A new neobisiid pseudoscorpion species from Crete (Greece), with notes on its morphology, distribution, evolution, and phylogeny

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Abstract
This study, based on an analysis of some palaeo-Mediterranean pseudoscorpions (Ernstmayria venizelesi n. sp. and E. apostolostrichasi Ćurčić and Dimitrijević from the family Neobisiidae) represents an outstanding improvement of our knowledge of the diversity of relict and distributionally limited false scorpions from the ancient (or proto-) Aegean area. Both E. venizelesi n. sp. and E. apostolostrichasi originated in the proto-Balkan region; their ancestors are to be sought among extinct forms. Since Ernstmayria species presently inhabit the ‘peripheral’ location of the ancient Aegeis, it is evident that their remote ancestor gave rise to a number of recent genera which presently constitute two generic groups inhabiting the Mediterranean region: Neobisium Chamberlin, Occitanobisium Heurtault, Roncobisium Vachon, Protoneobisium Ćurčić, and Pennobisium Ćurčić, on the one hand, and Acanthocreagris Mahnert, Balkanoronorcus Ćurčić, Insulocreagris Ćurčić, and Roncocreagris Mahnert, on the other.

Keywords: Biogeography, Ernstmayria, evolution, Greece, morphology, new species, phylogeny, pseudoscorpions

Geographical frame
Situated in the eastern part of the Mediterranean area and occupying the region between the Adriatic Sea in the west and the Black Sea in the east, the Balkan Peninsula faces Asia Minor, with which it formed, until the Pleistocene, an uninterrupted continental mass (or ancient Aegeis). As a consequence of later radial movements and especially in the breakdown of the Aegean basin, the bridge linking the Peninsula with Asia Minor was submerged, its last remnants being numerous extant Aegean islands (Stanković 1960; Ćurčić 1998).

An important tectonic unit (the depression of Peć, South Serbia) separates the northern Dinarids from the Hellenids and it is here that the main mass of the vast karst zone ends, to
come into unusual contact with a completely different tectonic unit, that of green rocks (‘nappe albanaise’; Bourcart 1925), continuing to the south through Albania to Greece.

The structure of the Hellenids appears rather different in its general details than that of the Dinarids *sensu stricto*. The two external zones, that of the autochthonous coastal foreground and of the Cukali-Pindus-Olonos zone, are separated from the inner zone by an extensive area of green rocks (ophiolites, serpentine), which are especially developed in Albania. The inner zone is formed by the mighty Pelagonian Massif (Kober 1952), a great montainous axis composed of ancient crystalline rocks which stretches over a distance of 420 km from the region of Prizren (South Serbia) in the north to the islands of Euboea.

The Pelagonian Massif is bordered in the northeast by the Vardar (=Axios) Zone, which extends from the basin of Skopje to the Thessaloniki Gulf. Unstable and highly disturbed (Kober 1952), the Vardar Zone separates the Hellenids from the ancient Rhodopes Massif. However, Petković (1958) thinks that the Hellenids extend even further eastward to the line of Osogovo-Plačkovica-Belasica, until now considered a part of the Rhodopes mass.

In addition to the overthrust tectonics characteristic of the Hellenids and Northern Dinarids (a phenomenon that is still being actively debated), a series of younger tectonic accidents, especially radial movements and above all the breaking-down by faulting, can be noted everywhere in the Dinaric system *sensu lato*. Following these movements, the area mentioned is fragmented in an extraordinary way, especially in the southern part (Greece).

To this should be added the intense movements which lifted Neogene sediments up to an altitude of 2000 m (Peloponnesus, Albania). These upliftings occurred especially during the Pliocene and Pleistocene and are still going on (Furon 1950, 1959).

**Geomorphological evolution of Crete**

The recent concepts of continental drift and plate tectonics (Hsü 1972, 1978) have as yet produced no uniform account of the area, and the Archaic (or pre-Cambrian) and Palaeozoic geological history of Crete and the surrounding land masses remains largely shrouded in darkness. In the very remote past, the island of Crete was part of a larger northern land mass consisting of Italy and the southern Balkan countries, bounded by the Alps, the central portion of the Danube River and the Rhodopes mountains in the south (Cvijić 1906, 1911; Hsü 1972, 1978).

The presence of igneous and metamorphic rocks, especially in the western Cretan provinces of Kissamos, Kydonia and Selino, but also in those of Rethymnon and Aghios Vassilios, Milopotamos, Malevisi, Pedhiada, Mirabelo, Ierapetra and Siteia—in short, clearly throughout Crete—reveals a crucial long convulsive history dating far back, perhaps to the Palaeozoic era, some 600 million years ago. Subsequent historical history tells of numerous complicated partial land elevations and depressions during an active orogenic period marked by the formation of new mountains and sea basins, which lasted until early Miocene times. These violent diastrophisms within a short geological interval of 50 million years marked the Helladic region with long mountain ranges and lakes (Dietz & Holden 1970). New geological activities, during Miocene and Pliocene times, broke up the Helladic area, and Mediterranean waters rushed in to cover up entire regions that had sunk. The present form of the island began to develop since lower Pleistocene times, when Crete was still joined to the Peloponnesus and the Dodecanese Islands.

From the middle of the Quaternary, when new fissures and fractures of the land mass occurred, Crete took its present shape, more or less. There have been no significant
changes in its shape since Middle Pleistocene times. This does not mean, however, that
geological activity has ceased. For some thousands of years, Crete has been slowly turning
from west to east. Yet, when generalized, this phenomenon is misleading because
depressions have been observed where elevations are occurring and vice versa. What is
more likely the case is that separate large areas of the island are undergoing elevations,
depressions, and rotation within a range of more general movements whose results are
observed in those coasts. As for the rotation of the island as a whole, it is being
accomplished at so slow a rate that for the past 5000 years it has not completed one full
degree (Vachrameev 1960; Vitali-Di Castri 1973).

**Diversity of some Aegean pseudoscorpions**

Although data on the diversity of pseudoscorpion groups in Mediterranean regions and the
tropics are still insufficient, even preliminary reports based on the analysis of these taxa
tend to indicate that the number of genera and species of these arachnids is greatest in
Mediterranean zones (including Crete), even when compared with tropical rain forests
(Vitali-Di Castri 1973; Čurčić 1983, 1988; El-Hennawy 1988; Harvey 1990). The Balkan
Peninsula, and especially its regions bordering the Adriatic, Ionian and Aegean Seas,
constitutes the richest area in the world in terms of diversity of the pseudoscorpion fauna.
Most of the genera and species of these arachnids belong to the families Chthoniidae and
Neobisiidae (Vandel 1964; Čurčić 1984a; Čurčić et al. 2004).

The relative purposes of the present paper are: to demonstrate the diversity of the
recently established pseudoscorpion genus *Ernstmayria* Čurčić and Dimitrijević, 2006
(Neobisiidae), otherwise a Cretan endemic and relict taxon; to present objective criteria for
both identification and diagnosing of *E. apostolostrichasi* Čurčić and Dimitrijević, 2006, and
*E. venizelosi* Čurčić, Dimitrijević and Trichas n. sp., the latter representing a species new to
science; to evaluate the evolutionary grounds for delimiting some archaic genera of the
Neobisiidae; and finally to offer new utilisable criteria for grouping more precisely
supraspecific taxa of the *Ernstmayria*-related genera (Čurčić et al. 2006).

The first section of the paper is devoted to the description of a newly established species
from Crete: *E. venizelosi* n. sp., and to the supplementary description of *Ernstmayria
apostolostrichasi* (based on the analysis of some recently collected new samples of the
species). The next part is concerned with both palaeobiogeography and phylogeny and
gives an analysis of the evolutionary status of different *Ernstmayria*-related genera,
otherwise being of great age and different origin.

**Systematic part**

**NEOBISIIDAE** J. C. Chamberlin, 1930

*Ernstmayria* Čurčić and Dimitrijević, 2006

*Ernstmayria venizelosi* Čurčić, Dimitrijević and Trichas, new species
(Figures 1–7; Table I; Map 1)

**Material examined**

Holotype male and paratype male, from Rouvas (ca 1500 m a.s.l.), Crete, Greece, 27
November 1990, collected by Dr. Apostolos Trichas (Map 1).
The specimens analysed are housed in the collections of the Institute of Zoology, Faculty of Biology, Belgrade, Serbia (IZB 1010–1011).

**Etymology**

After the name of Eleftherios Venizelos, a noted Cretan humanist and politician.

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**Figures 1–7. Ernstmayria venizelosi** n. sp., holotype male, from Rouvas, Crete, Greece. (1) Pedipalpal chela. (2) Epistome. (3) Carapace. (4) Pedipalp. (5) Leg IV. (6) Genital area. (7) Chelicera. Scale bars: 0.50 mm (1, 3–6); 0.25 mm (2, 7).
Table I. Linear measurements (in mm) and morphometric ratios in *Ernstmayria apostolostrichasi* Čurčić and Dimitrijević, and *E. venizelosi* n. sp. (both from Crete, Greece).

| Character                  | *Ernstmayria apostolostrichasi* |           |           | E. venizelosi |           |
|---------------------------|----------------------------------|-----------|-----------|---------------|-----------|
|                           | Ierapetra                        | Chrysi Isl.| Keratidi  | Omalos        | Rouvas    |
|                           | F       | M       | T     | F       | M       | F       | M       | F       | T     | Two M                      |
| Body                      | Length (1) | 4.325   | 3.20    | 2.44   | 3.975   | 3.57    | 3.865   | 3.095   | 3.83   | 2.31 | 2.68–2.72                  |
| Cephalothorax             | Length (2) | 0.99    | 0.825   | 0.60   | 1.00    | 1.06    | 0.90    | 0.825   | 0.95   | 0.56 | 0.60–0.62                  |
|                           | Breadth (2a) | 0.91    | 0.805   | 0.62   | 0.95    | 0.85    | 0.97    | 0.78    | 0.84   | 0.60 | 0.53–0.55                  |
|                           | Ratio 2/2a | 1.09    | 1.02    | 0.97   | 1.05    | 1.25    | 0.93    | 1.06    | 1.13   | 0.93 | 1.13–1.18                 |
| Abdomen                   | Length    | 3.33    | 2.37    | 1.84   | 2.975   | 2.51    | 2.965   | 2.27    | 2.88   | 1.75 | 2.08–2.10                  |
| Chelicerae                | Length (3) | 0.76    | 0.65    | 0.44   | 0.78    | 0.67    | 0.825   | 0.67    | 0.75   | 0.49 | 0.45–0.47                  |
|                           | Breadth (4) | 0.43    | 0.36    | 0.26   | 0.42    | 0.38    | 0.41    | 0.36    | 0.41   | 0.25 | 0.25–0.26                  |
|                           | Length of movable finger (5)     | 0.51    | 0.43    | 0.33   | 0.52    | 0.44    | 0.54    | 0.44    | 0.51   | 0.315 | 0.33–0.34                  |
|                           | Ratio 3/5 | 1.49    | 1.51    | 1.47   | 1.50    | 1.55    | 1.53    | 1.52    | 1.47   | 1.56 | 1.36–1.38                  |
|                           | Ratio 3/4 | 1.77    | 1.805   | 1.69   | 1.86    | 1.76    | 2.01    | 1.86    | 1.83   | 1.96 | 1.80                      |
| Pedipalps                 | Length with coxa (6) | 5.845   | 5.04    | 3.30   | 5.83    | 4.90    | 5.745   | 5.115   | 5.56   | 3.12 | 3.805–3.89                 |
|                           | Ratio 6/1 | 1.35    | 1.575   | 1.35   | 1.47    | 1.37    | 1.49    | 1.165   | 1.45   | 1.35 | 1.42–1.44                  |
|                           | Length of coxa | 0.805   | 0.67    | 0.46   | 0.845   | 0.75    | 0.845   | 0.75    | 0.79   | 0.47 | 0.53–0.54                  |
|                           | Length of trochanter | 0.68    | 0.54    | 0.39   | 0.69    | 0.61    | 0.67    | 0.58    | 0.63   | 0.35 | 0.43–0.44                  |
|                           | Length of femur (7) | 1.21    | 1.10    | 0.72   | 1.20    | 1.15    | 1.23    | 1.10    | 1.20   | 0.56 | 0.84–0.86                  |
|                           | Breadth of femur (8) | 0.33    | 0.25    | 0.20   | 0.295   | 0.285   | 0.315   | 0.29    | 0.305  | 0.19 | 0.21–0.22                  |
|                           | Ratio 7/8 | 3.66    | 4.40    | 3.60   | 4.07    | 4.035   | 3.90    | 3.79    | 3.93   | 2.95 | 3.91–4.00                  |
|                           | Ratio 7/2 | 1.22    | 1.33    | 1.20   | 1.20    | 1.08    | 1.37    | 1.33    | 1.26   | 1.00 | 1.40                      |
|                           | Length of patella (tibia) (9)    | 1.00    | 0.87    | 0.52   | 0.99    | 0.91    | 0.95    | 0.825   | 0.91   | 0.48 | 0.62–0.64                  |
|                           | Breadth of patella (tibia) (10)  | 0.41    | 0.34    | 0.22   | 0.41    | 0.37    | 0.39    | 0.34    | 0.40   | 0.22 | 0.24–0.25                  |
|                           | Ratio 9/10 | 2.44    | 2.56    | 2.36   | 2.41    | 2.46    | 2.435   | 2.43    | 2.275  | 2.18 | 2.56–2.58                  |
|                           | Length of chela (11) | 2.15    | 1.86    | 1.21   | 2.11    | 1.48    | 2.05    | 1.86    | 2.03   | 1.26 | 1.385–1.41                 |
|                           | Breadth of chela (12) | 0.67    | 0.53    | 0.36   | 0.61    | 0.54    | 0.61    | 0.54    | 0.54   | 0.35 | 0.36–0.37                  |
|                           | Ratio 11/12 | 3.21    | 3.51    | 3.36   | 3.46    | 2.74    | 3.36    | 3.44    | 3.76   | 3.60 | 3.81–3.85                  |
|                           | Length of chelal palm (13)       | 1.04    | 0.89    | 0.56   | 1.07    | 0.94    | 1.04    | 0.90    | 0.99   | 0.57 | 0.67–0.68                  |
Table I. (Continued)

| Character                        | Ierapetra | Chrysi Isl. | Keratidi | Omalos | E. venizelosi |
|----------------------------------|-----------|-------------|----------|--------|--------------|
|                                  | F         | M           | T        | F      | M            | F       | M       | T     |
| Ratio 13/12                      | 1.55      | 1.68        | 1.555    | 1.75   | 1.74         | 1.71    | 1.67    | 1.83  | 1.63 |
| Length of chelal finger (14)     | 1.11      | 0.98        | 0.65     | 1.04   | 0.96         | 1.00    | 0.97    | 1.04  | 0.69 |
| Ratio 14/13                      | 1.07      | 1.10        | 1.16     | 0.97   | 1.02         | 0.97    | 1.08    | 1.05  | 1.21 |

Leg IV

| Total length                     | 4.33      | 3.79        | 2.65     | 4.12   | 3.915        | 4.23   | 3.835   | 4.095 | 2.45 |
| Length of coxa                   | 0.59      | 0.45        | 0.43     | 0.60   | 0.55         | 0.61   | 0.53    | 0.545 | 0.34 |
| Length of trochanter (15)        | 0.50      | 0.46        | 0.33     | 0.52   | 0.50         | 0.53   | 0.49    | 0.50  | 0.305|
| Breadth of trochanter (16)       | 0.22      | 0.19        | 0.15     | 0.24   | 0.24         | 0.23   | 0.21    | 0.25  | 0.14 |
| Ratio 15/16                      | 2.27      | 2.42        | 2.20     | 2.17   | 2.08         | 2.30   | 2.33    | 2.00  | 2.18 |
| Length of femur+patella (17)     | 1.20      | 1.09        | 0.71     | 1.13   | 1.12         | 1.19   | 1.06    | 1.16  | 0.63 |
| Breadth of femur+patella (18)    | 0.36      | 0.33        | 0.22     | 0.37   | 0.33         | 0.36   | 0.36    | 0.38  | 0.22 |
| Ratio 17/18                      | 3.33      | 3.30        | 3.23     | 3.05   | 3.39         | 3.305  | 2.94    | 3.05  | 2.86 |
| Length of tibia (19)             | 1.06      | 0.90        | 0.58     | 0.96   | 0.825        | 0.95   | 0.845   | 0.93  | 0.52 |
| Breadth of tibia (20)            | 0.18      | 0.17        | 0.12     | 0.17   | 0.17         | 0.18   | 0.17    | 0.17  | 0.11 |
| Ratio 19/20                      | 5.89      | 5.29        | 4.83     | 5.65   | 4.85         | 5.28   | 4.97    | 5.47  | 4.73 |
| Length of metatarsus (21)        | 0.46      | 0.40        | 0.25     | 0.43   | 0.42         | 0.41   | 0.40    | 0.42  | 0.21 |
| Breadth of metatarsus (22)       | 0.13      | 0.12        | 0.09     | 0.12   | 0.12         | 0.13   | 0.12    | 0.12  | 0.08 |
| Ratio 21/22                      | 3.54      | 3.33        | 2.78     | 3.58   | 3.50         | 3.15   | 3.33    | 3.50  | 2.625|
| Length of tarsus (23)            | 0.52      | 0.49        | 0.35     | 0.48   | 0.50         | 0.54   | 0.51    | 0.54  | 0.305|
| Breadth of tarsus (24)           | 0.10      | 0.10        | 0.08     | 0.10   | 0.09         | 0.10   | 0.09    | 0.10  | 0.07 |
| Ratio 23/24                      | 5.20      | 4.90        | 4.375    | 4.80   | 5.555        | 5.40   | 5.67    | 5.40  | 4.36 |
| TS ratio—tibia IV                | 0.42      | 0.43        | 0.40     | 0.31   | 0.38         | 0.43   | 0.46    | 0.34  | 0.235|
| TS ratio—metatarsus IV           | 0.18      | 0.15        | 0.18     | 0.12   | 0.15         | 0.20   | 0.15    | 0.17  | 0.19 |
| TS ratio—tarsus IV               | 0.24      | 0.16        | 0.21     | 0.21   | 0.21         | 0.20   | 0.20    | 0.18  | 0.20 |
| Tactile seta                     | 0.485     | 0.42        | 0.41     | 0.36   | 0.42         | 0.38   | 0.38    | 0.38  | 0.47 |

F, female; M, male; T, tritonymph; TS, tactile seta. Bold numbers refer to distinct characters of *E. venizelosi* n. sp. in relation to different samples (males) of *E. apostolostrichasi* from all available collecting sites.
Carapace slightly longer than broad (Table I); epistome as in Figure 2. The carapacal formula is $6+8+8+10=32$ setae. With two pairs of eyes, anteriors larger than posteriors (Figure 3).

Tergal formulae: $12-12-15-16-14-13-13-11$ and $12-12-14-17-16-15-14-13-12$.

Sternite II with seven or eight setae (in two groups, 4+3 and 4+4), sternite III with 22 or 23 anterior and posterior setae, and two suprastigmatic microsetae on either side; sternite IV with 11 or 12 posterior setae and two microsetae along each stigma (Figure 6). Sternites V–X with $18-17-17-14-14$ and $17-18-19-18-15-15$ setae, respectively. Of these, two median setae on each of the sternites are somewhat anterior—at a distance of 2.20–3.50 diameters of their bases—to other posterior setae.

The movable and fixed cheliceral finger carry 11–12 and 14–16 small teeth, apically rounded. On the movable finger these teeth end well below the galeal setae. A single chaeta is borne on the movable finger, and six such setae are present on the fixed cheliceral finger (Figure 7). Flagellum eight-bladed, characteristic of the genus.

Apex of pedipalpal coxa with five long and acuminate setae. Form of pedipalpal articles as in type species (Čurčić et al. 2006). Pedipalpal femur with some interior and lateral granulations (Figure 4) and with few interior and distal larger tubercles (Figure 4; open arrow). Pedipalpal chela granulated interiorly and distally; a sickle-shaped swelling on the base of the fixed pedipalpal finger, protruding laterally as an outstanding tubercle (Figures 1, 4; open arrow).

Fixed chelal finger with 58, movable finger with 54 small and contiguous teeth only. Small chitinous points on tibial and chelal palm handle present, similar to those in *E. apostolostrichasi*.

Fixed cheliceral finger with eight, movable finger with four trichobothria (Figure 1). Pedipalpal femur is 3.91–4.00 times as long as broad, pedipalpal patella is 2.56–2.58 times.
longer than broad, pedipalpal chela length to breadth ratio is 3.81–3.85, and pedipalpal chela is 1.935–1.96 times shorter than carapace+abdomen (Table I). Chelal fingers slightly longer than chelal palm (Figure 1; Table I).

Tibia IV and metatarsus IV each carry a long tactile seta, but tarsus IV has two such setae (Figure 5; Table I).

All measurements of different body structures and morphometric ratios are presented in Table I.

**Differential diagnosis of E. venizelosi n. sp.**

These two congeners clearly differ in the total number of carapacal setae (28 in *E. apostolostrichasi* versus 32 in *E. venizelosi* n. sp.). Additionally, the new species of *Ernstmayria* is easily distinguished from *E. apostolostrichasi* by the number of posterior carapacal setae (10 versus 12), by the number of setae on sternite II of the male (seven or eight versus four), by the number of pedipalpal chelal teeth of the male (fixed finger: 58 versus 66 teeth; movable finger: 54 versus 65 teeth), by the body length of the male (2.68–2.72 mm versus 3.095–3.57 mm), by the carapace length of the male (0.60–0.62 mm versus 0.825–1.06 mm), by the length of the male (2.08–2.10 mm versus 2.27–2.51 mm), by the pedipalpal abdominal length of the male (3.85–3.89 mm versus 4.90–5.115 mm), by the pedipalpal chelal length to breadth ratio of the male (3.81–3.85 versus 2.74–3.51) and by the leg IV length of the male (2.97–3.03 mm versus 3.79–3.915 mm); in addition, all bold numbers refer to distinct characters of *E. venizelosi* n. sp. in relation to different samples (males) of *E. apostolostrichasi* from all available collecting sites (Table I).

**Distribution**

This new species is an endemic inhabitant of the epigean and mountainous areas in Crete, Greece. It might also represent an ancient vestige of the once existing tropical and/or subtropical Tertiary or even pre-Tertiary fauna in SE Europe (Map 1).

*Ernstmayria apostolostrichasi* Ćurčić and Dimitrijević, 2006
(Figures 8–42; Table I; Map 1)

**Material examined**

One female and one male, Chrysi Isl., Crete, Greece, 15 June 1992, collected by Dr. Apostolos Trichas; one female and one male, Keratidi, Crete, Greece, 15 November 1990, same collector; one female and one tritonymph, Omalos, Crete, Greece, 27 June 1990, same collector (Map 1).

The biotope of this species includes supralittoral as well as some macchia and woody areas up to 1400 m a.s.l.; all specimens were collected by the use of Barber traps. The carbonate substrate is characterized by diverse vegetation, consisting of different species of *Quercus, Tamarix smyrnensis* Bunge, *Tamarix parviflora* DC., *Tamarix dalmatica* Baum, *Sarcopoterium spinosum* (L.) Spach, and a few representatives of some Poaceae.

The specimens analysed are housed in the collections of the Institute of Zoology, Faculty of Biology, Belgrade, Serbia (IZB 1004–1009).
Supplementary description

The carapace is somewhat longer than broad or broader than long (Table I; Figures 12, 19, 24, 34, 41). The epistome is triangular and apically rounded (Figures 10, 18, 23, 33, 40). With four eyes (Figures 12, 19, 24, 34, 41). The carapacal setal formulae are:

- 7+6+6+10=29, and 4+6+6+9=25 setae (males; Figures 12, 24), 6+6+6+12=30, 4+6+6+11=27, and 4+6+6+10=26 setae (females, Figures 19, 34), and 4+6+6+8=24 setae (tritonymph; Figure 41).

Figures 8–14. *Ernstmayria apostolostrichasi* Čurčić and Dimitrijević, 2006, male, from Chrysi Isl., Crete, Greece. (8) Pedipalpal chela. (9) Pedipalp. (10) Epistome. (11) Leg IV. (12) Carapace. (13) Genital area. (14) Chelicera. Scale bars: 0.50 mm (8, 9, 11–13); 0.25 mm (10, 14).
The number of setae borne on tergites I–X is variable: 9–11–12–14–14–12–12–11, 9–12–13–14–14–13–13–12 (males), 9–13–14–16–16–14–14–13–12–11 (female) and 8–12–13–13–12–11–11–11–10 (tritonymph). In the male, sternite II carries 16–18 setae, and 13 and two setae are borne in the female and tritonymph, respectively. Sternite III has 27–29 setae and three or four suprastigmatic microsetae on either side (male), 17 setae and four or five microsetae along each stigma (females), and eight setae and two small setae along each of the stigma (Figures 13, 25). Sternite IV has 15–19 setae and three or four suprastigmatic microsetae along each of the stigma (males), 14–17 setae and three or four tiny suprastigmatic setae on either side (females; Figures 17, 29, 35), and 10 setae and two small setae on either side (tritonymph). Sternites V–X each with 19–21–17–18–15–14, 18–15–14–13–12 (males), 19–18–19–17–14–13, 20–18–17–15–14, 21–18–17–18–14–13 (females) and 13–13–13–13–12 setae (tritonymph). Of these, two median setae on each of the sternites are slightly anterior—at a distance of 2.00–3.20 diameters of their bases—to other posterior setae.

Figures 15–19. Emustmayria apostolostrichasi Ćurčić and Dimitrijević, 2006, female, from Chrysi Isl., Crete, Greece. (15) Pedipalpal chela. (16) Pedipalp. (17) Genital area. (18) Epistome. (19) Carapace. Scale bars: 0.50 mm (15–17, 19); 0.25 mm (18).
The movable and fixed cheliceral fingers carry 8–12 (males), 9–11 (females), and nine small teeth, apically rounded (worn or lamellar in some ‘old’ specimens), and 12–17 (males), 13–16 (females) and 14 such teeth (tritonymph). On the movable finger, these end well below the galeal seta (gl) (Figures 14, 26, 36, 42). A single chaeta is borne on the movable cheliceral finger (adults, tritonymph), and six to seven (males), and six such setae are carried by males and tritonymph, respectively.

Flagellum seven- or eight- (males), eight- (females), and eight-bladed (tritonymph), characteristic of the genus.
Manducatory process with five (adults) and four long setae (tritonymph). Pedipalpal articles (Figures 9, 16, 21, 28, 32, 38) as in the type specimens (Čurčić et al. 2006). The movable chelal finger with 63–66 (males), 60–63 (females), and 48 small teeth (tritonymph). Trichobothriotaxy as in type specimens (Figures 8, 15, 20, 27, 30, 37) (Čurčić et al. 2006). Fixed chelal finger with 63–68 (males), 63–66 (females) and 53 small and close-set teeth (tritonymph).

Figures 27–29. *Ernstmayria apostolostrichasi* Čurčić and Dimitrijević, 2006, female, from Keratidi, Crete, Greece. (27) Pedipalpal chela. (28) Pedipalp. (29) Genital area. Scale bars: 0.50 mm.
The pedipalpal femur is 3.79–4.40 (males), 3.66–4.07 (females), and 2.95–3.60 times as long as broad (tritonymphs) (Table I). The pedipalpal patella is 2.43–2.56 (males), 2.275–2.44 (females), and 2.18–2.36 (tritonymphs) times longer than its breadth (tritonymphs). The pedipalpal chela length to breadth ratio is 2.74–3.51 (males), 3.21–3.76 (females) and 3.36–3.60 (tritonymph). Chelal fingers of the same length or slightly longer than chelal palm (Figures 8, 15, 20, 27, 30, 37; Table I).

Tibia IV and metatarsus IV each carry a single long tactile seta, but tarsus IV bears two such setae (Figures 11, 22, 31, 39; Table I).

Figures 30–36. Ernstmayria apostolostrichasi Ćurčić and Dimitrijević, 2006, female, from Omalos, Crete, Greece. (30) Pedipalpal chela. (31) Leg IV. (32) Pedipalp. (33) Epistome. (34) Carapace. (35) Genital area. (36) Chelicera. Scale bars: 0.50 mm (30–32, 34); 0.25 mm (33, 35, 36).
The measurements of different body structures and morphometric ratios are presented in Table I.

Generally, the additional examples analysed conform to the original description of *E. apostolostrichasi*. Some minor distinctions are due to the intra- and interpopulation variability of this taxon from different localities.

**Distribution**

This taxon is an endemic and palaeorelict inhabitant of different ecosystems (ranging from supralittoral to mountainous areas) in Crete, Greece.

Figures 37–42. *Ernstmayria apostolostrichasi* Ćurčić and Dimitrijević, 2006, tritonymph, from Omalos, Crete, Greece. (37) Pedipalpal chela. (38) Pedipalp. (39) Leg IV. (40) Epistome. (41) Carapace. (42) Chelicera. Scale bars: 0.50 mm (37–39, 41); 0.25 mm (40, 42).
Evolution, palaeobiogeography, phylogeny

Biogeographically, the pseudoscorpion genera *Neobisium* J. C. Chamberlin and *Roncus* L. Koch, otherwise phenetically similar to the new genus, are characterized by extreme diversity, especially in southern Europe. These genera are distributed over a broad area from west Europe to southwestern Russia and northern Iran and from northern Europe to the northern coast of Africa, including the Mediterranean islands (Čurčić 1988). As currently defined (Harvey 1990; Čurčić et al. 2006), they comprise almost 350 species and subspecies each.

Since the distribution centres of *Neobisium* and *Roncus* are in southern Europe, it is probable that both genera evolved there. This assumption is further supported by the discovery of several *Neobisium*-related (*Roncobisium* Vachon, *Occitanobisium* Heurtault, *Protoneobisium* Čurčić, *Pennobisium* Čurčić, *Trisobisium* Čurčić, *Novobisium* Muchmore) and *Roncus*-related genera (*Acanthocreagris* Mahnert, *Balkanoroncus* Čurčić, *Insulocreagris* Čurčić, *Microcreagris* Balzan, and *Bisotocreagris* Čurčić) (Čurčić 1988) inhabiting Eurasia and North America. These facts suggest that their ancestral or primordial population was broadly distributed over the ancient continent of Laurasia (Vachrameev 1960; Pantić 1967; Dietz & Holden 1970). Subsequently, with the breakup of this supercontinent, North American and Eurasian neobisiid genera and species evolved differently. As already mentioned, in Southern Europe (in the Pyrenees, Appennines, and Balkans) some ancient proto-neobisiid species have survived; however, the majority of *Neobisium* species probably originated during the Tertiary period. The members of the Neobisiidae, then, are of different age and origin, including many taxa of Laurasian, palaeo-Mediterranean, proto-Balkan, and south- and north-Aegean origin (Čurčić 1978, 1984a, 1986, 1988).

Let us reconsider the phylogeny of some pseudoscorpions related to the neobisiid genus *Microcreagris* Balzan (from China) that are otherwise distributed over the Eurasian and North American continents (Čurčić 1984b, 1984c). Of these, only three genera inhabit the Balkan Peninsula: *Acanthocreagris* Mahnert (SW Europe to Iran), *Balkanoroncus* Čurčić (Appennines and Balkans) and *Insulocreagris* Čurčić (the Balkan Peninsula) (Harvey 1990).

The interrelationships between *Roncoocreagris* Mahnert and the three cited genera are still insufficiently clear. Among the suprageneric group *Acanthocreagris–Balkanoroncus–Insulocreagris*, *Insulocreagris* exhibits the most plesiomorphic character states; its primitive traits and limited geographical distribution suggest that both *Acanthocreagris* and *Balkanoroncus* probably differentiated either from some ancestral population whose members were similar to *Insulocreagris*, or directly from this taxon. The three mentioned genera represent both palaeoendemics and relicts of pre-Tertiary age, while their species have very limited distributions, thus appearing to constitute the last vestiges of a Laurasian pseudoscorpion stock that have survived until the present day almost intact. The most intense endemic differentiation of these archaic forms evidently took place both during the evolution of karstic relief and in the course of the subsequent Alpine Orogeny, which affected much of the northern hemisphere. Interestingly, the origin and genesis of new, lower taxa (species and subspecies) has taken place mainly on the periphery of their original areas of distribution (Mayr 1969; Čurčić 1975).

Most scientists have been preoccupied with one issue only: the origin of biodiversity of the Dinarid and Hellenid karst at the beginning of existence of the Balkan Peninsula. It would appear that these animals lived on the floors of some ancient tropical forests (Lapschoff 1940; Birstein 1947; Furon 1950, 1959; Balazuc et al. 1951; Stanković 1960; Jeannel 1965; Birstein & Ljovuschkin 1967; Deeleman-Reinhold 1978). However, the present endemic and relict pseudoscorpions must have gone through a long evolutionary
history, which resulted in the current composition of the Hellenid (and Cretan) fauna. This process must have been complicated and cannot be solely ascribed to climatic changes. It must have taken place with an uneven intensity in different areas and affected different groups of organisms. Thus, the disappearance of archaic pseudoscorpions was least intense in the shelters where the fauna was able to maintain itself (Čurčić 2002). Certain species disappeared, while others evolved at different geological times. The composition of the old thermophilous fauna was not uniform, and regional differences no doubt existed. With the Ice Age, its distribution changed (Furon 1950, 1959; Vandel 1964; Culver 1970). Many species disappeared in central and northern Europe (as well as in Siberia and North America), having been for the most part pushed south into refugia where climatic and other changes were least infavourable.

Biogeographically, the Mediterranean and the Pannonian-Ponto-Caspian regions are the two main refuge zones in Europe. Kosswig (1955) and Kosswig and Battalgil (1943) claimed that the Mediterranean region was populated by a more thermophilous fauna as a refugium to many Tertiary elements of central Europe that migrated southward due to climatic and other changes. The better an area was sheltered, the richer it is in relicts (Cain & Harrison 1960; Mayr 1969, 1970). This is indeed the case with the proto-Balkan dry land (or the ancient Aegeis, to which Crete also belongs) whose wealth in relicts inhabiting different epigean and hypogean habitats is impressive; similar cases are encountered with other faunal groups, for instance diplopods (Makarov et al. 2003), spiders (Deeleman-Reinhold 1978), and coleopterans (Prentner 1968; Guéorguiev 1977; Beron 1994).

The colonization of different habitats must have begun a long time ago and passed through successive stages during different geological times and the development of karstic phenomena. It is evident that the ancient Aegeis (including Crete) was colonized at the beginning of its existence by pseudoscorpions which already inhabited either the then existing atolls or the subsequently evolved Mediterranean forests. The existence of the recently discovered pseudoscorpions *Ernstmayria apostolostrichasi* and *E. venizelosi* n. sp. fits perfectly into this scheme. In fact, *Ernstmayria* represents an example of the ancient circum-Mediterranean fauna, its origin to be sought in the proto-Balkan (or Aegean) region. Since the continuity of its habitat has certainly played an outstanding role in its preservation or conservation until the present day, it is clear that its present distribution corresponds to its ancestral area, more or less. Living conditions have certainly changed during the existence of the Island of Crete, but not in a manner to have provoked the disappearance of such relicts, probably of the late Mesozoic or early Tertiary age and origin. Since *Ernstmayria* holds an isolated position with no close relatives in the Recent fauna, it definitely belongs to the most ancient relicts whose closely related species are to be sought among extinct or fossil forms.

Let us now consider the evolutionary position of *Ernstmayria* and some neobisiid pseudoscorpions belonging to the same complex *sensu lato*. Needless to say, ‘during the continuous faunal turnover … older elements are often forced to retreat to the south … These relicts of formerly more widespread taxa often possess exactly the ancestral characters from which the character states of more modern type can be derived’ (Mayr 1969). Our study of *Ernstmayria*, now found at the ‘peripheral’ location of the ancient Aegeis, is of particular importance for reconstruction of the inferred ancestral characters. Thus, it is evident that this ‘living fossil’ and its remote ancestor perfectly fill the evolutionary gap between two old groups of pseudoscorpion genera of the Mediterranean region: (1) *Neobisium–Occitanobisium–Roncobisium–Protoneobisium–Pennobisium*, on the one hand and (2) *Acanthocreagris–Balkanoroncus–Insulocreagris–Roncocreagris*, on the other.
Finally, since Popadic (2002) clearly illustrated diversification of the arthropod (including pseudoscorpion) body plan through the evolutionary process, it must be noted that the expression pattern of some (Hox) genes is manifested either through determination of activities at the molecular level in order to change the expression pattern of a gene, or through the time component of the whole process. Going a step further, one can make the argument that the putative sharing of gene regulation is actually an ancestral state, resembling the situation in a proto-pseudoscorpion lineage immediately following the duplications that generated the relevant genes. In more general terms, pseudoscorpions may exemplify organisms with relatively ‘open’ developmental programs in which developmental circuitry still contains a high level of redundancy. Thus, further (molecular) characterization of Hox genes in chelicerates (including pseudoscorpions) holds promise as a way to gain a much better understanding of how changes in the expression of homeotic genes influenced morphological evolution in the pseudoscorpions studied (Telford and Thomas 1998).

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