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# Molecular phylogeny of the crab genus Brachynotus (Brachyura: Varunidae) based on the 16S rRNA gene

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The crab genus Brachynotus de Haan, 1833 is restricted to the intertidal and shallow subtidal of the Mediterranean and northeastern Atlantic. It is presently recognized to consist of four species, of which three (B. foresti, B. gemmellari and B. sexdentatus) are endemic to the Mediterranean. The fourth species, B. atlanticus, is found along the Atlantic coasts of northern Africa and southern Europe, but also extends into the western Mediterranean. This high level of endemism suggests that speciation within Brachynotus is strongly correlated with the geography and geology of the Mediterranean Sea. A molecular phylogeny based on the mitochondrial large subunit (16S) rRNA gene indicates that the four species of Brachynotus form a monophyletic group within Atlantic Varunidae. The DNA sequence data also show that the genus Brachynotus can be subdivided into two species groups, one comprising B. atlanticus and B. foresti, and the other one B. gemmellari and B. sexdentatus. While B. atlanticus and B. foresti are clearly genetically distinct, B. gemmellari and B. sexdentatus are identical in the studied region of the 16S rRNA gene, suggesting a recent separation or continuing gene flow.

# Introduction

Abstract

Crabs of the genus Brachynotus de Haan, 1833 are restricted to the western Atlantic and Mediterranean, despite the fact that many species from different parts of the world, which are now classified in Cyrtograpsus, Hemigrapsus, Leptograpsodes, Tetragrapsus or Thalassograpsus, had been previously placed in this genus (see for example Rathbun, 1893; Tesch, 1918; Tweedie, 1942; Phillips et al., 1984). Today, Brachynotus consists of four species. B. atlanticus Forest, 1957 is found along the Atlantic coasts of northern Africa and southern Europe extending into the western Mediterranean (García-Raso, 1984; d'Udekem d'Acoz, 1999). The other three species, B. foresti Zariquiey Alvarez, 1968, B. gemmellari (Rizza, 1839) and B. sexdentatus (Risso, 1827), are mostly endemic to the Mediterranean, with occasional findings from the Black Sea, the Suez Canal, and the Gulf of Cádiz (Zariquiey Alvarez, 1968; d'Udekem d'Acoz, 1999).

The geographical confinement of its species, makes *Brachynotus* a very interesting genus for the study of speciation and biogeography within the Mediterranean Sea.

The ecological distribution of the crabs belonging to *Brachynotus* is typically the intertidal and shallow subtidal zone of rocky or soft bottom shores (d'Udekem d'Acoz, 1999). The resurrection of the species *B. gemmellari* by Froglia & Manning (1978) was mainly based on bathymetric and morphometric differences of this species and *B. sexdentatus*. Otherwise, these two species have overlapping distributions and a practically identical morphology. The taxonomic status of *B. gemmellari* is widely accepted, and several studies on its distribution, ecology and larval stages, have been published since its recognition (Almaça, 1985; Stevcic, 1990; Guerao et al., 1995; Paula, 1996; Atkinson et al., 1997; d'Udekem d'Acoz, 1999).

The remaining species of *Brachynotus* are easily separable on the basis of morphological characters. On

the other hand, the important question about underlying phylogenetic relationships among these mostly sympatric species was never resolved. In this study, we compared a 580 basepair region of the mitochondrial DNA (large subunit rRNA) in order to test whether *Brachynotus* forms a monophyletic group, to help resolve phylogenetic relationships within the genus, and to establish the degree of genetic differentiation between the closely related *B. genumellari* and *B. sexdentatus*.

# Material and methods

For the molecular phylogenetic analysis of Bruchynotus and allied crabs, we included representatives of all the genera of Varunidae occurring in the Atlantic, i.e. four species (six specimens) of Brachynotus, as well as Cyrtograpsus affinis, C. angulatus, Chasmagnathus granulatus, Cyclograpsus integer, Eriocheir sinensis and Hemigrapsus penicillatus (see Table 1). The latter two are East Asian species that have been introduced into European waters during this century (Schnakenbeck, 1924; Noël et al., 1997). 16S mtDNA sequences of Chasmagnathus granulatus (EMBL accession number AJ250640), Cyclograpsus integer (AJ250639), Cyrtograpsus affinis (AJ130801), Eriocheir sinensis (AJ250642), Hemigrapsus oregonensis (AJ250644), Sesarma reticulatum (Sesarmidae) (AJ130799) and Tetragrapsus jouvi (AJ250647) had been used in a previous study to show that the genera Chasmagnathus and Cyclograpsus need to be classified within the Varunidae (see Schubart et al., 2000a). Other sequences obtained from genetic databases and included in the present study were Eriocheir japonica (AF105242) and Grapsus grapsus (Grapsidae) (AJ250650). The latter species served as an outgroup for the phylogenetic analyses. New sequences were submitted to the EMBL genetic database and can be retrieved under the accession numbers AJ278831 - AJ278836. The crabs specimens used for DNA extraction and sequencing were deposited as museum vouchers (Table 1).

Genomic DNA was extracted from the muscle tissue of walking legs or claws using a phenol-chloroform or Puregene extraction. An approximately 580 basepair region of the mitochondrial large ribosomal subunit rRNA (16S rRNA) gene was amplified by polymerase-chain-reaction (PCR) (38–40 cycles; 1 min 94°/1 min 48–55°/2min 72° denaturing/annealing/extension temperatures) with the

primers listed in Table 2. PCR products were purified and sequenced by dideoxy chain termination with \$35 radioactive labeling (at the Pennsylvania State University) or with the ABI Prism 310 Genetic Analyzer using the ABI BigDye terminator mix (at the University of Louisiana at Lafayette). All sequences were aligned manually using the multisequence editing program ESEE (Cabot & Beckenbach, 1989). Distance matrices of sequence divergence were analyzed using Kimura 2-parameter distances and neighbor joining (NJ) (Saitou & Nei, 1987) with the program MEGA (Kumar et al., 1993). Maximum parsimony (MP) analyses were carried out with PAUP (Swofford, 1993), using the heuristic search method with tree bisection and reconnection branch swapping. Gaps were treated as missing and the tree was rooted by a user-defined outgroup. Statistical significance of groups within inferred trees was evaluated by bootstrapping with 2000 replications.

#### Results

The complete alignment of the sequenced 16S rRNA gene region consisted of 580 positions. Of these, 186 were variable and 114 parsimony-informative. Pairwise transition to transversion ratios ranged between 0.74 (outgroup vs. ingroup) and 6.5 (closely related species). The MP heuristic search, with transversions versus transitions weighted 3/1, resulted in two most parsimonious trees. The MP bootstrap analysis (2000 replicates) yielded a consensus tree of the length 722 with the following tree-fit values: CI: 0.665, RI: 0.569, RCs 0.378 (Fig. 1). Results obtained by NJ agreed in the tree topology with MP (only considering bootstrap values > 50%) and are, therefore, combined in Fig. 1.

All phylogenetic analyses suggest that Brachynotus forms a monophyletic group within the other Varunidae tested in this analysis (bootstrap values of 100 / 100). The sister group of this eastern Atlantic and Mediterranean genus cannot be determined with certainty, due to low nodal support (lower than 50%). According to our results, the genus Brachynotus can be further subdivided into two species groups: B. atlanticus and B. foresti (bootstrap values of 88 / 91), as well as B. gemmellari and B. sexdentatus (100 / 100) (Fig. 1). While B. atlanticus and B. foresti are clearly genetically distinct. B. gemmellari and B. sexdentatus turn out to be identical in the 16S mtDNA region that was analyzed. This was confirmed after comparing sequences of additional specimens of both species

Table 1. Localities, dates of collection and genetic database accession numbers of the specimen of Brachynotus (4 species), Hemigrapsus penicillanus, Cyrtograpsus angulatus and Eriocheir sinensis used for genetic comparisons, Abbreviations of museums where animals were deposited as voucher specimens: BMNH: British Museum of Natural History, London: SMF. Senckenberg Museum und Forschungsinstitut. Frankfur. a. M.: ULLZ: University of Louisiana at Lafayette Zoological Collection. Lafayette: USNM: United States National Museum, Smithsonian Institution. Washington

Brachynotus sexdentatus (Risso, 1827) (EMBL AJ278832)

- Spain: Cadiz: Puerto de Santa María; El Toruño, in aquaculture ponds up to 1,5 m depth; 14. June 1999; coll. A. Rodríguez; SMF 25794
- Greece: Gulf of Amvrukikos: Menidi; '0.5 m = 1.5 m deep muddy bottom with seu grasses", 17. July 1993; coll. C. d'Udekem d'Acoz; SMF 25795

Brachynoms genunellari (Rizza, 1839) (EMBL AJ278833)

- 1taly: Ancona, 3 miles off, 15 m depth; 7, July 1963; coli, Froglia; USNM 172093
- England: Swansea: Queens Dock, March-June 1957; coll. E. Naylor; BMNH 1957, 11, 11, 1-6

Brachynotus atlanticus Forest, 1957 (EMBL AJ278831)

Spain: Cádiz: Cabo de Trafalgar: June 1996: coll. J.A. Cuesta; SMF 25706

Brachynoius foresti Zariquiey Alvarez, 1968 (EMBL AJ278834)

Greece: Gulf of Amyrakikos: Agia Triada, 4 July 1993; coll. C. d'Udekem d'Acoz; SMF 25796

Hemigrapsus penicillatus (de Haan, 1835) (EMBL AJ278835)

France: La Gironde Estuary, Talmont (~ 45° 32′ N - 0° 54′ W); 9 May 1996; coll. P. Noel; SMF 25798

Cyriograpsus angularus Dana, 1851 (EMBL AJ278836)

Argentina: Mar Chiquita: January 1996; coll. K. Anger; SMF 24546

Eriocheir sinensis H. Milne Edwards, 1853 (EMBL AJ250642)

U.S.A. California: San Francisco Bay: Byron; State Fish facility: 11.11.1996; coll. K. Hieb; ULLZ 4175

from different localities (see Table 1), which rendered identical results.

The present results also show significant support for other phylogenetic groupings. The Varunidae (sensu Schubart et al., 2000a) is confirmed as a monophyletic family (Fig.1: node 'VAR'; 99 / 99) (see also Cuesta & Schubart, 1997; Schubart & Cuesta, 1998). Congeneric species belonging to two other varunid genera were grouped together with relatively high bootstrap values: Cyrtograpsus (98 / 98) and Eriocheir (100 / 100), thereby confirming current taxonomy. The monotypic genus Tetragrapsus from the Gulf of California is nested within two species of the genus Hemigrapsus. If future results confirm that the eastern Pacific Hemigrapsus (e.g. H. oregonensis) are closer related to Tetragrapsus than to the western Pacific Hemigrapsus (e.g. H. penicillatus), the genus Hemigrapsus has to be considered paraphyletic.

Table 2. Primers used for PCR amplification and sequencing of parts of the 16S rRNA gene

16Sur: 5'- CGCCTGTTTATCAAAAACAT -3'

16L15: 5'- GACGATA AGACCCTATA A AGCTT -3'

1472 J - AQATAQAAACCAACCTGG -3

16Sbr: 5'- CCGGTCTGAACTCAGATCACGT -3'

16H16: 5'-TTATCRCCCCAATAAA.4TA-3'

## Discussion

In this study, the monophyly of the crab genus *Brachynotus* was supported by a phylogeny based on a 580 basepair region of the 16S rRNA gene. This finding is not only important in terms of corroberating present taxonomic classification. It is also useful for understanding evolutionary relationships among

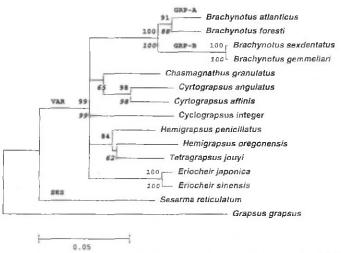


Figure 1. Molecular phylogeny of the genus Brachynotus and other representatives of the Varunidae based on 580 basepairs of the 165 rRNA gene. Upper values: Kimura 2-parameter distances, neighbor joining, 2000 bootstrap replications. Lower values in italies: maximum parsimony, 2000 bootstrap replications (transversions/transitions weighted 3/1). Only bootstrap values above 50% are shown. Abbreviations: VAR: Varunidae, SES: Sesamidae, GRP: Group.

the comprised species and for developing a model of speciation.

Three species of *Brachynotus* are almost exclusively found in the Medirerranean Sea (d'Udekem d'Acoz. 1999). It is, therefore, most likely that they also evolved there. The fourth species, *B. atlanticus*, has an eastern Atlantic distribution from southern Spain to Mauritania (d'Udekem d'Acoz, 1999). In the Mediterranean, it is only found in the westernmost part (Sea of Alborán) (García-Raso, 1984). The geology of the Mediterranean Basin gives evidence for at least one major isolation event from Atlantic waters (Por. 1989). Assuming that crabs survived in the Mediterranean, despite possible water level decrease and hypersaline conditions (e.g. Messinian crisis in the Pliocene), allopatric speciation from the Atlantic form would have been the logical consequence.

According to our data, the oldest split within Brachynotus is the separation of B. atlanticus and B. foresti (Group-A) from B. sexdentatus and B. gemmellari (Group-B) (Fig. 1). Assuming that the documented speciation events occurred by Atlantic-Mediterranean allopatric differentiation, we suggest that the ancestor of Group-A was originally isolated as an Atlantic population from its Mediterranean counterpart (Group-B). After reconnection of Atlantic

and Mediterranean waters took place, introgression of Group-A into parts of the Mediterranean, and a subsequent second isolation event could explain speciation of the Atlantic B. atlanticus and the Mediterranean B. foresti. The chronologically last split took place when the Mediterranean Group-B separated into B. sexdentatus and B. gemmellari. This separation most likely occurred within the Mediterranean Sea, but the completion and mechanisms of this possible speciation event are unconfirmed.

Based on our speciation model, most species did only slightly redisperse after reconnection of Atlantic and Mediterranean waters. Today's distribution of species shows only marginal redispersal beyond the Gibraltar Straits (B. sexdentatus in Bay of Cádiz, B. atlanticus in Sea of Aiborán). The sister species B. atlanticus and B. foresti even seem to exclude each other, since the latter species is absent from the Sea of Alborán, which represents the westernmost distribution of B. atlanticus (see García-Raso, 1984; García-Raso et al., 1987). The lack of redispersal is probably due to long-term adaptation to different local conditions encountered in the Atlantic Ocean and the Mediterranean Sea during isolation (e.g. temperature, salinity, substratum). Occasionally, some of the Mediterranean species of Brachynotus have been recorded from localities clearly outside their normal distributionary range. *B. sexdentatus* has been reported from Swansea, U.K. (Naylor, 1957) and the French Atlantic coast (Noel et al., 1997; d'Udekem d'Accz. 1999), but never established breeding populations (except at the warmed docks of Swansea). We found that specimens from Swansea deposited in the Bristish Museum of Natural History were labeled as *B. sexdentatus gemmellari*. This identification was confirmed by C. Froglia (perscomm.. 1999) and they are thus here considered to belong to *B. gemmellari* (see Table 1).

Four specimens of Brachynotus sexdentaius and B. gemmellari were included in this study (Table 1), and all of them shared the same 16S mtDNA haplotype. This gene is normally variable enough to be used for population studies in marine crabs (e.g. Cuesta & Schubart, 1998; Schubart et al., 2000b). The lack of variation between the two species of Brachynotus is thus an indication for a very recent separation or for continuing gene flow. A close relationship between B. gemme flari and B. sexdentatus can already be inferred from the fact that adults of both species can only be separated on the basis of morphometry and bathymetry (Ficelia & Manning, 1978). New results on comparative larval morphology of these two species reveal only minor differences in setation of appendages that are known to vary intraspecifically (Cuesta et al., 2000).

Morphological and molecular comparisons of many populations of Brachynotus sexdentatus and B. gemmellari throughout the Mediterranean need to be undertaken to determine how consistently these two 'forms' can be separated and how likely it is that they represent good species. These studies can be supported by crossbreeding experiments in the laboratory in order to determine whether B. sexdentatus and B. genunellari can produce fertile offspring. As far as future molecular work is concerned, we will use a second, more variable gene (cytochrome oxidase subunit I, COI) to compare a large number of different populations. Preliminary results revealed differences in 4 out of 640 positions between two specimens of B. sexdentatus (Greece and Spain). Unfortunately, specimens of B. gemmellari had probably been preserved in formalia (judging from tissue and PCR sucess), and amplification of the long COI fragment was so far unsuccessful. Based on the present results, it seems at least possible that Brachynotus gemmellari (subtidal) and B. sexdentatus (intertidal to shallow subtidal) represent different ecophenotypes of a single species.

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# Austinogebia, a new genus in the Upogebiidae and rediagnosis of its close relative, Gebiacantha Ngoc-Ho, 1989 (Crustacea: Decapoda: Thalassinidea)

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Key words: Crustacea, Thalassinidea, Austinogebia, new genus, taxonomy, Indo-Pacific

### Abstract

New material described recently permits the separation of six upogebiid species into the new genus Austinogebia, for which the diagnostic characters and a key are presented. The new taxon is compared to its close relative, Gebiacuntha Ngoc-Ho, 1989, and the opportunity is taken to rediagnose the latter.

Abbreviations: cl – carapace length measured from the tip of the rostrum to the posterior border of the carapace; tl – total length measured from the tip of the rostrum to the posterior border of the telson; AMS – Australian Museum, Sydney; BLT – Biological Laboratory, Shikoku Women's University, Japan; MNB – Museum für Naturkunde, Berlin; MNHN – Museum national d'Histoire naturelle, Paris; NTOU – Graduate School of Fisheries, National Taiwan Ocean University; SMF – Senckenberg Museum, Frankfurt.

'Teeth'—refers to structures mainly rounded at base, with a blunt tip which is sometimes corneous. These are found on the upper parts of the rostrum, the carapace and the lateral ridges of the gastric region: 'Spines'—refer to structures often not rounded at base with a pointed, non-corneous tip; 'Upper' and 'lower'—considered as equivalent to 'dorsal' and 'ventral', respectively, are used where they seem more appropriate, especially in the description of appendages

# Introduction

In 1995, Sakai and Türkay studied two upogebiid species collected in the Persian-Arabian Gulf, both with infrarostral spines: Upogebia nobilii Sakai & Türkay, 1995 and Upogebia plantae Sakai, 1982 (the latter was placed in the genus Gebiacantha by Ngoc-Ho, 1989). Upogebia spinifrons (Haswell, 1881) was also briefly discussed. To these authors 'it got clear that all three species treated herein are quite similar and cannot be separated generically.' They concluded: 'therefore we prefer to leave the species treated herein in Upogebia s.l. and suppose that Gebiacantha should be treated as a synonym of Upogebia'.

I have now re-examined all upogebiid species with infrarostral spines and compared *Upogebia nobilii* and *Upogebia plantae*. The excellent figures provided by Sakai & Türkay (1995) show several important differ-

ences between them (Figs 1 and 2). I believe these species represent two similar upogebiid groups that are distinct from each other and from the remaining species of the Upogebiidae. In this contribution, both groups are given generic rank. Austinogebia gen. nov. and Gebiacantha are diagnosed and their type species figured.

Seven American upogebiid species with infranostral spines have now been described: *U. affinis* (Say, 1818), *U. spinistipula* Williams & Heard, 1991, *U. felderi* Williams, 1993, *U. paraffinis* Williams, 1993, *U. pillsbury* Williams, 1993, *U. schmitti* Williams, 1993 and *Upogebia bermudensis* Williams, 1993. All of these are excluded from *Austinogebia* and also from *Gebiacantha*, except for *U. bermudensis*.

Likewise, two other species with infrarostral spines are excluded from both *Austinogebia* and *Gebiacantha*; they are: *Upogebia poensis* De Saint Laurent