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

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Abstract

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

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; Števčić, 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. gemmellari* and *B. sexdentatus*.

Material and methods

For the molecular phylogenetic analysis of *Brachynotus* 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 jouyi* (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 S35 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, RC: 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 penicillatus*, *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, Frankfurt 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: Cádiz: 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 Amvrakikos: Menidi; '0.5 m – 1.5 m deep muddy bottom with sea grasses", 17. July 1993; coll. C. d'Udekem d'Acoz; SMF 25795
	Brachynotus gemmellari (Rizza, 1839) (EMBL AJ278833)
*	Italy: Ancona, 3 miles off, 15 m depth; 7. July 1963; coll. 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
	Brachynotus foresti Zariquiey Alvarez, 1968 (EMBL AJ278834)
*	Greece: Gulf of Amvrakikos: 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 ($\sim 45° 32' N - 0° 54' W$); 9 May 1996; coll. P. Noël; SMF 25798
	Cyrtograpsus angulatus 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

16Sar: 5′- CGCCTGTTTATCAAAAACAT -3′
16L2 5′- YGCCTGTTTATCAAAAACAT -3′
16L15: 5′- GACGATAAGACCCTATAAAGCTT -3′
1472 5′- AGATAGAAACCAACCTGG -3′
16Sbr: 5′- CCGGTCTGAACTCAGATCACGT -3′
16H16: 5′-TTATCRCCCCAATAAAATA-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 corroborating present taxonomic classification. It is also useful for understanding evolutionary relationships among

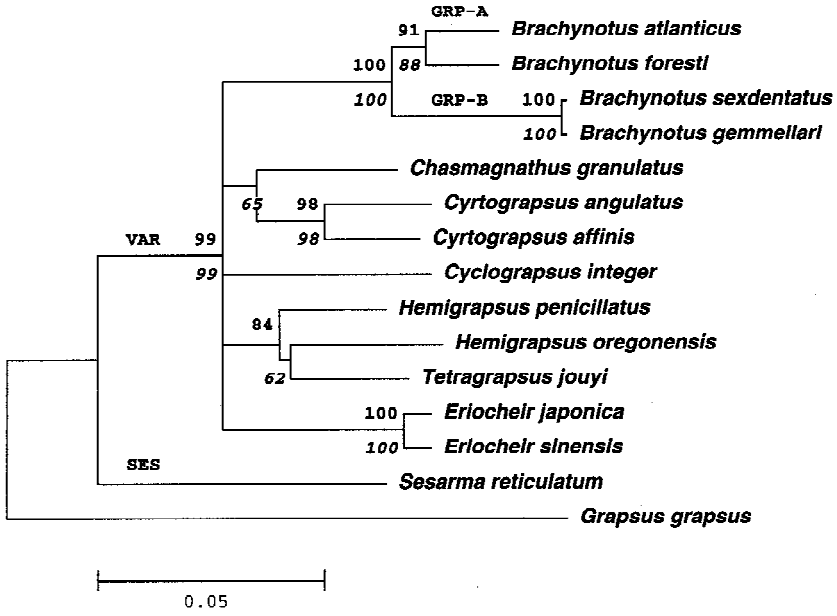

Figure 1. Molecular phylogeny of the genus *Brachynotus* and other representatives of the Varunidae based on 580 basepairs of the 16S rRNA gene. Upper values: Kimura 2-parameter distances, neighbor joining, 2000 bootstrap replications. Lower values in italics: maximum parsimony, 2000 bootstrap replications (transversions/transitions weighted 3/1). Only bootstrap values above 50% are shown. Abbreviations: VAR: Varunidae, SES: Sesarmidae, GRP: Group.

the comprised species and for developing a model of speciation.

Three species of *Brachynotus* are almost exclusively found in the Mediterranean 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 Alborán). 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 local-

ities clearly outside their normal distributionary range. *B. sexdentatus* has been reported from Swansea, U.K. (Naylor, 1957) and the French Atlantic coast (Noël et al., 1997; d'Udekem d'Acoz, 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 identifcation was confirmed by C. Froglia (pers. comm., 1999) and they are thus here considered to belong to *B. gemmellari* (see Table 1).

Four specimens of *Brachynotus sexdentatus* 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. gemmellari* 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 (Froglia & 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. gemmellari* 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 formalin (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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