



## Cladistic analysis of the *Eudaniela* species complex (Crustacea: Decapoda: Pseudothelphusidae)

R. von Sternberg<sup>1\*</sup>, L. A. Galindo<sup>2</sup> & E. M. González<sup>2</sup>

<sup>1</sup>Department of Biology, Northern Michigan University, Marquette, MI 49855-5341, U.S.A.

<sup>2</sup>Departamento de Acuicultura, Escuela de Ciencias Aplicadas del Mar, Universidad de Oriente, Boca del Río, Nueva Esparta, Venezuela

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### Abstract

Freshwater crabs of the genus *Eudaniela* s.l. (Pseudothelphusidae: Kingsleyini) are found along the Andean and Coastal Cordillera of Venezuela and in the highlands of Isla Margarita, Trinidad and Tobago. Four of the five species in the genus are very similar in both genital and somatic morphology and may constitute a sibling species complex. A cladistic analysis of morphological characters was conducted to test the monophyly of the genus by using multiple outgroups from the tribe Kingsleyini and to resolve the relationships of the sibling species complex. As presently constituted, *Eudaniela* is a paraphyletic group, with *E. pestai* positioned as the most basal taxon within all kingsleyinine taxa compared. The internal relationships within *Eudaniela* s.s. are [*E. garmani* [*E. iturbei* [*E. ranchograndensis*, *E. trujillensis*]]].

### Introduction

Pseudothelphusid freshwater crabs of the tribe Kingsleyini constitute a monophyletic taxon based on a unique male 1st pleopod (gonopod) morphology (Rodríguez, 1982; Rodríguez & Pereira, 1992). Nine genera are currently recognized within this tribe: *Eudaniela* Pretzmann, 1971; *Fredius* Pretzmann, 1967; *Guinotia* Pretzmann, 1965; *Kingsleya* Ortmann, 1897; *Microthelphusa* Pretzmann, 1968; *Neopseudothelphusa* Pretzmann, 1965; *Oedothelphusa* Rodríguez, 1980; *Orthothelphusa* Rodríguez, 1980; and *Priothelphusa* Rodríguez, 1980. With the exception of *Guinotia* (found on islands of the West Indies), members of the Kingsleyini are distributed along the highlands of north-eastern South America, ranging across Venezuela, Guyana and the northern basins of the Amazon in Brazil. New kingsleyinine taxa are still being described (e.g. Rodríguez & Suárez, 1994; Rodríguez & Campos, 1998) and additional species will undoubtedly be discovered as remote mountain-

ous streams that flow into the Amazon basin are sampled. Relationships within the Kingsleyini are unresolved, because cladistic studies so far have been restricted to the analysis of species groupings in the genus *Fredius* (Rodríguez & Pereira, 1992; Rodríguez & Campos, 1998). Several genera within the tribe are probably artificial (e.g. *Kingsleya*, *Orthothelphusa* and *Neopseudothelphusa*). Delineating natural relationships within the tribe (even within the family Pseudothelphusidae as a whole) is hampered by the paucity of somatic characters that can be used in cladistic studies, whereas the complexity and disparity of gonopodal anatomies further hinders comparative analyses. Nevertheless, progress can be made by attempting to identify the derived groundpatterns of monophyletic pseudothelphusid genera.

The genus *Eudaniela* consists of five fluviatile species found predominantly along the Venezuelan coastal Cordillera and part of the Andes (see Rodríguez, 1982, for specific information regarding species distributions). *Eudaniela pestai* (Pretzmann, 1965) exhibits the least derived 1st gonopod morphology of any species within the Kingsleyini (in that the

\* Author for correspondence

complex 1st gonopodal folds and processes seen in the other taxa are absent or reduced; Rodríguez, 1982) and is endemic to the western region of the Venezuelan coastal Cordillera (Estado Falcon). A second species, *E. ranchograndensis* (Rodríguez, 1966) is found immediately east of the range of *E. pestai* (Estados Aragua, Carabobo and the Distrito Federal). To the east of this species are *E. iturbei* (Rathbun, 1919) (Estados Guarico and Miranda) and then *E. garmani* (Rathbun, 1898) (Estados Monagas and Sucre), with the latter species also inhabiting the islands of Margarita, Trinidad and Tobago. *Eudaniela trujillensis* (Rodríguez, 1967) is found where the northeastern range of the Andes meets the coastal Cordillera (Estados Barinas, Portuguesa and Trujillo), just south of the range of *E. ranchograndensis* and is partially sympatric with *E. pestai*. Of the five *Eudaniela* taxa, four (*E. garmani*, *E. iturbei*, *E. ranchograndensis* and *E. trujillensis*) form a sibling species complex, with specific distinctions based upon slight differences in the subapical morphology of the 1st gonopod. However, the latter four species clearly form a monophyletic group on the basis of their nearly identical 1st gonopods, and appear to be only distantly related to *E. pestai*. For example, *E. pestai* has a simple gonopod architecture and a 3rd maxilliped exopod which is half the length of the 3rd maxilliped ischium, both of which constitute the plesiomorphic condition, not only within *Eudaniela*, but also in the Kingsleyini in general (see Rodríguez & Pereira, 1992; Rodríguez & Campos, 1998). Although the geographical range of *E. pestai* is close to that of *E. ranchograndensis*, the morphological distinctions between *E. pestai* and the sibling species complex raises the possibility that *Eudaniela* (as currently recognized) is a paraphyletic taxon. In addition, the underived 1st gonopod morphology and the relatively long 3rd maxilliped exopod of *E. pestai* compared to other taxa within the tribe, strongly suggests that this species occupies a basal position within the Kingsleyini.

The purpose of this study is threefold. First, to test the monophyly of *Eudaniela s.l.* by a parsimony analysis of somatic and 1st gonopodal characters; second, to resolve cladistic relationships within the sibling species complex; and third, to identify possible sister taxa of *Eudaniela*.

Table 1. Data matrix of the 22 characters used in the parsimony analysis of *Eudaniela* relationships (plesiomorphic state = 0; 1 and 2 - apomorphic conditions)

	0000000001	1111111112	22
	1234567890	1234567890	12
Outgroup	0000000000	0000000000	00
<i>E. garmani</i>	1110122211	0111111201	11
<i>E. iturbei</i>	1102111211	0102111101	11
<i>E. pestai</i>	0100000000	0000000000	00
<i>E. ranchograndensis</i>	1112111112	1222011111	10
<i>E. trujillensis</i>	1101122112	1222111111	11
<i>Fredius</i>	1000100000	000000201	11
<i>Guinotia</i>	1002000000	000000201	11
<i>Kingsleya</i>	1000100000	000000201	02
<i>Microthelphusa</i>	100000200	000000000	10

## Material and methods

Twenty-two somatic and 1st gonopod characters (outlined in the 'Results' section) were compared among male specimens of five species of *Eudaniela*: *E. garmani* (IVIC-1054); *E. iturbei* (IVIC-515, 518); *E. pestai* (IVIC-529); *E. ranchograndensis* (IVIC-541); and *E. trujillensis* (IVIC-547). (Taxonomic distinctions at the species level are based on the male genitalia.) Characters revealing intrageneric differences were examined in specimens of the outgroup taxa *Fredius estevisi* (Rodríguez, 1966) (XI-2682, Universidad Central de Venezuela); *Guinotia dentata* (Latreille, 1825) (IVIC-589); *Kingsleya latifrons* (Randall, 1840) (IVIC-635); and *Microthelphusa racenisi* (Rodríguez, 1966) (IVIC-648). *Fredius estevisi* was chosen to represent *Fredius* because this species is the sister taxon of all other members of the genus (Rodríguez & Pereira, 1992; Rodríguez & Campos, 1998). Aside from *Guinotia*, which is monotypic, *K. latifrons* and *M. racenisi* were included in the analysis because their respective first gonopods lack the elaborated processes seen on other members of each genus. Character states were categorized into apomorphies and plesiomorphies using outgroup comparison and a data matrix (Table 1) was compiled using MacClade 3.06 (Maddison & Maddison, 1996). The data was subjected to parsimony analysis using the 'Exhaustive' search option of PAUP 4.0b for Macintosh (Swofford, 1999), with characters run both as ordered and unordered transformation series and with no outgroup designated. A hypothetical taxon with all characters in the plesiomorphic state ('outgroup') was used to

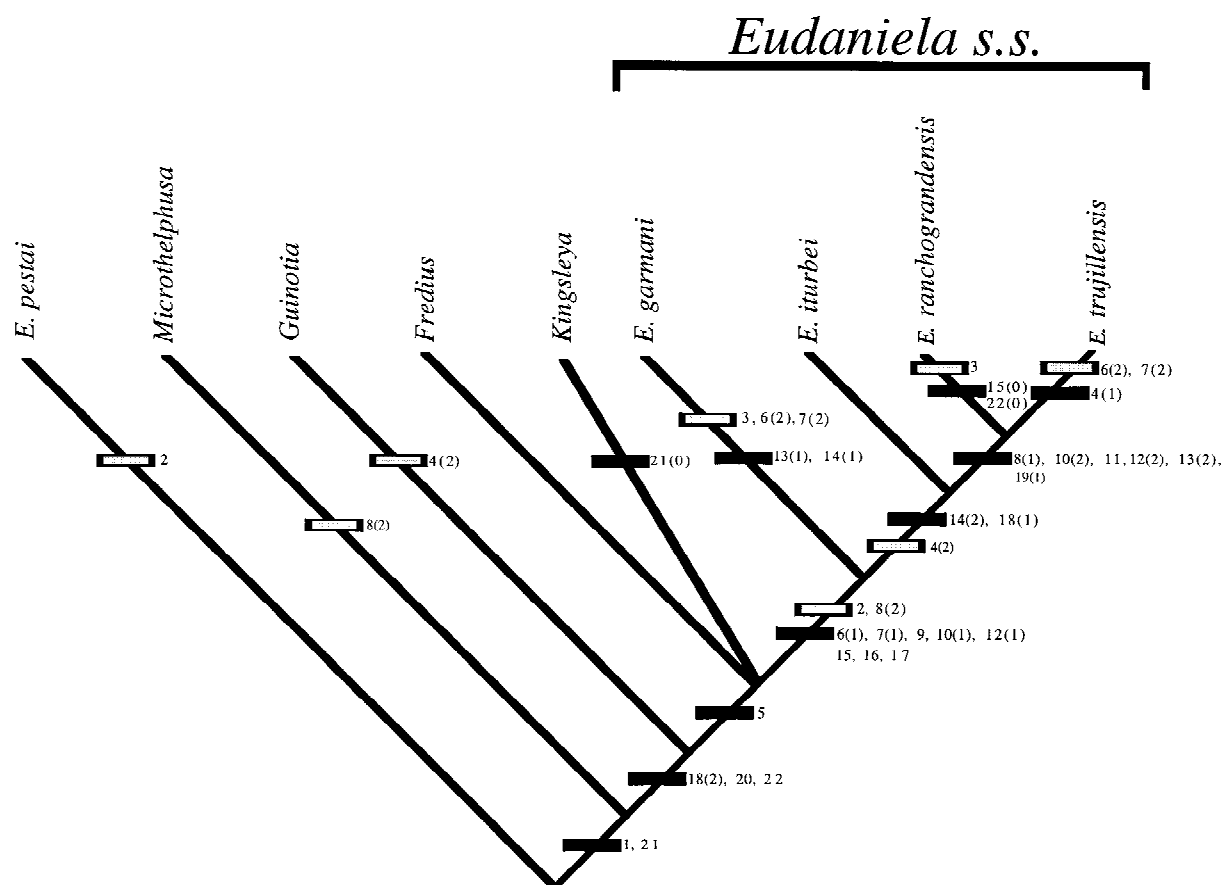


Figure 1. Cladogram of the single most parsimonious tree (length = 40 steps, CI = 0.775, RI = 0.816) obtained from the PAUP 4.0b analysis of 22 *Eudaniela* morphological characters. Filled boxes indicate character apomorphies, stippled boxes indicate homoplasies.

root the tree. Character state distributions on the most parsimonious cladogram were analyzed using MacClade 3.06 although character state optimization was based upon character argumentation (Wägele, 1994).

## Results

The exhaustive parsimony search of the data with unordered transformation series (Table 1) resulted in the identification of a single most parsimonious tree (out of 2 027 025 possible trees) with a length of 40 steps, consistency index (CI) of 0.775 and a retention index (RI) of 0.8163. Conducting the search with characters as ordered transformation series likewise resulted in a single most parsimonious cladogram, six steps longer, CI = 0.6739, RI = 0.7829, that had an identical topology to that found with characters run as unordered series. The most parsimonious cladogram with nodal character states is presented in Figure 1. *Eudaniela*

*pestai* is positioned as the most basal taxon among all kingsleyinine taxa analyzed and *E. pestai* does not group with the other four species of *Eudaniela*, so *Eudaniela* is evidently a paraphyletic taxon. No taxonomic changes are proposed here. The paraphyletic taxon '*Eudaniela*' is simply referred to as *Eudaniela s.l.*, and the monophyletic sibling species complex as *Eudaniela s.s.* or simply as *Eudaniela*.

Before discussing the distribution of character states, it is necessary to overview the rudiments of *Eudaniela s.s.* 1st gonopod morphology.

### *Eudaniela s.s.* 1st gonopod general description

Figure 2 presents the topological 'landmarks' of a generalized *Eudaniela* 1st gonopod morphotype and shows the general aspects of this organ in *Eudaniela*. The male 1st gonopod in *Eudaniela* is straight in overall conformation, proximally broad and tapered distally (Rodríguez, 1980, 1982). This organ is formed

by two main endopodal divisions referred to hereafter as 'vertical plates' (VP). Both VP extend from the gonopod base to the subapical area and there is a field of spines adjacent to the distal opening of the sperm channel (Rodríguez, 1982): the two plates are termed the 'thick vertical plate' (VP<sub>1</sub>) and the 'thin vertical plate' (VP<sub>2</sub>). The apical spine field is obscured by the subapical lobes.

The thick vertical plate (VP<sub>1</sub>) is visible from the caudal view (Figure 2), and is broader in extent relative to the other plate. The VP<sub>1</sub> plate curves round and is partly visible on the cephalic side and is strongly indented on the lateral side (Rodríguez, 1982). The VP<sub>1</sub> plate also has a prominent thorn-like process, that is designated here as the 'marginal thorn' (this is the 'spiniiform mesial lobe' in Rodríguez & Pereira, 1992) (T<sub>1</sub>); this process is one of the main characters typifying kingsleyinine genera.

The thin vertical plate (VP<sub>2</sub>) is partially overlapped by VP<sub>1</sub> on the latero-caudal side and curves to meet VP<sub>1</sub> caudo-mesially. The VP<sub>2</sub> forms the main axis of the gonopod around which the VP<sub>1</sub> partially extends. The extreme distal end of VP<sub>2</sub> constitutes a pronounced vertically oriented thorn-like process (the 'cephalic lobe' of Rodríguez & Pereira, 1992) (T<sub>2</sub>), which lies superior to the marginal thorn.

The vertical plates (VP<sub>1</sub> and VP<sub>2</sub>) and thorn-like processes (T<sub>1</sub> and T<sub>2</sub>) serve as topographical markers for locating other important gonopodal features, such as subapical lobes (L<sub>1</sub>, L<sub>2</sub> and L<sub>3</sub>) and depressions (C<sub>1</sub> and C<sub>2</sub>) which are variably found in kingsleyinine taxa. These 'minor' subapical gonopodal characters are also depicted in Figure 2.

#### Characters and codification

1. Exopod of 3rd maxilliped: partially reduced (0); vestigial (1).

The exopod of the 3rd maxilliped is reduced in length to a considerable extent in many pseudothelphusine genera (Rodríguez, 1982). Of the taxa investigated here, *E. pestai* has the longest exopod with the length of this unit 0.5X that of the endopodal ischium; in *Fredius*, *Guinotia* and *Microthelphusa* the ratio of the exopod to ischium length is 0.3. *Eudaniela garmani*, *E. iturbei*, *E. ranchograndensis*, *E. trujillensis* and *Kingsleya* all have exopods 0.2X the ischial length. Given the topology of the most parsimonious tree, state (1-1) unites all the taxa studied here (except *E. pestai*) into a monophyletic group. Another possible interpretation would be that state (1-1) is a rampant

parallelism within pseudothelphusine genera, and not a synapomorphy for any clade.

2. Postfrontal longitudinal groove: obsolete or absent (0); well defined (1).

All species of *Eudaniela s.l.* possess a well defined longitudinal groove separating the epigastric lobes (2-1). This groove originates at the point where the carapace front deflects vertically downward and extends back between the epigastric lobes. The derived state cannot be considered a diagnostic feature of *Eudaniela s.l.* but is instead a homoplastic development in *Eudaniela s.s.* and *E. pestai*.

3. Prominent tubercle at the external base of the cheliped propodus-dactylus junction: absent (0); present (1).

A prominent, round tubercle at the external base of the cheliped propodus-dactylus articulation point is found in many pseudothelphusid genera. For example, a number of species of the genus *Hypolobocera s.l.* exhibit the derived condition (Rodríguez, 1982). *Eudaniela garmani* and *E. ranchograndensis* each have state 3-1 although this condition must be considered a homoplastic development for the two species, given the topology of the most parsimonious tree (Figure 1).

4. Punctae on the cheliped dactylus: absent (0); small (1); distinct (2).

*Eudaniela garmani*, *E. pestai* and some species in the genera *Microthelphusa*, *Fredius* and *Kingsleya* lack punctae on the pereopod 1 dactylus (4-0). The presence of distinct dactyl punctae (4-2) is a synapomorphy for the placement of *E. iturbei* as the sister species of *E. ranchograndensis* and *E. trujillensis*, and this character is also seen in some species of *Fredius*, *Kingsleya* and *Guinotia* (which is monotypic). Within *Eudaniela s.s.*, *E. trujillensis* has small punctae (4-1), a state also present in *Microthelphusa racenisi*.

5. Overall gonopod 1 conformation: columnar (0); proximally broad, tapering distally (1).

The genera *Fredius*, *Kingsleya* and *Eudaniela s.s.* can be differentiated from *Guinotia*, *Microthelphusa* and *E. pestai* by having a 1st gonopod with a broad base, that gradually tapers toward the apex (5-1).

6. Caudal, subapical lobe-1 of the 1st gonopod (L<sub>1</sub>): simple or absent (0); moderately developed (1); highly developed (2).

All species of *Eudaniela s.s.* have a unique 1st go-

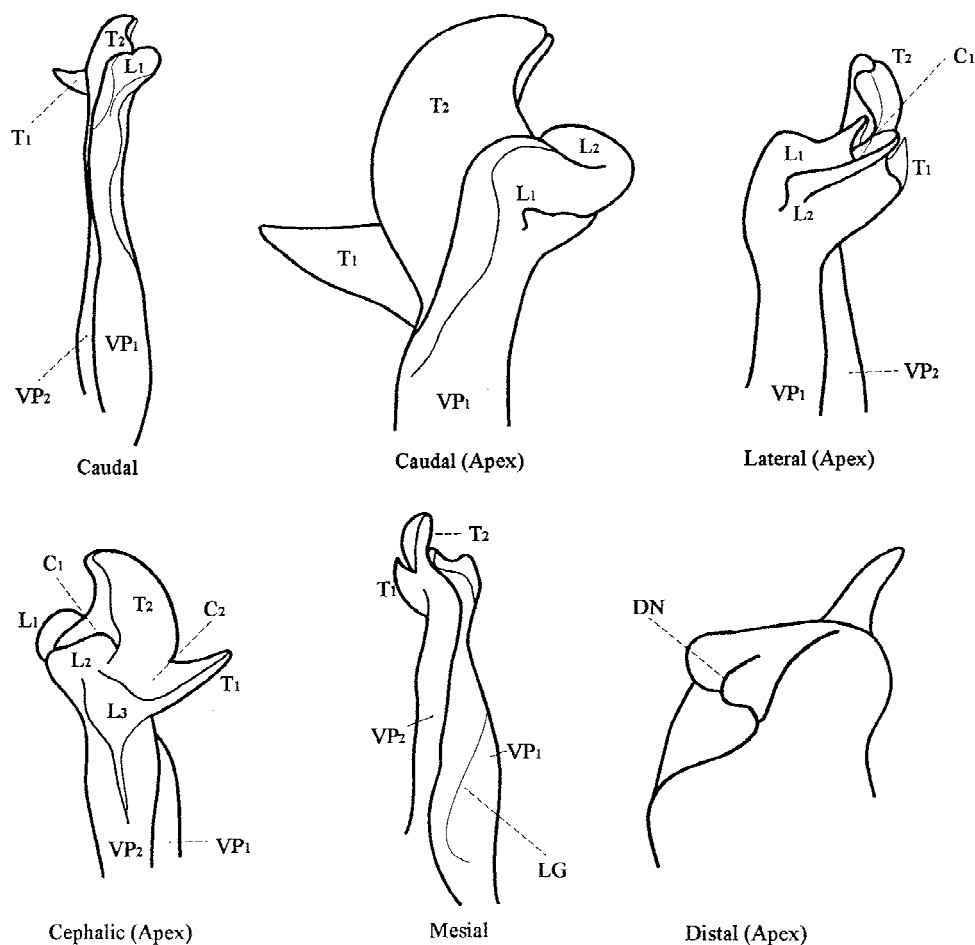


Figure 2. Topological landmarks of a generalized *Eudaniela* 1st gonopod morphotype. Characters are as follows: C<sub>1</sub> = latero-apical cavity-1; C<sub>2</sub> = cephalo-apical cavity-2; DN = distal notch; LG = lateral groove; L<sub>1</sub> = caudal, subapical lobe-1; L<sub>2</sub> = caudal, subapical lobe-2; L<sub>3</sub> = cephalic, subapical lobe-3; T<sub>1</sub> = marginal thorn; T<sub>2</sub> = vertical thorn; VP<sub>1</sub> = thick vertical plate; and VP<sub>2</sub> = thin vertical plate.

nopod morphotype. From the caudal perspective, a distinct subapical lobe-1 (L<sub>1</sub>) can be detected (referred to as the 'subapical bulge' in Rodríguez & Pereira, 1992) (Figure 2). Homologues of this lobe may be present in other genera within the tribe Kingsleyini, although striking differences in gonopod topology make unambiguous comparisons difficult. The derived groundpattern of *Eudaniela s.s.* includes a 1st gonopod lobe-1 which is moderately developed (6-1), that is, it is considerably larger in size and more well defined relative to the lobe-1 seen in *E. pestai*. *Eudaniela garmani* and *E. trujillensis* both have a very prominent caudal lobe (6-2), considered here to be a parallel elaboration of state (6-1).

7. Caudal, subapical lobe-2 of the 1st gonopod (L<sub>2</sub>): absent (0); small (1); distinct (2).

All species of *Eudaniela s.s.* possess a lobe-2 (L<sub>2</sub>), which (as with L<sub>1</sub>) can also be seen from the caudal view of the 1st gonopod, where it is positioned cephalic to lobe-1 (Figure 2). Lobe-2 is absent in *Eudaniela pestai* (7-0). This morphological unit is distinct in *E. garmani* and *E. trujillensis* (7-2), whereas *E. itubei* and *E. ranchograndensis* exhibit a relatively weak development of this process (7-1). Given the basal position of *E. garmani vis-à-vis* the other species of *Eudaniela s.s.*, it is here postulated that state (7-2) arose twice from state (7-1).

8. Cephalic, subapical lobe-3 of the 1st gonopod (L<sub>3</sub>): absent (0); simple (1); prominent (2).

A large lobe-3 ( $L_3$ ) can be observed on the cephalic side of the 1st gonopod in *Eudaniela s.s.* (8-2); this lobe emerges at the base of the marginal thorn ( $T_1$ ). Lobe-3 is undetectable in the genera *Fredius*, *Kingsleya* and *Guinotia* (8-0).  $L_3$  is prominent in *Eudaniela iturbei* and *E. garmani* (8-2), a condition which is homoplastically present in *Microthelphusa*. *Eudaniela trujillensis* and *E. ranchograndensis* possess a simple lobe (8-1), which is a derived, reductive state. Lobe-3 is very vaguely differentiated in *E. pestai* (8-0).

9. Latero-apical cavity-1 of the 1st gonopod ( $C_1$ ): absent (0); present (1).

A large depression is formed between the distal ends of lobe-1 and lobe-2 due to the partial overlapping of the two lobes. An analogous cavity is found in *Guinotia*, although the conformation is different from that found in *Eudaniela s.s.* All species of *Eudaniela s.s.* have the derived character state (9-1); *E. pestai* and most other species in the tribe Kingsleyini lack this character (e.g. *Microthelphusa racenisi*).

10. Cephalo-apical cavity-2 of the 1st gonopod ( $C_2$ ): absent (0); distinct (1); very deep (2).

The cephalo-apical cavity-2 is located between lobe-3 and the base of the marginal thorn ( $T_1$ ) of all *Eudaniela s.s.* taxa. This depression is notably absent in *E. pestai*, (10-0). *Eudaniela garmani* and *E. iturbei* possess a rather inconspicuous cavity-2 (10-1), which may be correlated with the presence of a prominent lobe-3 and a wide and short marginal thorn ( $T_1$ ). On the contrary, *E. trujillensis* and *E. ranchograndensis* exhibit a very deep cavity-2 (10-2), possibly linked with the simple lobe-3 and the slender and large marginal thorn ( $T_1$ ) observed in these two species.

11. Proportional size of the 1st gonopod marginal thorn base: wide base (0); slim base (1).

This character pertains to the proximal end of the  $T_1$ , which originates at the terminus of lobe-3 on the meso-cephalic side. *Eudaniela ranchograndensis* and *E. trujillensis* each has a slim marginal thorn base (11-1), which is a unique character state in the genus. All other *Eudaniela s.l.* taxa have a wide  $T_1$  base (11-0), as do the outgroup taxa (*Microthelphusa*, *Fredius*, *Kingsleya* and *Guinotia*). Character state (11-1) supports a sister species relationship for *E. ranchograndensis* and *E. trujillensis*.

12. Proportional overall size-length of the 1st gonopod marginal thorn: short (0); medium (1); large (2).

The overall relative size-length of the  $T_1$  was compared between the different taxa studied. This attribute of  $T_1$  (size and length) was considered from the base to the terminus, which can be viewed from the cephalomesial perspective. All kingsleyinine taxa examined have homologues of  $T_1$  and *E. pestai* is notable in that this species has the shortest thorn of all the genera, (12-0). *Eudaniela trujillensis* and *E. ranchograndensis*, on the other hand, have the largest and longest thorn-1 (12-2) among both the ingroup and outgroup taxa. The  $T_1$  of these two sister species is quite similar and can not be easily used to distinguish between the two. The marginal thorn of *E. garmani* and *E. iturbei* is intermediate between the most underived and derived conditions in overall size and length (12-1).

13. Sharply pointed cephalo-mesial terminus of the 1st gonopod marginal thorn: inconspicuous (0); present (1); very distinct (2).

The shape of the marginal thorn cephalo-mesial terminus was categorized into three states based upon comparisons made within the genus *Eudaniela s.l.* *Eudaniela garmani* has an intermediate (and independently derived) condition for this character in that the terminus of the  $T_1$  is produced into a moderately sharp point, (13-1). *Eudaniela ranchograndensis* and *E. trujillensis* possess a very sharp  $T_1$  end (13-2), a synapomorphy for the two taxa. On the other hand, the marginal thorn terminus in *E. iturbei* and *E. pestai* is not conspicuously pointed, (13-0).

14. Overall vertical thorn conformation ( $T_2$ ): flattened triangle (0); conical (1); pyramidal (2).

The conformation of the vertical thorn appears to be related to the development of the subapical processes, especially the three lobes already described (characters 6, 7 and 8); and also with the degree of overlapping of the two vertical processes (see character 19 below). *Eudaniela pestai* has a simple  $T_2$  which is flattened, appearing to be the union of two sheets that have a sharp angular junction at the terminus, (14-0). *Eudaniela garmani* has a conical  $T_2$  (14-1), where the unit appears rolled over; the  $T_2$  in this species originates from a subapical position more reduced in size than that seen in other *Eudaniela* species, due the presence of a unique process formed by the aggregation of lobe-1, lobe-2 and the base of the vertical thorn, all of which makes the apex more complicated in detail. *Eudaniela iturbei*, *E. ranchograndensis* and *E. trujillensis* have a  $T_2$  with a pyramidal shape (14-2), a synapomorphy positioning *E. iturbei* as the sister

species of the latter two. In contrast to the subapical organization seen in *E. garmani*, the T<sub>2</sub> has a relatively wider base in these three taxa.

15. Round 1st gonopod vertical thorn: absent (0); present (1).

*Eudaniela garmani*, *E. iturbei* and *E. trujillensis* have a vertical thorn which is round in overall shape, (15-1). The vertical thorn in *E. pestai* and *E. ranchograndensis* presents a more spade-like outline, (15-0). Given the topology of the most parsimonious cladogram, state (15-1) is an autapomorphy for *Eudaniela s.s.* with *E. ranchograndensis* exhibiting a reversal to the underived condition.

16. Inclination of the 1st gonopod vertical thorn: straight (0); strong inclination (1).

All species in the genus *Eudaniela s.s.* have a T<sub>2</sub> with an inclined lateral margin, 16-1. In *E. pestai*, possibly due to the absence of some subapical processes, or to the simplicity of the subapical lobes present, the T<sub>2</sub> exhibits no inclination and this is considered the underived condition, (16-0). In *Fredius* and *Microthelphusa*, the vertical thorn is highly inclined (in some cases doubled-over), which is interpreted as evidence supporting the hypothesis that the conformation of the T<sub>2</sub> in *E. pestai* is the plesiomorphic condition. However, the type of inclination seen in *Fredius* and *Microthelphusa* is different from that exhibited by *Eudaniela s.s.*

17. Base of the 1st gonopod vertical thorn: exposed (0); positioned in C<sub>1</sub> (1).

This character, like the previous one, clearly differentiates between *E. pestai* and all other species of the genus. *Eudaniela pestai* has an exposed vertical thorn base (17-0), whereas the *Eudaniela s.s.* taxa have the base located in the cephalo-apical depression present between lobe-1 and lobe-2 (C<sub>1</sub>) (17-1).

18. Distal notch (DN) on the 1st gonopod vertical thorn terminus: complete (0); incomplete(1); absent (2).

In some taxa of the Tribe Kingsleyini [e.g. *Eudaniela* and *Microthelphusa* (variable)], a distal notch (incision) is present on the terminus of the vertical thorn ('apical notch' of Rodríguez & Pereira, 1992), which can be seen from the distal view of the gonopod apex. This character varies considerably in *Eudaniela s.l.* *Eudaniela pestai* has a conspicuous notch which extends from one side to the other of the T<sub>2</sub> (18-0). In

*Eudaniela iturbei*, *E. ranchograndensis* and *E. trujillensis* a partially fused notch is apparent, a modification of the plesiomorphic state (18-1). In the case of *E. garmani* and the genera *Guinotia*, *Kingsleya* and *Fredius*, the vertical thorn lacks the distal notch completely, (18-2). It is here hypothesized that state (18-1) constitutes an intermediate state reversed for *Eudaniela s.s.* with the exception of *E. garmani*.

19. Sides of the distal notch overlapping: absent (0); present (1).

The distal notch (when present) exhibits two distinct developments. The rims of the notch can be observed overlapping (19-1); or can be found in a parallel arrangement (i.e. one rim in front of the other). Overlapping sides of the distal notches are a condition that only can be observed in two species of the genus *Eudaniela s.s.*, specifically in *E. ranchograndensis* and *E. trujillensis*. Character state (19-1) might also be present in some taxa of *Microthelphusa* (which exhibits polymorphism).

20. 1st Gonopod thick vertical plate (TPT) 'twisted': absent (0), present (1).

The VP<sub>1</sub> appears twisted when seen from the caudal view in some taxa. *Eudaniela pestai* presents a straight thick vertical plate, a condition similar to that seen in *Microthelphusa* (20-0). *Eudaniela s.s.*, and most of the outgroup genera studied (*Fredius*, *Kingsleya* and *Guinotia*) possess a twisted thick vertical plate, giving the effect of a more complex gonopod anatomy, (20-1).

21. Degree of 1st gonopod vertical plate overlap: approximately half of the caudal VP<sub>2</sub> covered by the VP<sub>1</sub> (0); greater than a half of the caudal VP<sub>2</sub> covered by the VP<sub>1</sub> (1).

The thick vertical plate covers the thin vertical plate in a manner that is differently proportioned in each species. Most of the taxa studied have a thick vertical plate which overlaps a significant region of the thin vertical plate, longitudinally and caudally, where the degree of overlap is approximately greater than half of the caudal VP<sub>2</sub> region. This condition can be observed in *Eudaniela s.s.*, *Microthelphusa*, *Fredius* and *Guinotia*, (21-1). *Eudaniela pestai* and *Kingsleya* have first gonopods in which the thick vertical plate overlaps the caudal region of the thin vertical plate to a lesser degree (21-0) so that the VP<sub>1</sub> covers almost half of the caudal thin vertical plate.

22. 1st gonopod lateral groove (LG): narrow (0); deep (1).

The thick vertical plate is characterized by a groove on the caudo-lateral side. *Eudaniela pestai*, *E. rancho-grandensis* and *Microthelphusa* have a narrow groove in this region (22–0). *Fredius*, *Kingsleya* and *Guinotia* have developed a deep lateral groove, this state being homologous with that seen in *E. garmani*, *E. iturbei* and *E. trujillensis*, (22–1). The presence of the underived state in *E. rancho-grandensis* is most parsimoniously interpreted as a reversal.

## Discussion

An exhaustive parsimony analysis of 22 morphological characters, four somatic characters and 18 1st gonopod characters, unequivocally presents the genus *Eudaniela* as a paraphyletic taxon. *Eudaniela pestai* is positioned basal not only to the monophyletic *Eudaniela s.s.* sibling species complex, but also to the representatives of the genera *Fredius*, *Guinotia*, *Kingsleya* and *Microthelphusa* examined. Rodríguez & Pereira (1992) stated the following regarding the status of *E. pestai* relative to *Fredius*:

“... the genus *Fredius* is grouped with eight other genera in the tribe Kingsleyini. The apomorphies which define this tribe are the following: 1. Reduction of the exognath of the third maxilliped to less than half the length of the ischium of the exognath; this trend is already present in all Pseudothelphusidae, but it is more accentuated in the Kingsleyini. In *Eudaniela pestai* ... and *Fredius* spp., the exognath is less reduced than in other members of the tribe. 2. Presence of a spiniform mesial lobe and a hoodlike cephalic lobe in the distal segment of the first gonopod. As theorized by Rodríguez ... the cephalic lobe originated from an ancestral type of gonopod with three independent apical plates, by apposition of the mesial and lateral plates, and reduction of the marginal plate. In *Eudaniela pestai*, the cephalic lobe is still formed by two separate plates, but in other species, only an apical notch remains as a vestige of the recess between both plates. For this reason *Eudaniela pestai* can be considered as approaching the ancestral pseudothelphusid condition ...”.

This conclusion, reiterated by Rodríguez & Campos (1998), is supported by our finding that *E. pestai* clearly has the least derived 1st gonopod and longest 3rd maxilliped exopod within the Kingsleyini. For this

reason, we concur with the opinion of Rodríguez & Pereira (1992) and Rodríguez & Campos (1998) that *E. pestai* exhibits the prototypical Strengerianini-like gonopod conformation from which the more complicated gonopodal anatomies in the Kingsleyini can be derived. Furthermore, *E. pestai* has a partially enclosed efferent channel, a condition intermediate between that seen in the Strengerianini (Rodríguez, 1982) and kingsleyinines.

Although the basal position of *E. pestai* within the Kingsleyini is a well-supported conclusion, the position of the other kingsleyinine taxa *vis-à-vis Eudaniela s.s.* needs to be resolved. Comparing the 1st gonopods of *Eudaniela s.s.* and the basal taxa of *Fredius* does provoke one to hypothesize that these two genera, possibly with *Guinotia*, are sister groups. No attempt was made in this study to definitively identify the sister taxon of *Eudaniela*; indeed, the highly specialized 1st gonopod seen in *Kingsleya s.l.*, *Microthelphusa* and *Oedothelphusa*, for example, underscores the need to robustly determine topological series across the genera in the tribe prior to undertaking such an analysis. Nevertheless, if the degree of gonopodal ‘complexity’ has any cladogenetic significance, then one can postulate the following series of relationships: [*E. pestai* [[*Fredius*, *Guinotia*], *Eudaniela s.s.* [*Microthelphusa* [*Kingsleya*, *Neopseudothelphusa* [*Oedothelphusa*, *Orthothelphusa*]]]]]. Such a scheme postulates that, for each genus, the taxon with the simplest gonopod conformation represents the most basal form. This postulate is partially substantiated by the observation that a trend toward the elaboration of subapical processes can be detected in cohesive kingsleyinine genera (e.g. *Fredius* and *Microthelphusa*) (see Figure 4 of Rodríguez & Pereira, 1992; see also Rodríguez, 1982). (The position of *Prionoethelphusa* relative to other kingsleyinines is very unclear.)

The *Eudaniela* sibling species complex was resolved into a dichotomously branching arrangement. Given that pseudothelphusid crabs have direct development and are geographically restricted because of limited dispersal capabilities (Rodríguez, 1986), a vicariance model appears to best explain the distribution of *Eudaniela* species. The most basal taxon, *E. garmani*, has a disjunct biogeography inasmuch as it is found not only along the northeastern coast of Venezuela but also on the coastal islands of Margarita, Trinidad and Tobago. Such a distribution suggests that proto-*Eudaniela* had already differentiated into *E. garmani* and the internode taxon (ancestral to the other members of the complex) prior to the barriers that



arose between the mainland and island populations of *E. garmani*. Following the fragmentation of the range of *E. garmani*, cladogenetic events proceeded in a westward direction, with the sister species *E. ranchograndensis* and *E. trujillensis* presumably being the youngest taxa. The morphological differences between the *Eudaniela* species are so slight, however, that one is tempted to postulate a young age for the genus. Such morphological similarity may on the other hand reflect stasis, and a test of this would be to date the geological events separating Isla Margarita, Tobago, and Trinidad from the mainland and each other.

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