Mandibular palp articles 2:3 (distal) is 1:1.15. Proximal palp article without setae; the second article with 12 setae groups and single setae; distal article with 1 A group of 16 setae; 6 B groups; 41 D single setae; 6 E single setae.
Maxilla I distal palp article with 10–12 apical setae. Outer lobe of maxilla I with 7 uni-, bi- or pluri-toothed spines; inner lobe with 8 setae.

Maxilla II inner lobe slightly smaller than outer lobe; both of them with numerous apical setae.

Maxilliped palp article 2 with 11 rows of setae along inner margin; distal article with a dorsal seta and a group of setae at the base of nail. Outer lobe of maxilliped with 15–16 flattened spines and 6–8 serrated setae. Inner lobe with 5 flattened spines and 9–11 serrated setae apically.

Coxal plates, gills (Figures 7, 21–23). Coxal plate I antero-ventrally produced; anterior and ventral margin of coxa I with 14–15 setae. Coxal plate II width:depth is 1:0.7–0.73; anterior and ventral margin with 17–18 setae. Coxal plate III width:depth is 1:0.55–0.6; antero-ventral margin with 23 setae. Coxal plate IV width:depth is 1:0.7–0.8; postero-distally remarkably widened (postero-distal lobe exceeds 0.2 coxa width); antero-ventral margin with 31 setae. Coxal plates V–VI: posterior lobe much larger than anterior lobe; along posterior margin 6–7 setae, distally spine/very strong seta. Coxal plate VII half-elliptic, ventral margin slightly concave; posterior margin with 2 setae. Gills II–VI large, irregularly ovoid.

Gnathopod I (Figure 21). Ischium with single postero-distal row of setae row. Carpus 0.6–0.65 of basis length and 0.95–1 of propodus length. Anterior margin of carpus with distal...
group of setae, additional groups may be present; carpus posteriorly with transverse rows of setae proximally, a row of lateral setae and submarginal setae groups; postero-proximal bulge large (1/3 of carpus length), positioned proximally. Propodus rectangular, palm short, convex and slightly inclined. Posterior margin with 14 rows of denticulated setae. Anterior margin with 35–40 setae in 5 groups; antero-distal group with 14–15 setae. Group of 3–4 facial setae proximally of palmar spine; small groups of surface setae present. Palmar corner with strong palmar spine, 1–2 supporting spines on inner surface and 4 denticulated spines on outer side. Nail length 0.23 of total dactylus length; along anterior margin 7–8 single setae and a distal group of 2 setae; short setae along inner margin present.

**Gnathopod II** (Figure 21). Basis width:length is 1:0.3. Ischium with single postero-distal row of setae. Carpus 0.6–0.65 of basis length and 1.1–1.15 of propodus length. Anterior margin of carpus with distal group of setae, sometimes additional groups of setae are present; carpus posteriorly with transverse rows of setae proximally, a row of lateral setae and submarginal setae groups; postero-proximal bulge large (1/3 of carpus length), positioned proximally. Gnathopod II propodus small (compared to the body) and larger than propodus of gnathopod I. Propodus rectangular, palm short, convex and slightly inclined. Posterior margin with 17–18 rows of denticulated setae. Anterior margin with 15 setae in 4–5 groups; antero-distal group with 12–15 setae. Group of 4–5 facial setae proximally of palmar spine; small groups of surface setae present. Palmar corner with strong palmar spine, single supporting spine on inner surface and 3 denticulated spines on
outer side. Nail length 0.2 of total dactylus length; along anterior margin 6–7 single setae and a distal group of 2 setae; short setae along inner margin present.

*Pereopods III–IV* (Figure 22). Lengths of pereopods III–IV equal (1:1). Dactylus IV 0.5 of propodus IV length; nail length 0.4 of total dactylus length. Dactyli III–IV with dorsal plumose setae; at the base of nail a spine and a seta.

*Pereopods V–VII* (Figure 23). Lengths of pereopods V:VI:VII is 1:1.15–1.2:1.01–1.15. Pereopod VII length 0.6–0.65 of body length.

Bases V–VI length:width is 1:0.75–0.8; anterior and posterior margins convex; disto-anterior lobe equally large or larger than disto-posterior lobe; posterior margin with 33–34 (basis V) and 24–25 (basis VI) setae; anterior margin with 10–13 single and/or groups of slender spines and/or setae. Dactyla V–VI with 2–3 plumose setae, at the base of nail a spine and a seta.

Basis VII length:width is 1:0.85–0.9; posterior margin convex with large disto-posterior lobe; posteriorly with 21–22 setae and spines; anteriorly with 10–11 single and/or groups of slender spines and/or setae. Propodus:dactylus is 1:0.2–0.25. Dactylus VII with 2–3 dorsal plumose seta; at the base of nail a spine and a seta, additional spine on inner margin may occur.

*Pleopods and uropods* (Figure 22). Pleopods I–III with 3-hooked retinacles and few setae; occasionally distally of retinacle occurs a spine. Pleopod II rami of 24–27 articles each.
Uropod I protopodit with 7 dorso-lateral spines and 6 dorso-medial spines. Exopodite:endopodite lengths is 1:1.1–1.15; rami straight. Uropod I rami with groups of spines and plumose setae along medial and lateral surface. Endopodite with 10–19 setae and/or spines in 4–7 groups of spines and/or setae; apically 5 spines. Exopodite with up to 24–25 setae and/or spines in 7–8 groups of spine and/or setae; apically 5 spines.

Uropod II exopodite:endopodite lengths is 1:1.1.

Uropod III length 0.17–0.18 of body length. Protopodite with 2 lateral setae; 9–10 apical spines and/or setae. Endopodite 0.55–0.7 of protopodite length; apically with spines and plumose setae; totally with 2–3 setae and/or spines; laterally 2–3 setae and/spines in 1–2 groups. Exopodite of uropod III distinctly flattened; distal article 0.13–0.14 of proximal article length. Proximal article with 7–8 groups of setae, plumose setae and spines along inner margin and 4 groups of spines and/or setae along outer margin. Distal article of exopodite with 0–1 lateral setae groups; setae set along single margin; apically 2–7 setae.

**Variability.** The paratype is without additional spine on dactyls VII as well as without additional setae groups along anterior margin of gnathopods I–II. Spine distally of retinacles occurs irregularly. Males not known.

**Remarks and affinities.** *Niphargus polymorphus* resembles *N. carcerarius* in most characters, from which it can be distinguished by larger body size, spines along the dorso-posterior margin of pleonites and three hooks in the retinacles of the pleopods. Otherwise *N. polymorphus* shares some characters with *N. longiflagellum* (wide bases and structure of distal lobes of pereopods V–VII, large disto-posterior lobe on coxa IV, shape of gnathopods) as well as *N. steueri* (shape of coxal plate I, much larger posterior lobe on coxae V–VI) and *N. pectinicauda* (narrow coxal plates of pereopods I–IV, large disto-posterior lobe on coxa IV, much larger posterior lobe on coxae V–VI). However, *N. polymorphus* can be easily distinguished from all these species by the presence of the three hooks in the retinacle of pleopods and a higher number of apical telson spines.

**Discussion**

**Phylogeny of “Orniphargus” taxa**

The results of the present study do not confirm the findings of an earlier allozyme analysis (Bullini and Sbordoni 1980) that put “Orniphargus” outside *Niphargus*, as a sister group to *Gammarus*. However, we cannot compare the results of both studies directly, since the only “Orniphargus” species used in the allozyme study was *N. patrizii* (Sbordoni pers. commun.) – a species not included in our analysis.

Descriptions of groups or subgenera of *Niphargus* were often accompanied by comments such as “some of the characters may be different” (S. Karaman 1950c) or “…distinctively mosaic type evolution […] makes exact delimitation of any group extremely difficult…” (Sket and Notenboom 1993). A comparison of our results with S. Karaman’s diagnosis summarized in Table II illustrates the pitfalls of previous classifications. The most prominent feature, a large and massive body, is a combination of a phylogenetically non-informative plesiomorphy (stout, gammariform shape) and convergently acquired large size typical of many subterranean crustaceans including other niphargids as well as unrelated amphipods, e.g. *Megagidiella* (Bogidiellidae) or *Trogloleleupia* (Ingolfiellidae) (Holsinger 1994; Koenemann and Holsinger 1999). Similar conclusions can be drawn also for less obvious characters.
In our case, an almost completely resolved cladistic hierarchy has been obtained. However, only some smaller groups of taxa can be considered as supported (e.g. clades a-2.1, b-1). Larger clades (e.g. clades A, a-2) suffer from weak node support, a high number of homoplasies (parallelisms, reversals) and, consequently, low character consistency. In addition, multistate characters and numerous polymorphic characters might indicate rapid character evolution or parallel evolution.

Homoplasies may be explained, at least in part, as a consequence of homogeneous selection forces acting in the subterranean environment. Nevertheless, characters derived on account of “subterranean selection”, so-called troglomorphisms, should not necessarily be a priori regarded as homoplasies and may provide substantial information on the phylogeny of subterranean animals. Marques and Gnaspini (2001) addressed that question and proposed a method for coding troglomorphisms to minimize both errors due to homoplasies as well as loss of phylogenetically relevant information. The method was flawed (Desutter-Grandcolas et al. 2003; Harris et al. 2003) and, to date, no other method has been proposed to solve the problem successfully.

However, troglomorphosis is not a general phenomenon in subterranean animals, and sometimes different, closely related species or even allopatric populations of the same species reveal different patterns of troglomorphic characters (Turk et al. 1996; Aden 2005) as well as different degrees of changes of ancestral states (Prevorčnik et al. 2004; Christiansen 2005). We may assume that parallel evolution in subterranean environments results in similar, but not the same morphological differentiation (Prevorčnik et al. 2004). Our case shows that defining character states as exactly as possible can considerably refine hypotheses of primary homology. The same character state of a multistate troglomorphic character found in two taxa may either be a synapomorphy or a homoplasy due to parallel evolution. In our study, extremely elongated antennae I and pereopods VII are synapomorphies of the clades B and b-1, respectively, while moderately elongated appendages emerge in several different lineages convergently.

In the “Orniphargus” case, the problem of troglomorphisms is far from being trivial. Several species exhibit traits that can be regarded as progressive (e.g. elongated appendages) or reductive (setae and spine reductions) troglomorphisms (Langecker 2000; Christiansen 2005). However, a discussion on troglomorphisms should be restricted to phylogenetically well-supported comparisons of non-troglomorphic ancestor and troglobiotic descendant relationships (Dessuter-Grandcolas et al. 2003). At present, all niphargids display at least two prominent reductive characters, which might be regarded as troglomorphic: lack of eyes and lack of integumental pigmentation. Furthermore, no epigean and non-troglomorphic niphargid ancestor is known. The presumably plesiomorphic species N. valachicus, hypothesized to have lived already in surface waters of the ancient Paratethys area (Skeť 1981), does not appear basally in the cladogram. Moreover, over 30-million-year-old fossils found in Baltic amber (Coleman and Myers 2000; Coleman and Ruffo 2002) closely resemble some recent species and display some features that can be regarded as troglomorphic.

West Balkan clades A and B

Most of the large plesio-troglomorphic “Orniphargus” species live in the western Balkans. Most of the taxa from that territory belong to clades A and B (Figure 1). Surprisingly, N. longiflagellum is excluded from either clade, although it was originally described as N. orcinus longiflagellum. The biogeographic patterns of clades A and B resemble each
other remarkably. Both clades are distributed across the western Balkans. The basal positions of both clades are held by south-eastern Dinaric species (\textit{N. podgoricensis} and \textit{N. lourensis} [clade A], \textit{N. zavalanus} [clade B]). Further, both clades contain holodinaric (a-2.2 vs. b-2) as well as southeastern Dinaric subclades (a-2.1 vs. b-1) (biogeography of the western Balkans \textit{sensu} Sket [1994]). Interestingly, the ranges of both southeastern Dinaric subclades overlap only slightly, possibly pointing to two independent centers of speciation.

\textit{Taxonomy of “Orniphargus” and remarks on species with ambiguous morphology}

While the most parsimonious trees rejected the monophyly of “\textit{Orniphargus}” or the “\textit{orcinus group}” of species, the support for this rejection, measured as consistency and Bremer support indices, is weak. We can, therefore, maintain that that the taxonomic validity of “\textit{Orniphargus}” remains doubtful. However, as a comprehensive revision of the whole genus is underway, new arguments for its rejection will probably emerge. The use of this and other large groups of niphargids remains problematic for further taxonomic practice. It can hardly be expected that these groups will prove monophyletic after phylogenetic scrutiny. The subdivision into smaller and well-supported monophyla that can readily be diagnosed morphologically seems to be more productive for the subgeneric taxonomy of \textit{Niphargus} (e. g. clades a-1, a-2, b-1, b-2).

\textit{Niphargus virei} Chevreux, 1896 from France, and \textit{N. miljeticus} Straškraba, 1959 from Mljet Island (southern Adriatic Sea) show some similarities with “\textit{Orniphargus}” (Straškraba 1959). In addition, \textit{N. hvarensis} was considered as a species that shares morphological features both with “\textit{Stygoniphargus}” and “\textit{Orniphargus}” (S. Karaman 1952b, 1952c). The French species \textit{N. virei} was recently shown to be genetically rather heterogeneous, and speciation within this “species” cannot be excluded (Lefèbure et al. 2006). However, early designations of \textit{N. virei} as \textit{N. orcinus virei} (Schellenberg 1935) or \textit{N. miljeticus} as \textit{N. virei} (Schellenberg 1937) were not correct. Both \textit{N. virei} and (\textit{N. miljeticus} and \textit{N. hvarensis}) are distinct lineages evolved independently from the rest of the studied species and from each other. Our analysis clearly positions the clade (\textit{N. miljeticus} and \textit{N. hvarensis}) among the so-called “\textit{stylgius sensu lato}” species. Interestingly, our results suggest that the two populations identified as \textit{N. hvarensis} do not constitute a monophylum. Furthermore, \textit{N. miljeticus} may be synonymous with \textit{N. hvarensis}. However, the high variability in these populations demands additional analyses with a wider sampling of different populations. Because we were not able to obtain the holotypes of \textit{N. miljeticus}, decisive taxonomic statements are not possible, neither are they within the scope of this paper.

Affinities between Italian and west Balkan species can only be discussed with reference to \textit{N. stefanellii}, the only Italian species studied. It occupies the basal-most position among the studied “\textit{Orniphargus}” taxa, and does neither form a monophylum with \textit{N. hebereri} nor with \textit{N. skopljensis}, as stated by Straškraba (1972) or G. Karaman (1985b). \textit{Niphargus polymorphus} sp. n. resembles both “\textit{Orniphargus}” (spines along posterior margin of pleonites and solid body) and \textit{N. pectinicauda} (very deep coxae II–IV, well-developed posterior lobe on coxae V–VI, widened and lobated bases on pereopods V–VII with three-hooked retinacles). The latter is along with \textit{N. longidactylus} a presumed member of the “\textit{transitivus}” group of species (Sket and Notenboom 1993). Sket and Notenboom (1993) recognized paraphyly of the \textit{transitivus sensu lato} group, whereas the present study suggests it is polyphyletic.
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Appendix A: Characters and character states used in the study

1. **Body size**: 0: large (adult size >15 mm); 1: middle (adult size 8–15 mm); 2: small (adult size <8mm). The remarkable difference in body lengths is illustrated in Sket (1999a, Figure 2). Recognised states in the study based on our measurements set three robust classes.

2. **Body shape**: 0: stout (Gammarus/orcinus/hebereri type); 1: slender (stygius-hvarensis type); 2: very slender (aquilex-longicaudatus type).

3. **Epimeral plates II–III – shape of posterior margin**: 0: sinusoid (croaticus type); 1: concave (orcinus type); 2: concave in juvenile and +/- convex in adults, always with distal corner pointed (stygius type); 3: always convex, corner completely surrounded, sometimes marked with seta (aquilex-longicaudatus type).

4. **Telson shape**: 0: wide (width:length >1); 1: narrow (width:length <1).

5. **Length of apical telson spines**: 0: short (<0.45 telson length); 1: long (>0.45 telson length). Juvenile have longer spines than adults. Present character states are designed on proportions of adult specimens.

6. **Depth of telson cleft**: 0: shallow (<0.6 telson length); 1: middle (0.6–0.7 telson length); 2: deep (>0.7 telson length).

7. **Dorsal telson spines**: 0: present; 1: absent.

8. **Lateral telson spines**: 0: present; 1: absent.

9. **Spines on margins of telson cleft**: 0: present; 1: absent.

10. **Apical telson spines, number on both lobes**: 0: few (less than 9); 1: elevated (over 10).

11. **Number of setae on disto-posterior margin of pereomera VII**: 0: 1, rarely 2; 1: 3 or more.

12. **Pereonite VII, number of dorsal spines on**: 0: absent; 1: present.

13. **Number of setae/spines along postero-dorsal margin of pleonites I–III**: 0: the most 5 setae; 1: 6 or more setae/spines.

14. **Type of setae/spines along postero-dorsal margin of pleonites**: 0: setae; 1: setae and few spines; 2: spines, sometimes accompanied with few setae.

15. **Number of dorso-posterior setae/spines on each side of urosomite I**: 0: single seta/spine; 1: several setae/spines; 2: single strong, curved and backward turned spine on elevation. The difference between seta and spine cannot be established for the following reasons: (1) gradual transition in structure between seta and spines was often noted in character state 0; (2) a seta is the most common case of character state 1, but it may be replaced by the spine especially in younger animals. Character state 2 seems to be autapomorphic for *N. valachicus*.

16. **Dorso-posterior spines on each side of urosomites I–II**: 0: number of spines/setae on urosomite I the same or more numerous than on urosomite II; 1: spines/setae on urosomite I less numerous than spines on urosomite II; 2: urosomites I–II with 1 seta/spine. Character state 2 is most probably a result of reduction and must be treated independently from the character state 0.

17. **Spines of urosomite III**: 0: absent; 1: present.

18. **Number of spines at the base of uropode I**: 0: spine absent; 1: single spine; 2: at least 2 spines.
19. **Length of antenna I**: 0: very long (0.9 body length or more); 1: long (0.6–0.8 body length); 2: middle (0.45–0.55 body length); 3: short (0.4 body length or less). Antenna length varies with body size (i.e. age) within a population; the character states are designed on measures of adults.

20. **Antenna I, peduncle**: 0: article lengths 1: (0.95–1.15):(<0.55); 1: article lengths 1: (0.95–1.15):(0.60); 2: article lengths 1: (<0.9):(0.60); 3: article lengths 1: (<0.9):(<0.55).

21. **Aesthetascs on flagellum of antenna I**: 0: 1 per article; 1: 1–2, rarely 3 per article.

22. **Antenna II, peduncle**: 0: article 4 distinctly shorter than article 5 (0.95); 1: article 4 subequal or longer than article 5 (0.95–1.1); 2: article 4 much longer than article 5 (1.15).

23. **Antenna II, flagellum**: 0: well developed; 1: extremely short (0.3 peduncle length) consisting of few articles (10). A code 0 was given also to *N. stenopus*, despite its short flagellum, since it has more articles in flagellum.

24. **Shape of coxa I**: 0: parallelogram-shaped; 1: rhomboid; ventro-anterior corner slightly pointed; 2: irregular parallelogram with antero-ventral corner distinctly produced anteriorly; 3: irregularly flattened trapezoid.

25. **Position of setae on article 3 of gnathopod I**: 0: only row of setae postero-distally; 1: at least 1 additional group of posterior setae present.

26. **Presence of additional anterior setae on gnathopod I article 5**: 0: absent; 1: present. Along anterior margin of carpus a distal group of setae is always present. “Additional” setae or setae groups may be present subapically.

27. **Length of article 5 of gnathopod I**: 0: short (0.65–0.9 art. 6 length); 1: middle (0.9–1.1 art. 6 length); 2: long (>1.2 art. 6 length).

28. **Shape of gnathopod I, article 6**: 0: *hebereri* type (a>b< c); 1: *dalmatinus* type (a>b< c, a< c); 2: *longiflagellum* type (a>b< c, a> c); 3: *orcinus* type I (a>b= c); 4: *orcinus* type II (a>b> c). The highly variable shape of propodus was abstracted from the shape of triangle defined as: propodus length (distance between joints carpus-propodus and dactylus-propodus; measured on outer side), palm length (distance between joint dactylus-propodus and palmar spine) and diagonal (distance between joint carpus-propodus and palmar spine). Different shape types were designed on relations between the three parameters: palm length:length (a), diagonal:length (b), diagonal:palm length (c). The shape of propodus may change during development; in present study only adult proportions were considered.

29. **Inclination of palm of gnathopod I, article 6**: 0: sharply inclined (41°); 1: normal (46–53°); 2: blunt (>63°). Angle between propodus length and palm was calculated from the length, palm length and diagonal.

30. **Shape of coxa II**: 0: very deep (height:length <0.8); 1: moderately deep (height:length 0.8–1); 2: extremely shallow (height:length >1.05).

31. **Presence of additional anterior setae on gnathopod II, article 5**: 0: absent; 1: present. See comments at character 26.

32. **Length of article 5 of gnathopod II**: 0: extremely short (<0.65); 1: short (0.7–0.9); 2: long (0.95–1.1); 3: elongated (>1.3).

33. **Shape of gnathopod II, article 6**: 0: *hebereri* type; 1: *dalmatinus* type; 2: *longiflagellum* type; 3: *orcinus* type I; 4: *orcinus* type II. See comments on character 28.

34. **Inclination of palm of gnathopod I, article 6**: blunt (>66°); 1: normal (66–57°); 2: sharp (53–41°); 3: very sharp (<40). See comments for character 29.
35. **Position of serrate spines in palmar corner of gnathopod II, article 6:** 0: behind the palmar spines; 1: on inner side.

36. **Shape of gnathopods I–II, articles 5:** 0: broadly widened postero-proximally; 1: narrowly widened postero-proximally; 2: broadly widened postero-centrally.

37. **Gnathopods I–II, articles 7-setae:** 0: setae in several groups; 1: a row of single setae; 2: only one seta. Character states 0 and 1 cannot be always unambiguously distinguished. If 1–2 groups of up to 2 setae appeared distally, the character was given state 1.

38. **Comparison of gnathopod I–II, articles 6 (propodi), size comparison:** 0: gnathopod I subequal or larger than gnathopod II (0.9–1); 1: gnathopod II moderately larger than gnathopod I (0.8–0.89); 2: gnathopod II distinctly larger than gnathopod I (<0.8). Propodus length, palm and diagonal (see character 28) change during development differently, e.g. propodus palm length often exceeds the length of propodus. To describe the size as exact as possible, the sum of all three parameters was compared; only adult specimens were regarded.

39. **Size of gnathopod II, article 6:** 0: small (<0.16 body length); 1: middle (gnathopod II 0.17–0.22 body length); 2: large (0.24–0.26 body length); 3: very large (0.28 body length). See comment on character 38.

40. **Shape of coxa III:** 0: extremely deep (height:length <0.75); 1: moderately deep (height:length 0.8–1.0); 2: extremely shallow (height:length >1.05).

41. **Coxa IV, posterior lobe:** 0: well developed (>0.2 coxa width); 1: recognised, but poorly developed (0.2–0.1 coxa width); 2: not developed (<0.1 coxa width).

42. **Spines on pereopod III–IV, articles 7 (dactyli):** 0: at the base of nail a spine and 1–2 setae (spine may be seta-like); 1: additional spines along the dactyl present. Pereopods III–IV are presumably serial homologues. According to our knowledge, both appendages always display similar spination of dactylus. In contrast, the comb-like structure on dactyls of pereopods V–VII may appear on VII, VI–VII or V–VII pereopod. The presence of additional spines is coded for every pereopod individually.

43. **Shape of coxae V–VI:** 0: anterior lobe well developed, posterior lobe not developed; 1: posterior lobe similar or larger than anterior lobe; 2: similar to character state 0, but ventro-posterior corner is slightly produced.

44. **Number of setae along posterior margin of coxae V–VI:** 0: single seta/spine; 1: several setae/spines.

45. **Width of pereopods V–VI, articles 2:** 0: extremely wide (width:length >0.75); 1: middle sized (width:length 0.55–0.73); 2: narrow (width:length <0.55). Measured on adult specimens.

46. **Shape of disto-posterior lobe of pereopod V–VII, articles 2:** 0: lobe small but distinct; 1: anterior and posterior distal lobes on pereopods V–VI equally developed, pereopod VII with large disto-posterior lobe; 2: disto-posterior lobe missing on all legs; 3: anterior lobe pronounced on pereopods V–VI; pereopod VII with small and distinct lobe.

47. **Spines on pereopod V, article 7:** 0: at the base of nail a spine and 1–2 setae (spine may be seta-like); 1: additional spines present. See comment on character 42.

48. **Spines on pereopod VI, article 7:** 0: at the base of nail a spine and 1–2 setae (spine may be seta-like); 1: additional spines present. See comment on character 42.

49. **Setae along posterior margin of coxa VII:** 0: at least 2 setae/spines; 1: single seta/spine.
50. **Proximal posterior lobe on pereopod VII, article 2**: 0: present; 1: absent.
51. **Posterior spines and setae on pereopod VII, article 2**: 0: setae; 1: setae and spines; 2: hook-like spines, almost no setae.
52. **Number of plumose setae on anterior/outer edge on pereopod VII, article 7**: 0: several setae in groups; 1: single seta; 2: at least 2 plumose setae.
53. **Spines on pereopod VII, article 7**: 0: at the base of nail a spine and 1–2 setae (spine may be seta-like); 1: additional spines present. See comment at character 42.
54. **Length ratio of pereopod VI and VII**: 0: VI distinctly longer than VII; 1: VI and VII of approximately equal length; 2: VII distinctly longer than VI; 3: VII much longer than VI.
55. **Length of pereopod VII**: 0: short (<0.35 body length); 1: medium (0.4–0.5 body length); 2: long (0.56–0.75 body length); 3: very long (>0.75 body length). All articles, except coxa were measured.
56. **Pleopod III**: 0: behind the retinacle a spine; 1: behind the retinacle a seta.
57. **Number of hooks on retinacula**: 0: 2; 1: 3 or more.
58. **Spines on rami of uropod I**: 0: single spines or spines in groups, almost no setae; 1: spines accompanied with numerous plumose setae; 2: setae (not plumose) and spines, single and in groups; 3: only few spines or setae.
59. **Differentiation of uropod I, rami**: 0: endopodite:exopodite length 1.5; 1: endo-:exopodite length 1.15–1.4; 2: endo-:exopodite length 1.0–1.1; 3: endo-:exopodite length <1.0.
60. **Distal hump on protopodite of uropod I in males**: 0: present; 1: absent.
61. **Differentiation of uropod II, rami**: 0: endopodite:exopodite length <1.0; 1: endo-:exopodite length 1.0–1.15; 2: endo-:exopodite length >1.15.
62. **Setae on proximal article of exopodite of uropod III**: 0: along inner margin at least 1.5× as many setae-spine groups as along outer margin; 1: along inner margin the most 1.5× more setae-spine groups than along outer margin.
63. **Setae on distal article of exopodite of uropod III**: 0: only apical setae; 1: lateral setae groups along one margin; 2: lateral setae groups along both margins.
64. **Length of uropod III**: 0: short (<0.23 body length); 1: middle (0.25–0.35 body length); 2: long (>0.38 body length).
65. **Shape of uropod III**: 0: flattened; 1: rod-shaped.
66. **Length of endopodite of uropod III**: 0: short (<0.55 of protopodite); 1: long (>0.65 of protopodite length).
67. **Length of distal article of exopodite of uropod III**: 0: short (<0.2 proximal article); 1: slightly prolonged in adult males (0.2–0.55 proximal article); 2: distinctly prolonged in adult males (>0.6 proximal article).
68. **Number of spines on outer plate on maxilla I**: 0: all the spines with several teeth; 1: only few spines with several teeth.
69. **Number of setae on inner plate of maxilla I**: 0: 1–2, rarely 3; 1: 3–4; 2: 5 or more.
70. **Number of spines on inner lobe of maxilliped**: 0: 1–2 spines; 1: at least 3 spines.
71. **Setae on nail of maxilliped palp**: 0: setae exclusively at the base of nail; 1: setae along the inner margin of the base of nail.
### Appendix B: Distribution of character states among studied taxa

| TAXON               | CHARACTERS 1 | 10 | CHARACTERS 11 | 20 | CHARACTERS 21 | 30 | CHARACTERS 23 | 40 |
|---------------------|--------------|----|---------------|----|---------------|----|---------------|----|
| G. fossarum         | 1 0 1 1 1 0 1 1 1 1 1 | 0 0 1 0 1 0 1 1 1 1 3 | 0 0 0 | 0 0 1 0 2 0 1 3 3 | 0 0 0 3 0 0 0 1 1 2 0 | 0 2 2 1 0 0 2 (01) 0 2 |
| N. aquilex          | 1 2 3 0 (01) 1 0 (01) 0 | 0 0 0 0 0 2 0 1 3 3 | 1 0 1 0 1 0 1 2 1 | 1 1 0 1 0 0 4 1 1 | 0 1 5 2 1 1 (01) 2 3 0 |
| N. arbiter          | 0 0 1 1 0 2 0 1 1 1 | 0 0 1 0 1 1 0 1 2 1 | 1 1 0 1 0 0 4 1 1 | 0 1 5 2 1 1 1 2 3 0 |
| N. arbiter-krk      | 0 0 1 1 0 2 0 1 1 0 | 0 0 1 0 1 1 0 1 2 1 | 1 1 0 1 0 0 4 1 1 | 0 1 5 2 1 1 1 2 3 0 |
| N. balcanicus       | 0 0 0 0 0 0 0 0 0 0 | 0 0 1 0 1 0 1 2 1 | 1 1 0 1 0 0 4 1 1 | 0 1 5 2 1 1 1 2 3 0 |
| N. costozze         | 0 1 2 1 0 2 0 0 0 0 | 1 0 1 0 1 (01) 0 1 3 3 | 0 (01) 0 0 0 0 2 1 1 | 1 1 5 2 0 0 0 1 1 1 |
| N. croaticus        | 0 0 0 1 0 0 0 0 1 1 | 0 1 2 1 0 1 0 1 1 0 | 1 2 1 0 1 0 1 2 0 1 | 1 2 3 2 0 0 0 1 1 1 |
| N. redensely        | 0 0 0 1 0 0 0 0 0 0 | 0 1 1 0 1 0 1 1 0 0 | 0 1 5 2 1 1 0 1 2 0 | 1 2 3 2 0 0 0 1 1 1 |
| N. daphniensis      | 0 0 0 1 0 0 1 1 0 | 0 1 2 1 0 1 0 1 1 0 | 1 2 1 0 1 0 1 2 0 1 | 1 2 3 2 0 0 0 1 1 1 |
| N. dolichopus       | 0 0 0 1 0 0 1 1 0 0 | 0 1 1 0 0 1 0 1 2 1 | 0 1 5 2 1 1 0 1 2 0 | 1 2 3 2 0 0 0 1 1 1 |
| N. elegans          | 0 1 (04) 0 1 0 0 0 0 | 0 1 1 0 0 1 0 2 3 3 | 0 0 0 0 0 0 0 0 1 1 1 | 0 1 5 2 1 1 0 1 2 0 |
| TAXON          | CHARACTERS 41 50 | CHARACTERS 51 60 | CHARACTERS 61 70 | 71 |
|---------------|------------------|------------------|------------------|----|
| *N. fossarum* | 0 0 0 1 1 0 0 0 1 0 0 | 0 0 1 0 0 (01) 1 1 0 3 2 1 | 0 2 0 0 0 1 1 0 1 1 | 0 0 |
| *N. aquilale* | 0 0 0 0 0 0 1 1 1 | 1 0 0 0 1 0 0 0 0 2 1 | 0 0 2 0 0 0 1 0 1 1 | 0 0 |
| *N. arbiter*  | 0 0 0 0 0 0 0 0 1 0 0 | 1 0 0 1 0 0 0 0 2 1 | 0 2 2 0 0 0 1 1 1 | 0 0 |
| *N. balcanicus* | 1 0 1 2 2 0 0 0 0 1 1 | 2 2 0 0 0 0 0 0 2 1 | 0 2 2 0 0 0 1 0 0 1 | 0 0 |
| *N. costozza* | 0 0 1 1 1 1 0 0 0 0 0 | 0 1 0 1 1 0 0 0 0 1 1 | 0 0 2 0 0 0 0 0 1 2 1 | 0 0 |
| *N. croaticus* | 0 0 0 0 0 0 0 0 1 0 0 | 1 0 0 1 0 0 0 0 2 1 | 0 2 2 0 0 0 1 1 1 | 0 0 |
| *N. hebereri* | 0 0 0 0 0 0 0 0 1 1 | 0 0 0 0 1 0 0 1 1 | 0 2 0 0 0 0 0 0 1 2 1 | 0 0 |
| *N. hercegovinensis* | 2 0 0 1 0 0 0 0 1 0 0 | 2 0 0 1 1 0 1 2 1 | 0 2 0 0 0 0 0 0 1 2 1 | 0 0 |
| *N. hyarenis* | 0 0 0 0 0 0 0 0 1 0 0 | 0 0 0 1 1 0 0 2 1 | 0 2 0 0 0 0 0 0 1 2 1 | 0 0 |
| *N. hyarenis-cavata* | 1 0 1 1 1 0 0 0 0 1 1 | 0 1 0 1 1 0 0 2 1 | 0 2 0 0 0 0 0 0 1 2 1 | 0 0 |
| *N. i. dalmatinus* | 2 1 0 1 1 0 1 1 | 1 1 0 0 0 0 2 1 | 0 2 0 0 0 0 0 0 1 2 1 | 0 0 |
| *N. kramer* | (12) 0 1 1 0 0 0 0 1 1 | 0 1 0 1 0 0 0 0 1 1 | 0 2 0 0 0 0 0 0 1 2 1 | 0 0 |
| *N. longicystus* | 1 0 1 0 0 0 0 0 1 0 0 | 0 1 0 1 1 0 0 2 1 | 0 2 0 0 0 0 0 0 1 2 1 | 0 0 |
| *N. longiflagellum* | 0 0 0 (01) 0 1 0 0 1 1 | 0 1 0 1 1 0 0 2 1 | 0 2 0 0 0 0 0 0 1 2 1 | 0 0 |
| *N. lourissens* | 1 0 0 1 0 0 0 0 1 0 0 | 0 1 0 1 0 0 0 0 1 1 | 0 2 0 0 0 0 0 0 1 2 1 | 0 0 |
| *N. lunaris* | 1 0 0 1 0 0 0 0 1 0 0 | 1 1 0 0 1 0 0 0 1 1 | 0 2 0 0 0 0 0 0 1 2 1 | 0 0 |
| *N. miljeticus* | 0 0 0 1 1 0 0 0 1 0 0 | 0 1 0 1 1 0 0 2 1 | 0 2 0 0 0 0 0 0 1 2 1 | 0 0 |
| *N. ornatus* | 1 0 1 1 0 1 0 0 0 0 0 | 0 0 1 0 1 2 0 0 0 2 1 | 0 2 0 0 0 0 0 0 1 2 1 | 0 0 |
| *N. pachyptelson* | 1 0 0 (01) 0 1 0 0 0 1 0 0 | 0 1 0 1 2 1 0 0 2 1 | 0 2 0 0 0 0 0 0 1 2 1 | 0 0 |
### Phylogeny of *Niphargus orcinus* species-aggregate

| Species          | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |
|------------------|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *N. pectinicauda*|   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
| *N. podgoricensis*|   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
| *N. polymorphus* |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
| *N. r. jadranko* | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 2 | 1 | 2 | 0 | 2 | 1 | 1 | 0 | 1 | 1 | 2 | 1 | 0 |
| *N. rejecti*     | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | ? | ? | 1 | 0 | 0 | 2 | 1 | 2 | 0 | 2 | 1 | 1 | 0 | 1 | 1 | 0 | 1 |
| *N. salonitamus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 2 | 1 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 |
| *N. sanctinaumi* | 2 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 2 | 1 | 1 | 0 | 2 | 2 | 1 | 1 | 1 | 2 | 2 | 1 | 0 | 2 | 1 | 0 | 1 |

| Species          | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 1 | 1 |
|------------------|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *N. schellenbergi*| 2 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 2 | 3 | 1 | 0 | 1 | 2 | 1 | 0 | 2 | 1 | 0 | 0 | 0 |   |   |   |   |
| *N. skopljensis* | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 3 | 2 | 1 | 2 | 1 | 1 | 0 | 1 | 1 |
| *N. spinuliferum* | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 2 | 0 | 1 | 2 | 1 | 2 | 1 | 1 | 2 | 1 |
| *N. stefanelli*  | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 1 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| *N. stenoptus*   | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 2 | 1 | 2 | 0 | 1 | 0 | 1 | 1 |
| *N. steueri*     | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| *N. s. kolombatovic* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *N. s. liburnicus* | 1 | 0 | 1 | 1 | 1 | 3 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 2 | 1 | 0 | 2 | 2 | 1 | 1 | 1 | (12) | 0 | 0 | 0 | 1 | 0 |
| *N. s. subtypicus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| *N. trullipes*   | 1 | 0 | 1 | 1 | 1 | 3 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 2 | 1 | 0 | 2 | 2 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 |

| Species          | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
|------------------|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *N. v. bilecanus*| 1 | 0 | 2 | 1 | 2 | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 1 | 2 | 1 | 0 | 1 | 2 | 1 | 0 | 1 | 0 | 1 | 2 | 1 | 0 | 1 |
| *N. valachicus*  | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| *N. virei*       | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 2 | 1 | 0 |
| *N. vjetrenicensis* | 1 | 0 | 2 | 1 | 2 | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 1 | 2 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 2 | 1 |
| *N. zavalanus*   | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 2 | 2 | 1 | 0 | 2 | 2 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 |

**Legend**:
- (xy): polymorphic character
- ?: unknown state
- -: inapplicable state
Appendix C: Taxa used in this study, remaining “Orniphargus” taxa

| Studied “Orniphargus” species | Previous classification | Geographical origin and number of studied specimens |
|-------------------------------|------------------------|-----------------------------------------------------|
| Niphargus arbiter             | G. Karaman, 1984       | Cave Zelena Pečina, Bunić, CRO; September           |
|                               |                        | 1963; coll. Sket B.; 4 ex. spring, Vrbnik, Krk,    |
|                               |                        | CRO; 29 April 2004; coll. Sket B.; 2 ex.           |
| Niphargus croaticus           | (Jurinac, 1887)        | Cave above the village, Pećina, Lika, CRO;          |
|                               |                        | October 1975; coll. Sket B.; 2 ex.                 |
|                               |                        | Cave Lukina jama, Hajdučki lukovi, Velebit, CRO;    |
|                               |                        | 8 August 1993; coll. Jalžič B.; 2 ex.              |
| Niphargus pachytelson         | Sket, 1960             | **Cave Luknja, Novo Mesto, SLO; 31 August          |
|                               |                        | 1958; coll. Sket B.; 5 ex.                          |
|                               |                        | Cave Podpeška jama, Dobropolje, SLO, 1970–1985;    |
|                               |                        | coll. Sket B.; 6 ex.                               |
| Niphargus hercegovinensis     | S. Karaman, 1950       | Vjetrenica Cave, Zavala, BIH; 23 September          |
|                               |                        | 1956; coll. Sket B.; 1 ex.                          |
|                               |                        | Cave Žira jama, Turkovci, BIH; 1960; coll. Sket B.; |
|                               |                        | 5 ex.                                               |
| Niphargus longiflagellum      | S. Karaman, 1950       | **Cave Podpeška jama, Dobropolje, SLO, 1970–1985;  |
|                               |                        | coll. Sket B.; 12 ex.                               |
| Niphargus lunaris             | G. Karaman, 1985       | Bubanji, D. Dolac, Sinj, CRO, 13 May 2001; coll.   |
|                               |                        | T. Radja; 2 ex.                                    |
| Niphargus orcinus             | Joseph, 1869           | **Cave Križna jama, Lož, SLO; 12 July 2002; coll.   |
|                               |                        | Sket B., Prevorčnik S., Fišer C.; 8 ex.            |
| Niphargus redenseki           | Sket, 1959             | **Cave Sinčić pećina, Brinje, Lika, CRO; 9         |
|                               |                        | September 1964; coll. Sket B.; 5 ex.               |
| Niphargus podgoricensis       | S. Karaman, 1934       | **Spring of Ribnica, Podgorica, SiCG; 11           |
|                               |                        | April 1964; coll. Sket B.; 3 ex.                   |
| Niphargus rejici              | Sket, 1958             | Spring near Poniške, Krk, CRO; May 1969; coll.      |
|                               |                        | B. Sket; 4 ex.                                     |
| Niphargus rejici jadranko     | Sket and Karaman, 1990 |                                                   |
|                               |                        |                                                   |
| Niphargus salomonanus         | S. Karaman, 1950       | Spring at the church Stomarija, Kaštel Stari,      |
|                               |                        | Split, CRO; 27 April 2004; coll. Kralj S. and      |
|                               |                        | Fišer C.; 8 ex.                                    |
| Niphargus stefanellii Ruffo   | and Vigna-Taglianti,   | Spring, Sorgente di Laura; Lago di Lesina;         |
|                               | 1968                   | Scannicandro, Gargano, ITA; 31 March 2004; coll.    |
|                               |                        | Fišer C.; 1 ex.                                    |
| Niphargus stenopus            | Sket, 1960             | **Luknja Cave, Novo Mesto, SLO; coll. Sket B.;      |
|                               |                        | 19 September 2004; 1 ex.                            |
| Niphargus steueri             | Schellenberg, 1935     | Cave Pra di Santa Brigida, Rovinj, CRO; 3 May 1958; |
| steueri                       |                        | coll. Sket B.; 2 ex.                               |
|                               |                        | Cave Osapska jama, SLO; 1 ex.                      |
|                               |                        | **Spring near Kaštel, Trogir, CRO, 27 April 2002;  |
|                               |                        | coll. Fišer C.; 1 ex.                              |
| Niphargus steueri             | S. Karaman, 1950       | Imotski, CRO; coll. Sket B.; 7 ex.                  |
| kolombatovici                 |                        | **Spring, Vrbnik, Krk, CRO; 29 April 2004; coll.    |
|                               |                        | Sket B.; 1 ex.                                     |
| Niphargus steueri             | G. Karaman and Sket,   | **Cave Jama v Stolbah, Črnomelj SLO, coll. Sket B.; |
| liburnicus                    | 1989                   | 2 ex.                                              |
|                               |                        | Vrlovka Cave, SLO, coll. Sket B.; 5 ex.            |
| Niphargus steueri             | Sket, 1960             | Cave near Špeharje, SLO, coll. Sket B.; 2 ex.       |
| subtypicus                    |                        |                                                   |
Studied "Orniphargus" species

| Species                        | Previous classification                                                                 | Geographical origin and number of studied specimens |
|--------------------------------|-----------------------------------------------------------------------------------------|--------------------------------------------------|
| Niphargus trullipes Sket, 1958 | Orcinus group¹, ⁴, Orniphargus⁸b                                                       | Vjetrenica Cave, Zavala, BIH; 23 September 1956; coll. Sket B. 4 ex. |
| Niphargus vjeternicensis kusseri f. bilecanus S. Karaman, 1953 | Orcinus group¹, ⁴, Orniphargus²                                                         | Cave near Bileća, BIH; September 1956; coll. Sket B.; 5 ex. |
| Niphargus vjeternicensis vjeternicensis S. Karaman, 1932 | Orcinus group¹, Orniphargus²                                                           | Vjetrenica Cave, Zavala, BIH; 26 August 1965; 5 ex. |
| Niphargus zavalanus S. Karaman, 1950 | Orcinus group¹, Orniphargus²                                                           | Spring Lukavac, Zavala, BIH; coll. B. Sket; 2 ex. |
| Niphargus balcanicus (Absolon, 1927) | Balcanicus group¹                                                                      | Vjetrenica Cave, Zavala, BIH; 24 September 1956; 4 ex. |
| Niphargus hvarensis S. Karaman, 1952 | Orcinus group¹, transitional form between Orniphargus and Stygoniphargus³             | Spring near Trsteno, Dubrovnik, CRO; coll. Sket B.; 12 ex. |
| Niphargus miljeticus Straškraba, 1959 | Orcinus group¹                                                                           | **Ostraševica Cave, Mljet, CRO; coll. Bole J.; 3 ex. |
| Niphargus virei Chevreux, 1896 | Virei group¹, orcinus group¹²                                                          | Grot Lang River Cave; Doubs, 5-10km NO van Montbentoit; FRA; 2 ex. |
| N. dolichopus sp. n.          |                                                                                         | Cave Suvaja pećina, Lušći polje, Sanski most, BIH, 26 July 2004; coll. Trontelj P.; 2 ex. |
| N. polymorphus sp. n.         |                                                                                         | Cave near Bileća, BIH; September 1956; coll. Sket B.; 2 ex. |
| N. lourensisp. n.             |                                                                                         | Spring of Louros River, Vouliasta, Ionannana, HEL; 25 April 2004; coll. Fišer C. and Verovnik R. |
| N. dabarensis sp. n.          |                                                                                         | Cave Dabarska pećina, BIH; August 2003; coll. Trontelj P.; 1 ex. |

¹Straškraba (1972); ²S. Karaman (1950c); ³S. Karaman (1952c); ⁴G. Karaman (1984); ⁵G. Karaman (1985a,b); ⁶G. Karaman and Sket (1989); ⁷Ruffo and Vigna-Taglianti (1968); ⁸S. Karaman (1958a,b); ⁹S. Karaman (1959); ¹⁰S. Karaman (1960); ¹¹S. Karaman and G. Karaman (1990); ¹²Schellenberg (1937). Note. 2c* S. Karaman did not see the type specimens of N. croaticus. While he was studying the yet undescribed species N. arbiter, he believed that he was dealing with toptype specimens of N. croaticus. He replaced the original description with a description of N. arbiter and, subsequently, caused some nomenclature errors. The mistake eliminated G. Karaman (1984). However, it is obvious that N. arbiter was considered as Orniphargus. ** Type locality. Countries are abbreviated as follows: BIH, Bosnia Herzegovina; CRO, Croatia; FRA, France; HEL, Greece; SiCG, Serbia Montenegro; SLO, Slovenia.
Table C-II. Other *Niphargus* taxa used in this study.

| Other *Niphargus* species studied | Previous classification | Role in the study | Geographical origin and number of studied specimens |
|-----------------------------------|------------------------|-------------------|---------------------------------------------------|
| *Niphargus longidactylus* Ruffo, 1937 | Kochianus group¹; transitivus group³ | Testing position of *N. polymorphus* | Well-pozzo, Via Muzo Padri, Verona, ITA; September 1938; 5 ex. |
| *Niphargus pectinicauda* Sket, 1971 | Transitivus group⁵ | Testing position of *N. polymorphus* | **Hyporheic of the Sava River, Tomachevo, Ljubljana, SLO; 22 December 2004; coll. Fišer C. and Bračko G.; 2 ex. |
| *Niphargus skopljensis* S. Karaman, 1929 | Skopljensis group¹ | Testing position of *N. stefanellii* | **Well in Skopje, MAK; coll. S. Karaman; 4 ex. |
| *Niphargus hebereri* Schellenberg, 1933 | Skopljensis group¹; hebereri group³ | Testing position of *N. stefanellii* | **Well, in S. Ciprijan, Rovinj, CRO; 6 May 1977; coll. Sket B.; 2 ex. Well in Rovinjsko polje, Rovinj, CRO; 1 May 1979; coll. Sket B.; 4 ex. Well in Vještar, Rovinj, CRO; May 1980; coll. Sket B.; 5 ex. |
| *Niphargus costozzae* Schellenberg, 1935 | Stygius-puteanus group¹ | Outgroup to *Orniphargus* | Cave Grotta della Guerra, Berici Mt., ITA; 16 September 2002; coll. Trontelj P., Sket B., Fišer C.; 12 ex. **Brook in San Pancrazio, Verona, ITA, 15 September 2002, Trontelj P., Polak S., Fišer C.; 10 ex. Fontanile Fontanino, Misamo, Bergamo, ITA, 3 May 1989, l. Consonni; 2 ex. **Spring near Vrana, Zadar, CRO, 12 September 1997; coll. Verovnik; 11 ex. |
| *Niphargus elegans* Garbini, 1894 | Elegans-valachicus group¹; Supraniphargus². ⁴ | Outgroup to *Orniphargus* | **Spring near Vrana, Zadar, CRO, 12 September 1997; coll. Verovnik; 11 ex. |
| *Niphargus illidzensis* dalmatinus, Šaëfferna 1922 | Elegans-valachicus group¹ | Outgroup to *Orniphargus* | Novaki, Pazin, CRO; coll. Sket B.; 9 ex. **Subsidiary flow of Foja Creek, Pazin; CRO; coll. Fišer C.; 4 ex. |
| *Niphargus krameri* Schellenberg, 1935 | Stygius-puteanus group¹; Supraniphargus². ⁴ | Outgroup to *Orniphargus* | Spring in Sv. Naum, Ohrid, MAK; 30 April 2004; coll. Fišer C. and Verovnik R., 3 ex. **Well in Avey’s Ditchling, Sussex, GB; 13 April 1954; 2 ex. Firleworth, Sussex, GB; October 1950; coll. G.H.Caswell, 1 ex. ** Tambach-Dietharz Sitterstollen, Thueinguer Wald, DEU; 2. July 1989; coll. Bellstedt; ZMA-Crust-Amph-204986; 8 ex. |
| *Niphargus sanctinaumi* S. Karaman, 1943 | Stygius-puteanus group¹ | Outgroup to *Orniphargus* | Well in Aveys, Ditchling, Sussex, GB; 13 April 1954; 2 ex. Firleworth, Sussex, GB; October 1950; coll. G.H.Caswell, 1 ex. ** Tambach-Dietharz Sitterstollen, Thueinguer Wald, DEU; 2. July 1989; coll. Bellstedt; ZMA-Crust-Amph-204986; 8 ex. |
| *Niphargus aquilex* Schiodte 1855 | Aquilex-tauri group¹ | Outgroup to *Orniphargus* | Spring of štulovca Creek, Grasšišče, SLO; coll. Fišer C.; 6 ex. Brook near Sokolići, SLO; coll. Fišer C.; 1 ex. Tunnel between Strunjan and Portoroz, SLO; coll. Fišer C.; 6 ex. |
| *Niphargus schellenbergi* S. Karaman, 1932 | Aquilex-tauri group¹ | Outgroup to *Orniphargus* | **Hagymas-lapos, Tiszafüred, Hortobagy reg., HUNG, leg. A. Mora; 7 ex. |
| *Niphargus spinulifemur* (S. Karaman), 1954 | Stygius-puteanus group¹; Supraniphargus⁴ | Outgroup to *Orniphargus* | **Hagymas-lapos, Tiszafüred, Hortobagy reg., HUNG, leg. A. Mora; 7 ex. |
| *Niphargus valachicus* Dobreanu and Manolache, 1933 | Elegans-valachicus group¹; Supraniphargus². ⁴ | Outgroup to *Orniphargus* | **Hagymas-lapos, Tiszafüred, Hortobagy reg., HUNG, leg. A. Mora; 7 ex. |

¹Strasškraba (1972); ²S. Karaman (1950a); ³G. Karaman (1985b); ⁴Sket (1958a); ⁵Sket and Notenboom (1993). ** Type locality. Countries are abbreviated as follows: CRO, Croatia; DEU, Germany; GB, Great Britain; HUNG, Hungary; ITA, Italy; MAK, Macedonia; SLO, Slovenia.
Table C-III. Described putative “Orniphargus” taxa not used in study.

| Other “Orniphargus” species (not studied) | Previous classification |
|------------------------------------------|-------------------------|
| Niphargus altagahizi Alouf, 1973         | Orcinus group<sup>10</sup> |
| Niphargus arcanus G. Karaman, 1988       | Orcinus group<sup>7a</sup> |
| Niphargus brevicupis Schellenberg, 1937  | Orcinus group<sup>1</sup>; Orniphargus<sup>12</sup> |
| Niphargus brevicupis sketi G. Karaman, 1966 | Orcinus group<sup>1</sup> |
| Niphargus carcerarius G. Karaman, 1989   | Orcinus group<sup>g</sup>; transitivus group<sup>14</sup> |
| Niphargus ictus G. Karaman, 1985         | Hebereri group<sup>3</sup> |
| Niphargus ictus G. Karaman, 1986         | Orcinus group<sup>6</sup> |
| Niphargus jalzici G. Karaman, 1988       | Orcinus group<sup>7b</sup> |
| Niphargus lindbergi S. Karaman, 1956     | Orcinus group<sup>1</sup>; Orniphargus<sup>3</sup> |
| Niphargus cornicolanus Iannilli and Vig.-Taglianti, 2004 | Orcinus group<sup>15</sup> |
| Niphargus macedonicus S. Karaman, 1929   | Orcinus group<sup>1</sup>; Orniphargus<sup>2</sup> |
| Niphargus nadarini Alouf, 1972           | Orcinus group<sup>6, 9</sup> |
| Niphargus parentzani Ruffo and Vigna-Taglianti, 1968 | Orcinus group<sup>1</sup>;<sup>11</sup> |
| Niphargus patrizii Ruffo and Vigna-Taglianti, 1968 | Orcinus group<sup>1</sup>;<sup>11</sup> |
| Niphargus pectencoronatae Sket and G. Karaman, 1990 | Orcinus group<sup>13</sup> |
| Niphargus pellagonicus S. Karaman, 1943  | Orcinus group<sup>1</sup>; Orniphargus<sup>2</sup> |
| Niphargus poianoi G. Karaman, 1988       | Orcinus group<sup>2a</sup> |
| Niphargus vjeternicensis kusceri S. Karaman, 1950 | Orcinus group<sup>114</sup>; Orniphargus<sup>2</sup> |
| Niphargus vadimi Birstein, 1961          | Orcinus group<sup>1</sup> |

<sup>1</sup>Strasˇkraba (1972); <sup>2</sup>S. Karaman (1950c); <sup>3</sup>S. Karaman (1956); <sup>4</sup>G. Karaman (1984); <sup>5</sup>G. Karaman (1985b); <sup>6</sup>G. Karaman (1986); <sup>7</sup>G. Karaman (1988a,b); <sup>8</sup>G. Karaman (1989); <sup>9</sup>Alouf (1972); <sup>10</sup>Alouf (1973); <sup>11</sup>Ruffo and Vigna-Taglianti (1968); <sup>12</sup>Sket (1958b); <sup>13</sup>Sket and G. Karaman (1990); <sup>14</sup>Sket and Notenboom (1993); <sup>15</sup>Iannilli and Vigna-Taglianti (2004).