Phylogenetic Relationships of Parasitic Pseudeca and Taxonomic Position of the Anopla*  

KE CHUNG KIM and HERBERT W. LUDWIG

ABSTRACT

Phylogenetic relationships of five taxa of the Pseudeca (Pseudeca, Acanthocerca, Ischnocerca, Rhynchoptera, and Anopla) are studied cladistically. Fourteen character complexes including taxonomic characters used by previous workers are analyzed. The major factors of change within these complexes are described and correlated with the evolution of character states. The evolutionary history of these taxa is thus divided into several stages, each characterized by a distinct combination of character states. This approach is used to reconstruct the evolutionary history of these taxa and to determine their relationships within the Linnaean system. The results indicate that the Pseudeca and Acanthocerca are sister taxa, whereas the Ischnocerca and Rhynchoptera are more closely related to the Anopla. The relationship between the Pseudeca and Anopla is also discussed in detail.
adapting zone does not alter its basic organization during the period of adaptive radiation, and it is not affected by ecological shifts of the member taxa. Furthermore, the expression of this character is usually seen. A taxonomic character is a taxonomic character, and the positive adaptation of the character is the result of a constellation of factors that can be identified as being related to the different ecological niches the species occupy. This is clearly demonstrated by the fact that the same character can be found in different species and that the same character can be found in the same species but at different times. Zinkowski and Nayar (1963) have shown that this is the case for the species of the genus Anolis. However, the number of species of the genus Anolis, which is a result of the fact that the species of the genus Anolis have a higher degree of variation, is higher than the number of species of the genus Anolis that have a lower degree of variation. This is also true for the species of the genus Anolis that have a lower degree of variation. Therefore, the fact that the same character can be found in different species and that the same character can be found in the same species but at different times, is due to the fact that the same character can be found in different species and that the same character can be found in the same species but at different times, is due to the fact that the same character can be found in different species and that the same character can be found in the same species but at different times.
Fibrous Tissues and Ovarioles in the Anopla. A fibrous plug of connective tissues, known as the ovariole, is developed in the head and gives support to the muscles of the trophic styles (Stejneger 1945). The enlargement of the connective tissues surrounding the head ganglia in the Ischnocera and Rhynchoptera is homologous to the ovariole (Symmons 1952). Pipa and Cook (1928) in the Anopla and the Archyopteryx development of the connective tissue is very similar to that found in other insects (Symmons 1952). The development of the ovariole and the connective tissues surrounding it, is thus, the aponomic condition in a morphogenetic series.

Mouthparts

The mouthparts in the Anopla are of a generalized type, comprising the maxilla, labium, and characteristic hypopharynx (Badonnel 1934). The mandible is sparsely toothed with a molar area at base. The maxilla is highly modified; the cardo is either lost or fused with the stipes, the galea is continuous with the stipes, the lacina is modified into a stellate stylet process, often called the "pick," and the maxillary palp is 4-segmented (Badonnel 1934). The labium is generalized, with the labial palp 1-segmented, or rarely, 2-segmented (Masuda 1965). The hypopharynx in the Anopla is characterized by (1) the presence of the swollen pars ovoidal soriaceous, (2) the absence of the larval arm, (3) the presence of a filiform ligament connecting the stipe and ovipositor and ovipositor sheath (Masuda 1965).

Ovipositor

The Mallophaga and the maxillary palp is provided with a sharp apical tooth, and a blunt projection on its basal inner margin (Masuda 1965). The arthroconical hypostomids differ from the mandibles in the Anopla: the hypostomids are situated in the preoral region and are not preoral, the labium is simplified and fused with the labium, and the cardo is always present. The maxillary palp is usually 4-segmented, rarely 3-segmented, and, in the Amblycera, but lacking in the Ischnocera (Richards and Davies 1970). The maxillopharynx is single-lobed and highly modified in the Anopla and the maxillae are joined by a common stalk and are generally fused with the labial palp, but the cardo is always present. The maxillary palp is usually 4-segmented, rarely 3-segmented, and, in the Amblycera, but lacking in the Ischnocera (Richards and Davies 1970). The maxillopharynx is single-lobed and highly modified in the Anopla and the maxillae are joined by a common stalk and are generally fused with the labial palp.
Thus, we conclude that the presence of symbiotes does not contribute to phylogenetic inference.

**Internal Reproductive Organs**

In the Pocodidae and Amblycera males the testis usually consists of three pyknotic follicules (some Pocodidae may have a single follicule), but in the Ischnocera, Rhyynchophtharia, and Anoplophora there are two follicules. In all the Pocodidae the ovary possesses polytrophic ovaries; in the Pocodidae and Amblycera each ovary consists of 3–5 ovarials and in all other Pocodidae there are 5 ovarials (Quadt 1937; Königsmann 1960; Richards and Davies 1970). It is interesting to note that in Trocomorpha and Trogomorpha (Pogoniidae) there are only 3 or 4 ovarials in the Pocodidae (Matsuoka 1976a).

**Eggs and Nymphs**

In the parasitic Pocodidae the egg is provided with an operculum, micropyle, and an egg stigma. Elision is assisted by the embryonic egg barbules.

In the Pocodidae there are usually six nymphal instars. The number of instars sometimes differs between male and female; male *Arachnopus* has 4–6 instars but the female always has 6 instars (Mockford 1957). Frequently, nymphalization in the Pocodidae is accompanied by reduction in the number of instars.

The Mallophaga and Anoplura have three nymphal instars (Königsmann 1960) considering the presence of three instars aponomorphic for the parasitic poecilocraea. Rich nutrition diet can increase the number of molts in some insects (Gillespie 1970; Wiegmann 1950; Tischack 1926), and in many parasitic insects, such as *Glossina* and *Haemagogus*, full-grown larvae are laid and almost immediately begin to develop. These phenomena suggest the fluidity of the number of molts in some insects. It is reasonable to speculate that the number of nymphal instars may have been reduced as the parasites adapted a new aedaphic zone (parasitic mode of life). Thus, this character state has little phylogenetic significance.

**Cladistic Analysis**

In cladistic analysis, phylogenetic relationships are inferred on the basis of shared derived character-states (= synapomorphy) and not of shared ancestral ones (= plesiomorphy). The sharing of primitive character-states does not necessarily indicate close phylogenetic relationships. However, character states plesiomorphically evolved at a higher level and in addition to synapomorphy, the entire suite of each morphospecific line should be examined, in order to recognize the resulting change from the evolutionary breakdown of related groups into similar new adaptive zones.

**Selection and Weighting of Taxonomic Characters**

From 14 character complexes analyzed, 21 characters were selected for cladistic analysis on the basis of criteria already described. These characters are considered to be morphological among the five taxon Pocodidae, Pogoniidae, Ischnocera, Rhyynchophtharia, and Anoplophora. Two character states for each character, plesiomorphy (0) and apomorphy (1), were identified. The proposed criteria by several workers (Campione 1961; Kuge and Fujita 1969; Schaefer et al. 1972; Kluge 1976a). In a morphofoenic series more than one aponomorphic state may be recognized: they are indicated by "1", "1", and "1". There are exactly two characters being synapomorphic in 0 = 1 → 1 → 3; or it may be a branched morpohphy 0 → 1 → 3, or it may be that three aponomorphic states are each independently derived from the pleosiomorphic state (Max et al. 1977). Each character is then weighted by a frequency of criteria of length and time (1976) and classified into one of the five types in order of increasing phylogenetic inference. The type 1 character refers to the least amount of inferred phylogenetic inference, and thus is given the lowest value of five. Those derived characters which are highly variable are discussed in this analysis. The character states and the weighting of type 21 characters are enumerated below:

1. Head hypognathous and globular (0) or prognathous and flattened (1). (Type 4).
2. Head mobile (0) or fixed (1). (Type 4).
3. Tenentia complete (0), with anterior tergal arms reduced (1), completely lacking but with terminal pro (2) or completely absent (3). (Type 2).
4. Antennae filiform (0) or capitate (1). (Type 4).
5. Antennae muscles originating on the tergum anterior (0), on the anterior tergal arm (1), on the tergal arms (2), or entirely on the head dorsum (3). (Type 3).
6. Terminal segment of antennae with only sensilla coeloconica (0), with only sensilla coeloconica and basiconica basiconica and saucer-shaped pore organs (1). (Type 4).
7. Early larval fibrils present around head ganglia (0), well-developed fibrillae present around the head ganglia (1) or absent (2). (Type 4).
8. Pinniforma teeth on arocharon (0) or specialized pincer-like (1). (Type 4).
9. Labial glands; 2 pairs (0) or one pair (1). (Type 2).
10. Lacinial gland present (0) or absent (1). (Type 1).
11. Stericore present (0) or absent (1). (Type 2).
12. Mandibular-hypopharyngeal muscles present (0) or absent (1). (Type 1).
13. Thoracic segmentation divided (0), meso- and metathorax fused (1) or all segments fused (2). (Type 4).
14. Parts articulated with forecoxae (0) or not (1). (Type 2).
15. Tarsus with 2 claws (0) or with one claw (1). (Type 2).
16. Order of 2 pairs of spiracles (0) or of one single pair of spiracle (1). (Type 2).
17. Spiracular glands absent (0) or present (1). (Type 4).
18. Head produced into a long, slender rostrum (1). (Type 5).
19. Tests with 3 follicules (0) or 2 follicules (1). (Type 1).
20. Two with 3 ovarials (0) or 3 ovarials (1). (Type 2).
21. Nymphs with 4–6 instars (0) or 3 instars (1). (Type 3).

The distribution of character states for the 21 characters is shown in Table 1. Of the 21 characters used we placed none in weighting types 1 and 2, two in type 3, eight in type 4, and two in type 5. Thus, 15 characters (11, 12, 19 and 21) are aponomorphy in all Pocodidae except Anoplophora. Five sympo-
Table 2.—Matrix for synapsmyophor based on 21 characters for the Psocodea. Number of synapsmyophor characters is shown in the lower triangular matrix. Number of synapsmyophor characters for weighting type 4 and 5 characters in the upper triangular matrix. Ps = Psocodea; Am = Amblycera; Is = Ischnoptera; Rh = Rhynchophasmatidae; An = Anomala.

<table>
<thead>
<tr>
<th></th>
<th>Ps</th>
<th>Am</th>
<th>Is</th>
<th>Rh</th>
<th>An</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dy</td>
<td>1</td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>X</td>
<td>2</td>
<td>1</td>
<td></td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>X</td>
<td>3</td>
<td>2</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>X</td>
<td>4</td>
<td></td>
<td></td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>X</td>
<td>5</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The numbers of sensory pegs and surface cavities, which are a type of sensillum coeloconicum, on the 5th segments are highly variable, and the details of saucers-shaped pore organs are also variable among different taxa of the Ichneumonidae and Anoplophora. These facts actually contradict the view of Clay (1970) that the Ichneumonidae are more closely related to the Anoplophora. The Anoplophora presence of a single basalica in Heterometra and Ichneumonidae as well as of sensilla coelica in Amblycera, Ichneumonidae and some Amblycera. The icnheumonid can cause the sensilla organs in the body to develop independently along parabolic lines. At least, this is a more parsimonious interpretation.

The Amblycera three-character states (1, 8, 9, 16, 21) with the Ichneumonidae and Rhynchophasmatidae (1) head prothongated and flattened, (2) mouthparts of the modified chewing type; (9) only one pair of labial glands; (16) thorax with a single pair of spiracles; and (21) with 3 nymphal instars (Table 2 and 1). Of these two synapsmyophor attributes (9, 16, 21) are unique to the three taxa, commonly known as the order Mecoptera, and the other three states (1, 16, 20) related to the parasitic mode of life as already discussed. The Anoplophora share the least number of character states with the Psocodea.

The Ichneumonidae possess seven synapsmyophor attributes (weighting type 4 and 5) with the Rhynchophasmatidae (Holometabola): (1) head prothongated and flattened; (2) terminal segment of antenna with sensillum coeloconicum; (3) saucer-shaped pore organs on the vertex and mid-dorsal parts of the head and thorax; (3) mouthparts modified chewing type; (12) mandible-hypopharyngeal muscles absent (except for the Rhynchophasmatidae); (13) sternite and metasternum fused; and (17) spiracular glands present. Of these, the two character-states (7 and 12) are unique to both taxa. Four synapsmyophor attributes (4, 5, 17, 19) are of the Amblycera plura were fairly well established on the earhicate taxon (Fig. 2). In the Psocodea early incipient (Fig. 2).

Quite early in psocodean evolution there occurred a major evolutionary shift into a new habitat, the body surface and dermal dellence (feathers and hairs) of birds and mammals. As a consequence, several characters and character complexes must have become modified by intense selection pressure to successfully exploit the new environment. These include: (a) dorsoventral flattening and pro-longation of the body, (b) reorganization of the mouth; (c) reduction in the number of spiracles; (d) shorter length of the immature stage by the number of instars and duration of stages; (e) modification of legs; (f) modification of some sensory organs; and (g) reproductive adaptations, in oviposition and fecundity. Such modifications are of coarse common among other ectoparasites of birds and mammals.

The parasitic Anoplophora, differentiated in the Psocodea line early in psocodean evolution. The Amblycera lineage naturally involved those character-states correlated with their parasitic mode of life already discussed; one autapomorphy-character state, the terminal antennal segment (the third terminal instar); the alternative developmental differentiation, which gave rise to the Psocodea and the Ichneumonidae-Rhynchophasmatidae stock, involved the following synapsmyophor: (a) development of saucer-shaped pore organs in addition to sensory coelica or sensilla basiconica on the terminal antennal segment; (b) presence of spiracular glands (c) ovary with five ovarioles. Furthermore, the polarity of several morphological series was already established for this phylogenetic stock.

The differentiation of the Ichneumonidae-Rhynchophasmatidae line from the main psocodean stock involved the following synapsmyophor: (a) reduction in the number of instars; (b) shift in the origin of antennal muscles from the ventral to the head dorsum; (c) development of thoracic muscles into head dorsum; (d) development of the meta- and hypopharyngeal muscles absent; and (e) fusion of the mental and metasternal muscles. The subspecies differentiation of the Ichneumonidae showed the reduction of the antennal ventralia series fol-

November 1978

Kim and Ludwig F. Procopio: Phylogenetic Relationships

<table>
<thead>
<tr>
<th>Taxa set</th>
<th>No of exclusive synapsmyophor or autapomorphies</th>
</tr>
</thead>
<tbody>
<tr>
<td>Am-Is-Rh</td>
<td>1</td>
</tr>
<tr>
<td>Rh-Is-An</td>
<td>1</td>
</tr>
<tr>
<td>Rh-Is-An</td>
<td>1</td>
</tr>
<tr>
<td>Rh-An</td>
<td>1</td>
</tr>
</tbody>
</table>

See Table 2 for character states and weighting types.
Key to the Orders and Suborders of Podecida

1. Antennae with more than 10 segments; hypognathous head; abdomen with 7 or 8 pairs of spiracles
   2. Promoterum highly reduced; stipes lacking; thorax wider than head
   2. Promoterum highly reduced; stipes lacking; thorax wider than head
      3. Antenna capitate with segment 3 pedunculate; maxillary palps present
         ...Suborder Asbycheria
      4. Antenna falciform with segment 3 not pedunculate; maxillary palps absent
         ...Suborder Rhynchothyrina

Acknowledgment

We have received numerous valuable comments from many fel low workers during the preparation of this paper. We owe special thanks for reading the manuscript and their suggestions to E. F. Cook and R. D. Price, University of Minnesota, St. Paul; K. M. C. Emerson, National Museum of Natural History, Smithsonian Institution; 2704 North Kennington St., Arlington, Va.; R. C. Delighie, the Edmond Niles Hacky Preserve Inc., Rosellinville, N.Y.V.; W. M. Moss, Academy of Natural Sciences, Philadelphia, Pa.; C. F. Wieser, Universität Heidelberg, Heidelberg, Germany; and B. F. Cook, R. B. Eckhardt, P. D. Long, M. T. Quinn, D. J. Shear, and R. Strauss, the Pennsylvania State University. We are indebted to Dr. Carl v. Linné for his critical review of the manuscript and valuable suggestions.

REFERENCES CITED

Morphology of the Internal Reproductive System of the Adult Female Army Cutworm, Euxoa auxiliaris.*1,4

H. GENE DRECKRAH

Biotechnology Department, University of Wisconsin, Oakfield 54901

ABSTRACT

The morphology of the internal reproductive system of the adult female army cutworm, Euxoa auxiliaris (Grote) (Lepidoptera; Noctuidae), is described and illustrated. The spermatheca is large and described.

The study shows the basic similarities and differences between the army cutworm and some other noctuid species previously studied.

The army cutworm, Euxoa auxiliaris (Grote), is an important pest of field crops in the plains area of the United States and Canada. Considerable work has been done on various aspects of its life cycle and behavior both in the field and in the laboratory (e.g., Cooley 1910, 1916, 1917; Jacobson and Blackley 1959; Jacobson 1960, 1964; and Prusa 1964). These studies, and others, have added much to our understanding of the rather complex life cycle of this pest which migrates from the Great Plains to the mountains during the spring and then returns to the plains in the fall to lay eggs (Prusa 1967). Since very little has been reported on the reproductive systems of the army cutworm, this study was undertaken to supply the necessary basic information for a more detailed study of the reproductive cycle of wild female moths to be collected at several sites along their migration path from late spring to early fall.

Methods and Materials

The morphology of the internal reproductive system of the adult female army cutworm was studied in specimens obtained from the continuous laboratory rearing program at the USDA Northern Grain Insects Research Laboratory, Brookings, S.D. The specimens were received as pupae via the mail and placed in an environmental chamber operated at 22°C-23°C and 70-75% RH with a 12-h photophase. Adult moths were allowed to emerge in quarts-sized cardboard boxes with one end screened and were maintained in the chamber for as long as four weeks on the diet described by Sutter and Miller (1977). All specimens were dissected in physiological saline solution under a stereo-microscope using a method similar to Drews and Broedley (1967). Observations were made on newly-emerged (0-24 h) females and on those of oviposition age. Measurements of the internal organs were made on 0-24 h-old females. Illustrations were made using a scaled ocular grid.

Results and Discussion

The reproductive system of the female army cutworm is of the ditrysian type, having two separate openings: the ovum bursa which receives the oocytes during mating, and the ovispose through which the eggs pass during oviposition.

Bursa Copulatrix and Seminal Duct

The external opening of the bursa copulatrix is the ovum bursa located ventrally in the intersegmental membrane between the 7th and 8th abdominal segments (Fig. 1, 2). The ovum bursa opens into the short, heavily-muscled ductus bursae which extends anterior to join the corpus bursae. Near its junction with the corpus bursae, the ductus bursae has a small, lateral pouch-like structure of unknown function. Immediately inside the ovum bursae, the ductus bursae has dorsal and ventral triangular, sclerotized plates, the apices of which point anterior. The medial surface of the dorsal plate is concave projecting ventrally into the lumen of the duct. The posterior anal plate of the ventral plate are reflected upwards lateral to the margin of the dorsal plate. If viewed in cross-section, the 2 plates would appear somewhat U-shaped, the dorsal plate fitting inside the ventral plate. This arrangement effectively occludes (completely or partially) the ductus bursae during mating, when the aedeagus penetrates the ovum bursae and thrusts between the 2 sclerotized plates.

The corpus bursae is the most conspicuous part of the reproductive system except for the ovaries in females of oviposition age. It is commonly slightly constricted near its middle, and an external surface is covered by well-developed muscles. The corpus bursae lacks an internal signum present in some other noctuids (Callahan 1958, Callahan and Calpin 1960) and several other lepidopteran species.

The semitum duct (Fig. 1) arises from the dorsoposterior region of the corpus bursae. The duct tapers to the right over the common duct and then back to the left before it joins the left anterior region of the vagina immediately lateral-ventral to the point of attachment of the spermatotheca. The duct varies considerably in diameter, and in midden is larger than either the proximal or distal ends. The corpus bursae lacks a cervix bursae, a structure found in some other noctuids. Callahan (1958) found a constricted cervix bursae extending from the corpus bursae to the seminal duct in the cuer cutworm, Helicoverpa zea (Bod.-die). The structure is morphologically distinct from either of the two structures with which it is associated. Callahan and Chapin (1960) also reported a similar cervix bursae in two other noctuids, Peridroma saucia (Flowrey) and Peridroma saucia (Hübner). In these 3 species the oviposition endophallus of the male penetrates at least part way up the cervix bursae during copulation and deposits the tip of the spermatotheca collicum, with its aperture, near the junction of the cervix bursae with the seminal duct. The corpus of the spermatotheca is dense, the corpus bursae being the underlying vesica. When the body of the spermatotheca progresses through the cervix bursae, the opening of the bursa copulatrix is not blocked. If the spermatotheca is blocked, there is no opening through which the eggs pass during oviposition.