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**Morphological variation in *Atyaephyra desmarestii* (Millet, 1831) within and among populations over its geographical range**

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**Abstract**

*In order to elucidate the distinction of *Atyaephyra desmarestii* subspecies (*A. d. desmarestii*, *A. d. orientalis*, *A. d. stankoi* and *A. d. mesopotamica*) and investigate their geographical distribution in Greece, the main morphological features and somatometric ratios were studied in numerous specimens collected from a dense station network of Greek fresh waters. Specimens from Belgium, Portugal, Albania and Turkey were also examined. *Atyaephyra desmarestii* was found in western and northern Greece while it was absent in eastern Greece, the Aegean and the Ionian islands. The comparison of the obtained data with those of the literature revealed a clearly overlapping variability of the main key morphological features among the four subspecies. The results of this study indicate that the current *A. desmarestii* subspecies are not valid on the basis of the used key features. There is only one very variable species with many ecophenotypes.*

**Keywords:** Decapoda; *Atyaephyra*; Morphological variation; Distribution.

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**Introduction**

The monotypic genus *Atyaephyra* de Brito Capello, 1867 includes the species *Atyaephyra desmarestii* (Millet, 1831) which extends its distribution in the fresh waters of Europe, North Africa and the Middle East up to Iran. A detailed revision of this genus synonyms and etymology has been given by HOLTHUIS (1993). BOUVIER (1913) was the first who distinguished the western (European and North African) from the eastern (Asian) populations

as different variations (*occidentalis* and *orientalis* respectively). HOLTHUIS (1961) distinguished two subspecies under the names *A. desmarestii desmarestii* and *A. desmarestii orientalis*, giving a detailed description of *A. desmarestii orientalis* from Turkey. KARAMAN (1972) described the third subspecies from Doirani Lake (F.Y.R.O.M.), *A. desmarestii stankoi*, while AL-ADHUB (1987) described the fourth subspecies from Iraq, *A. desmarestii mesopotamica*.

In any case, the status and the geographical distribution of *Atyaephyra desmarestii*

subspecies seem to be uncertain. HOLTHUIS (1961) has recorded considerable morphological variations in *A. d. orientalis* populations from different areas of Turkey. KINZELBACH & KOSTER (1985) noticed the necessity for a more comprehensive study of *Atyaephyra* populations, particularly from the Balkan region. Finally, GORGIN (1996), studying two *A. d. mesopotamica* populations from Iran, questioned the validity of this subspecies concluding: ‘... more studies should be undertaken to establish the validity of these three subspecies’.

The present study aims at determining the variability range of the key characters used to distinguish *A. desmarestii* subspecies, in order

to check the subspecies validity, which could result in the knowledge of the geographical distribution of this species.

## Materials and Methods

*Atyaephyra desmarestii* individuals were collected with a hand net from a dense station network, covering all the Greek fresh waters (Fig. 1). Furthermore, a significant number of individuals from Belgium, Portugal, Albania and Turkey were examined. The Turkish specimens belong to the type-material of *A. d. orientalis* (HOLTHUIS, 1961) and were borrowed from the Nationaal Natuurhistorisch

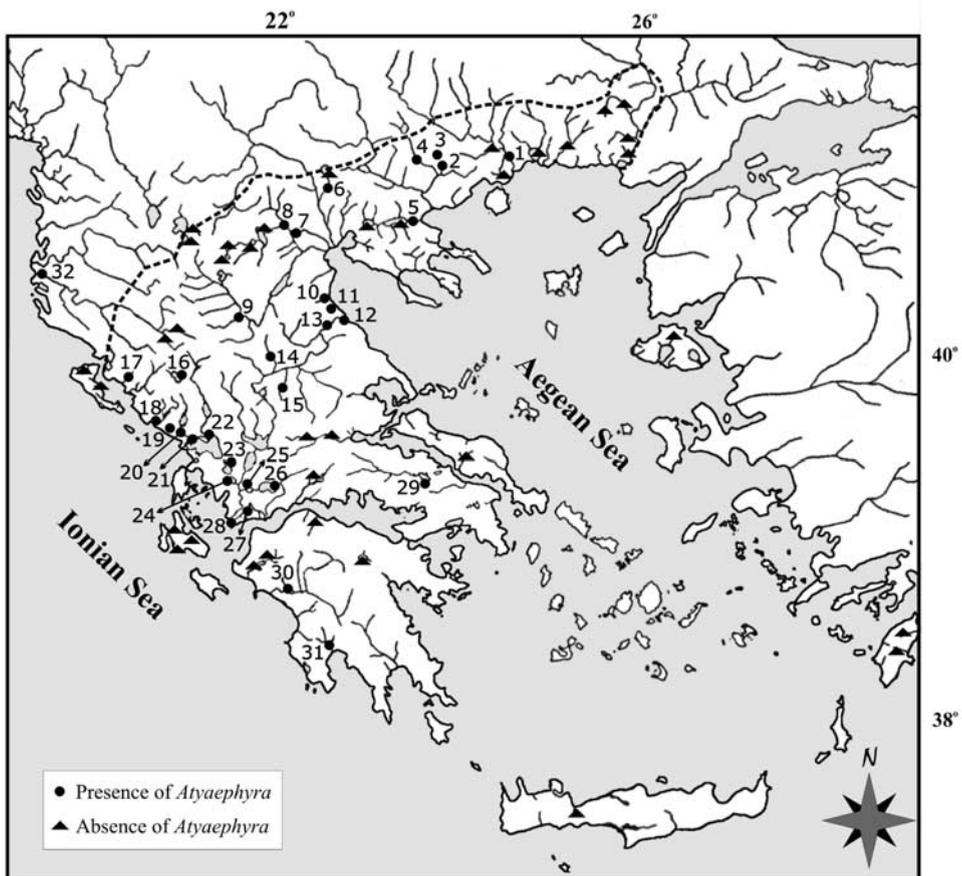


Fig. 1: Map indicating the sampling stations of Greek and Albanian fresh waters.

Museum of Leiden. The data on all material studied are given in Table 1.

In all specimens, approximately 80 morphological features and somatometric ratios were studied. Data were processed with the SPSS software package in an IBM compatible computer, for each station separately. For every studied feature the most frequent values (bulk) that are appearing in more than 70% of the population individuals and the variability range of the feature were calculated.

The review of the relevant literature indicated that 14 features are used as key characters to distinguish *A. desmarestii* subspecies. The variability of these features was estimated among populations from different geographical areas and compared with the relevant literature data (Table 2). Greece was divided into three areas and the most variable populations in each area were selected and grouped (northern Greece, stations 3, 5, 8; central Greece, stations 9, 17, 26; southern Greece, station 30). The data analysis allowed the distinction of the constant features from those overlapping among the populations and the evaluation of their validity as key characters.

## Results

In Greece, *Atyaephyra desmarestii* was found in the western and northern part of the mainland (Fig. 1), in lakes and rivers with rich riparian vegetation and a constant water flow of low velocity. On the contrary, this species was not found in the Aegean and Ionian islands.

In all populations studied, the female maximum post-orbital carapace length was longer than that of the males (Table 1).

From Table 2 it is obvious that most of the studied features (e.g. the rostral formula and the number of median setose spines on telson) are variable, overlapping among the populations, while the other features (e.g. the endopod shape of male first pleopod) are not

variable. The same patterns are followed concerning the examined material from Turkey (not included in Table 2).

## Discussion

The only previous records of *Atyaephyra desmarestii* from Greece were those from the area north of Thessaloniki (BOUVIER, 1913), Koronia Lake (HOLTHUIS, 1961) and Vegoritida Lake (KOUKOURAS, 1973). The collected material revealed that *A. desmarestii* extends its geographical distribution only in the fresh waters of western and northern Greece. This pattern of distribution seems to be the reflection of the mean annual rainfall values in each area. In eastern Greece, where rainfall is low, rivers periodically drain (especially during summer) prohibiting the presence of this shrimp. The deviation of the western Greece rivers, through dams, to the Yliki Lake (station 29) can justify the presence of *A. desmarestii* in this station, which is located in eastern Greece. On the other hand, in Corfu, Crete and Rodos Islands, where permanent inland waters exist, *Atyaephyra* is replaced by *Palaemonetes* species as fact that could be explained by the paleogeography of these areas (PRETZMANN, 1987).

The larger female body size has been previously observed in *A. desmarestii* subspecies (BOUVIER, 1913; HOLTHUIS, 1961; AL-ADHUB, 1987) and is characteristic of this species' populations.

Based on the descriptions of *A. desmarestii* subspecies, *A. d. desmarestii* has a straight and high rostrum (HOLTHUIS, 1961; ZARIQUIEY ÁLVAREZ, 1968), *A. d. stankoi* (KARAMAN, 1972) has a straight and shallow rostrum, *A. d. orientalis* has a shallow rostrum bending upwards (HOLTHUIS, 1961) and *A. d. mesopotamica* has a shallow rostrum bending downwards (AL-ADHUB, 1987). However, this feature is variable. DE BRITO CAPELLO (1867: pl.1, Fig.1) figured *A. d. desmarestii* (under the name *A. rosiana*) from Portugal having a shallow rostrum, while KINZELBACH

**Table 1**  
**Data of *Atyaephyra* material studied. (N.I.: number of individuals, CL<sub>max</sub>: maximum post-orbital carapace length).**

| Station               | Location                              | Date         | ♂♂   |                           | ♀♀      |                           |
|-----------------------|---------------------------------------|--------------|------|---------------------------|---------|---------------------------|
|                       |                                       |              | N.I. | CL <sub>max</sub><br>(mm) | N.I.    | CL <sub>max</sub><br>(mm) |
| <b>Greece</b>         |                                       |              |      |                           |         |                           |
| 1                     | Nestos River, Kirnos, Xanthi          | 30/ix/2002   | 26   | 5.0                       | 19 (1)  | 8.0                       |
| 2                     | Kephalari Stream, Drama               | 4/iv/2001    | 17   | 5.0                       | 13 (7)  | 7.0                       |
| 3                     | Agia Varvara spring, Drama            | 4/iv/2001    | 16   | 5.5                       | 14 (10) | 7.0                       |
| 4                     | Mylopotamos spring, Drama             | 4/iv/2001    | -    | -                         | 22 (19) | 9.0                       |
| 5                     | Richios River, Thessaloniki           | 22/x/1997    | 11   | 6.0                       | 19 (1)  | 8.0                       |
| 6                     | Axios River, Kilkis                   | 12/xi/1998   | 8    | 5.0                       | 7       | 6.0                       |
| 7                     | Kariotissa River, Pella               | 18/x/2001    | 13   | 5.0                       | 17      | 5.5                       |
| 8                     | Edesseos River, Pella                 | 19/x/2001    | 7    | 5.5                       | 14      | 7.0                       |
| 9                     | Litheos River, Trikala                | 14/xi/2001   | 9    | 6.0                       | 21      | 7.0                       |
| 10                    | Gritsas River, Pieria                 | 15/xi/2001   | 7    | 5.0                       | 5       | 7.0                       |
| 11                    | Litochoro marshes, Pieria             | 15/xi/2001   | 2    | 4.5                       | 3       | 6.5                       |
| 12                    | Pinios River, Stomio, Larisa          | 15/xi/2001   | 10   | 5.0                       | 8 (1)   | 7.0                       |
| 13                    | Pinios River, Agia Paraskevi, Larisa  | 25/x/2001    | 3    | 5.0                       | 2       | 7.0                       |
| 14                    | Enipeas River Karditsa                | 14/xi/2001   | 3    | 5.0                       | 17      | 8.0                       |
| 15                    | Stream near Karditsa city             | 14/xi/2001   | 1    | 4.0                       | 3       | 5.5                       |
| 16                    | Lake Pamvotida, Ioannina              | 24/x/2001    | 5    | 5.5                       | -       | -                         |
| 17                    | Thiamis River, Sagiada, Thesprotia    | 27/x/2001    | 8    | 5.0                       | 32      | 8.0                       |
| 18                    | Acherontas River, Preveza             | 27/x/2001    | 11   | 5.0                       | 36 (23) | 7.4                       |
| 19                    | Ziros Lake, Arta                      | 28/x/2001    | 13   | 5.5                       | 21      | 7.0                       |
| 20                    | Louros River, Flabouro, Preveza       | 28/x/2001    | 16   | 6.0                       | 13      | 8.0                       |
| 21                    | Louros River, estuary, Preveza        | 28/x/2001    | 3    | 5.5                       | 7       | 8.0                       |
| 22                    | Arachthos River, Arta                 | 28/x/2001    | 4    | 4.5                       | 4       | 7.0                       |
| 23                    | Amvrakia Lake., Aetoloakarnania       | 23/xi/2001   | 1    | 4.0                       | -       | -                         |
| 24                    | Ozeros Lake, Aetoloakarnania          | 22/xi/2001   | 7    | 4.5                       | 28      | 6.5                       |
| 25                    | Lysimachia Lake, Aetoloakarnania      | 22/xi/2001   | 2    | 4.0                       | 16      | 7.0                       |
| 26                    | Trichonida Lake, Aetoloakarnania      | 22/xi/2001   | 3    | 5.0                       | 27      | 6.2                       |
| 27                    | Stream near Aetoliko, Aetoloakarnania | 4/v/2002     | 3    | 5.0                       | 25 (9)  | 7.0                       |
| 28                    | Acheloos River, Aetoloakarnania       | 22/xi/2001   | 3    | 4.0                       | 2       | 4.5                       |
| 29                    | Yliki Lake, Biotia                    | 10/viii/2000 | -    | -                         | 20      | 5.0                       |
| 30                    | Alphios River, Achaia, Peloponnisos   | 24/ix/2001   | 15   | 5.5                       | 33      | 6.0                       |
| 31                    | Pamisos River, Achaia, Peloponnisos   | 26/ix/2001   | 4    | 4.6                       | 3       | 6.5                       |
| <b>Other material</b> |                                       |              |      |                           |         |                           |
| 32                    | Aoos River, Avlona, Albania           | 24/v/2001    | 22   | 6.0                       | 17      | 7.0                       |
| 33                    | Sao Barnabe River, Algarve, Portugal  | 23/vii/1988  | 17   | 5.5                       | 13 (8)  | 7.0                       |
| 34                    | Ombret, Belgium                       | 3/vii/1979   | 23   | 5.5                       | 27 (3)  | 8.0                       |
| 35                    | Bileybi, SW of Antalya, Turkey        | 18/vi/1959   | 6    | 4.5                       | 9 (9)   | 6.0                       |

& KOSTER (1985) and GORGIN (1996) observed individuals of *A. d. orientalis* and *A. d. mesopotamica*, respectively, with a straight rostrum. In our material, the three different rostral shapes appeared even in the same population (station 26). Furthermore, in all populations (Table 2), specimens with high and shallow rostrum co-existed. So, the rostral shape and height cannot be used as key characters. Similarly, the rostral dentition that may vary a lot even in the same population (Table 2), is overlapping among the four subspecies and thus is not suitable as a key character.

The variability of the rostral height, even though it has no systematic value, appears to have a geographical gradation, with a high rostrum dominating in NW Europe populations (ZARIQUIEY ÁLVAREZ, 1968; HOLTHUIS, 1961), while the southern European and Asian populations have mainly shallow rostra. The relation between rostral variability and the geographic latitude was also observed in *Palaemonetes varians* (LEACH, 1814) populations (DE GRAVE, 1999). This geographical gradation of rostral height possibly confused KARAMAN (1972) who described *A. d. stankoi* based mainly on rostral differences to distinguish it from the other subspecies. Thus, *A. d. stankoi* should be considered a junior synonym of *A. d. desmarestii*.

The pterygostomian angle bears a tooth only in some specimens from southern and central Greece (Table 2). Similarly, the posterolateral angle of the fifth abdominal somite can be more or less acute appearing round or pointed even in the same population (Table 2). Therefore, both characters have no taxonomic value.

The number of spines on the dactylus of the third pereopod, the number of spinules on the dactylus of the fifth pereopod and the number of median setose spines on the telson, as well as the number of spines on the appendix masculina of the male second pleopod vary widely among the studied populations (Table

2). These features are overlapping among *A. d. desmarestii* subspecies and have also no taxonomic value.

BOUVIER (1913) noticed the triangular shape of the posterior male thoracic sternite on some specimens from Greece and France. Our data confirms this (Table 2). According to the same author, the position of setae on the posterior male thoracic sternite is different between the eastern and western populations distinguishing *A. d. desmarestii* from *A. d. orientalis*. This feature should not be considered as valid, since in the examined *A. d. orientalis* material there are setae all over the posterior male thoracic sternite as in *A. d. desmarestii*.

The distinction between *A. d. desmarestii*, *A. d. orientalis* and *A. d. mesopotamica* is based mainly on features of the endopod of the male first pleopod (BOUVIER, 1925; AL-ADHUB, 1987). From Table 2, it is obvious that the number of setae on the outer margin, and the number of spines on the inner margin, varies in our material and overlaps with the literature data. BOUVIER (1913, 1925) considered the endopod shape as the strongest key character even though he noted that the male sex characters might alter as a result of particular local conditions. Furthermore, HOLTHUIS (1961), referring to a studied male from Koronia Lake (Greece), stated: '...the endopod is heavier and more distinctly curved than in the typical western form, forming more or less a transition to the shape of the endopod of the eastern form'. Eventually, GORGIN (1996) questioned the validity of *A. d. mesopotamica* based on the variability of this character. In our European specimens the endopod is slightly curved, similar to that figured by BOUVIER (1913: 68, Fig. 2 G, I, J) for *A. d. desmarestii*. On the contrary, in the studied Turkish population of *A. d. orientalis* it is strongly curved, but in a few individuals it is less curved, similar to European specimens. Thus even this character is variable and for this reason is not valuable for the distinction of *A. d. desmarestii* subspecies.

Table 2

The most frequent values and their range (in parenthesis) of *Ayaephyra desmareszi* subspecies key features, in the studied populations from selected areas, in comparison with the literature data.

(CL<sub>max</sub>: maximum post-orbital carapace length; L/H: Length / Height ratio; rostral formula – literature: dorsal teeth / ventral teeth; rostral formula – studied populations: post-orbital teeth | orbital tooth | pre-orbital dorsal teeth / ventral teeth)

| Literature      | Belgium  | Portugal   | Albania  | S. Greece  | Central Greece   | N. Greece  |
|-----------------|--|--|--|--|--|--|
|                 | 23 ♂♂, CL <sub>max</sub> = 5.5<br>27 ♀♀, CL <sub>max</sub> = 8.0 | 17 ♂♂, CL <sub>max</sub> = 5.5<br>13 ♀♀, CL <sub>max</sub> = 7.0 | 22 ♂♂, CL <sub>max</sub> = 6.0<br>17 ♀♀, CL <sub>max</sub> = 7.0 | 23 ♂♂, CL <sub>max</sub> = 5.5<br>27 ♀♀, CL <sub>max</sub> = 8.0 | 20 ♂♂, CL <sub>max</sub> = 6.0<br>80 ♀♀, CL <sub>max</sub> = 8.0 | 34 ♂♂, CL <sub>max</sub> = 6.0<br>47 ♀♀, CL <sub>max</sub> = 9.0 |
| <i>A.d.d.</i>   | Straight   |  |  |  | Straight   |  |
| <i>A.d.o.</i>   | Bends upwards  |  |  | Straight or Bends upwards  | Straight or Bends downwards                                      | Straight or Bends downwards                                      |
| <i>A.d.s.</i>   | Straight   | Straight   | Straight   | Straight or Bends upwards  | Straight or Bends downwards                                      | Straight or Bends downwards                                      |
| <i>A.d.m.</i>   | Bends downwards  |  |  | Bends downwards  | Bends downwards  |  |
| <i>A.d.d.</i>   | High ♂   |  |  |  |  |  |
| <i>A.d.o.</i>   | Shallow  |  |  |  |  |  |
| <i>A.d.s.</i>   | Shallow ♀  |  |  |  |  |  |
| <i>A.d.m.</i>   | Shallow  |  |  |  |  |  |
| <i>A.d.d.</i>   | 24-33(21-36)   |  |  |  |  |  |
| <i>A.d.o.</i>   | 2-10   |  |  |  |  |  |
| <i>A.d.s.</i>   | 19-20(12-27)   |  |  |  |  |  |
| <i>A.d.m.</i>   | 4(3-6)   |  |  |  |  |  |
| Shape           |  |  |  |  |  |  |
| L/H             |  |  |  |  |  |  |
| Rostrum         |  |  |  |  |  |  |
|                 | 1-2(1-3)   1(0-1)   19-23(17-25)   5-8(4-8)                      | 0-1(0-2)   1(0-1)   24-31(15-38)   4-7(1-7)                      | 1-2(0-2)   1(0-1)   20-24(16-30)   4-6(3-8)                      | 2-3(1-3)   1(0-1)   18-23(12-24)   4-7(3-8)                      | 0(0-2)   1(0-1)   18-22(14-24)   4-8(2-8)                        | 0-1(0-2)   0-1   14-21(13-27)   0-3(0-5)                         |
| Rostral formula |  |  |  |  |  |  |
|                 | 2-3(1-4)   0-1   19-24(17-25)   7-10(5-10)                       | 2(1-3)   1   26-28(16-31)   4-5(1-6)                             | 1-2(0-3)   1(0-1)   21-23(14-24)   4-6(3-8)                      | 1-2(1-3)   1(0-1)   21-24(20-33)   5-6(4-8)                      | 0-1(0-4)   1(0-1)   18-22(16-25)   4-8(2-10)                     | 0-2(0-3)   0-1   14-22(10-25)   0-3(0-5)                         |

Table 2 (Continued)

| Literature                               | Belgium<br>23 ♂♂, CL <sub>max</sub> = 5.5<br>27 ♀♀, CL <sub>max</sub> = 8.0 | Portugal<br>17 ♂♂, CL <sub>max</sub> = 5.5<br>13 ♀♀, CL <sub>max</sub> = 7.0 | Albania<br>22 ♂♂, CL <sub>max</sub> = 6.0<br>17 ♀♀, CL <sub>max</sub> = 7.0 | S. Greece<br>23 ♂♂, CL <sub>max</sub> = 5.5<br>27 ♀♀, CL <sub>max</sub> = 8.0 | Central Greece<br>20 ♂♂, CL <sub>max</sub> = 6.0<br>80 ♀♀, CL <sub>max</sub> = 8.0 | N. Greece<br>34 ♂♂, CL <sub>max</sub> = 6.0<br>47 ♀♀, CL <sub>max</sub> = 9.0 |
|--|---|--|---|---|--|---|
| <i>A.d.d.</i> Present                    |   |  |   | Present   | Present  |   |
| <i>A.d.o.</i> Present or Absent          | Absent  | Absent   | Absent  | Present or Absent   | Present or Absent  | Absent  |
| <i>A.d.s.</i> ?                          |   |  |   |   |  |   |
| <i>A.d.m.</i> Present or Absent          |   |  |   |   |  |   |
| <i>A.d.d.</i> Pointed                    |   |  |   |   |  |   |
| <i>A.d.o.</i> Pointed                    |   |  |   |   |  |   |
| <i>A.d.s.</i> Round                      | Pointed   | Pointed  | Pointed   | Pointed or Round  | Pointed  | Pointed or Round  |
| <i>A.d.m.</i> Pointed or Round           |   |  |   |   |  |   |
| Number of spines on P3 dactylus          | 8 ♂<br>5-6  | 6-7 (5-8)  | 6-7 (5-7)   | 6-7 (6-8)   | 6-7 (6-8)  | 6-8 (4-8)   |
| <i>A.d.s.</i> ?                          | ♀   | 6-8 (5-8)  | 5-6 (5-7)   | 6-8 (6-9)   | 6-9 (5-9)  | 6-8 (3-8)   |
| <i>A.d.m.</i> 7-10                       | 5-7 (4-8)   |  |   |   |  |   |
| Number of spinules                       | 35<br>40  | 26-34 (21-40)  | 26-33 (24-35)   | 27-33 (25-34)   | 28-36 (25-41)  | 29-35 (20-39)   |
| <i>A.d.d.</i> 35                         | ♂ (11-32)   |  |   |   |  |   |
| <i>A.d.o.</i> 40                         |   |  |   |   |  |   |
| <i>A.d.s.</i> ?                          | ♀   | 28-35 (22-37)  | 23-32 (15-36)   | 28-34 (23-35)   | 30-40 (23-44)  | 30-40 (27-47)   |
| <i>A.d.m.</i> 50                         | 26-38 (21-39)   |  |   |   |  |   |
| Number of median setose spines on telson | Usually 6<br>4-6  | 4-6 (2-7)  | 7-8 (5-9)   | 4-5   | 4-6 (2-8)  | 4-8 (2-10)  |
| <i>A.d.d.</i> Usually 6                  | ♂ (3-9)   |  |   |   |  |   |
| <i>A.d.o.</i> 4-6                        |   |  |   |   |  |   |
| <i>A.d.s.</i> ?                          | ♀   | 5-6 (3-8)  | 6-7 (5-8)   | 4-5 (2-6)   | 4-6 (2-8)  | 4-9 (3-11)  |
| <i>A.d.m.</i> 4                          | 7-10 (4-11)   |  |   |   |  |   |

Table 2 (Continued)

| Literature   | Belgium<br>23 ♂♂, CL <sub>max</sub> = 5.5<br>27 ♀♀, CL <sub>max</sub> = 8.0 | Portugal<br>17 ♂♂, CL <sub>max</sub> = 5.5<br>13 ♀♀, CL <sub>max</sub> = 7.0 | Albania<br>22 ♂♂, CL <sub>max</sub> = 6.0<br>17 ♀♀, CL <sub>max</sub> = 7.0 | S. Greece<br>23 ♂♂, CL <sub>max</sub> = 5.5<br>27 ♀♀, CL <sub>max</sub> = 8.0 | Central Greece<br>20 ♂♂, CL <sub>max</sub> = 6.0<br>80 ♀♀, CL <sub>max</sub> = 8.0 | N. Greece<br>34 ♂♂, CL <sub>max</sub> = 6.0<br>47 ♀♀, CL <sub>max</sub> = 9.0 |
|--|---|--|---|---|--|---|
| Shape  | Styliform or<br>Triangular  | Styliform  | Styliform   | Styliform<br>or<br>Triangular   | Styliform<br>or<br>Triangular  | Styliform   |
| <i>A.d.d.</i>  | ?   | ?  |   |   |  |   |
| <i>A.d.o.</i>  | ?   |  |   |   |  |   |
| <i>A.d.s.</i>  | ?   |  |   |   |  |   |
| <i>A.d.m.</i>  | ?   |  |   |   |  |   |
| Setae  | All over  | All over   | All over  | All over  | All over   | All over  |
| <i>A.d.d.</i>  | All over  |  |   |   |  |   |
| <i>A.d.o.</i>  | Only on base  |  |   |   |  |   |
| <i>A.d.s.</i>  | ?   |  |   |   |  |   |
| <i>A.d.m.</i>  | ?   |  |   |   |  |   |
| Shape  | Rectilinear or<br>Slightly curved   | Slightly<br>curved   | Slightly<br>curved  | Slightly<br>curved  | Slightly<br>curved   | Slightly<br>curved  |
| <i>A.d.d.</i>  |   |  |   |   |  |   |
| <i>A.d.o.</i>  |   |  |   |   |  |   |
| <i>A.d.s.</i>  |   |  |   |   |  |   |
| <i>A.d.m.</i>  |   |  |   |   |  |   |
| Number of setae<br>in outer margin                               | numerous  | 10-14<br>(9-17)  | 10-13<br>(9-16)   | 6-10<br>(6-12)  | 7-11<br>(6-14)   | 6-13<br>(4-18)  |
| <i>A.d.d.</i>  |   |  |   |   |  |   |
| <i>A.d.o.</i>  |   |  |   |   |  |   |
| <i>A.d.s.</i>  |   |  |   |   |  |   |
| <i>A.d.m.</i>  |   |  |   |   |  |   |
| Number of spines<br>in inner margin                              | 12-20   | 14-18  | 13-15<br>(7-17)   | 9-14<br>(8-14)  | 8-10<br>(7-14)   | 12-19<br>(9-21)   |
| <i>A.d.d.</i>  |   |  |   |   |  |   |
| <i>A.d.o.</i>  |   |  |   |   |  |   |
| <i>A.d.s.</i>  |   |  |   |   |  |   |
| <i>A.d.m.</i>  |   |  |   |   |  |   |
| Number of spines on<br>appendix masculina<br>of 2nd male pleopod | 15-18   | 18-23<br>(7-28)  | 18-23<br>(10-23)  | 17-24<br>(13-30)  | 21-27<br>(15-30)   | 16-30<br>(14-35)  |
| <i>A.d.d.</i>  |   |  |   |   |  |   |
| <i>A.d.o.</i>  | Much more<br>than A. d. d.  |  |   |   |  |   |
| <i>A.d.s.</i>  | Much more<br>than A. d. d.  |  |   |   |  |   |
| <i>A.d.m.</i>  | ?   |  |   |   |  |   |

Based on the results of this study, it is certain that the key characters currently used to separate *A. desmarestii* subspecies are invalid. It seems that there is only one very variable species with many ecophenotypes. Nevertheless, taking into account the wide distribution of this species and the isolation degree of its populations, it is very likely that the detailed examination of other morphological features will reveal real differences among the different populations of this species.

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