



**Assessment
of the Phylogenetic Relationship Between
Octopus vulgaris CUVIER, 1797 and *O. mimus* GOULD 1852,
Using Mitochondrial 16S rDNA
in Combination with Morphological Characters**

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1 Text-Figure and 1 Table

Chile
Mediterranean
Cephalopods
Mitochondrial 16S rDNA

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**Beurteilung der phylogenetischen Beziehungen zwischen
Octopus vulgaris CUVIER, 1797 und *O. mimus* GOULD 1852
durch mitochondriale 16S rDNA
in Kombination mit morphologischen Merkmalen**

Zusammenfassung

Von sieben Individuen verschiedener *Octopus-vulgaris*- bzw. *O.-mimus*-Populationen und zwei weiteren Oktopoden (*O. bimaculoides* und *Scaevargus unicolor*) wurde ein ca. 500 Basenpaare langes Fragment des mitochondrialen 16S-rDNA-Gens sequenziert.

Die phylogenetische Auswertung der Sequenzen zeigte deutlich, dass es sich bei *Octopus vulgaris* und *O. mimus* um getrennte Arten handelt. Damit werden frühere Ergebnisse aus Sequenzvergleichen des Gens für die mitochondriale Cytochromoxidase-Untereinheit III (mtCOIII), der RAPD sowie rezenter morphologischer Untersuchungen bestätigt. Die Ergebnisse der DNA-Sequenzvergleiche werden im Zusammenhang mit den morphologischen Daten diskutiert und erweisen sich als hilfreich, da zwar sämtliche morphologischen Daten für getrennte Arten sprechen, teilweise aber widersprüchlich und nicht klar definiert sind.

Abstract

Seven specimens from different populations of *Octopus vulgaris* and *O. mimus* and two additional octopods (*Octopus bimaculoides* and *Scaevargus unicolor*) were investigated using the mitochondrial large subunit ribosomal RNA gene (mt16S rDNA) as a target sequence.

The results obtained through a phylogenetic analysis of partial mt16S rDNA sequences support the status of *Octopus mimus* as a species distinct from *O. vulgaris* and confirm the conclusions drawn from earlier investigations based on cytochrome oxidase subunit III (mtCOIII) DNA sequence comparison and random amplified polymorphic DNA (RAPD) typing. The results are also discussed in the context of recent morphological studies focusing on the taxonomic position of *O. mimus*. Although most of the morphological characters so far used are poorly defined with respect to the range of variability, the status of *O. mimus* as a species distinct from *O. vulgaris* is supported by all of these characters.

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1. Introduction

The common octopus *Octopus vulgaris* is the benchmark species in the genus. With hundreds of publications devoted to it, this species is better known than any other octopus (HOCHBERG, 1997). However, ROPER et al. (1984) remarked that the taxonomic parameters of *O. vulgaris* are not precisely defined.

The *Octopus* working group members of CIAC (Cephalopod International Advisory Council) realized, during their 1988 workshop, that a type of *O. vulgaris* (CUVIER 1797) had never been designated. Consequently they selected a neotype from the Catalan Sea off Banyuls-sur-Mer (western Mediterranean) (MANGOLD & HOCHBERG, 1991). Although MANGOLD (1997; 1998) gave short descriptions of *O. vulgaris*, a detailed morphological study is not yet published (HOCHBERG & MANGOLD, MS).

Likewise, the geographic details of the wide distribution are not defined precisely. Voss (1977) stated that a detailed study of *O. vulgaris*, using careful statistical approaches, would probably show that *O. vulgaris* is a series of closely related species or perhaps a world-wide series of subspecies. ROPER et al. (1984) questioned the distribution of *O. vulgaris* in the western Pacific. For a long time the common octopus of the Chilean coast, once described as *O. mimus* (GOULD, 1852), was listed as *O. vulgaris* (OSORIO, 1979; GUERRA & FERNANDEZ, 1990; FAO, 1995). Only recently *O. mimus* has been recognized again as a valid species (CORTEZ, 1995; GUERRA et al., 1999; GUERRA pers. comm.; HOCHBERG pers. comm.). However, most of the morphological differences between *O. vulgaris* and *O. mimus* reported by CORTEZ (1995) and GUERRA et al. (1999) are poorly defined when compared to data from the literature (see Discussion). Only one clear morphological feature attributable to *O. mimus* remained valid, namely the angular, mosaic-like chromatophore pattern of live, undisturbed *O. mimus*, as described already by GOULD (1852). The skin pattern of adult *O. vulgaris* is characterized by round and polygonal patches (PACKARD & HOCHBERG, 1977). Unfortunately, in preserved material the pattern of *O. mimus* is very difficult to recognize.

Recent studies using molecular methods aimed at the identification of new features that may further support the species status of *Octopus mimus*. A phylogenetic analysis of DNA sequences from the mitochondrial cytochrome oxidase subunit III (mtCOIII) (SÖLLER et al., 1997; WARNKE, 1999a; SÖLLER et al., 2000) based on a number of *O. vulgaris* and *O. mimus* specimens supported the affiliation of *O. mimus* to a distinct species. Since these results were based on a single gene, in the present study we used an additional gene, the mitochondrial ribosomal 16S DNA. This gene was already used for phylogenetic analysis of cephalopods by WRAY et al. (1995) and BOUCHER-RODONI et al. (1996). The results of the present study are discussed also in relation to morphological data.

2. Material and Methods

Tissue samples from the *O. vulgaris/mimus* complex were obtained in coastal areas of the Atlantic Ocean (northern and southern Brazil) and the Pacific Ocean (Costa Rica and northern Chile). *O. vulgaris* s.s. were collected in the Mediterranean (coast of France). Two additional octopods (*O. bimaculoides* and *Scaevurgus unicolor*) were sampled for ingroup comparison or as outgroup representatives. Table 1 lists specific sampling localities for the specimens in this study (for donors of tissue samples see Acknowledgements). Whole specimens, or arm tissue, of various sizes were preserved directly in 70 % (v/v) ethanol.

From each sample, up to 500 base pairs of mt16S rDNA were amplified by PCR using universal primers 16Sar and 16Sbr (SIMON et al., 1991), sequenced and arranged in a multiple sequences alignment assisted by secondary structure (OKIMOTO et al., 1992; BONNAUD et al., 1994). The putative phylogenetic relationships were calculated using both the distance and character based analysis option of the PAUP* program (Swofford, Smithsonian Institution, Washington, D. C., USA) for the construction of phylogenetic trees (for details see WARNKE, 1999a).

3. Results

Both distance and character based analyses assign *Octopus vulgaris* from the Mediterranean and western Atlantic (except northern Brazil, see below) to a different cluster than *O. mimus* from Chile. Each cluster is well supported by high bootstrap values, and the *O. vulgaris* cluster (Bootstrap 100, Decay 9) by a very high decay index. The well described species *O. bimaculoides* from California clusters with *O. mimus*. As mentioned above, the *O. vulgaris* cluster does not include the northern Brazilian octopus. The latter clusters with *O. mimus* and *O. bimaculoides* (see Text-Fig. 1).

The sequence divergence between *Octopus mimus* (Chile) and *O. vulgaris* (Mediterranean) is 6.7 %. For comparison the distance between *O. mimus* and the well described *O. bimaculoides* from California is only 4.2 %.

Only minor genetic differences were found when comparing the sequences of specimens obtained from France and southern Brazil (data not shown, details will be given in WARNKE et al., in prep.). A low level of genetic variation was also detected among the *Octopus* sp. sampled near Costa Rica (Cocos Island) and *O. mimus* from Chile.

4. Discussion

The mt16S rDNA nucleotide sequence appears useful in attempts to answer phylogenetic questions at the species level in octopods because only little homoplasy was detectable between closely related *Octopus* species (see consistency and retention indices, Text-Fig. 1).

Table 1.

List of specimens used in this study. Sampling regions, number of specimens sequenced and accession number of DNA sequences submitted to the EMBL database.

Species	Sampling Region	No of specimens	Acc. No.
<i>Octopus vulgaris</i>	Banyuls, France, Mediterranean	2	AJ390310
<i>Octopus</i> cf. <i>vulgaris</i>	Itajaí, South Brazil, Atlantic	1	AJ390314
<i>Octopus</i> cf. <i>vulgaris</i>	Recife, North Brazil, Atlantic	1	AJ390315
<i>Octopus mimus</i>	Iquique, North Chile, Pacific	2	AJ390318
<i>Octopus</i> sp.	Isla del Cocos, Costa Rica, Pacific	1	AJ390319
<i>Octopus bimaculoides</i>	Santa Barbara, California, USA, Pacific	1	AJ390321
<i>Scaevurgus unicolor</i>	Banyuls, France, Mediterranean	1	AJ390324

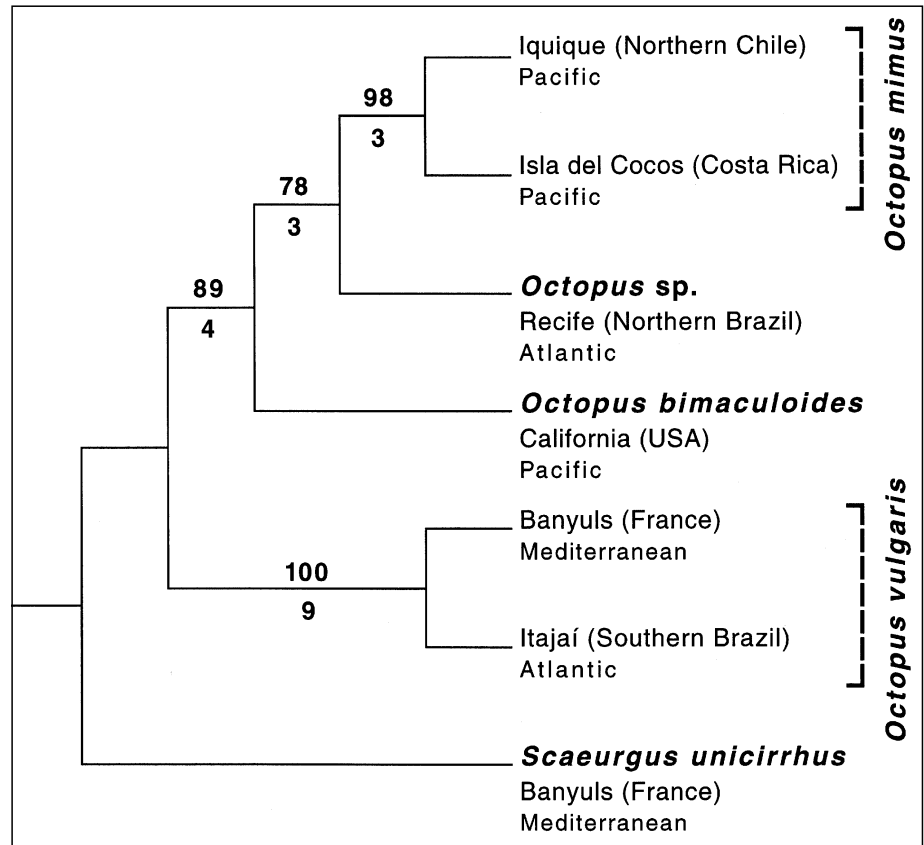
Text-Fig. 1.
 Maximum parsimony (MP) reconstructions based on 37 parsimony-informative positions of the alignment (exhaustive search). Step-length of "most parsimonious tree" = 98; consistency index = 0.857; retention index = 0.741. Bootstrap values in percentages obtained from resampling of 500 Bootstrap replications are indicated above, decay index below branches. The tree was rooted with *Scaevargus unicirrhus*.

The assumption that *Octopus mimus* is a species distinct from *O. vulgaris* is supported by a high nucleotide 16S rDNA divergence (6.7 %) when compared with the Mediterranean and Atlantic (southern Brazil) haplotype. The range of divergence of mt16S rDNA sequences is comparable to interspecific distances from other coleoids like the genus *Loligo* with about 9.5 %, *Sepia* with 8.1 to 13.8 % and *Nautilus* with 5.5 % (BOUCHER-RODONI et al., 1996). Other invertebrates, e.g. *Emerita* or *Calanus* exhibit the same range of interspecific divergence for this portion of the mt16S rDNA: 3.9 to 17 %, (TAM et al., 1996) and 7.3 to 23.9 % (BUCKLIN et al., 1992), respectively.

The phylogenetic relationships calculated from both distance and character based analyses clearly showed the separation between *O. mimus* and *O. vulgaris* in two different clusters. These results also match the conclusions drawn from other molecular investigations based on mtCOIII (SÖLLER et al., 1997; WARNKE, 1999a; SÖLLER et al., 2000), and RAPD typing (WARNKE et al., 2000). Moreover, PÉREZ-LOSADO et al. (2000) suggested, based on alloenzyme data, that *O. mimus* and *O. maya* should be considered as belonging to a different confamilial genus than *O. vulgaris*. Although *O. maya* was not examined in the present study the affiliation of *O. mimus* and *O. vulgaris* to different genera seemed at least unlikely when compared to the results of our mtCOIII and 16S rDNA analysis (WARNKE, 1999a; SÖLLER et al., 2000).

NESIS (1998) stressed that the best approach to solve taxonomy problems is to use as many taxa and characters as possible and to check one methodology (e.g. molecular phylogenetic analysis) by a different, independent method (e.g. morphological based studies). The molecular phylogenetic results of the present analysis also match the data from recent embryological (WARNKE, 1997; OLIVARIO et al., 1998; WARNKE, 1999b) and morphological studies (CORTEZ, 1995; GUERRA et al., 1999) which also suggested the existence of two distinct species.

Unfortunately, the embryological and morphological data cited above revealed contradictory details under closer scrutiny. In contrast to CORTEZ (1995) and OLIVARIO et al. (1998) WARNKE (1997, 1999b) found no clear differences between the chromatophore patterns of hatchlings observed in *O. mimus* (Chile) and those described by FIORONI (1965) and HOCHBERG et al. (1992) for *O. vulgaris* (Mediterranean) or the figure for hatching Stage XX given by NAEF (1928). FIORONI (1965) postulated, for *O. vulgaris*



hatchlings, a relatively high natural variability in chromatophore patterns.

However, a clear difference was observed in the number of outer gill lamellae per demibranch at the time of hatching: 5 for *Octopus vulgaris* (BOLETZKY, 1969) and 7 for *O. mimus* (WARNKE, 1997, 1999b).

In contrast, the number of gill lamellae of adult *Octopus vulgaris* and *O. mimus*, viewed as characteristic for these two species by CORTEZ (1995) and GUERRA et al. (1999), is another example of controversial literature data. The number of outer gill lamellae per demibranch is 7 to 8 for *O. mimus* in northern Chile, and 9 to 10/11 for *O. vulgaris* (CORTEZ, 1995; GUERRA et al., 1999). Other authors indicated 8 to 10 for *O. vulgaris* from the Atlantic and the Mediterranean (ROBSON, 1929), 7 to 11 for *O. vulgaris* in the western Atlantic (PICKFORD, 1945), 8 to 9 for *O. vulgaris* in the northwestern Mediterranean (BOLETZKY, 1969), 7 to 11 for *O. vulgaris* in the southern Atlantic/Brazil (PALACIO, 1977; HAIMOVICI et al., 1994), 9 to 11 for adult *O. vulgaris* from the Mediterranean MANGOLD (1998).

Further morphometric characters described in CORTEZ (1995) and GUERRA et al. (1999) are difficult to use for the determination of single specimens. The ranges of sucker numbers on the hectocotylized arm between *Octopus vulgaris* (140 to 180 suckers [MANGOLD, 1998]) and *O. mimus* (129 to 149 suckers [CORTEZ, 1995; GUERRA et al., 1998]) overlap. NORMAN (1992) divided the number of suckers in three categories. His third category with high sucker numbers is characterized by more than 130 suckers. Another example of variability is the diameter of enlarged suckers. Whereas GUERRA et al. (1999) indicated a diameter of 16.1 to 16.9 mm for *O. mimus* and 18.2 to 21.1 mm for *O. vulgaris*, CORTEZ (1995) stated for *O. mimus* 14 to 19 mm and for *O. vulgaris* 18 to 29. WARNKE (1999a) found for *O. mimus* a maximum of 23 mm and for *O. vulgaris* 25 mm. BOLETZKY (pers. comm.) measured a diameter of 27 to 30 mm in *O. vulgaris*.

GUERRA et al. (1999) confirmed the angular, mosaic-like chromatophore pattern of undisturbed *O. mimus* (GOULD 1852) and described faint paired ocelli at the base of the second and third arm as characteristic for live *O. mimus*. But no ocellus could be found for *O. mimus* by WARNKE (1999a) (observation confirmed by HOCHBERG, pers. comm.).

The present work shows that molecular data can be of help to distinguish sibling species, in this case *O. vulgaris* and *O. mimus*, when it is difficult to find distinctive morphological characters. The final species description must include further morphological data and more detailed comparative analyses of morphological characters.

In addition to these results, this study provides evidence for the presence of *Octopus mimus* in the eastern tropical Pacific. The octopuses from this region indeed show nearly identical DNA-sequences with *O. mimus* from Chile.

The molecular data obtained in this study indicate the presence of *Octopus vulgaris* in both the Mediterranean and the western Atlantic. An additional molecular investigation is in preparation to clarify the distribution of *O. vulgaris* based on DNA sequence data. The redescription of *O. vulgaris* s.s. by HOCHBERG & MANGOLD (MS) and a detailed comparative study of *O. vulgaris*-like octopods worldwide are urgently needed.

The distinction between *Octopus vulgaris* of southern Brazil and the north Brazilian *O. vulgaris*-like octopus, which is possibly based on a molecular phylogenetic analysis, suggests the existence of "cryptic" species within the hitherto accepted species *O. vulgaris*. Again, more detailed comparative analyses of morphological characters combined with an extended molecular genetic population survey are also needed to clarify the position of the northern Brazilian *Octopus*.

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References

BOLETZKY, S. V., 1969: Zum Vergleich der Ontogenesen von *Octopus vulgaris*, *O. joubini* und *O. briareus*. – Rev. suisse Zool., **76**, 716–726.

BONNAUD L., BOUCHER-RODONI R. & M., MONNEROT, 1994: Phylogeny of decapod cephalopods based on the partial 16S rDNA nucleotide sequence. – CR. Acad. Sci. (III), **317**, 581–588.

BOUCHER-RODONI, R. & L. BONNAUD, 1996: Biochemical and molecular approach to cephalopod phylogeny. – Amer. Malac. Bull. **12**, 79–85.

BUCKLIN, A., FROST, B.W. & T.D. KOCHER, 1995: Molecular systematics of six *Calanus* and three *Metridia* species (Calanoida: Copepoda). – Mar. Biol. **121**, 655–664.

CORTEZ, T., 1995: Biología y ecología del pulpo común *Octopus mimus* GOULD, 1852 (Mollusca: Cephalopoda) en aguas litorales del norte de Chile. – Doctoral dissertation, Universidad de Vigo, España, 292 p.

CUVIER, G., 1797: Tableau élémentaire de l'histoire naturelle des Animaux. – Paris, 14 Plates, 710 p.

FAO, 1995: Fishery statistics. Catches and landings. – Yearbook. Food and Agriculture Organisation of the United Nations. Rome, Vol. **80**, 646 p.

FIORONI, P., 1965: Die embryonale Musterentwicklung bei einigen mediterranen Tintenfischarten. – Vie Milieu **16** (2A), 655–756.

GOULD, A.A., 1852: Mollusca and Shells. – In: United States Exploring Expedition 1838–1842, Under the Command of Charles Wilkes. Washington, D.C. **12**, 473–474.

GUERRA, A. & M.T. FERNANDEZ, 1990: Pesquería de pulpo en Chile. – Industrias Pesqueras, No. **1508**, 9–10.

GUERRA, A., CORTEZ, T. & F. ROCHA, 1999: Redescrípción del pulpo de los Changos, *Octopus mimus* GOULD, 1852, del litoral chileno-peruano (Mollusca, Cephalopoda). – Iberus, **17** (2), 37–57.

HAIMOVICI, M., PEREZ, J.A. & R.A. SANTOS, 1994: Class Cephalopoda. – In: RIOS, E.C. (ed.): Seashells of Brazil, Furg, Rio Grande, 311–320.

HOCHBERG F.G., 1997: Presentation of the Issues. – In: M.A. LANG & F.G. HOCHBERG (eds.): Proceedings of the Workshop on The Fishery and Market Potential of *Octopus* in California. Smithsonian Institution, Washington D.C., 192 pp.

HOCHBERG, F.G., M. NIXON & R.B. TOLL, 1992: Order Octopoda Leach, 1818. – In: M.J. SWEENEY, C.F.E. ROPER, K.M. MANGOLD, M.R. CLARKE & S. V. BOLETZKY (eds.): "Larval" and Juvenile Cephalopods: A manual for their identification. Smiths. Contr. Zool., **513**, 213–280.

MANGOLD, K., 1997: *Octopus vulgaris*: review of the biology. – In: M.A. LANG & F.G. HOCHBERG (eds.): Proceedings of the Workshop on The Fishery and Market Potential of *Octopus* in California. Smithsonian Institution, Washington D.C., 85–90.

MANGOLD, K., 1998: The Octopodinae from the eastern Atlantic Ocean and the Mediterranean Sea. – In: N.A. VOSS, M. VECCHIONE, R.B. TOLL & M.J. SWEENEY (eds.): Systematics and Biogeography of Cephalopods. Smiths. Contr. Zool., **586** (2), 521–528.

MANGOLD K. & F.G. HOCHBERG, 1991: Defining the genus *Octopus*: Redescription of *Octopus vulgaris*. – Bull. mar. Sci., **49**, 665.

NAEF, A., 1928: Die Cephalopoden (Embryologie). Fauna und Flora des Golfes von Neapel und der angrenzenden Meeresabschnitte. – Monographie **35** (2), Verlag R. Friedländer & Sohn, Berlin, 357 pp.

NESIS, K.N., 1998: Biodiversity and systematics in cephalopods: unresolved problems require an integrated approach. – In: A.I.L. PAYNE, M.R. LIPINSKI, M.R. CLARKE & M.A.C. ROELEVELD (eds.): S. Afr. J. mar. Sci., **20**, 165–173.

NORMAN, M., 1992: Systematics and biogeography of the shallow-water octopuses (Cephalopoda) of the Great Barrier Reef, Australia. – Dissertation. University of Melbourne, Australia, 281 pp.

OKIMOTO, R., MACFARLANE, J.L., CLARY, D.O. & D.R. WOLSTENHOLME, 1992: The mitochondrial genomes of two nematodes, *Caenorhabditis elegans* and *Ascaris suum*. – Genetics, **130**, 471–498.

OLIVARES, A., CASTRO, H. & O. ZUNIGA, 1998: Desarrollo embrionario *Octopus mimus*, GOULD 1852 (Mollusca, Cephalopoda) en cautiverio. – Resúmenes XVIII Congreso de Ciencias del Mar. 4–8 de mayo de 1998, Iquique, Chile, 147–148.

OSORIO, R.C., ATRIA, C. & F.S. MANN, 1979: Moluscos marinos de importancia económica en Chile. – Biol. Pesq. (Chile), **11**, 3–47.

PACKARD, A. & F.G. HOCHBERG, 1977: Skinpatterning in *Octopus* and other genera. – Symp. zool. Soc., Lond., **38**, 191–231.

PALACIO, J.F., 1977: A study of coastal cephalopods from Brazil with a review of Brazilian zoogeography. – Dissertation, University of Miami, USA, 311 p.

PÉREZ-LOSADA, M., GUERRA, A. & A. SANJUAN, 2000: Allozyme divergence supporting the taxonomic separation of *Octopus mimus* and *O. maya* from *O. vulgaris* (Cephalopoda: Octopoda). – Abstracts Book, International Symposium and Workshops, CIAC 2000 (Cephalopod International Advisory Council): "Cephalopod Biomass & Production", July 3rd–7th. University of Aberdeen, Scotland, 96–97.

- PICKFORD, G.E., 1945: Le poulpe Americain – A study of the littoral octopoda of the western Atlantic. – Trans. Conn. Acad. Sci. **36**, 701–811.
- ROBSON, G.C., 1929: A monograph of the recent Cephalopoda. – British Museum (N.H.), London, 236 p.
- ROPER, C.F.E., SWEENEY, M.J. & C.E. NAUEN, 1984: FAO species catalogue. Cephalopods of the world. – FAO Fish. Synop., **3** (125), 278 p.
- SÖLLER, R., WARNKE, K., SAINT-PAUL, U. & D. BLOHM, 1997: Molecular phylogenetic evidence supporting the taxonomic separation of *Octopus vulgaris* and *Octopus mimus* (Cephalopoda: Octopoda) from the genus *Octopus*. – Programmes and Abstracts Book, International Symposium and Workshops, CIAC 97 (Cephalopod International Advisory Council): „Cephalopod Biodiversity, Ecology and Evolution“, 31. August to 14. September. South African Museum, Cape Town, South Africa, 86.
- SÖLLER, R., WARNKE, K., SAINT-PAUL, U. & D. BLOHM, 2000: Sequence divergence of mitochondrial DNA indicates cryptic biodiversity in *Octopus vulgaris* and supports the taxonomic distinctiveness of *Octopus mimus* (Cephalopoda: Octopodidae). – Mar. Biol. **136**, 29–35.
- TAM, Y.K., KORNFIELD, I. & F.P. OJEDA, 1996: Divergence and zoogeography of mole crabs, *Emerita* spp. (Decapoda: Hippidae) in the Americas. – Mar. Biol. **125**, 489–497.
- VOIGHT, J.R., 1998: An overview of shallow-water *Octopus* biogeography. – In: N.A. VOSS, M. VECCHIONE, R.B. TOLL & M.J. SWEENEY (eds.): Systematics and Biogeography of Cephalopods. Smiths. Contr. Zool. **586** (2), 549–559.
- VOSS, G. L., 1977: Present status and new trends in cephalopods systematics. – Symp. zool. Soc., Lond. **38**, 49–60.
- WARNKE, K., 1997: Observations on the embryonic development of *Octopus mimus* (Mollusca: Cephalopoda) from northern Chile. – Programmes and Abstracts Book, International Symposium and Workshops, CIAC 97 (Cephalopod International Advisory Council): „Cephalopod Biodiversity, Ecology and Evolution“, 31. August to 14. September. South African Museum, Cape Town, South Africa, 89.
- WARNKE, K., 1999a: Diversität des Artenkomplexes *Octopus* cf. *vulgaris* CUVIER, 1797 in Beziehung zu seiner Verbreitung an der Ost- und Westküste Lateinamerikas. – Shaker Verlag, Aachen, Zugl. Dissertation 1998, Universität Bremen, Germany, 141 p.
- WARNKE, K., 1999b: Observations on the embryonic development of *Octopus mimus* (Mollusca: Cephalopoda) from northern Chile. – The Veliger, **42** (3), 211–217.
- WARNKE, K., SÖLLER, R., BLOHM, D. & U. SAINT-PAUL, 2000: Rapid differentiation between *Octopus vulgaris* CUVIER (1797) and *Octopus mimus* GOULD (1852), using randomly amplified polymorphic DNA. – J. Zool. Syst. Evol. Research **38**, 119–122.
- WRAY, C.G., LANDMANN, N.H., SAUNDERS W.B. & J. BONACUM, 1995: Genetic divergence and geographic diversification in Nautilus. – Paleobiology **21**, 220–228.

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