

THE PHYLOGENY AND EVOLUTIONARY BIOLOGY OF THE PIMPLINAE  
(HYMENOPTERA: ICHNEUMONIDAE)

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## ABSTRACT

7

The phylogeny and evolutionary biology of the Pimplinae are investigated using a cladistic compatibility method.

Cladistic methodology is reviewed in the introduction, and the advantages of using a compatibility method explained. Unweighted and weighted compatibility techniques are outlined.

The presently accepted classification of the Pimplinae is investigated by reference to the diagnostic characters used by earlier workers. The Pimplinae do not form a natural grouping using this character set. An additional 22 new characters are added to the data set for a further analysis. The results show that the Pimplinae (*sensu lato*) form four separate and unconnected lineages. It is recommended that the lineages each be given subfamily status. Other taxonomic changes at tribal level are suggested.

The host and host microhabitat relations of the Pimplinae (*sensu stricto*) are placed within the evolutionary framework of the analyses of morphological characters. The importance of a primitive association with hosts in decaying wood is stressed, and the various evolutionary pathways away from this microhabitat discussed.

The biology of the Rhyssinae is reviewed, especially with respect to mating behaviour and male reproductive strategies. The Rhyssinae (78 species) are analysed cladistically using 62 characters, but excluding characters thought to be connected with mating behaviour. Morphometric studies show that certain male gastral characters are associated with particular mating systems. These characters are used in a reanalysis of the data set, and indicate that one genus (*Megarhyssa*) appears to have evolved an extreme scramble competition system uniquely. The reanalysed results are used to recommend changes in the generic limits within the Rhyssinae. Explanations for the evolution of rhyssine mating systems are evaluated. The evolutionary biology and biogeography of the group is discussed.

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2

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# CONTENTS

|                                                              | Page |
|--------------------------------------------------------------|------|
| Abstract                                                     | 2    |
| Acknowledgments                                              | 3    |
| Contents                                                     | 4    |
| List of figures                                              | 9    |
| List of tables                                               | 15   |
| <br>                                                         |      |
| 1 Introduction and methods                                   | 19   |
| 1.1 Introduction                                             | 19   |
| 1.2 Choice of methods of phylogenetic reconstruction         | 21   |
| 1.2.1 Phenetics (numerical taxonomy)                         | 22   |
| 1.2.2 Evolutionary taxonomy                                  | 22   |
| 1.2.3 Cladistics                                             | 22   |
| 1.2.4 What can cladistics tell us?                           | 23   |
| 1.2.5 Methodology of cladistics - parsimony or compatibility | 24   |
| 1.2.6 Which method is suitable here?                         | 29   |
| 1.3 Definitions and assumptions                              | 32   |
| 1.4 Techniques of compatibility analysis                     | 33   |
| 1.4.1 LEQU/PROB\$ analyses                                   | 33   |
| 1.4.2 O'NOMOD analyses                                       | 36   |
| 1.4.3 Reintroducing incompatible characters                  | 39   |
| 1.5 Sources of homoplasy                                     | 40   |
| 1.6 Cladograms, trees and scenarios                          | 41   |
| <br>                                                         |      |
| 2 The Pimplinae: the present classification                  | 44   |
| 2.1 Introduction                                             | 44   |
| 2.2 Historical review                                        | 44   |
| 2.3 The Townes classification                                | 46   |
| 2.4 Testing the Townes classification                        | 48   |
| 2.4.1 Outgroups                                              | 48   |

|       |                                   |     |
|-------|-----------------------------------|-----|
| 2.4.2 | The holophyly of the Pimplinae    | 48  |
| 2.4.3 | The character states              | 50  |
| 2.5   | Results                           | 55  |
| 2.5.1 | Cladograms: initial output        | 55  |
| 2.5.2 | Trees: phylogenetic hypotheses    | 58  |
|       |                                   |     |
| 3     | The phylogeny of the Pimplinae    | 63  |
| 3.1   | Introduction                      | 63  |
| 3.2   | Head                              | 63  |
| 3.2.1 | Back of the head                  | 63  |
| 3.2.2 | Mouthparts                        | 65  |
| 3.2.3 | Antennal structure                | 65  |
| 3.3   | Thorax                            | 71  |
| 3.3.1 | Introduction                      | 71  |
| 3.3.2 | The prothorax                     | 71  |
| 3.3.3 | The mesothorax                    | 77  |
| 3.3.4 | Thoracic musculature              | 82  |
| 3.3.5 | Wings                             | 83  |
| 3.3.6 | Legs                              | 83  |
| 3.4   | Abdomen                           | 85  |
| 3.4.1 | Propodeal carination              | 85  |
| 3.4.2 | Attachment of gaster to propodeum | 85  |
| 3.4.3 | Gastral tergites                  | 85  |
| 3.5   | Ovipositor complex                | 86  |
| 3.5.1 | Tergite 9                         | 86  |
| 3.5.2 | Ovipositor                        | 88  |
| 3.5.3 | Gonostylus 9 (ovipositor sheath)  | 88  |
| 3.6   | Larval structures                 | 90  |
| 3.7   | Results                           | 91  |
| 3.7.1 | Cladograms: initial analyses      | 91  |
| 3.7.2 | Trees: phylogenetic hypotheses    | 93  |
| 3.7.3 | Subset analyses                   | 94  |
| 3.8   | The holophyletic groups           | 95  |
| 3.8.1 | The poemeniine group              | 95  |
| 3.8.2 | The Ephialtini                    | 98  |
| 3.8.3 | The Polysphinctini                | 100 |

|       |                                                               |     |
|-------|---------------------------------------------------------------|-----|
| 3.8.4 | The Pimplini                                                  | 102 |
| 3.9   | The relative positions of the groups                          | 105 |
| 4     | Evolutionary biology of the Pimplinae                         | 110 |
| 4.1   | Introduction                                                  | 110 |
| 4.2   | Node 1: (outgroups), the Poemeninae and Rhyssinae             | 119 |
| 4.2.1 | Microhabitat 1: Hard, dead wood                               | 119 |
| 4.2.2 | Microhabitat 2: aculeates in pre-existing workings            | 124 |
| 4.3   | Node 2: The Pimplinae ( <i>sensu stricto</i> )                | 125 |
| 4.4   | Node 3: The <i>Ephialtes</i> -group                           | 125 |
| 4.4.1 | Microhabitat 3: soft wood and bark                            | 125 |
| 4.4.2 | Microhabitat 4: soft non-woody plant tissue                   | 127 |
| 4.4.3 | Microhabitat 5: exposed or lightly concealed pupae            | 128 |
| 4.5   | Node 4: Polysphinctini and allies                             | 129 |
| 4.5.1 | Microhabitat 6: spider egg sacs                               | 129 |
| 4.6   | Node 5: the Polysphinctini                                    | 130 |
| 4.6.1 | Microhabitat 7: free-living spiders                           | 130 |
| 4.7   | Node 6: the Pimplini                                          | 132 |
| 4.7.1 | Microhabitat 8: Exposed or weakly concealed Lepidoptera pupae | 133 |
| 4.8   | General trends                                                | 135 |
| 4.8.1 | From concealed to exposed hosts                               | 136 |
| 4.8.2 | From concealed to very deeply concealed hosts                 | 137 |
| 4.8.3 | From newly fallen to rotting timber                           | 138 |
| 4.9   | Conclusions                                                   | 139 |
| 5     | The biology of the Rhyssinae                                  | 143 |
| 5.1   | Introduction                                                  | 143 |
| 5.2   | Distribution                                                  | 143 |
| 5.3   | Sexual dimorphism                                             | 144 |
| 5.4   | General adult behaviour                                       | 144 |

|        |                                                                              |     |
|--------|------------------------------------------------------------------------------|-----|
| 5.4.1  | Emergence timings                                                            | 146 |
| 5.4.2  | Meteorological effects on emergence                                          | 151 |
| 5.5    | Male reproductive behaviour                                                  | 152 |
| 5.5.1  | Male reproductive behaviour in <i>Rhyssa</i> and<br><i>Megarhyssa</i>        | 152 |
| 5.5.2  | Male reproductive behaviour in <i>Rhyssella</i>                              | 158 |
| 5.5.3  | Male reproductive behaviour in <i>Lytarmes</i>                               | 161 |
| 5.5.4  | Mating systems                                                               | 165 |
| 5.5.5  | Conclusions                                                                  | 166 |
| 5.6    | Host searching and oviposition behaviour                                     | 167 |
| 5.7    | Larval biology                                                               | 170 |
| 6      | The phylogeny of the Rhyssinae, and the<br>evolution of their mating systems | 171 |
| 6.1    | Historical review                                                            | 171 |
| 6.2    | The present classification                                                   | 171 |
| 6.3    | Outgroups                                                                    | 172 |
| 6.4    | The holophyly of the group                                                   | 172 |
| 6.5    | Material examined                                                            | 177 |
| 6.6    | Character states                                                             | 178 |
| 6.7    | Preliminary results                                                          | 185 |
| 6.7.1  | Cladograms: initial results                                                  | 186 |
| 6.7.2  | Trees: phylogenetic hypotheses                                               | 188 |
| 6.7.3  | The LEQUB/PROBS analysis                                                     | 189 |
| 6.7.4  | The O'NOMOD analysis                                                         | 189 |
| 6.7.5  | Subset analyses                                                              | 191 |
| 6.7.6  | Comments on the two trees                                                    | 193 |
| 6.8    | Male gasters and mating systems                                              | 195 |
| 6.8.1  | Mating strategies in the Rhyssinae                                           | 198 |
| 6.8.2  | Direct evidence                                                              | 200 |
| 6.8.3  | Indirect evidence                                                            | 201 |
| 6.9    | Is <i>Megarhyssa</i> a holophyletic group?                                   | 212 |
| 6.9.1  | Cladograms and trees                                                         | 213 |
| 6.9.2  | <i>Megarhyssa</i> : phylogenetic conclusions                                 | 218 |
| 6.10   | Phylogeny: overall conclusions                                               | 221 |
| 6.10.1 | Comments on the final tree                                                   | 225 |

|            |                                                             |     |
|------------|-------------------------------------------------------------|-----|
| 6.11       | Possible explanations for the distribution of gaster shapes | 230 |
| 6.11.1     | Size factors                                                | 230 |
| 6.11.2     | Intruder male numbers                                       | 230 |
| 6.11.3     | Mimicry complexes                                           | 234 |
| 6.11.4     | Phylogenetic constraints                                    | 235 |
| 6.12       | Alternative male strategies                                 | 237 |
| 6.13       | Evolutionary biology and biogeography of the Rhyssinae      | 240 |
| 6.13.1     | Present day distribution of holophyletic groups             | 240 |
| 6.14       | The evolution of the Rhyssinae: a speculative scenario      | 245 |
| 6.14.1     | Background                                                  | 245 |
| 6.14.2     | <i>Rhyssa</i>                                               | 248 |
| 6.14.3     | <i>Megarhyssa</i>                                           | 248 |
| 6.14.4     | <i>Lytarmes</i>                                             | 250 |
| 6.14.5     | <i>Epirhyssa</i>                                            | 250 |
| 6.14.6     | <i>Myllenyxis</i>                                           | 252 |
| 6.15       | General conclusions                                         | 252 |
|            | References                                                  | 254 |
| Appendix 1 | Pimpline OTUs                                               | 281 |
| Appendix 2 | Rhyssine OTUs                                               | 282 |
| Appendix 3 | Pimpline data set                                           | 284 |
| Appendix 4 | Rhyssine data set                                           | 286 |
| Appendix 5 | LEQUB initial run data                                      | 289 |
| Appendix 6 | Emergence timing data for <i>Rhyssella</i>                  | 293 |
| Appendix 7 | Gastral and forewing data                                   | 294 |

## LIST OF FIGURES

### CHAPTER 2

|                                                                       | Page |
|-----------------------------------------------------------------------|------|
| Fig 2.1. LEQU/PROB cladogram for the Townes data set.                 | 56   |
| Fig 2.2. O'NOMOD cladogram for the Townes data set.                   | 57   |
| Fig 2.3. Final combined hypothetical tree for the<br>Townes data set. | 61   |

### CHAPTER 3

|                                                                                                          |    |
|----------------------------------------------------------------------------------------------------------|----|
| Fig 3.1. Post genal region of <i>Dolichomitus imperator</i><br>showing partial fusion of postgena.       | 64 |
| Fig 3.2. Notch on post-occiput of <i>Dolichomitus</i><br><i>imperator</i> .                              | 64 |
| Fig 3.3. Foramen of <i>Neoxorides collaris</i> showing<br>expanded lateral hollow.                       | 66 |
| Fig 3.4. Smooth basiconic sensillum (type A) of<br><i>Liotryphon cydiae</i> .                            | 66 |
| Fig 3.5. Smooth basiconic sensillum (type B) of<br><i>Acrotaphus tibialis</i> .                          | 70 |
| Fig 3.6. Tip of apical segment of antenna of<br><i>Theronia lurida</i> showing projections.              | 70 |
| Fig 3.7. Tip of apical segment of antenna of <i>Pimpla</i><br><i>hypochondriaca</i> showing projections. | 72 |

|           |                                                                                                                                             |    |
|-----------|---------------------------------------------------------------------------------------------------------------------------------------------|----|
| Fig 3.8.  | High magnification view of <i>Pimpla hypochondriaca</i> antennal projections.                                                               | 72 |
| Fig 3.9.  | Tip of apical segment of <i>Itoplectis maculator</i> showing projections.                                                                   | 73 |
| Fig 3.10. | Penultimate antennal segment of antenna of <i>Neoxorides collaris</i> .                                                                     | 73 |
| Fig 3.11. | Apical segments of antenna of <i>Podoschistus scutellaris</i> .                                                                             | 75 |
| Fig 3.12. | Pronotum of <i>Neoxorides collaris</i> .                                                                                                    | 75 |
| Fig 3.13. | Posteriorly dipping pronotum and pronotal collar of <i>Afrephialtes cicatricosa</i> .                                                       | 76 |
| Fig 3.14. | Anteriorly dipping pronotum and pronotal collar of <i>Epirhyssa flavopictum</i> .                                                           | 76 |
| Fig 3.15. | Raised parascutal carina of <i>Pimpla hypochondriaca</i> .                                                                                  | 78 |
| Fig 3.16. | Propodeum of <i>Neoxorides collaris</i> , showing bowed pattern of the posterior transverse carina.                                         | 78 |
| Fig 3.17. | (a) Dorsal view of mesoscutum of <i>Pseudorhyssa sternata</i> . (b) Higher magnification view of mesoscutum showing punctate line.          | 79 |
| Fig 3.18. | (a) Dorsal view of mesoscutum of <i>Rhyssa persuasoria</i> . (b) Higher magnification view of mesoscutum showing absence of punctate lines. | 79 |

|                                                                                                                                                                   |     |
|-------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----|
| Fig 3.19. Forewing of <i>Dolichomitus imperator</i> .                                                                                                             | 84  |
| Fig 3.20. Forewing of <i>Rhyssella approximator</i> .                                                                                                             | 84  |
| Fig 3.21. Forewing of <i>Epirhyssa flavopictum</i> .                                                                                                              | 84  |
| Fig 3.22. Posterior gastral tergites of <i>Pseudorhyssa alpestris</i> female.                                                                                     | 87  |
| Fig 3.23. Posterior gastral tergites of <i>Rhyssella approximator</i> female.                                                                                     | 87  |
| Fig 3.24. Diagram of ovipositor complex of <i>Exeristes roborator</i> , showing phragmata on tergite 9.                                                           | 89  |
| Fig 3.25. Diagram of Gonostylus 9 (ovipositor sheath) of <i>Pimpla hypochondriaca</i> showing bulbous gonocoxostylar apodeme and the large gonocoxostylar muscle. | 89  |
| Fig 3.26. LEQU/PROB cladogram for the pimpline data set.                                                                                                          | 92  |
| Fig 3.27. Final hypothetical tree for the pimpline data set.                                                                                                      | 96  |
| Fig 3.28. Unanalysed hypothetical tree for the Polysphinctini.                                                                                                    | 103 |
| Fig 3.29. Unanalysed hypothetical tree for the Pimplini.                                                                                                          | 103 |
| Fig 3.30. Hypothetical tree showing possible phylogenetic relationships within the lower "pimpliformes" groups.                                                   | 108 |

## CHAPTER 4

- Fig 4.1. Host and microhabitat associations  
superimposed on the combined hypothetical  
tree for the pimpline data set. 111
- Fig 4.2. Diagram showing possible pathways of  
biological evolution at the base of the  
'pimpliformes' clade. 140
- Fig 4.3. Simplified scenario diagram for the  
biological evolution of the Pimplinae  
(*sensu stricto*). 142

## CHAPTER 5

- Fig 5.1. Plots of emergence times for male and  
female *Rhyssella approximator* specimens,  
1955-1957. 147
- Fig 5.2. Plots of emergence times for male and  
female *Rhyssella approximator* specimens,  
1958-1960. 148
- Fig 5.3. Line drawing of partially inserted male of  
*Megarhyssa praezellens*. 157
- Fig 5.4. Line drawing of fully inserted male of  
*Megarhyssa praezellens*. 157
- Fig 5.5. Male aggregation in *Rhyssella approximator*,  
prior to female emergence. 159
- Fig 5.6. Male aggregation in *Rhyssella approximator*,  
showing characteristic abdomen-bending  
behaviour. 159

|           |                                                                                                                                   |     |
|-----------|-----------------------------------------------------------------------------------------------------------------------------------|-----|
| Fig 5.7.  | Male insertion in <i>Rhyssella approximator</i> .                                                                                 | 160 |
| Fig 5.8.  | Loose male aggregation in <i>Lytarmes maculipennis</i> , prior to female emergence.                                               | 163 |
| Fig 5.9.  | Magnified view of large <i>Lytarmes maculipennis</i> male guarding emergence site.                                                | 163 |
| Fig 5.10. | Line drawing of guarding male of <i>Lytarmes maculipennis</i> , showing abdomen-bending behaviour close to female emergence hole. | 164 |

## CHAPTER 6

|          |                                                                                                                     |     |
|----------|---------------------------------------------------------------------------------------------------------------------|-----|
| Fig 6.1. | Tubercles on sternites 2-4 (ovipositor guides) of A. <i>Rhyssa persuasoria</i> ; B. <i>Rhyssella approximator</i> . | 174 |
| Fig 6.2. | Longitudinal carina on trochantellus of mid leg of <i>Rhyssella approximator</i> .                                  | 174 |
| Fig 6.3. | Pattern of radial hamuli on hindwing of <i>Rhyssa persuasoria</i> .                                                 | 175 |
| Fig 6.4. | Pattern of radial hamuli on hindwing of <i>Rhyssella approximator</i> .                                             | 175 |
| Fig 6.5. | Pattern of radial hamuli on hindwing of <i>Epirhyssa flavopictum</i> .                                              | 175 |
| Fig 6.6. | Front of head of <i>Megarhyssa emarginatoria</i> .                                                                  | 181 |
| Fig 6.7. | Mandibles of (a) <i>Triancyra scabra</i> ; (b) <i>Myllenyxis bernsteinii</i> .                                      | 181 |

- Fig 6.8. Epicnemium and epicnemial carina of  
(a) *Sychnostigma validum*; (b) *Sychnostigma flavopictum*; (c) *Cyrtorhyssa mesopyrrha*. 183
- Fig 6.9. LEQU/PROB cladogram for the rhyssine data set without male gastral characters. 187
- Fig 6.10. O'NOMOD cladogram for the rhyssine data set without gastral characters. 187
- Fig 6.11. LEQU/PROB hypothetical tree for the rhyssine data set without gastral characters. 190
- Fig 6.12. O'NOMOD hypothetical tree for the rhyssine data set without gastral characters. 192
- Fig 6.13. Final gastral segments of males of *Megarhyssa emarginatoria*. A. Small male (forewing length 10.5mm). B. Large male (forewing length 21.4mm). 196
- Fig 6.14. Dorsal view of gastral tergite 5 of *Rhyssella approximator*: (a) large male; (b) small male. 197
- Fig 6.15. High magnification view of gastral tergite 5 of *Rhyssella approximator*: (a) large male; (b) small male. 197
- Fig 6.16. Final gastral tergite of *Rhyssa* showing absence of strongly developed anal gland. 199
- Fig 6.17. Final gastral tergite of *Epirhyssa flavopictum* showing the strongly developed brush-like anal gland. 199

- Fig 6.18. Plots of male gastral tergite 5  
length:width. v. forewing length for: A.  
*Megarhyssa greenei*; B. *Megarhyssa macurus*;  
C. *Rhyssella approximator*. 202
- Fig 6.19. Plots of male gastral tergite 5  
length:width v. forewing length for: A.  
*Lytarmes maculipennis*; B. *Rhyssa*  
*persuasoria*; C. *Rhyssa amoena*. 203
- Fig 6.20. Plots of male gastral tergite 5 length:width  
v. forewing length for: A. *Rhyssa lineolata*  
B. *Rhyssella obliterator*; C. *Lytarmes fasciatus*. 206
- Fig 6.21. Plots of male gastral tergite 5  
length:width v. forewing length for: A.  
*Epirhyssa cruciatum*; B. *Megarhyssa*  
*emerginatoria*; C. *Epirhyssa flavopictum*. 207
- Fig 6.22. Plots of male gastral tergite 5  
length:width v. forewing length for: A.  
*Epirhyssa* sp.29; B. *Epirhyssa mexicana*; C.  
*Epirhyssa phoenix*. 208
- Fig 6.23. Plots of male gastral tergite 5  
length:width v. forewing length for: A.  
species with known mating systems; B. +  
species with unknown mating systems; C.  
+ species with fewer than 6 specimens  
available. 210
- Fig 6.24. Plots of male gastral tergite 5  
length:width v. forewing length for: A.  
*Megarhyssa* and *Rhyssella* species only; B.  
All species except *Megarhyssa* and  
*Rhyssella*. 211

|                                                                                                          |     |
|----------------------------------------------------------------------------------------------------------|-----|
| Fig 6.25. LEQU/PROB cladogram for the rhyssine data set with male gastral characters added.              | 214 |
| Fig 6.26. O'NOMOD cladogram for the rhyssine data set with male gastral characters added.                | 215 |
| Fig 6.27. LEQU/PROB hypothetical tree for the rhyssine data set with male gastral characters added.      | 217 |
| Fig 6.28. O'NOMOD hypothetical tree for the rhyssine data set with male gastral characters added.        | 220 |
| Fig 6.29. Final combined hypothetical tree for the rhyssine data set.                                    | 224 |
| Fig 6.30. Histogram of largest male gastral tergite 5 shape, for tropical and north temperate latitudes. | 233 |
| Fig 6.31. Distribution of <i>Rhyssa</i> .                                                                | 241 |
| Fig 6.32. Distribution of <i>Megarhyssa</i> .                                                            | 241 |
| Fig 6.33. Distribution of <i>Lytarmes</i> .                                                              | 243 |
| Fig 6.34. Distribution of <i>Epirhyssa</i> .                                                             | 243 |
| Fig 6.35. Distribution of <i>Myllenyxis</i> .                                                            | 244 |
| Fig 6.36. Simplified area cladogram (tree diagram) for the Rhyssinae.                                    | 248 |

## LIST OF TABLES

### CHAPTER 1

|                                                               | Page |
|---------------------------------------------------------------|------|
| Table 1.1 LEQUB single run analysis of an artificial data set | 34   |
| Table 1.2 LEQUB boil-down analysis of an artificial data set  | 36   |
| Table 1.3 O'NOMOD analysis of an artificial data set          | 38   |

### CHAPTER 2

|                                                                                      |    |
|--------------------------------------------------------------------------------------|----|
| Table 2.1 Nomenclatural problems in the Pimplinae                                    | 45 |
| Table 2.2 Present tribal status of study OTUs                                        | 47 |
| Table 2.3 Summary of differences between analysis results and present classification | 60 |

### CHAPTER 3

|                                                                           |     |
|---------------------------------------------------------------------------|-----|
| Table 3.1 Distribution of smooth basiconic sensilla amongst the Pimplinae | 69  |
| Table 3.2 Summary of proposed taxonomic changes amongst the Pimplinae     | 109 |

### CHAPTER 4

|                                                                        |     |
|------------------------------------------------------------------------|-----|
| Table 4.1 Host preference summaries                                    | 112 |
| Table 4.2 Adaptive character suite in deep wood associated parasitoids | 120 |

## CHAPTER 5

|           |                                                                                    |     |
|-----------|------------------------------------------------------------------------------------|-----|
| Table 5.1 | Numbers of rhyssine species in each biogeographical region                         | 145 |
| Table 5.2 | Median tests for earlier male emergence of <i>Rhyssella approximator</i> , 1955-60 | 149 |
| Table 5.3 | Sex ratio of emergences of <i>Rhyssella approximator</i> , 1955-60                 | 149 |

## CHAPTER 6

|           |                                                                 |     |
|-----------|-----------------------------------------------------------------|-----|
| Table 6.1 | Defining characters of the presently recognised rhyssine genera | 176 |
| Table 6.2 | Summary of initial results                                      | 188 |
| Table 6.3 | Summary of known male mating systems in the Rhyssinae           | 200 |
| Table 6.4 | Correlations for species with known mating systems              | 204 |
| Table 6.5 | Correlations for species with unknown mating systems            | 205 |

### 1.1 Introduction

This project looks in some detail at a subfamily of ichneumonids, the Pimplinae, and constructs phylogenetic hypotheses about them. From these phylogenetic hypotheses ideas about the evolution of the group's biology are developed. The work is intended to straddle phylogenetics, taxonomy and biology. Several workers have stressed that one of the main aims of comparative biology should be to explore the evolutionary history of biological traits across groups of related organisms (see, Simpson, 1944, Tinbergen, 1963; Gould & Lewontin, 1979; Clutton-Brock & Harvey, 1984; Ridley, 1983; for example). That aim is pursued here, both in terms of mating behaviour and of host-related biology (Gauld, 1988).

Very little is known about the phylogenetic relationships within the Ichneumonidae. Only recently have limited parts of the family been investigated cladistically (Gauld, 1983, 1985, 1987a; Wahl, 1984, in press). As the Pimplinae is considered to be a rather primitive subfamily (Gauld, 1984b) investigation of its phylogeny has given some insights into the early evolution of the family as a whole. Several taxonomic changes are also recommended in the light of the phylogenetic analyses.

Members of the subfamily have very varied biologies, especially with respect to how they deal with their hosts. Some genera of pimplines are ectoparasitoids of deeply concealed beetle hosts; some are endoparasitoids of exposed Lepidoptera pupae; and some are even koinobiont parasitoids (that is they paralyse the host only temporarily) of mature spiders (Gauld, 1984b; Fitton *et al*, 1988). This wide spectrum of host associations within one apparent lineage makes investigations of how these associations may have developed, in an evolutionary sense, of special interest. Gauld (1988) has pointed out that an evolutionary pathway can be discerned from one host to

another, and the work here will investigate if this is a phylogenetic pathway.

Early on in the work it was discovered that the genera within the Pimplinae could not easily be fitted into any evolutionary scheme which postulated that they were holophyletic. For this reason the work has been split into two sections. The first deals with the phylogenetic relationships within the pimelines as presently recognised (chapters 2 and 3), and the evolution of the host-preferences of a more limited demonstrably holophyletic group (chapter 4). The second explores in some detail the phylogeny and biology of a group which is shown to be paraphyletic with respect to the rest of the pimelines, the Rhyssini (chapters 5 and 6). In both cases a detailed cladistic analysis (using a compatibility method) forms the framework for the consideration of biological evolution. A secondary aim of the project is to see how far biological characters can be used to make phylogenetic hypotheses in themselves. This applies especially to male gastral characters associated with male mating systems in the rhyssine analysis (chapter 6).

The second group of ichneumonids considered here, the Rhyssini, have been the focus of a great deal of study because several of the Holarctic genera have been used in biological control programmes (for references, see section 5.1). This has meant that the biology of a number of the species is very well known. This, again, means that biological patterns can be compared with phylogenetic ones, and possible evolutionary pathways for biological evolution can be postulated.

One particular area of biological interest has been rhyssine male mating systems. Individuals of this group develop on hosts deep beneath the surface of fallen logs. When they have fully developed they must chew their way up to the surface, and because of this, males congregate at female emergence sites (Thornhill & Alcock, 1983) in order to mate with them. Not all rhyssines show the same behavioural adaptations for maximising the number of females they copulate with. Some guard the spot where the female is emerging,

2

while others have extremely long gasters which they insert into the hole the female makes as she chews her way to the surface. These copulate with her *before* she has emerged. The phylogenetic analysis enables the observed patterns of rhyssine mating systems to be placed in a framework, and the possible evolutionary explanations for the differences in mating system are explored.

The idea for this PhD project arose originally from the preliminary preparations for a Royal Entomological Handbook on pimpline ichneumon-flies (Fitton, Shaw & Gauld, 1988). During the work undertaken for that volume it was discovered that a wealth of new biological information existed for the group. This, it was felt, could profitably be placed in an evolutionary framework, in a way that would not be suitable in a handbook.

## 1.2 Choice of methods of phylogenetic reconstruction

Given the nature of the project it is important to choose a method of phylogenetic reconstruction which allows of easy comparison of biology and phylogeny. The methods are discussed below as well as the rationale for using them. This is not intended to be a comprehensive review of contemporary cladistic methodology. Excellent reviews exist on this topic (Wiley, 1981; Ridley, 1986; Felsenstein, 1982), summarising the vast body of literature on the subject.

To make evolutionary sense of biological (i.e. non morphological) data it is necessary to have hypotheses about phylogenetic relationships between groups. The number of ways to construct these hypotheses have multiplied, making it harder and harder to justify using one rather than another. The methods used here have been chosen for fairly pragmatic reasons, but it seems worth discussing the alternatives in a little detail to show the theoretical basis underlying them. For simplicity's sake the main evolutionary methodologies have been split into two: evolutionary taxonomy and cladistics and one non-evolutionary methodology, phenetics, will be mentioned briefly.

### 1.2.1. Phenetics (numerical taxonomy)

A method developed by Sneath & Sokal (1973) which relies on comparing characters to give an index of overall similarity. As many characters are used as possible and these characters are usually neither weighted nor assigned polarity. This leads to a non-evolutionary classification of the taxa involved. For the purposes of this work the approach has few attractions as phylogenetically meaningful characters are likely to be swamped by highly homoplastic ones.

### 1.2.2. Evolutionary Taxonomy

A method whose best known adherents are Mayr (1942, 1963, 1969) and Simpson (1944, 1953, 1961). This involves intuitive judgments based on systematic experience. In the hands of an experienced taxonomist this may turn out to be the best option. However, its methodology is not explicit and some of the 'intuitive' aspects are not easily transferable from one group to another.

### 1.2.3. Cladistics.

Hennig (1950, 1979) began the growth industry which is now referred to as cladistics or phylogenetic systematics. His original ideas were simple and quite elegant, even if they were couched in rather opaque language. He suggested that characters acquired at speciation (cladogenetic characters) could be used as markers indicating common descent. If these characters could be identified then the evolutionary history (phylogeny) of groups could be reconstructed. From these beginnings came a rich but at times confusing vocabulary, which led to disagreements which often seem more semantic than real. However, cladistics as originally formulated by Hennig has great advantages over the two previously mentioned methodologies.

2

The first is that it explicitly excludes groups that do not consist of a taxon and *all its descendants*. These groups are called **paraphyletic** by Hennig (1950). The classic example is the group 'reptiles' which is a paraphyletic group because it excludes the groups 'mammals' and 'birds' (if you put all three together, however, you do get a cladisitically acceptable group - 'the amniotes'). Groups that contain a taxon and all its descendants Hennig called monophyletic, but are called **holophyletic** here (Ashlock 1971). This is due to an ambiguity of meaning. Hennig (1950) used the word in the restricted sense as explained above, but earlier workers had used it to mean any group which was evolutionarily related, even if all the descendants were not included (Mayr, 1963, for example) . However, for the purposes of this thesis, Hennig's ideas enable evolutionarily meaningful groups to be delineated, and so the evolutionary history of biological characters to be investigated. The difference between the evolutionary taxonomic and cladistic approach can clearly be seen.

The second, and more mixed, blessing that came from Hennig is that algorithms could be devised to analyse data containing potential phylogenetic information. This has meant that a number of methodologies have been devised to cope with phylogenetic data. These methods can broadly be described as **parsimony** and **compatibility** (Felsenstein, 1982), and are discussed in some detail below.

Cladistics gives an explicit methodology for constructing hypotheses about evolutionary relationships which is repeatable and can be used to look at biological patterns. It would seem therefore to be the most suitable approach for this work, although there is still a lot of uncertainty about what a cladistic analysis actually produces - a true evolutionary history or just a convenient ordering of sense data?

#### 1.2.4. What can cladistics tell us?

Originally, cladistics concentrated upon cladogenesis and aimed to find

the true branching pattern of speciation events. Since then it has been realised that is an impractical goal. A diagram obtained by a cladistic analysis does necessarily show the true relationships of taxa. This led to a distinction between **cladograms** - patterns of shared similarities thought to be evolutionary novelties (synapomorphies); **trees** - the evolutionary history of a group; and **scenarios** - descriptions of the evolution of a group including other data such as ecology and adaptation (Tattersall & Eldredge 1978; Eldredge 1979).

This conception of a cladogram has led many cladists to the point where they are no longer interested in the topology of speciation events (trees) but only in the pattern of synapomorphies (Platnick, 1980; Panchen 1982). This does not imply that these cladists are uninterested in evolution, merely that they are no longer looking for markers of speciation events, and now allow a greater role for anagenetic processes. At the extreme end of this tendency, however, the **pattern cladists** see their constructed dendrograms as nested sets of specialised characters within generalised ones, with no *necessary* evolutionary significance. One leading exponent of this school (Patterson 1980) says "cladistics is not necessarily about evolution... It is about a simpler and more basic matter, the pattern in nature".

It is accepted that the diagrams that have been produced in the analyses are not trees, but asserted that they can be used to construct plausible hypotheses about trees. These ideas are discussed in more detail in section 1.6.

#### 1.2.5. Methodology of cladistics - parsimony or compatibility?

Two main methodologies have arisen for the construction of hypotheses of evolutionary relationships. They may broadly be termed **compatibility** and **parsimony**.

Compatibility methods were first suggested by Wilson (1965) and by

8

Le Quesne (1969). The methods rely on simple logic. Consider the distribution of two two-state characters in a given group of taxa. If all four possible combinations of the characters occur in any four taxa then one of the characters cannot have been derived uniquely. There must be either a reversal or parallelism between the two characters and there is some degree of homoplasy in the data set. By comparing each character against every other, it is then possible to identify highly homoplastic characters (by how many times they are 'marked' as incompatible according to the above method) and remove them one by one until a clique (Estabrook *et al* 1977) of characters is obtained with no homoplasy.

Additionally, if all the states are present except the double-plesiomorphic one (this still refers to the four-taxa situation above), then a polar incompatibility arises. Here the incompatibility can be resolved by reversing the polarity of the characters, turning the double-apomorphic state into the double-plesiomorphic. When a clique has been produced polar incompatible characters can be dealt with in this fashion (Gauld & Underwood, 1986).

Compatibility methods try to minimise the effect of homoplasy in the data set by removing characters which are incompatible with a core of other characters, which, in their turn, are assumed to be reasonable indicators of evolutionary relationship. Parsimony methods, on the other hand, assume that evolution has taken the least number of steps to derive the observed character set. That is to say that algorithms are used that minimise the number of character state changes in each lineage (Gaffney, 1979; Nelson, 1979, among many).

These methods have their strong supporters and critics, and there has been much discussion, especially within the pages of *Systematic Zoology*, as to which is best to use, in theory. The arguments for and against each method will be discussed and it is explained why a compatibility method is used in this work.

It is perhaps not an exaggeration to say that 90% of all cladistic analyses use some sort of a parsimony approach. Because this is the

case, voices have been raised most strongly for and against this method. In comparison, the attacks on compatibility methods have been relatively muted. They concentrate most strongly on the fact that a compatible clique will often contain only a small fraction of the original character set used in the analysis. This means that there is an appreciable loss of information from homoplastic characters outside the clique (Farris, 1979; Hill, 1975). However methods exist for reintroducing rejected characters into the clique by postulating reversals or parallelisms in them. In addition characters can be reintroduced into the analysis as subsets (Estabrook, 1978, Estabrook & Anderson, 1978; see below).

Parsimony methods have suffered a more concerted series of attacks over the years. The first is a philosophical point related to the scientific status of the methodology. Cladists have long claimed that parsimony methods can be considered *Hypothetico-deductive sensu Popper*). The essence of this idea is that a properly framed scientific hypothesis should be falsifiable by another hypothesis that explains more of the observed states and patterns of a phenomenon. In parsimony cladistics the hypotheses are cladograms and the best hypothesis is assumed to be the cladogram with the smallest number of character transformations. However, parsimonists treat their analyses as a succession of three-taxon problems at every branch of a cladogram. This involves examining each of these problems in turn and identifying which of the three possible arrangements of the taxa is "falsified the fewest number of times" (Gaffney, 1979). This leads to a step with the fewest number of transformations, and, hopefully, a cladogram with the fewest character-state changes. The problem which then arises is that a hypothesis which may already have had many of its branches "falsified", is then tested to see if it is "falsifiable". Panchen (1982) argues persuasively that this is not the hypothetico-deductive method in its Popperian sense. This may seem a rather arid point to make, but in fact it is quite important given some parsimonist's attitude to their approach. They have often claimed a scientific authority which may in the light of the above conclusions, turn out to be questionable (Panchen, op cit).

2

A less esoteric line of argument relates to the sort of evolutionary processes that parsimony analyses assume are occurring. Underwood (1982) and Gauld & Underwood (1986) point out that orthodox parsimony methods assume that markers will appear at speciation and label this event, presumably in the newly arising species. Tracing the pattern of these characters will give the history of speciation events for this group. The implication is that evolution minimises the amount of anagenesis ( modifications occurring in a single line without speciation). This is considered by many authors to be an unreasonable assumption (Gauld & Underwood 1986: "Parsimony analysis.... appears to assume that the best estimate of phylogeny is one which maximises the descent and minimises the modification. In the absence of evidence to support it this is a gratuitous assumption which is better avoided if possible").

Parsimony methods presumably work well for groups where levels of homoplasy are low - when, broadly speaking, homoplasy can be equated with anagenetic processes. However, reversal and parallelisms that remain undetected and arise from post-speciation events inevitably will add a significant amount of noise to the analysis. It seems then, in the absence of fixed, uniplastic markers of cladogenesis, that the search for the pattern of speciation within a group is unprofitable. The practical result of this seems to be (Gauld, 1985) that a parsimony method means that "a large set of coincidental 'bad' characters will be favoured at the expense of even a very slightly smaller set of 'good' characters". In the Ophioninae data set which Gauld studied this often meant that taxa were grouped together by characters that would be considered by classical taxonomists to be 'bad'. Wiley (1975) defends the parsimony approach against such arguments by saying that a cladogram which implies the least parallel and convergent evolution and the fewest reversal is most applicable " not because nature is parsimonious, but because only parsimonious hypotheses can be defended by the investigator without resorting to authoritarianism or apriorism".

Some workers have pointed out that there are number of almost

equally parsimonious cladograms that can be produced from the same data set (Strauch, 1984), and that the position of taxa in a cladogram can be dependent upon the order in which the taxa are fed into the analysis (Gauld, 1985). Indeed it is not possible to predict, for large data sets, the actual minimum tree length (Felsenstein, 1982; Day, 1983) since the number of trees becomes larger than Avogadro's number at around 20 taxa, and it is therefore computationally impracticable to produce all trees and then choose the most parsimonious. Some methods however do exist that will produce the most parsimonious tree in cases with small data sets (see Felsenstein, 1982). However, as is discussed later, the discovery of the largest clique in a data set can be burdened with the same kind of difficulties.

More recently, workers have tried to look for the occasions where either method might be applicable. This has involved a statistical approach related to maximum likelihood methods. Felsenstein (1981): "...unequal weights are a corollary of unequal rates of evolution of different characters. When rates of evolution are very low... the weights become more equal, leading in the extreme to the support for unweighted parsimony methods. When rates of evolution are known to be very unequal, the use of compatibility methods is supported provided that we do not know in advance which characters have the high rates of evolution." Parsimony and compatibility methods only work where there are low overall rates of evolution, Felsenstein (1978) has shown that at high rates of evolution neither method will produce the correct phylogeny even if an infinite number of characters are employed. He points out that the problem becomes especially acute if rates of evolution in different lineages are very unequal.

Finally, Day & Sankoff (1986) have shown that "... computationally ... efficient algorithms cannot be designed to obtain globally optimal solutions for important compatibility problems". They are NP-complete (Felsenstein, 1982), meaning that they are in a class of computational problems which are known to have no efficient algorithm to solve them. The same has been proven to be true of compatibility methods (Day 1983). Practically, this means that any

parsimony or compatibility methods rely on locally optimal solutions, and can therefore never be considered totally reliable. It is always possible that there is a statistically less likely clique or a more parsimonious cladogram than that revealed by contemporary methods.

#### 1.2.6. Which method is suitable here?

The major question to ask here relates to what we know about the rates of evolution in ichneumonids and other Hymenoptera. To summarise Felsenstein (1982) the following conditions apply:

1. Rates of evolution are uniformly high across all characters in the data set. Neither method is applicable.

2. Rates of evolution are low across all characters in the data set.

- A. Rates of evolution are low and uniformly spread across the data set. An unweighted parsimony method is applicable.

- B. Rates of evolution are low but unevenly scattered across the characters in a way not predictable before the analysis. A compatibility method is applicable.

So what do we know about overall rates of evolution and the scatter of individual rates of evolution in ichneumonids? The major studies which examine ichneumonids using a method giving some objective idea about levels of homoplasy (Gauld & Underwood 1986) are Gauld (1983; 1985) on the subfamilies Labeninae and Ophioninae respectively. In both studies the 'observed:expected LeQuesne test failures' (see below) were used as a relative measure of homoplasy. In the labenine study the failure rates varied from between 0.00 and 0.97; in the

7

ophionine study the failure rates were from 0.00 to 1.25. Values close to 0 indicate characters with low relative homoplasy. In both cases some characters were clearly very highly homoplastic, while others were of low homoplasy. In both cases the scatter of homoplasy is very great which suggests that a compatibility method would be more appropriate. The same sorts of patterns of homoplasy are found in the data sets used here (chapters 2, 3 and 6). However, there are three problems associated with accepting this evidence as an endorsement for a simple compatibility approach.

First, Felsenstein (1982) gives no clue as to the sorts of scatter of homoplasy which should lead to the adoption of either method. The levels of homoplasy in ichneumonid data sets is undoubtedly high in comparison with other groups (Strauch's data set for Alcidae which has an overall ratio of 0.19 and a scatter from between 0.00 and 0.8, for example; Gauld & Underwood, 1986) but there is no way of telling whether these other groups have intrinsically low scatters or just relatively low scatters.

Second, leading on from the first point; are the levels of overall homoplasy so high that neither method is appropriate? Ophionines have an overall randomness ratio of 0.83 and pimelines an overall ratio of 0.76. Even accepting the problem discussed above this is still enormously higher than the Alcidae data ratio (0.16) mentioned above. It does not seem to be the case that a few homoplastic characters account for the bulk of the ratio either; there are a significant number of characters with medium levels of homoplasy. This is all very unfortunate, and must point to the possibility that homoplasy levels are too high in ichneumonids for the true cladogram to be found. However, no method seems to exist to tell either way.

Third, it could be argued that the sources of homoplasy are clear in ichneumonid data sets: the large number of loss characters which are employed. If this were the case then these could be removed beforehand and an unweighted parsimony method undertaken on the remaining character set. The problem with this approach is that a very high proportion of characters in ichneumonid data sets are loss characters. For example,

7

in the ophionine data set 24 out 89 characters are loss characters. This situation means that it is very difficult to construct cladograms without using loss characters and so it is usually not possible to remove them beforehand. The alternative to this might be to run the characters through a Lequesne test programme before hand and then take out the worst. It is not clear whether this would (1) be any different from the normal compatibility method; (2) statistically valid (due to data dredging; Selvin & Stuart, 1966).

The conclusion to the above discussion must be that if any method is appropriate in this case then it is a compatibility method. In addition, as pointed out by Le Quesne, (1982) "compatibility methods... are close to the implicit, sometimes subconscious, judgments long made by taxonomists when assessing relationships... Classical taxonomists tend to think in terms of 'stable' and 'unstable' characters, and hope to find some in the former category that are good indicators of the history of the group." In data sets where there is a high degree of homoplasy, methods that allow the identification of 'unstable' characters must represent the most reasonable procedure.

The other major reason why a compatibility method is chosen here is because it gives a measure of how compatible character states (of any kind, whether biological or morphological) are with each other. This means that it is possible to conjecture how many times a certain feature may have evolved in a given group, by explaining where parallelisms or reversals may have occurred. This is especially important in chapter 6, where the evolution of structures related to male mating systems are discussed, and the male mating system structures turn out to be more compatible with the overall character set than the characters which imply that they have evolved a number of times in separate lineages. Here, the compatibility method shows more clearly actual pattern of incompatibilities than would a parsimony method. This ability to judge the evolutionary significance of one character against another, in the context of a large character set, is perhaps the most useful feature of a compatibility analysis, and the one that makes its use essential here.

### 1.3. Definitions and assumptions made in this study

Throughout this work the terms holophyletic, paraphyletic and polyphyletic are used in the sense of Ashlock (1971). Holophyletic has been used rather than 'monophyletic' in order to reduce confusion. Homoplasy includes all instances of (1) convergence - species evolving similar structures along different phyletic lines; (2) parallelism - closely related species evolving similar structures due to similar selective pressures, but not due to a single evolutionary acquisition in a shared ancestor; (3) reduction - lack of a character due to a double apomorphy indistinguishable from the plesiomorphic state. The three are not distinguishable by direct phylogenetic analysis. The randomness ratio indicates the relative levels of all three in any given data set. Only by looking at the patterns of incompatibility between characters can the probable nature of the homoplasy be ascertained.

Polarity determination is as much as possible by outgroup comparison. The criteria of ingroup comparison, morphological specialisation, ecological specialisation and geographical restriction were not allowed or used, except in some restricted cases where the outgroups have a confusing distribution of character states. Here, ingroup comparison was reluctantly employed. Paraphyletic groups have been identified whenever possible as the outgroups for the reasons outlined by Underwood (1982); a sister-group outgroup may show a derived state of a presumed plesiomorphic condition and thus prove confusing. The choice of outgroups is discussed for each individual analysis.

The characters chosen were, by and large, those of morphology of adult and larval specimens. Characters which provide circumstantial evidence for evolutionary patterns - such as geographical distribution, ecology, biology and the fossil record - were not used in the initial analyses. Such data were admitted after the analyses were completed, however, when the intention was to examine the evolution of characters - in this case predominantly biological characters.

There was no *a priori* character weighting. Hecht & Edwards (1977) suggest a character weighting scheme, this has been modified by Underwood (1982) and has been referred to in the text occasionally. However, as suggested by Gauld & Underwood (1986), it has proved necessary to occasionally discount the result of an analysis for biologically plausible reasons. For example, if a grouping is supported by several characters which seem biologically to be rather unlikely then another 'outvoted' but biologically more likely character might be chosen. This is, of course, a form of intuitive character weighting, and in some respects can also be seen as a compromise between cladistics and evolutionary taxonomy.

#### 1.4. Techniques of compatibility analysis

The methods used in this thesis are based on those of Underwood (1982) and Gauld & Underwood (1985). In addition several new computer programs were designed by Underwood (pers comm). The following programs were used during the thesis - LEQUA; LEQUB; LEQUC; PROBS; and O'NOMOD. All these programs were run on either an ACT Apricot or BBC Master personal computer. Throughout this discussion the tables and figures are for an artificial data set devised by Underwood (pers comm).

##### 1.4.1. LEQU/PROBS analyses

The LEQU programs are those outlined in Gauld (1985) and Gauld & Underwood (1986). The LEQUA program simply prints out the raw data in an easily digestible form (appendix 3 and 4).

The LEQUB program computes the number of polar and non-polar incompatibilities for each character across the taxa. The ratio of observed incompatibility failures to expected incompatibility failures is then calculated to give the *randomness ratio*. In addition the randomness ratio of the whole data set is calculated. The PROBS program is a faster running version of LEQUB, which does not indicate the number of polar incompatibilities.

Table 1.1. LEQUB single run analysis of artificial data set

| Taxa analysed: 1 2 3 4 5 6 7 8 9 10 11 12 |     |     |   |   |   |   |   |   |     |     |   |   |    |    |    |    |    |    |
|-------------------------------------------|-----|-----|---|---|---|---|---|---|-----|-----|---|---|----|----|----|----|----|----|
|                                           | 1.1 | 1.2 | 2 | 3 | 4 | 5 | 6 | 7 | 7.1 | 7.2 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 |
| 16                                        | -   | -   | - | - | - | - | - | - | -   | X   | - | - | -  | -  | -  | -  | -  | -  |
| 15                                        | -   | -   | - | - | - | - | - | - | -   | -   | - | X | -  | -  | -  | -  | -  | -  |
| 14                                        | -   | -   | - | - | - | - | - | X | X   | X   | X | - | X  | -  | -  | -  | -  | -  |
| 13                                        | -   | X   | X | X | - | X | - | X | X   | X   | X | X | X  | X  | X  |    |    |    |
| 12                                        | -   | -   | X | X | - | - | - | X | X   | X   | X | X | X  | X  |    |    |    |    |
| 11                                        | X   | -   | X | - | : | : | X | - | X   | -   | X | - |    |    |    |    |    |    |
| 10                                        | -   | -   | : | X | : | : | - | - | -   | -   | X |   |    |    |    |    |    |    |
| 9                                         | X   | X   | X | X | - | X | X | X | X   | X   |   |   |    |    |    |    |    |    |
| 8                                         | X   | -   | X | - | : | : | X | - | X   |     |   |   |    |    |    |    |    |    |
| 7.2                                       | -   | X   | X | X | - | X | - |   |     |     |   |   |    |    |    |    |    |    |
| 7.1                                       | -   | -   | X | X | : | : | - |   |     |     |   |   |    |    |    |    |    |    |
| 6                                         | -   | -   | - | X | - | - |   |   |     |     |   |   |    |    |    |    |    |    |
| 5                                         | -   | -   | - | : | - |   |   |   |     |     |   |   |    |    |    |    |    |    |
| 4                                         | -   | :   | - | : |   |   |   |   |     |     |   |   |    |    |    |    |    |    |
| 3                                         | X   | -   | X |   |   |   |   |   |     |     |   |   |    |    |    |    |    |    |
| 2                                         | -   | -   |   |   |   |   |   |   |     |     |   |   |    |    |    |    |    |    |
| 1.2                                       |     |     |   |   |   |   |   |   |     |     |   |   |    |    |    |    |    |    |

LeQuesne's coefficient of character state randomness =  
ratio x 100%. Taxa analysed: 1 2 3 4 5 6 7 8 9 10 11 12

TEST DATA 20.5.88

Incompatibilities: observed expected ratio - polar

|     |   |    |       |      |   |   |     |   |   |       |      |   |   |
|-----|---|----|-------|------|---|---|-----|---|---|-------|------|---|---|
| 1.1 | : | 4  | 11    | 0.36 | - | 0 | 1.2 | : | 3 | 5.88  | 0.51 | - | 1 |
| 2   | : | 8  | 9.59  | 0.83 | - | 1 | 3   | : | 9 | 9.93  | 0.91 | - | 2 |
| 4   | : | 0  | -     | -    | - | 6 | 5   | : | 3 | 6.41  | 0.47 | - | 5 |
| 6   | : | 4  | 11.53 | 0.35 | - | 0 | 7.1 | : | 6 | 8.94  | 0.67 | - | 2 |
| 7.2 | : | 11 | 11.1  | 0.99 | - | 0 | 8   | : | 8 | 11.84 | 0.68 | - | 2 |
| 9   | : | 14 | 12.62 | 1.11 | - | 0 | 10  | : | 5 | 6.71  | 0.74 | - | 3 |
| 11  | : | 7  | 10.97 | 0.64 | - | 2 | 12  | : | 9 | 9.59  | 0.94 | - | 0 |
| 13  | : | 11 | 11.53 | 0.95 | - | 0 | 14  | : | 4 | 8.65  | 0.46 | - | 0 |
| 15  | : | 1  | 0.54  | 1.86 | - | 0 | 16  | : | 1 | 6.71  | 0.15 | - | 0 |

Grand total - 54 76.78 0.7

Ranking ratios

|    |    |   |     |    |     |     |    |     |   |
|----|----|---|-----|----|-----|-----|----|-----|---|
| 4  | 16 | 6 | 1.1 | 14 | 5   | 1.2 | 11 | 7.1 | 8 |
| 10 | 2  | 3 | 12  | 13 | 7.2 | 9   | 15 |     |   |

The pattern of incompatibilities is printed out as shown in table 1.1, for a demonstration set of data. An 'X' indicates a non-polar incompatibility; a ':' a polar incompatibility; and a '-' no incompatibility. For example, character 16 has a non-polar incompatibility with respect to character 7.2, while 10 and 2 share a polar incompatibility. The overall scores for the characters are also presented. Each character is shown with its observed number of non-polar failures; expected number of non-polar failures; ratio of the two; and finally number of polar failures. For instance character 1.1 reads 1.1: 4 11 0.36 - 0, indicating that there are 4 non-polar failures against an expected number of 11, which gives a randomness ratio of 0.36; also there are 0 polar incompatibilities. The 'grand total' figures indicates the overall observed non-polar failures (54); the expected (76.78) and the randomness ratio for the whole set (0.7, which is fairly high). Finally the characters are given in order of their randomness ratios character 4 being the best and character 15 the worst.

The LEQUB program can then be used to boil down the data. The character with the worst randomness ratio is removed and the data are reanalysed. After this reanalysis the next worse character is removed, and this process continues until there are no non-polar

incompatibilities remaining. (Note: there may still be polar incompatibilities in the data set). The characters which then remain form the compatible clique. This process is shown in table 1.2.

The first character removed is 15 which reduces the number of non-polar incompatibilities from 54 to 53, the next is character 9 which reduces the number from 53 to 40, and so on. The final clique was obtained by removing character 6 which reduced the number of non-polar incompatibilities from 2 to 0.

Table 1.2. LEQUB boil down analysis of an artificial data set

| total | expected | ratio | character<br>removed |
|-------|----------|-------|----------------------|
| 54    | 76.78    | 0.7   | 15                   |
| 53    | 76.24    | 0.7   | 9                    |
| 40    | 64.15    | 0.62  | 7.2                  |
| 30    | 54.04    | 0.56  | 13                   |
| 21    | 44.33    | 0.47  | 12                   |
| 15    | 37.17    | 0.4   | 3                    |
| 10    | 30.25    | 0.33  | 14                   |
| 7     | 25.38    | 0.28  | 2                    |
| 4     | 20.02    | 0.2   | 1.1                  |
| 2     | 14.77    | 0.14  | 6                    |
| 0     | 9.96     | 0     |                      |

Once the compatible clique is obtained a cladogram can be drawn from it. If there are any polar incompatibilities, character polarities can be reversed easily using the LEQUB program. The LEQUC program labels taxa instead of characters. In this way OTUs which have a disproportionate contribution to the overall randomness ratio can be identified. This can often be useful as the offending OTU can be removed, and plausible reasons can be devised as to why it should be so frequently labelled. In fact, this program very rarely gave any interesting results for the data sets presented here. In addition, the removal of highly marked taxa must be considered methodologically rather difficult to justify.

#### 1.4.2. The O'NOMOD analyses

The O'NOLAN program gives a probability weighted analysis. The algorithm for this method was developed by O'Nolan (unpublished manuscript; Moody & O'Nolan, 1987). This method relies on the

2

weighting of characters according to how compatible they are with other characters. The algorithm is given below:

- (a) All characters are assigned a weight of one.
- (b) A character compatibility matrix is constructed.
- (c) The number of compatibilities are counted for each character.
- (d) A new matrix is constructed, new pairwise compatibility tests are made:
  - (i) if character A is compatible with character B, then their compatibility scores are added together.
  - (ii) if character A is incompatible with character B, then (B's compatibility total X the weight of B). are subtracted from A. (This is done to reduce somewhat the penalty for incompatibility, and to minimise the number of characters with negative weights
- (e) each row is divided by  $(n-1)2$ ; this scales the data from -1 to +1. For each row this value is assigned as the weight of the corresponding character. If no iterations have yet occurred, then (a) is executed again (this is to ensure that the influence of poor characters is minimised)
- (f) the character with the lowest (or characters with equal lowest) weight is removed. Characters are assigned the weights they had when they were eliminated. The characters eliminated last have the highest weights.
- (g) the process is reiterated until no incompatibilities remain (all characters have a weight of 1).

This analytical method attempts to overcome one of the problems of unweighted compatibility - that bad characters may pull good characters out of a clique. In fact the results of the two types of

Table 1.3. O'NOMOD first and final iterations on an artificial data set.

Taxa analysed

1 2 3 4 5 6 7 8 9 10 11 12

Ch.nos.    Weights

1.1    : 0.3  
 2       : 0.16  
 4       : -  
 6       : 0.33  
 7.2    : -0.27  
 9       : -0.35  
 11      : 0.16  
 13      : -0.15  
 15      : -

Ch.nos.    Weights

1.2    : 0.44  
 3       : 1E-2  
 5       : 0.45  
 7.1    : 0.23  
 8       : 7E-2  
 10      : 0.28  
 12      : 6E-2  
 14      : 0.29  
 16      : 0.5

Ranking weights    2    5       6       16       1.1    1.2       10       14  
 7.1    12    11    8    3       13       7.2    9

1.1    : 1  
 2       : 1  
 4       : -  
 6       : 1  
 7.2    : 4E-2  
 9       : -0.35  
 11      : 0.37  
 13      : 7E-2  
 15      : -

1.2    : 1  
 3       : 0.27  
 5       : 1  
 7.1    : 0.59  
 8       : 0.32  
 10      : 1  
 12      : 0.49  
 14      : 0.75  
 16      : 1

Ranking weights

1.1    1.2    2       5       6       10       16       -14       -7.1    -12  
 -11    -8    -3       -13    -7.2    -9

analyses often differ only in the last character that is thrown out of a data set (Fergusson, pers comm; this volume, chapters 2, 3 and 6). It is only in the final rhyssine analysis that a real difference appears between the two analyses, and this is undoubtedly due to the high level of homoplasy in certain parts of that data set (chapter 6).

The only alteration to this made by Underwood (pers comm) in the O'NOMOD program is that binary state characters are not compared with each other, in order to make the program fit with the LEQU programs.

The first and final printouts are shown in table 1.3. The O'NOMOD program can often give a different result from the other programs. There is again a clique of 7 characters but instead of the clique consisting of characters [1.2, 5, 7.1, 8, 10, 11, 16] it consists of characters [1.1, 1.2, 2, 5, 6, 10, 16]. These sorts of differences are discussed later in the context of particular analyses.

#### 1.4.3. Reintroducing incompatible characters

Once a cladogram has been produced, the last few characters rejected can be examined to see how they can be fitted into the clique. This means postulating parallelisms or reversals which would explain the incompatibilities observed. This is best illustrated by the actual examples where this process has been undertaken, in chapters 2, 3 and 6 of this thesis (cf Gauld & Underwood, 1986).

Another way of explaining homoplasy is by examining subsets, that is reanalysing groups which the initial analysis showed as being holophyletic, thus removing the incompatibilities associated with parallelisms in other lines. This approach turned out to be rather ineffective in this work, usually because the parallelisms revealed by subset analyses were associated with characters thrown out of the clique late on, in any case. Subset analyses are discussed under each individual analysis.

7

In the main body of the text the compatible cliques are presented as cladograms (the characters in the clique can easily be read off each branch). Each analysis (see above) throws out certain characters late on, and these are discussed during the process of reintroduction in order to explain their homoplasy. The initial LEQUB randomness ratios and numbers of polar incompatibilities are referred to in the text and the tables are presented as part of the appendices.

### 1.5. Sources of homoplasy

Many of the characters which show the greatest homoplasy probably do so due to the effect of on/off toggling of regulatory genes during evolutionary history. Structural genes may be present within the genome yet not expressed due to the suppression of genes that regulate their development. Under renewed selective pressures of certain kinds, mutations in these regulatory genes may lead to the re-expression of the original structural genes. This will give the impression of parallelism when, in fact, there has always been homology at the genome level. These kinds of hidden synapomorphies are amongst the worst problems facing those who are attempting phylogenetic reconstructions. At times this may mean that the investigation of a particular character boils down to a search for the suppression and re-expression of regulatory genes, which is clearly of no phylogenetic significance in itself. Compatibility analyses have at least the advantage of recognising the high noise in these characters.

In opposition to this however a case can be made for certain highly homoplastic characters sometimes possessing phylogenetically useful information beyond their apparent homoplasy. This is especially true of the sorts of characters that I have described as **basal group characters** - that is character-states that have emerged at the base of groups and define those groups. These, although often highly homoplastic, have been used in certain places in this work. The reasoning behind this is that autapomorphies of any large and biologically diverse group will be characteristic of the least

biologically specialised taxa. Therefore, the most specialised and biologically most divergent taxa are extremely likely to show reduction homoplasy. However, this rule of thumb has been used with caution as, taken to its logical extreme, it would mean that all the most<sup>apparently</sup> underived groups in a phylogenetic analysis would be assumed to have no autapomorphies, and this would amount to an *a priori* assumption that they are paraphyletic. It may be just this kind of reasoning that leads to presumed ancestral taxa so often having no defining characters.

### 1.6. Cladograms, trees and scenarios

As mentioned above, the most basic information that is obtained from a cladistic analysis is that of the pattern of homologies between taxa. This is called, strictly speaking, a *cladogram*. In a compatibility analysis a cladogram is any compatible clique of characters obtained from a data set without consideration of characters which would be compatible if reversals or parallelisms were postulated. This means, in practice, the primary results of a LEQUB, PROBS or O'NOMOD computation. This result actually implies something about patterns in nature, it shows a nested set of synapomorphies. However, it has no essential evolutionary significance. In fact, no assumptions about evolution are necessary at all - and there is no need to *interpret* the pattern; it simply exists as an ordering of sense data. It cannot be refuted except where mistakes have been made in the construction of the data matrix.

The construction of a tree implies that a hypothesis is being made about the *true* evolutionary relationships within a group. This is not implied in a cladogram. At the point in a compatibility analysis when rejected characters are placed back into the clique and considerations made about parallelisms and reversals, assumptions are made about how evolution is occurring, and the resulting diagram must be considered a hypothetical diagram representing a tree. If evolution is really occurring, however, in the sorts of ways it is believed to be, then these decisions must be made. To be satisfied

2

with considerations of how characters are organised in space, as if they were timeless entities, seems theoretically sound but entirely unsatisfactory in practice. In this work cladograms are presented separately, and the emphasis is on how they can be used to construct trees.

From the construction of a tree comes consideration of the biological, ecological and biogeographical evolution of a group. Any hypotheses based on the combination of trees and other information of the above kind is a *scenario* (although this is a clumsy word it is used here for the sake of conformity with other workers (Tattersall & Eldredge, 1978, for example). In this work several scenarios will be discussed, presented as biological pathways derived from the original cladograms.

Cladograms are reflections of real patterns in nature, and as they do not presuppose that evolution has occurred (as long as the concept of homology is used in its non-phylogenetic sense) they are irrefutable. Trees, however, imply evolutionary processes are occurring which may or may not be true. As so little is known about evolutionary processes this implies that all trees are subjective - they imply impossible knowledge of cladogenetic and anagenetic events. This is why, quite reasonably, pattern cladists do not accept them. However, without trees and without the assumption of the existence of certain evolutionary processes no hypotheses about evolutionary patterns can be made.

Beyond this, scenarios are even more subjective. A consideration of how the parasitoid lifeway might have evolved from primitive sawflies, for example, requires assumptions about the evolutionary relationships within the Hymenoptera and how food-preferences may have changed which are impossible to prove and can be considered essentially as imaginative fiction. Hopefully, the scenarios constructed here represent a compromise between just-so stories and the arid presentation of patterns of apomorphies.

The analysis of data will be presented in the three forms discussed

2

above. Cladograms based on cliques will be discussed first and then trees constructed from them. The scenarios that will then be postulated will have a two-fold value. First, the trees will enable hypotheses about how ecological and biological characters may have evolved. Second, biological patterns will be compatible or incompatible with the trees, and enable more complex, if less rigorous and objective, patterns of relationships to be ascertained.

### 2.1. Introduction

In this chapter the status and interrelationships of the Pimplinae will be discussed in historical and phylogenetic terms. The characters used to define groups in the present classification will be examined, to see if, as phylogenetic markers, they support that classification.

### 2.2. Historical Review

The first worker, after Linnaeus, to attempt a classification of the ichneumonids was Gravenhorst (1829). He placed the large genus *Pimpla* amongst those genera with 'depressed and sessile' abdomens. Later, Wesmael (1844) split the ichneumonids up into 6 groups - the Ichneumones, Crypti, Pimplae, Banchi and Ophiones. Then Holmgren (1857) erected five subfamilies; calling them the Ichneumonides, Crypti, Ophionides, Tryphonides and Pimplariae. This classification formed the basis for the work of Thomson and Schmiedeknecht.

Modern classifications began with Perkins (in Beirne, 1941) and Townes (1944). It is Townes work that is the most important in this context. He divided the ichneumonids up into a much larger number of subfamilies and put the genera discussed in this study into the subfamily, called at that time the Ichneumoninae (= Pimplinae, and not to be confused with the present Ichneumoninae). Subsequently, Townes and his fellow workers (1960-1969) revised the classification of the Pimplinae and removed the Lycorini, Eugaltini, Labenini, Xoridini and Acaenitini from it. He erected five tribes - the Ephialtini, Pimplini, Polysphinctini, Poemeniini, Theroniini, Rhyssini and Diacritini. Essentially these are the groupings that will be discussed in this work.

Townes has not followed the *International Code of Zoological Nomenclature* and has not accepted several opinions of the Commission which relate to group names in the Pimplinae (see Townes 1969; Fitton & Gauld, 1976). This means that there are several taxonomic groupings which are referred to by different names by different authors. Fitton & Gauld's (1976) nomenclature has been adopted here. The table below shows how this differs from Townes (1969) and is reproduced from Gauld (1984a). In addition to these problems, one tribe, the Theroniini, should correctly be called the Delomeristini and is referred to as such here.

Table 2.1. Nomenclatural problems in the Pimplinae.

| Townes, 1969                                                                                                                               | Fitton & Gauld, 1976                                                                                                                                           |
|--------------------------------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Subfamily EPHIALTINAE                                                                                                                      | Subfamily PIMPLINAE                                                                                                                                            |
| Tribe PIMPLINI (Type-genus <i>Pimpla</i> F. <i>sensu</i> Curtis, 1828)<br>[This became a misidentification on publication of Opinion 159.] | Tribe EPHIALTINI (Type-genus <i>Ephialtes</i> Schrank <i>sensu</i> Gravenhorst, 1829)<br>[This became a correct identification on publication of Opinion 159.] |
| Genus <i>Pimpla</i> F.                                                                                                                     | Genus <i>Ephialtes</i> Schrank                                                                                                                                 |
| Tribe EPHIALTINI (Type-genus <i>Ephialtes</i> Schrank)<br>[This became a misidentification on publication of Opinion 159.]                 | Tribe PIMPLINI (Type-genus <i>Pimpla</i> F. <i>sensu</i> Gravenhorst, 1829)<br>[This became a correct identification on publication of Opinion 159.]           |
| Genus <i>Ephialtes</i> Schrank                                                                                                             | Genus <i>Apechthis</i> Foerster                                                                                                                                |
| Genus <i>Coccygomimus</i> Saussure                                                                                                         | Genus <i>Pimpla</i> F.                                                                                                                                         |

Recently some workers (Carlson 1979, Gupta 1987) have raised the sub-genera of *Theronia* to generic rank, and these genera have been placed in a separate tribe the Theroniini. These changes in generic limits are accepted in this work although their actual taxonomic validity is somewhat in doubt (see chapter 3).

Other changes have been suggested. Kazmierczak (1979, 1980, 1981) has reclassified *Pseudorhyssa* within the Rhyssini. Constantineau & Pisica (1977) also place *Pseudorhyssa* in the Rhyssini, and recognise two other tribes, the Scambini and Schizopygini.

### 2.3. The Townes Classification.

Townes revised the pimplines as part of a comprehensive treatment of the genera of ichneumonids (Townes, 1969); his procedures being those of a traditional taxonomist. In the 1969 revision there are diagnoses both at generic and tribal level (as well as an overall diagnosis for the subfamily which is discussed below). These diagnoses give the raw material for considerations of what the present classification means in an evolutionary context. Although Townes is presenting an intuitive interpretation of relationships, his characters can be analysed using cladistic techniques. The characters that he uses at subfamily level, and below, have been used as a basis for a compatibility analysis.

The present classification (Townes, 1969; Gauld, 1984b; Fitton, Shaw & Gauld, 1988) has 7 tribes: the Ephialtini (Pimplinae sensu Townes, see above); the Polysphinctini; the Pimplini (Ephialtini sensu Townes, see above); the Delomeristini; the Poemeniini; the Diacritini; and, the Rhyssini. It is this arrangement of tribes toward which this work is especially addressing itself (table 2.2).

The choice of genera for this study has been rather arbitrary and necessarily constrained by shortage of material of some groups. In addition taxa have been generally chosen where something is known about their biology. An unfortunate side-effect of this is that

Holarctic groups tend to predominate, and some tropical groups are poorly represented. The species chosen in each genus as the Operational Taxonomic Unit (OTUs) has also been fairly arbitrary, although as many other species have been examined as possible. Occasionally a character has been in its plesiomorphic state in the OTU yet in its apomorphic state in other congeneric species. This has led to the difficult problem of knowing when a real apomorphy is being obscured. As a general rule, if a character is in the plesiomorphic state in only a few species within a genus and in its apomorphic state in the majority I have assumed that the apomorphic state has been lost in the minority of cases. This has the effect that some scores for OTUs are composite and indicative of the genus as a whole rather than a particular species. Table 2.2 shows which of the study genera are in which tribes. The numbers refer to OTUs, which are listed in appendix 1.

Table 2.2. Present tribal status of OTU's used in the analyses.

| Tribe          | Study group members |
|----------------|---------------------|
| Ephialtini     | 1-15                |
| Polysphinctini | 16-24               |
| Pimplini       | 25-29               |
| Delomeristini  | 31-33               |
| Diacritini     | 34                  |
| Poemeniini     | 35-38               |
| Rhyssini       | 39-42               |

## 2.4. Testing the Townes classification

### 2.4.1. Outgroups

It is not clear which subfamily of ichneumonids should provide the outgroup for comparison with the pimelines. The suggestion has been made recently that the pimelines belong in a clade along with the Acaenitinae, Diplazontinae, Oxytorinae and Orthocentrinae (Brooks & Wahl, 1987). More recently Wahl (in press) has suggested an informal taxonomic grouping for the above subfamilies and also constructed a tentative cladogram which shows the Pimplinae as the basal group of the clade. This position is discussed in chapter 3. Although not all the fine details of Wahl's tree are accepted in this work, its overall conclusions are endorsed.

Throughout the other members of the clade have been used as outgroups, especially the Acaenitinae which seems to be the least specialised of them and is probably paraphyletic with respect to the pimelines (see chapter 1 and Underwood, 1982). Along with these groups I have used two subfamilies which appear to be close to the base of ichneumonid phylogeny: the Labeninae and the Tryphoninae. At an even lower phylogenetic level the braconid subfamilies, Braconinae and Doryctinae have been examined and finally, siricoid symphytan material has been investigated on occasions.

### 2.4.2. The holophyly of the Pimplinae

The first requirement of a cladistic analysis is to show that the study group is holophyletic. This means that one has to be able to identify derived characters that are shared by every member of the study group and no other taxa (autapomorphies). Townes (1969) mentions several shared characters of the Pimplinae. The strength of these is discussed below.

- (1) Absence of the precoxal sulcus (*sternaulus sensu* Townes 1969).

2

This groove on the mesopleurum may mark the boundary between it and the mesosternum. The only pimpline amongst the study group to have it seems to be *Rhyssella* where it is very weak. It is not present, however, in most acaenitines, labenines, tryphonines or xoridines. If its presence is plesiomorphic then it has been lost independently in several lineages and there is no reason to believe that its loss is an autapomorphy of the pimelines. It might be, but there is no way of telling either way. This is an unfortunate characteristic of loss characters and one which makes reconstructions of phylogeny throughout the Hymenoptera problematical (Gauld, 1985, 1987a).

(2) Absence of the posterior transverse carina of the mesosternum. This carina does seem to be universally absent in pimelines. It is strong in some species of labenines and tryphonines but absent in others. As parallel loss of carinae seems to be common amongst the ichneumonids this is not an unambiguous autapomorphy. Carination is very much reduced in all pimelines, compared with the outgroups. However, most specialised groups of ichneumonids have reduced carination, and the same general comments apply here as in (1) above.

(3) 2m-cu (Second recurrent vein) of forewing with 2 bullae. This character state is very common amongst the outgroup taxa, suggesting that it is the plesiomorphic state. In addition, the tribe Poemeninii has the two bullae so close together that they often appear as one bulla (see character 51 in chapter 3) and this is undoubtedly apomorphic. Clearly this character could only lead to the delineation of a paraphyletic taxon.

(4) Short's larval autapomorphy. Short (1978): "The outstanding character for this subfamily is the position of the hypostomal spur meeting the stipital sclerite on or near its point of meeting with the labial sclerite" (p. 14). This seems on the face of it to be the best candidate for an autapomorphy. Examination of the larvae in the BM(NH) collection and Wahl's investigations (1984, in press) have confirmed that the hypostomal spur does meet the stipital spur in the manner described above in all studied final instar larvae of

pimplines. However Wahl (op. cit.) believes that this is the first stage in a transformation series which leads to the development of a hypostomal-stipital plate by the fusion of the two processes. If this is true, and it seems plausible, then the character state in pimplines is symplesiomorphic and not indicative of holophyly.

(5) In addition to the Townes characters Wahl (in press) has suggested that the only autapomorphy of the Pimplinae might be "apical margin of the clypeus thin and with median notch - apparently bi-lobed". Within the Pimplinae this character state is found only in certain ephialtine, polysphinctine and delomeristine genera - it would require a very unlikely number of reversals to be a good autapomorphy.

The characters discussed above do not seem to satisfactorily delineate a holophyletic group. It may be, of course, that the group is polythetic (Gauld & Mound, 1982) and this possibility is discussed below. In any case, for the purposes of this preliminary analysis it is assumed that the Pimplinae are a holophyletic group with an undiscovered autapomorphy. The character states used in the Townes (1969, and contemporary works generally) classification are now described, and polarity is assigned to each.

#### 2.4.3. The Character States

All of these characters are taken from the descriptions of subfamily, tribe and genus level characters in Townes (1969). Characters which are autapomorphies of genera or are extremely variable within genera have not been included. Where the outgroups show a confused or uncertain condition a comment has been made in the text. Where no comment is made it is implied that the outgroups show the assumed plesiomorphic condition. The characters are figured in Townes (1969), Gauld (1984b) and Fitton *et al* (1988).

One character which is used by Townes has been left out of the character set. This is the *presence of two mandibular teeth in the final instar larvae*, which is one of the characters presently used to define the tribe Delomeristini. This is due to two problems: first, the lack of larval specimens; second, the related problem of interpretation of the character, which is made impossible by the inconsistencies of the published drawings. Spradbery (1970a) shows *Pseudorhyssa maculicoxis* as having only one mandibular tooth, while Short (1978) shows the same species with two mandibular teeth. In addition Spradbery's (*op cit*) drawing of *Megarhyssa emarginatoria* has two mandibular teeth while Short's (*op cit*) clearly shows only one. Without reference to new and old specimens a sensible set of character-state markings cannot be made.

The characters are placed in a roughly anterior to posterior order in respect to an ichneumonid body, and the numbering system has no other significance. Multistate character (Gauld & Underwood, 1986) are indicated in decimal - i.e. the first character state in a series is referred to as x.1, the second x.2 and so on. (1) indicates an apomorphy; (0) a plesiomorphy.

1. Inner margin of compound eyes strongly concave at level of antennal sockets (1); inner margin of compound eye straight, slightly convex, or slightly concave at or above the level of the antennal sockets (0).

2.1,2.2. Clypeus with median apical notch (1,0); convex apically, or at most slightly concave (0,0); with median apical tubercle (0,1).

3.1,3.2. Mandible unidentate (1,1); bidentate with lower tooth shorter than upper tooth (0,1); bidentate with upper tooth shorter than lower tooth (1,0); bidentate with upper and lower teeth coequal (0,0).

4. Mandible bidentate with upper tooth chisel shaped (1); not like this (0).

5. Occipital carina complete or absent at midline, undipped (0); complete and dipped above midline (1).

6. Occipital carina complete (0); absent at midline (1)
7. Dorsal half of temple with scale-like ridges (1); dorsal half of temple without scale-like ridges (0)
- 8.1,8.2. Notaulus absent (1,1); present but short and weak (1,0); present, long and strong (0,0). This character is discussed in more detail in Chapter 3.
9. Epomia present and strong (0); absent or very weak (1).
10. Presence of sharp transverse ridges on the mesoscutum (1), their absence (0). A difficult character to polarise easily as there are many wood-boring groups with mesoscutal ridges (ibaliids, aulacids, some siricids). *Certonotus* (in the Labeninae) has very clear mesoscutal ridges, but these may be analogous rather than homologous structures.
11. Epicnemial carina (prepectal carina) present (0), absent (1).
12. Mesopleural furrow angled opposite episternal scrobe (0); not angled or weakly angled (1).
13. Pleural carina of propodeum present and strong (0), absent, weak or obsolescent (1). Tryphonines and labenines have among the most complete propodeal carination in ichneumonids. In addition fossil ichneumonids seem to have strongly carinate propodea (Rasnitsyn, 1980). As with other characters related to carination a general trend toward reduction can be seen, but all ichneumonids with no carinae on their propodeum look the same, so real homologies are obscured.
- 14.1,14.2. Lateral longitudinal carina of propodeum complete (0,0), posteriorly preserved (1,0), absent (1,1).
- 15.1,15.2. Lateromedian longitudinal carina of propodeum complete,

forming 'cell' with apical and basal transverse carinae (0,0); basally present (1,0); absent (1,1).

16. Sub-metapleural carina of metapleurum complete (0), incomplete (1). Usually far better developed in the outgroups than in pimelines. Labenines often have it present as a large flange between mid- and hind-coxae.

17. Last tarsal segment enlarged (1), not enlarged (0).

18.1,18.2. Female tarsal claws with basal tooth (1,1); basal tooth only on front and/or middle claws (1,0); without basal tooth (0,0).

19. Tarsal claw hair with hair with flattened tip (1); without hair with flattened tip (0).

20. Vein 3rs-m of forewing present forming a closed cell (the areolet) (0), Vein 3rs-m of forewing absent not forming a closed cell (1). In general, wing vein reduction throughout the Hymenoptera seems to be an apomorphic feature. However it is a character highly susceptible to homoplasy as a result of parallel reduction.

21.1,21.2,21.3. Distal abscissa of Cul in hindwing closer to M than 1A (0,0,0); midway between M and 1A (1,0,0); further away from M than 1A (1,1,0); absent (1,1,1). Very uncertain polarity (see Gauld 1985). Labenines and tryphonines broadly agree with this polarity, xoridines and acaenitines do not.

22. First tergite of gaster free from its sternite (0); fused to its sternite (1).

23.1,23.2. Dorsolateral carina of first tergite of gaster present (0,0); vestigial (1,0); absent (1,1).

24.1,24.2. Mediodorsal longitudinal carina of tergite 1 of gaster extending greater than 0.5X length of tergite (0,0); extending between 0.25 to 0.5X length of tergite (1,0); extending less than 0.25X length

of tergite (1,1).

25. Tergites 3 and 4 of gaster with punctures present (0); absent (1).  
A somewhat arbitrary coding based on commonality.

26. Tergite 3 and 4 of gaster with tubercles definitely present (1); absent (0). The tergite is rounded and sometimes has humps on either side of the mid-line. Several primitive braconid genera seem to show this character, but few ichneumonids.

27.1, 27.2. Female subgenital plate completely sclerotised (0,0); weakly sclerotised at anterior edge (and sometimes around edges) (1,0); completely membranous (except sometimes at edges) (1,1).

28. Tergite 9 of gaster of female extended apically (1); not extended (0). The usual ichneumonid condition is to have a fairly short tergite 9. Tryphonines have short tergite 9s, but they don't bore into wood. Labenines have long tergite 9s where they are wood-boring.

29. Tergite 9 apical horn or boss present (1); absent (0). None of the outgroups (even the wood-boring *Certonotus* and *Coleocentrus*) have this character in the apomorphic state.

30. Ovipositor length greater than forewing length (1); less than forewing length (0).

31. Ovipositor sub-median swelling present (1); absent (0).

32. Epistomal arch of the Larva complete and heavily sclerotised (1); incomplete (0). Short (1978) suggests that the apomorphic state of this character is associated with the endoparasitic habit. The outgroups are confusing as they do not seem to have a typical state. This polarity somewhat in doubt.

33.1, 33.2. Larval median dorsal tubercles absent (0,0); one per segment (1,0); two per segment (1,1).

## 2.5. Results

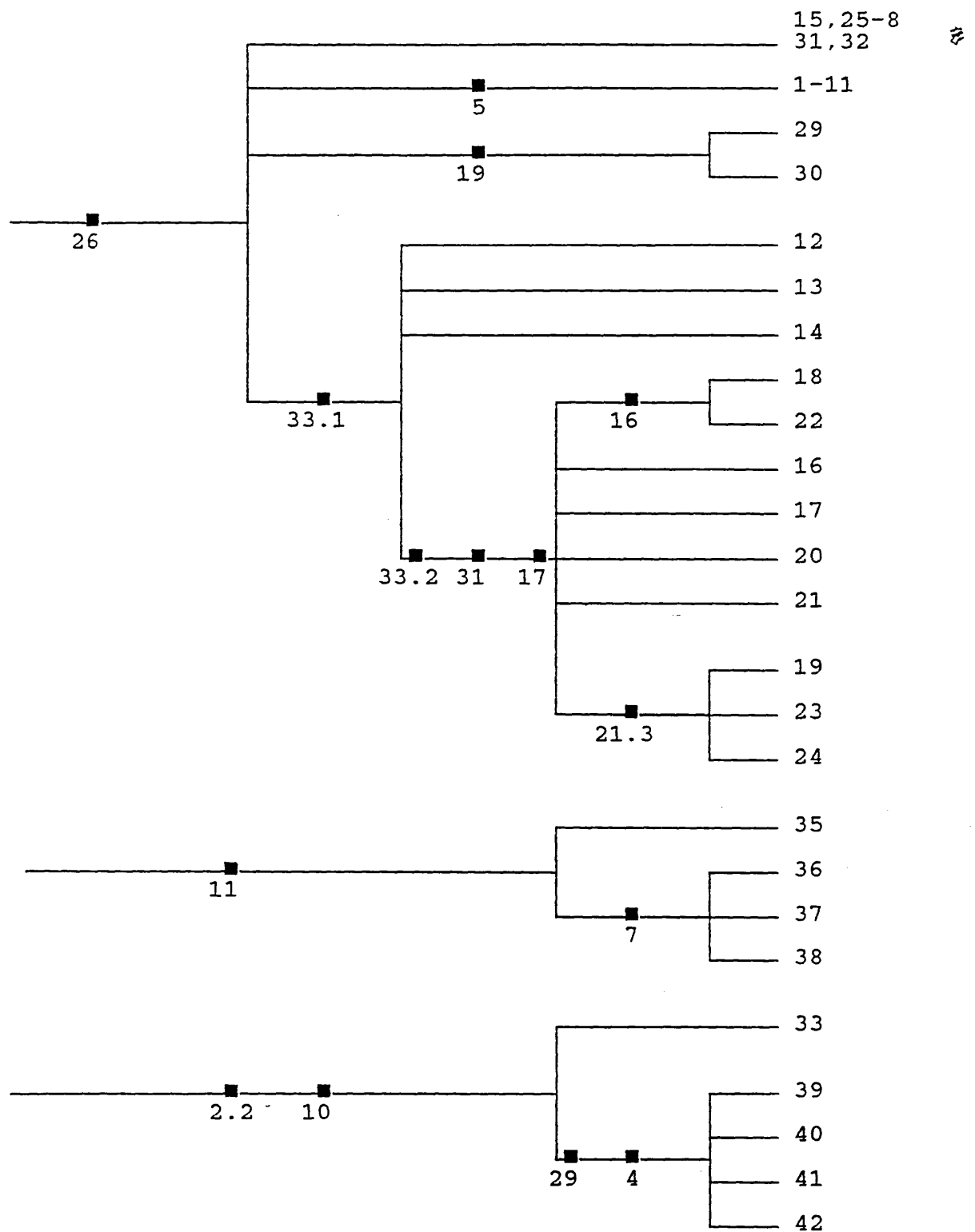
As indicated in chapter 1, the results will be presented as cladograms - the direct output from the compatibility programs; then as hypothetical trees - the cladograms with other homoplastic characters added, so that considerations of reversal or parallelism are involved. For more details on the methodology, see chapter 1.

The LEQUB program produced an overall randomness ratio of 0.75, and this indicates a high level of homoplasy (see chapter 1). There are only two polar incompatibilities and as one of the characters (14.1) does not enter any clique and was thrown out early in the analysis, its polar incompatibility did not effect either the cladogram or tree construction.

### 2.5.1. Cladograms: initial output

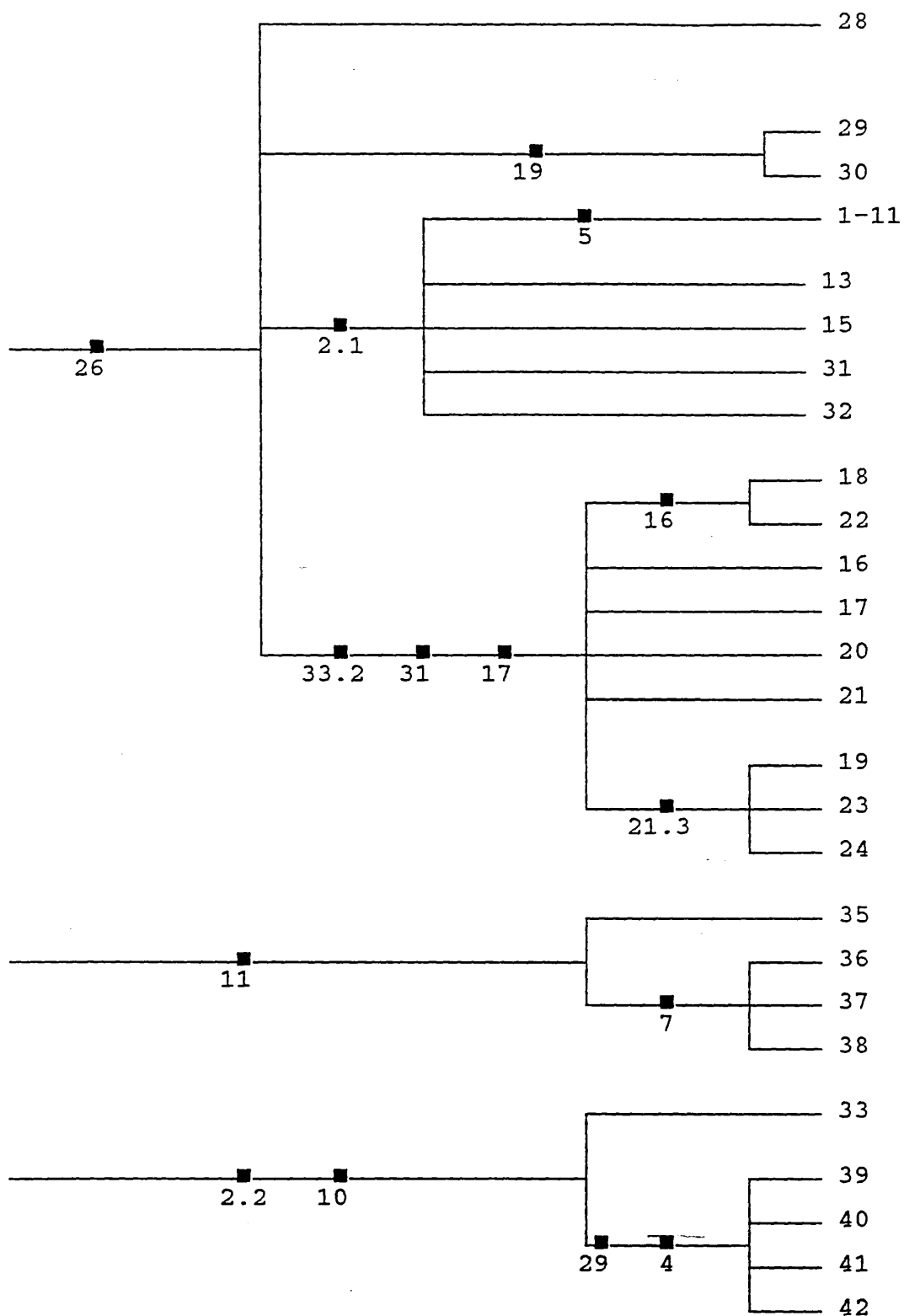
The results of the LEQU and O'NOMOD analyses are shown in fig 2.1 and fig 2.2. There are only small differences between them. Both cladograms split the pimelines into three: an ephialtine+polysphinctine group (by character 26); a poemeniine group (by character 11) and a rhyssine+*Pseudorhyssa* group (by characters 2.2 and 10). The last two groupings are not changed between the analyses while the first is altered only by the swapping of two characters (2.1 in the LEQU and 33.1 in the O'NOMOD). In essence this simply increases or decreases the number of unplaced taxa and shifts taxa 12, 13 and 14 from the ephialtine group to the polysphinctine group or vice-a-versa.

The major problem with both cladograms is that several groups that the Townes 1969 classification implies are natural are not placed together. The most obvious of these is the tribe Pimplini (presumed autapomorphic character, 12) which is split across the cladogram (see below). This is due to the presence of a straight mesopleural furrow in taxa 41 and 42, making character 12 homoplastic. In addition character 19 (tarsal claw hair) combines the genus *Xanthopimpla* (29; Pimplini) with the genus *Theronia* (30; Delomeristini). In addition,



Key: ■ - apomorphy.

Fig 2.1. LEQUB/PROB cladogram for the Townes data set.



Key: ■ - apomorphy.

Fig 2.2. O'NOMOD cladogram for the Townes data set.

7

the tribe Ephialtini is characterised as paraphyletic, leaving the holophyly of only 2 tribes supported by the analysis - the Polysphinctini (by 31, 33.2 and 17) and the Rhyssini (by 4 and 29). However, the analysis groups the Rhyssini and *Pseudorhyssa* together, the latter normally placed within the Delomeristini. Overall, it does not support the Townes classification, or present a coherent alternative. Some characters seem to have dragged taxa away from their probable homes and without some discussion of the sources of homoplasy in the data set it is not of much practical use.

#### 2.5.2. Trees: phylogenetic hypotheses

These poorly resolved cladograms can be tidied up somewhat by looking at where parallelisms and reversal might occur. However, there is one problem which cannot be solved by this method. It is that the genus *Diacritus* does not group with any other taxa in either of the two analyses (and is the only OTU that does not), this and the evidence presented in the next chapter suggests that it does not belong amongst the Pimplinae even in the sense of Townes. For this reason it is not presented in the cladograms - simply because it would be represented by a single line with no related branches, a representation that has no information content.

The characters which were thrown out of the clique last are now considered:

(a) Character 33.1. This larval character requires one parallelism in character 2.1 in taxon 13 to place it in the paraphyletic group delineated by possessing character 33.1 but not characters 17, 31 or 33.2.

(b) Character 28. This would link together taxon 15, 33, 36, 37, 38, 39, 40, 41 and 42. To fit this into the clique would involve a parallelism in taxon 15 (or two parallelisms in characters 26 and 2.1, which seems extremely unparsimonious) and one reversal in taxon

35. The result of this is to link the presently accepted tribes Poemeniini, Rhyssini and the genus *Pseudorhyssa* into a single clade unconnected with the rest of the pimelines.

(c) Character 1. One parallelism is required in taxon 18 (or alternatively 4 parallelisms in characters 17, 33.2, 31 and 16, once again less likely) to place this in the clique. The character links together taxa 25, 26, 29 and 30; that is, part of the present Pimplini and *Theronia*.

(d) Character 24.2. To fit this character into the clique would require a total of 5 separate parallelisms (in taxon 15, 27, 28, 31 and 34) - accepting character 28 as valid. This and the nature of the character - which is a reduction in its apomorphic state, suggests that the character is too homoplastic to be phylogenetically informative. In cases where this number of parallelisms are required it seems entirely a matter of subjective choice whether the parallelisms are imputed in taxa which would fit in with a clique (i.e. make the character less homoplastic) or in taxa which would be incompatible with the clique (i.e. make the character more homoplastic). In these cases the character must be rejected.

(e) Character 18.2. This character requires 2 parallelisms (taxon 36 and 37) and 7 reversals (taxa 25, 27, 28, 29, 30, 31 and 32) and therefore the comments for (d) above should apply. However, this pattern of reversals could be indicative of a character which was evolved early in the phylogenetic history of a group and has been lost in several lines. These sort of characters are very difficult to deal with objectively as although they often seem very useful (being right at the base of large groups) they also show a great deal of reduction homoplasy. At this stage the character must be rejected for the reasons given in (d), but a further consideration of this character and others like it is given in chapter 3 (cf. section 1.5).

(f) Character 18.1. The same general comments apply to this character as for its related character 18.2 (e) above.

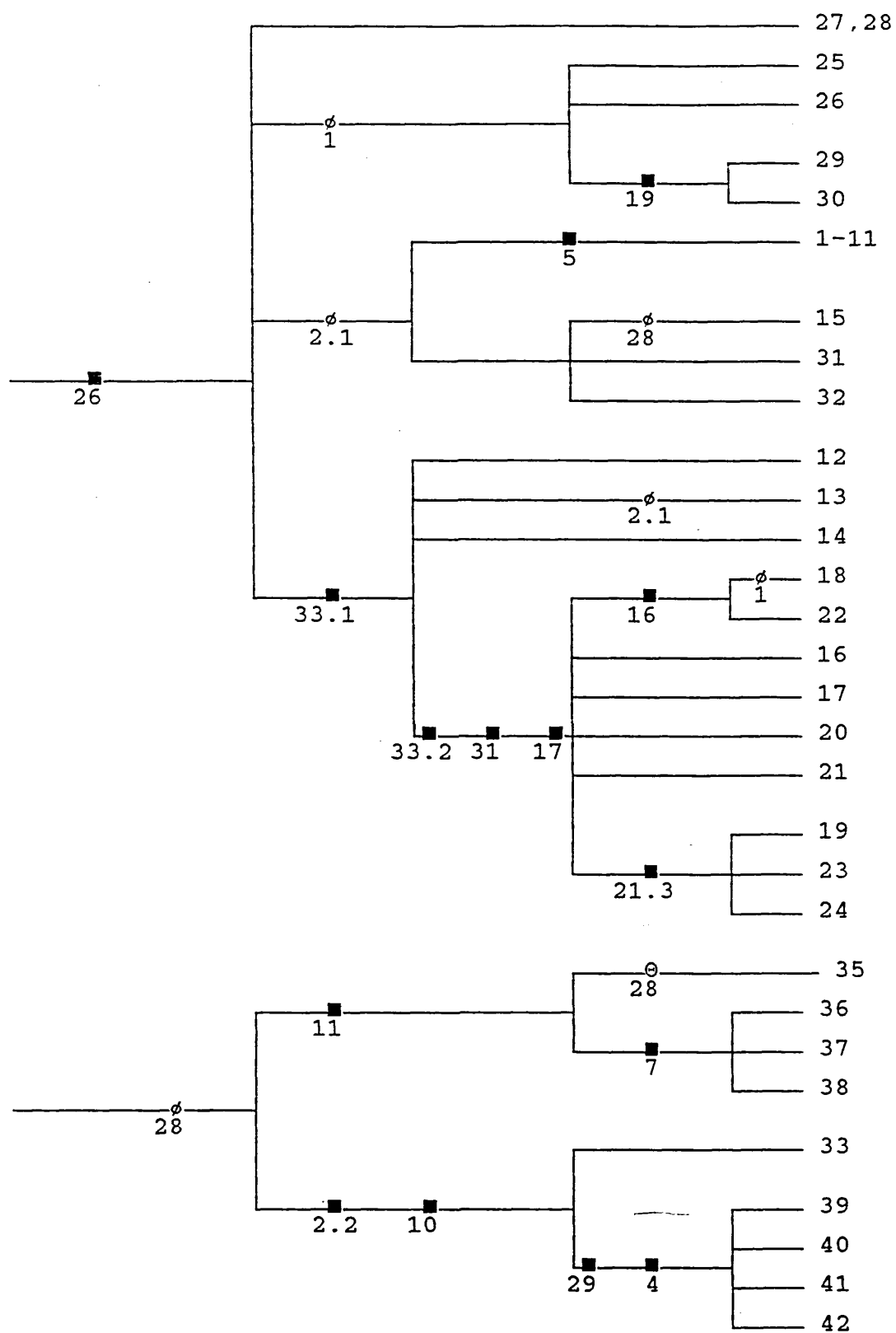
The hypothetical tree is shown in fig 2.3. How does this analysis compare with Townes classification (1969)? The results for the classification are shown in tabular form below.

Table 2.3. Summary of differences between analysis results and present classification.

| Group          | Townes     | Analysis                       |
|----------------|------------|--------------------------------|
| Pimplinae      | sub-family | paraphyletic?<br>polyphyletic? |
| Polysphinctini | tribe      | holophyletic                   |
| Ephialtini     | tribe      | paraphyletic                   |
| Pimplini       | tribe      | polyphyletic                   |
| Delomeristini  | tribe      | polyphyletic                   |
| Poemeniini     | tribe      | holophyletic                   |
| Rhyssini       | tribe      | holophyletic                   |

The data set derived from the Townes data therefore implies: first, that the Pimplinae are not a holophyletic group - and that at best they can be split into two holophyletic groups only tentatively (or three including *Diacritus*); second, that many of the tribes in the accepted classification are unnatural.

However, there is much that is unsatisfactory in this initial analysis of the Pimplinae. To start with, some of the groups which appear as polyphyletic or paraphyletic in the analysis seem intuitively to be holophyletic. The best example of this is the Pimplini, which seem biologically to be a good group and have an autapomorphy (character 12 - mesopleural furrow angle), but one which does not end up in any of the cliques. This seems to be due to a



parallelism between two of the rhyssine genera (*Lytarmes* and *Epirhyssa*) and the Pimplini. The weight of other evidence in the analysis is strongly against a Pimplini-Rhyssini grouping, and taking out the two parallelisms reinstates the Pimplini as a holophyletic group. Similarly characters 10 and 2.2 suggest that *Pseudorhyssa* is the sister-group of the Rhyssini. Both the characters which support this grouping are associated with the deep wood-associated habit (see chapter 4), and therefore are likely to be parallelisms in this case. These problems are dealt with in more detail in chapter 3.

A final point which is worth stressing is that the characters used in Townes' classification are not meant to constitute a comprehensive listing of diagnostic characteristics. They are the characters that he considers to be the most appropriate; either because they are simplest to see, are most easily described or have traditionally been employed. This means that they are a subset of the total number of characters which might be investigated in a cladistic analysis. For this reason it is not safe to rely on these characters alone, which are indicators for an intuitive classification. In the next chapter an analysis of new characters and reassessment of some of the old will lead to a different perspective phylogeny and classification of the "pimplines".

### 3.1. Introduction

The Townes data set consists of a series of characters which do not enable clear phylogenetic patterns to be resolved. In this section I will briefly examine features of pimpline morphology which appear to be of potential phylogenetic significance. This is not meant to be review of pimpline morphology, but an exercise in examining character states and an attempt to analyse these cladistically. The obtained data set will then be combined with the Townes one to obtain a better idea of relationships.

### 3.2. Head

#### 3.2.1. Back of the head

Rasnitsyn (1980) suggests that the back of the head is fairly primitive in ichneumonids. It does not seem to change much within the Pimplinae. In all pimelines a hypostomal bridge is present, nearly always with the postgena fused ventrally along the midline to form a postgenal bridge (fig 3.1). The extent of this fusion varies from taxon to taxon but as all states are widely spread throughout the pimelines and their outgroups, it is rejected as having no phylogenetic value.

On the post-occiput of a number of pimelines is a raised platform with a notch (fig 3.2). Amongst the outgroups it certainly occurs in the Acaenitinae, which implies that its presence is plesiomorphic at this level. *Character 34. Raised platform and/or notch on vertex below the occipital carina (0); no platform or notch (1).*

There is an expansion of the Foramen (posterior tentorial pits) to

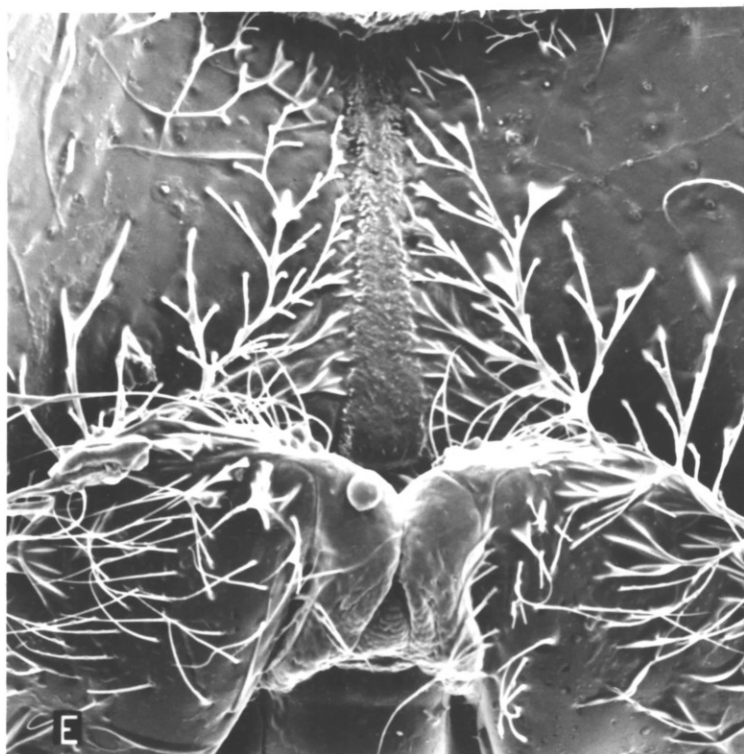


Fig 3.1. Post genal region of *Dolichomitrus imperator* showing partial fusion of postgena . X 110.

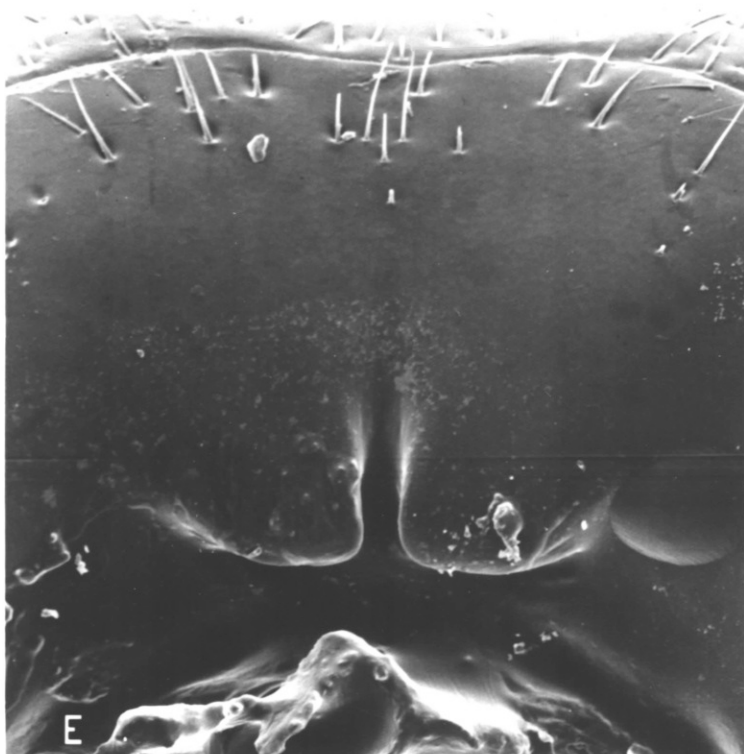


Fig 3.2. Notch on post-occiput of *Dolichomitrus imperator*. X 110.

7

form paired extended cavities in some taxa (fig 3.3.). This structure is present but not particularly well developed in *Poemenia* and *Deuteroxoides*; it is more strongly developed in *Neoxorides* and extremely well developed in *Podoschistus*.

*Character 35. Anterior part of foramen expanded on either side to form a pair of hollows or more extended cavities (1); foramen not expanded (0)*

### 3.2.2. Mouthparts

The primitive number of maxillary and labial palps segments amongst the Hymenoptera is 6 maxillary and 4 labial (Richards, 1977); this is modified in most Ichneumonidea to 5 maxillary and 4 labial. In a few pimplines the number of labial palp segments is reduced from 4 to 3. There is often also a reduction of the number of maxillary palp segments from 5 to 4, although this is due to a reduction in size of the 1st maxillary palp segment so that it is not clearly visible.

*Character 36. Labial palps 3-segmented (1); labial palps 4-segmented (0)*

There are a few divergences from the general pattern of ichneumonid palps. *Neoxorides* has very long thin maxillary palps and this is autapomorphic; *Deuteroxoides*, *Poemenia* and *Podoschistus* have narrow barrel-shaped 2nd and 3rd labial palp segments.

*Character 37. Narrow 2nd and 3rd labial palpar segments (1); palps not narrowed (0)*

### 3.2.3. Antennal Structure

Several studies have examined the sensilla found within the Hymenoptera (Slifer & Sekhon, 1960, 1961; Slifer & Sekhon, 1968; von Walther, 1979; Barlin & Vinson, 1981; Barlin et al, 1981 Bin & Vinson, 1986; for example), and one investigating ichneumonoids is of special interest here (Norton & Vinson, 1974). In support of these a survey of the probable pimpline outgroups has been performed and a general idea of the polarities has emerged. The following represent

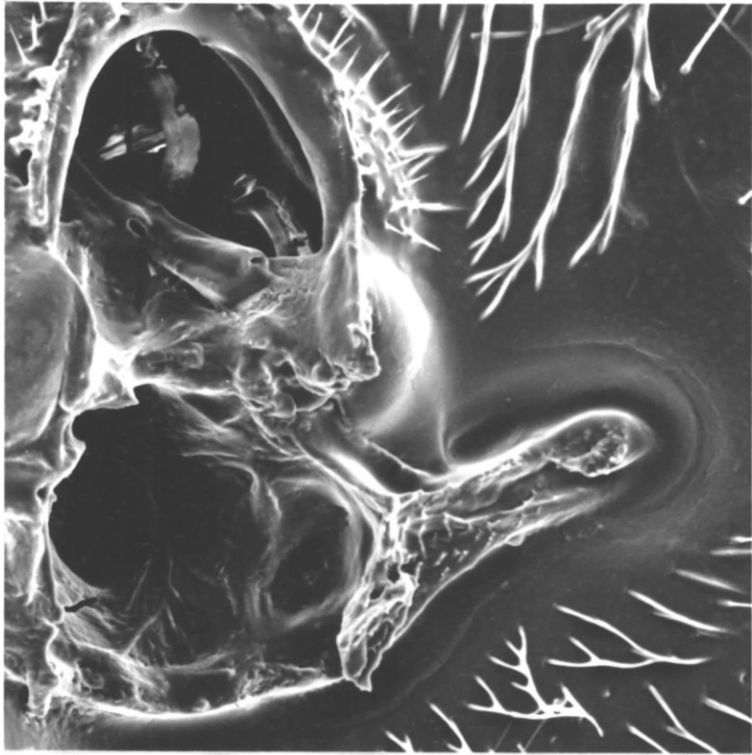


Fig 3.3. Foramen of *Neoxorides collaris* showing expanded lateral hollow. X 110.



Fig 3.4. Smooth basiconic sensillum (type A) of *Liotryphon cydiae*. X 13 000.

the probable plesiomorphic condition within ichneumonids as a whole:

(a) Trichoid sensilla. Hair-like with shallow longitudinal grooves and sharply pointed tips. Lengths varying from 15-24  $\mu\text{m}$ , basal diameters from 1-3 $\mu\text{m}$ .

(b) Placoid sensilla. Plate-like structures slightly elevated above the flagellar surface. They have a smooth surface and are surrounded by a cuticular ridge. Their lengths varying from 15-60  $\mu\text{m}$ , diameters from 1.5-18  $\mu\text{m}$  (extreme case of *Odontocolon*). Present on all (or nearly all ) flagellar segments of both sexes.

(c) Basiconic sensilla. There seem to be four morphologically distinct types of these sensilla:

(i) Fluted. Projecting perpendicularly from the antennal surface. They possess fluted surfaces and slightly blunt tips. Lengths varying from 15-60  $\mu\text{m}$ . These seem to be present on all flagellar segments of both sexes. Often large hairs are associated with the distal ends of segments.

(ii) Fluted bent-tipped. Often found only on female antennae, they seem to be commoner in braconids than ichneumonids (Norton & Vinson, 1974). They are characterised by having a fluted surface , abruptly bent apical region and a small bulb-like tip. The average length from base to beginning of bend is from 16-22 $\mu\text{m}$ , the basal diameter varies from 1.8-2.2  $\mu\text{m}$ .

(iii) Curved non-fluted. Common and usually from 5-8  $\mu\text{m}$  long. These usually have reasonably sharp tips, although in some cases they can be blunt (in *Cardiochiles nigriceps* as described by Norton & Vinson, 1974, for example.)

(iv) Smooth. These are sensilla of various shapes and sizes which often consist of pegs in pits. Primitively they are often large bulbous structures arising from the antennal surface. This primitive condition only seems to be found in *Podoschistus* amongst the study OTUs.

All the studied taxa have trichoid and placoid sensilla in the plesiomorphic state described above. Fluted, fluted bent-tipped and curved non-fluted basiconic sensilla are also found in their plesiomorphic state. These characters do not vary and therefore are of no phylogenetic significance. Only in the distribution of smooth basiconic sensilla does there seem to be any real variation.

There seem to be two types of smooth basiconic sensilla of potential phylogenetic significance found amongst the pimelines. The first structure is a peg in a pit, surrounded by a cuticular ring (fig 3.4). The peg can either end in a blunt or a swollen tip. The width of the ring varies from 1.5-2.5  $\mu\text{m}$ , and the length of the peg from 1.7-2.8  $\mu\text{m}$ . These seem to be the sensilla described in Norton & Vinson (1974). Their presence in outgroup taxa implies that the absence of the character state is apomorphic. *Character 38. Presence of smooth basiconic sensilla (type a) (1); absence of these sensilla (0)*

The second sensillum is much larger. It again consists of a peg in a pit with a surrounding ring. However, in this case there is a central area of variable structure between the peg and the ring (fig 3.5). The peg varies from 2-3  $\mu\text{m}$  in length and the total diameter of the ring from 6 - 9  $\mu\text{m}$ . As no outgroups seem to possess this character state its presence is apomorphic. *Character 39. Presence of smooth basiconic sensilla (type b) (1); absence of these sensilla (0)*

Table 3.1 shows the taxonomic distribution of smooth basiconic sensilla amongst the study OTUs. The notes show the variation in structures and distributions of structures observed.

Table 3.1. Distribution of smooth basiconic sensilla amongst the Pimplinae

| Genus                | SBS(a)         | SBS(b)         |
|----------------------|----------------|----------------|
| <i>Exeristes</i>     | -              | -              |
| <i>Endromopoda</i>   | -              | -              |
| <i>Afrieptialtes</i> | -              | -              |
| <i>Eptialtes</i>     | + <sup>1</sup> | -              |
| <i>Liotryphon</i>    | +              | -              |
| <i>Townesia</i>      | -              | -              |
| <i>Paraperithous</i> | -              | -              |
| <i>Dolichomitus</i>  | +              | -              |
| <i>Acropimpla</i>    | +              | -              |
| <i>Gregopimpla</i>   | -              | -              |
| <i>Iseropus</i>      | -              | -              |
| <i>Tromatobia</i>    | -              | -              |
| <i>Zaglyptus</i>     | + <sup>2</sup> | -              |
| <i>Clistopyga</i>    | +              | -              |
| <i>Pseudopimpla</i>  | -              | + <sup>3</sup> |
| <i>Dreisbachia</i>   | -              | -              |
| <i>Schizopyga</i>    | -              | -              |
| <i>Acrotaphus</i>    | -              | +              |
| <i>Acrodactyla</i>   | -              | -              |
| <i>Piogaster</i>     | *              | *              |
| <i>Oxyrrhexis</i>    | -              | -              |
| <i>Polysphincta</i>  | +              | -              |
| <i>Sinarachna</i>    | +              | -              |
| <i>Zatypota</i>      | +              | -              |
| <i>Itoplectis</i>    | +              | -              |
| <i>Apechthis</i>     | -              | -              |
| <i>Pimpla</i>        | -              | -              |
| <i>Strongylopsis</i> | +              | -              |
| <i>Xanthopimpla</i>  | -              | -              |
| <i>Theronia</i>      | -              | -              |
| <i>Perithous</i>     | -              | -              |
| <i>Delomerista</i>   | -              | -              |
| <i>Pseudorhyssa</i>  | -              | + <sup>4</sup> |
| <i>Diacritus</i>     | -              | -              |
| <i>Poemenia</i>      | -              | +              |
| <i>Deuteroxoides</i> | -              | +              |
| <i>Podoschistus</i>  | -              | +              |
| <i>Neoxorides</i>    | + <sup>5</sup> | + <sup>4</sup> |
| <i>Rhyssa</i>        | -              | + <sup>6</sup> |
| <i>Rhyssella</i>     | -              | +              |
| <i>Lytarmes</i>      | -              | +              |
| <i>Epirhyssa</i>     | -              | +              |

Key: +, structure present; -, structure not present; \*, information not available; 1, found only in males; 2, found in large numbers in fields; 3, two types of atypical SBS(b)'s; 4, SBS(b)'s with a double ring structure; 5, SBS(a)'s in deep pits and in fields; 6, flat SBS(b)s with much reduced projections.

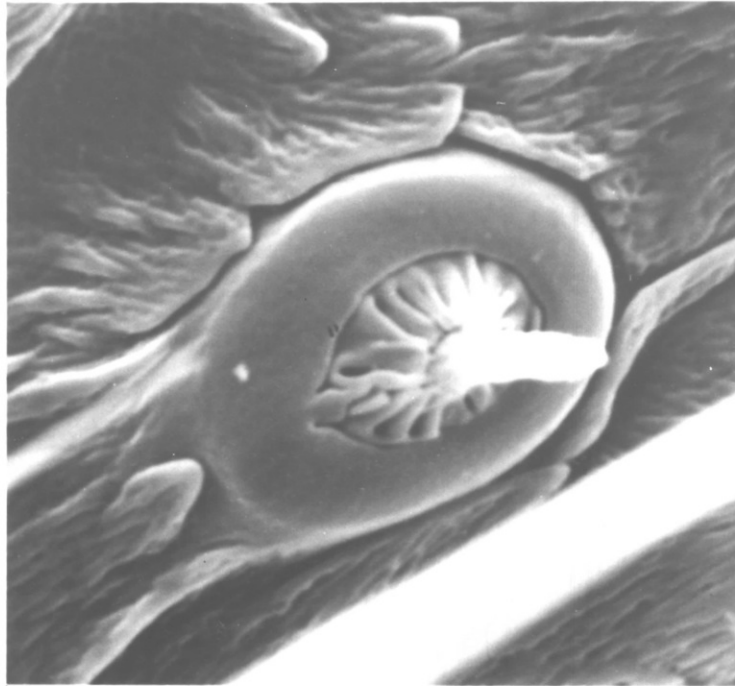


Fig 3.5. Smooth basiconic sensillum (type B) of *Acrotaphus tibialis*.  
X 660.

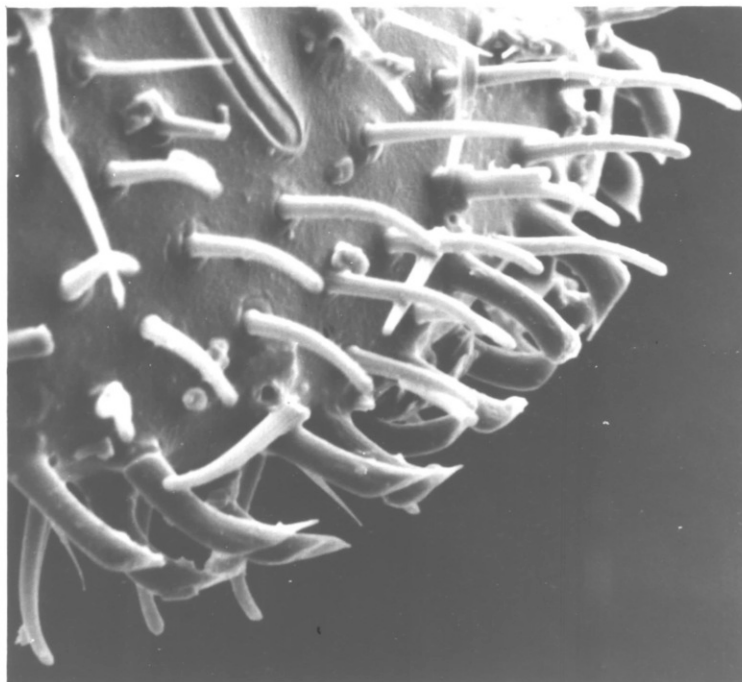


Fig 3.6. Tip of apical segment of antenna of *Theronia lurida* showing  
projections. X 1 050.

Another particularly noteworthy feature of some of the study OTUs is the structure of the most distal antennal segment. In various taxa there are large projections arising from the antennal tip which seem to be outgrowths of the antennal surface rather than conventional sensilla. Behind, and ringing these projections are blunt-headed non-fluted basiconics (figs 3.6 - 3.9). *Character 40. End of antennae with projections arising as an outgrowth from the antennal surface (1); No such projections (0).*

The genera traditionally grouped in the tribe Poemenini have the most varied antennal structures among the study OTUs. *Deuteroxoides* and *Podoschistus* both have antennae with a very short penultimate distal segment (fig 3.11). *Neoxorides* shares this character state but has a very distinct structure to the last few segments of the antenna (fig 3.10). *Character 41. Penultimate segment of the antenna less than 0.5 the length of the final segment (1); penultimate segment greater than 0.5 the length of the final segment (0).*

### 3.3 Thorax

#### 3.3.1. Introduction

The thoracic terminology used here comes from Gibson (1985), Richards (1977) and Gauld & Bolton (1988).

#### 3.3.2. The prothorax

Three conditions of the dorsal part of the pronotum are found in pimplines. The first is a **posteriorly dipped collar**, where there is a dip just anterior to the mesoscutum which rises to run flat along the dorsal part of the pronotum and ends in a collar which may be reflexed posteriorly to form a lip or unreflexed (fig 3.13). This condition is found in a modified form in most acaenitines, except in *Coleocentrus* which has a very similar pronotal structure to that

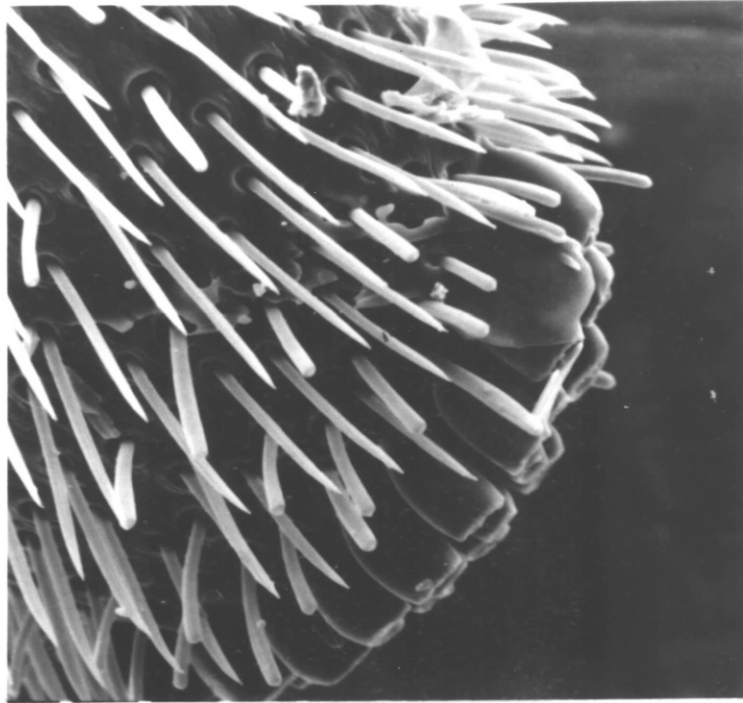


Fig 3.7. Tip of apical segment of antenna of *Pimpla hypochondriaca* showing projections. X 1 020.

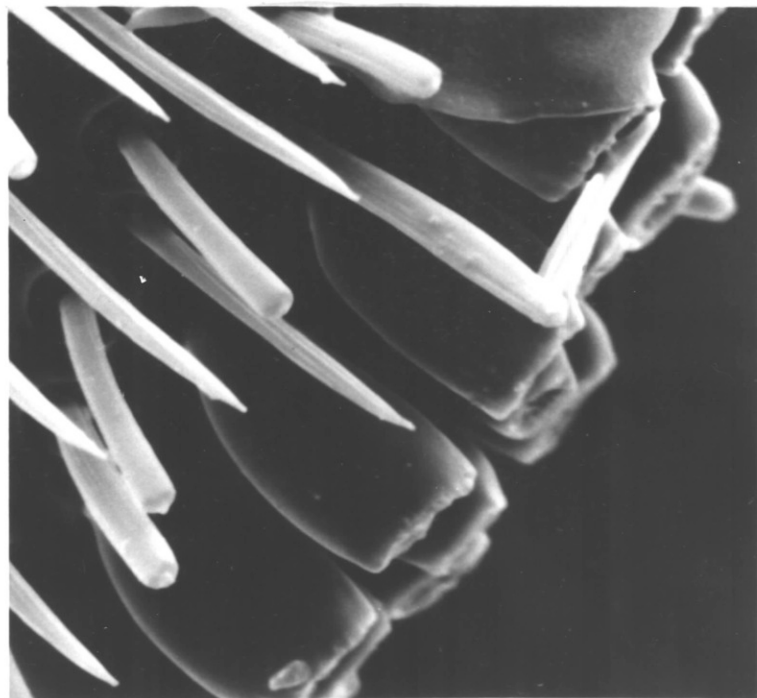


Fig 3.8. High magnification view of *Pimpla hypochondrica* antennal projections. X 2 600.

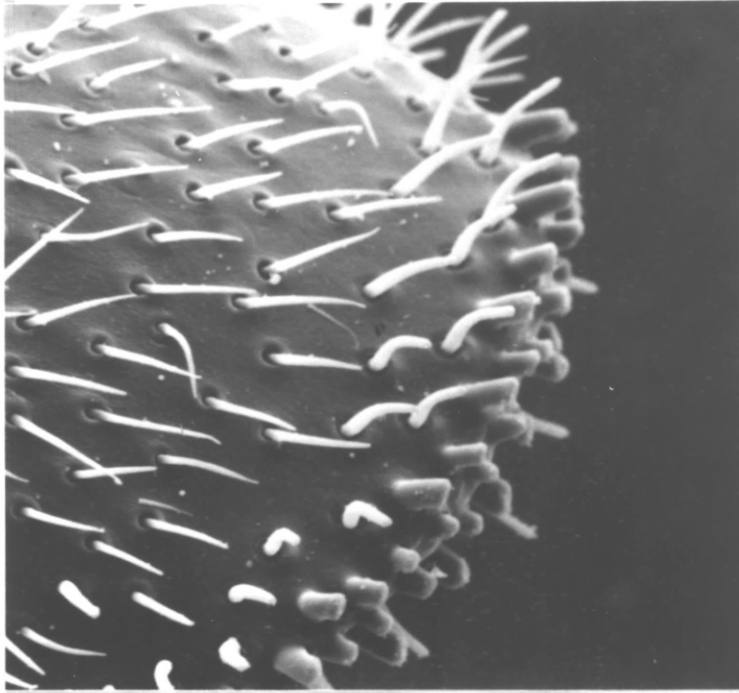


Fig 3.9. Tip of apical antennal segment of *Itoplectis maculator* showing projections. X 1 070.

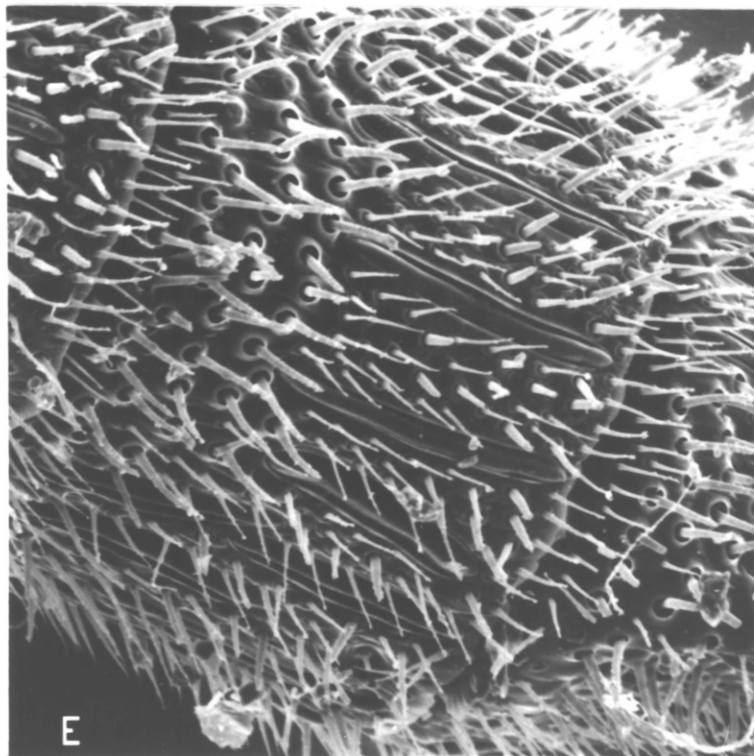


Fig 3.10. Penultimate apical segment of antenna of *Neoxorides collaris*. X 800.

described here. Presence of this structure is therefore plesiomorphic. *Character 42. Pronotum posteriorly dipped, with a weak to strong anterior collar (0); pronotum not like this (1)*

A variant of the posteriorly dipped collar occurs in a few taxa. The dip occurs immediately at the mesoscutal edge so that the collar itself is closely adjacent to the mesoscutum. This character state is apomorphic. *Character 43. Pronotum dorsally very short, collar, if present, close to the anterior edge of the mesoscutum (1); pronotum dorsally not short, collar, if present, not close to the mesoscutum (0).*

In the second condition of the pronotum the area between mesoscutum and collar is flat, forming a wide banded collar. This occurs only in the genus *Diacritus* and so is not phylogenetically informative.

The third condition is referred to here as the anteriorly dipped collar; where the area between the mesoscutum and pronotum is undipped but there is dip at the anterior of the pronotum which often forms a wide flange, often perforate, over the neck region (fig 3.14). No outgroup taxon has this character state. *Characters 44.1, 44.2. Pronotum dorsally forming a pronounced collar which drops immediately into a deep groove - collar perforate (1,1); pronotum dorsally forming a pronounced collar which drops immediately into a shallow groove (1,0); pronotum not dropping immediately behind collar, or no collar present (0,0).*

In addition to these dorsal features of the pronotum some OTU's have the lower part of the epomia sharp and on a ridge which runs parallel to the ventral margin of the pronotum (fig 3.12). This ridge is clearly visible on either side of the mesoscutum looking on to the dorsal surface of the thorax. This character is not present in any of the outgroup taxa, where the epomia, when present, runs up the pronotum at an angle to its ventral surface. *Character 45. Epomia strong basally and on a ridge that runs parallel to the lower margin of the pronotum (1); epomia not like this (0).*

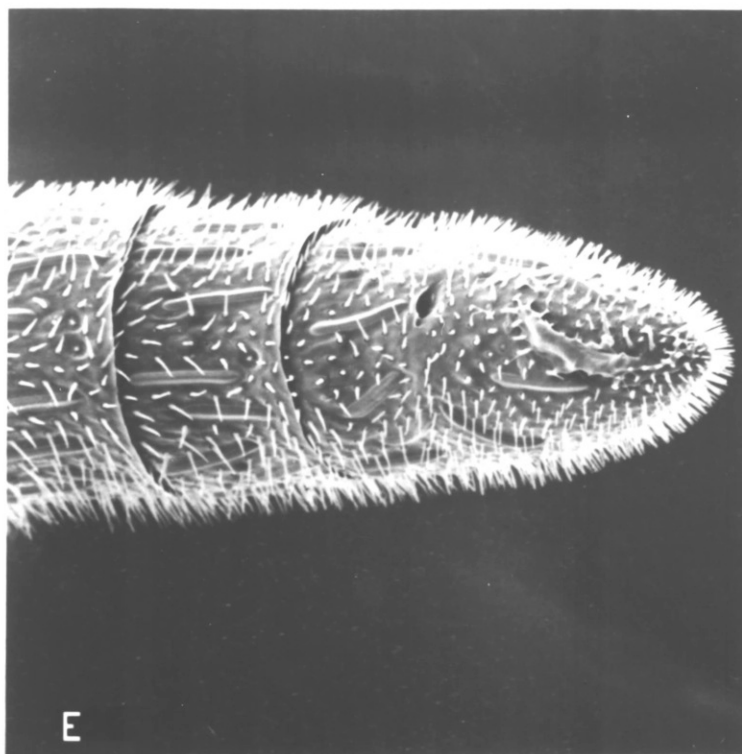


Fig 3.11. Apical segments of antenna of *Podoschistus scutellaris*.  
X 300.

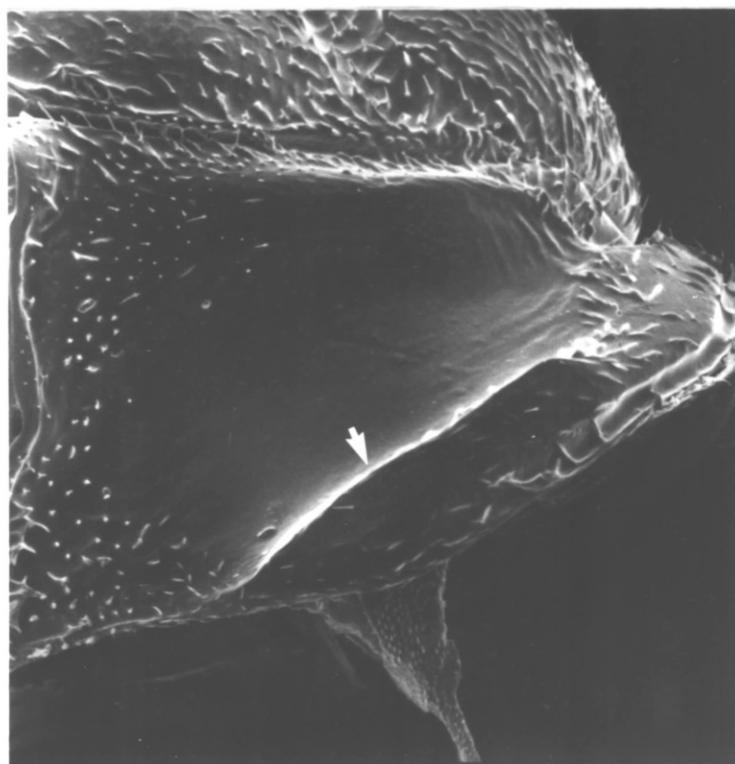


Fig 3.12. Pronotum of *Neoxorides collaris*. White arrow points to  
raised epomia. X 60.

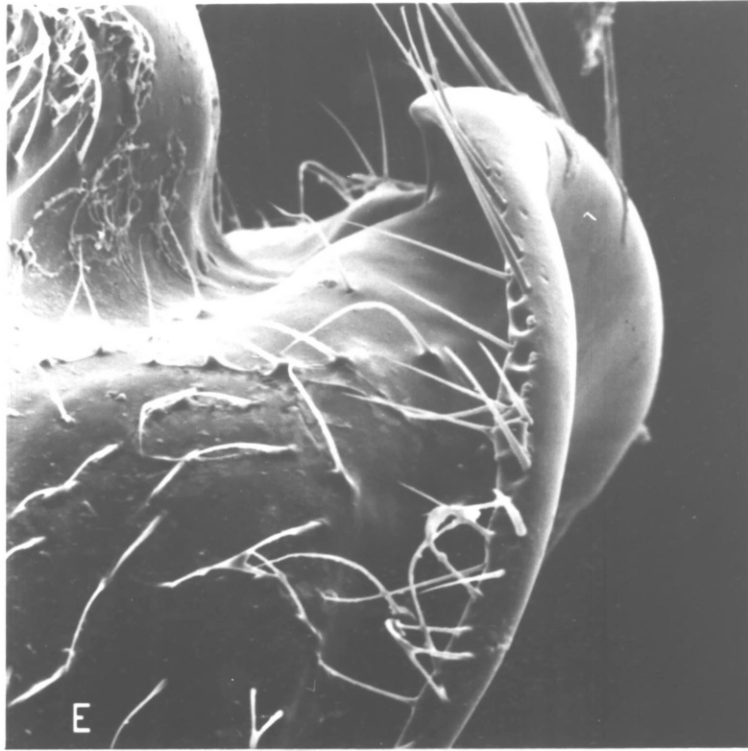


Fig 3.13. Posteriorly dipping pronotum and pronotal collar of *Afrephialtes cicatricosa*. X 250.

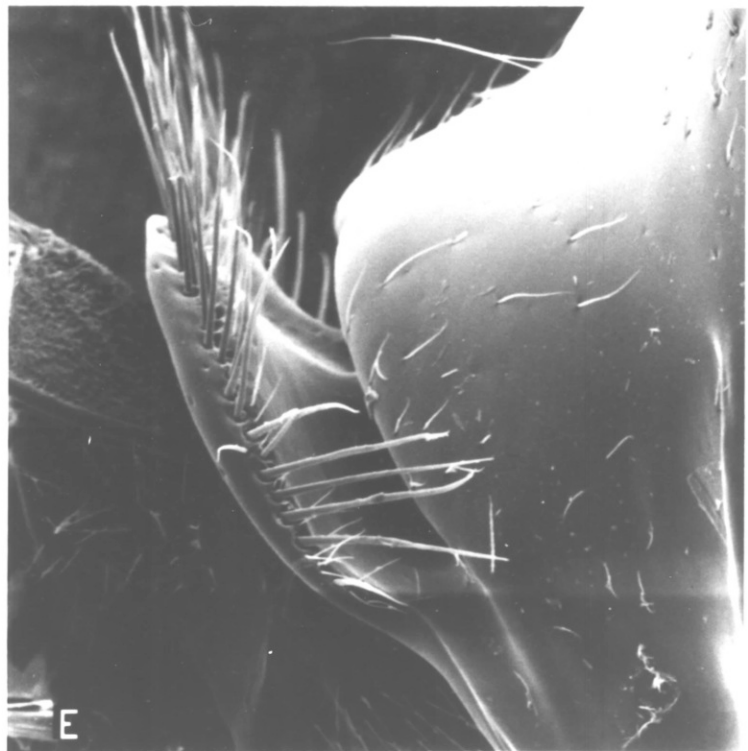


Fig 3.14. Anteriorly dipping pronotum and pronotal collar of *Epirhyssa flavopictum*. X 150.

### 3.3.3. The mesothorax

The mesothorax consists, dorsally, of a two flat slightly rounded structures the scutellum and the mesoscutum. The mesoscutum usually ends anteriorly in a median mesoscutal lobe bounded on both sides by the notauli which converge posteriorly. The notauli are primitively the site of phragmata and mark the separation of the dorsolongitudinal and dorsoventral indirect flight muscles (Gibson, 1985). In outgroups the notauli are variably present and seem, throughout the Ichneumonoidea to have been lost in many lines. For example, within the presumably holophyletic labenine genus *Certonotus* there are species with very strong through weak and even vestigial notauli. Within the pimelines this is also true, with all states of this character being found in most groups. This character forms part of the Townes data set (see section 2.4.3). The presence of the median mesoscutal lobe is intimately connected with this character as the lobe is delineated by the carinae or sulci of the notauli. This makes it a correlated character and it is of little phylogenetic significance.

Transverse mesoscutal ridges can be found in many non-pimpline groups (labenines, aulacids, ibaliids). Within the study OTUs, they are found in all the rhyssines and the genus *Pseudorhyssa*. They are almost definitely not homologous. No trace of parapsidal lines can be seen in rhyssines while in *Pseudorhyssa* two punctate lines arise from the lateral portions of the anterior of the mesoscutum and continue to the posterior portion parallel to each other. They there mark the boundary of the ridged area (fig 3.17) and are thus unlike the rhyssine condition (fig 3.18). *Revised character 10. Mesoscutal ridges clearly present on dorsal part of mesoscutum but never with a pair of punctate grooves running antero-posteriorly close to the side of the mesoscutum (1); ridges absent, only faintly or incompletely present, or with a pair of punctate grooves (0)*

Running forward from the posterior end of the mesoscutum as a pair of lines, sulci or carinae, are the parapsidal lines. These are the

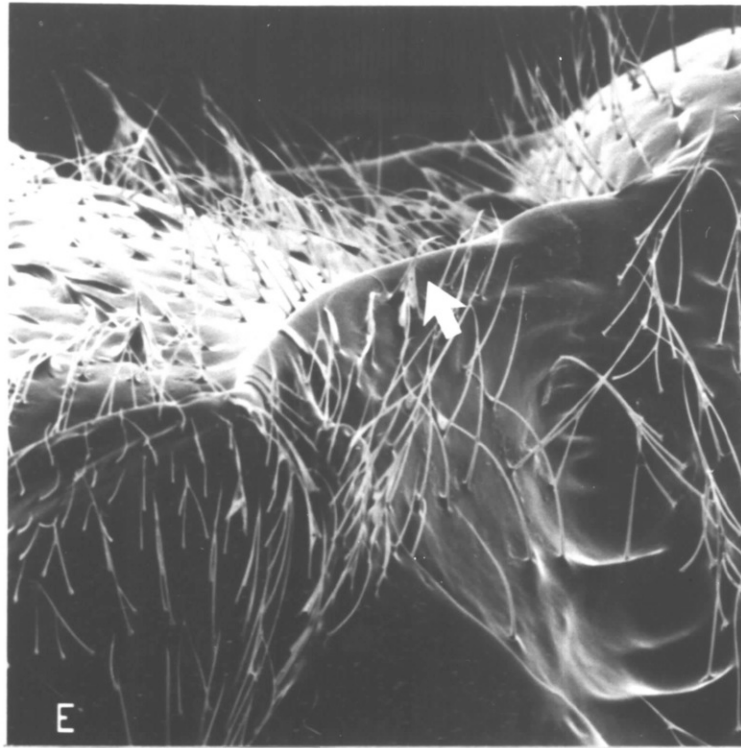


Fig 3.15. Raised parascutal carina of *Pimpla hypochondriaca*. Arrow shows position of carina.

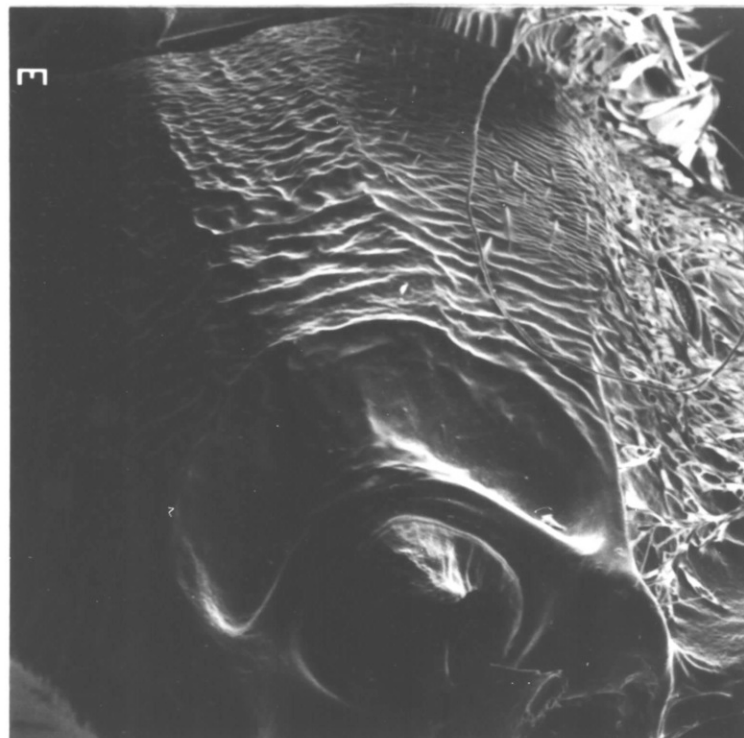


Fig 3.16. Propodeum of *Neoxorides collaris*, showing bowed pattern of the posterior transverse carina. X 70.

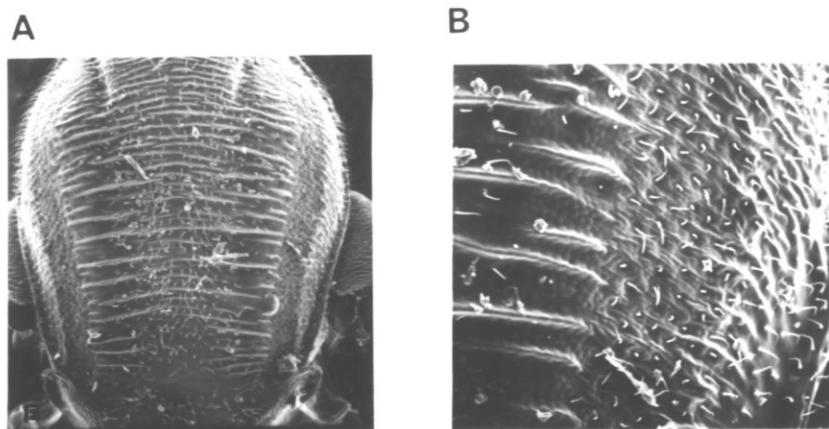


Fig 3.17. (a) Dorsal view of mesoscutum of *Pseudorhyssa sternata*. X 50. (b) Higher magnification view of mesoscutum showing punctate line. X 200.

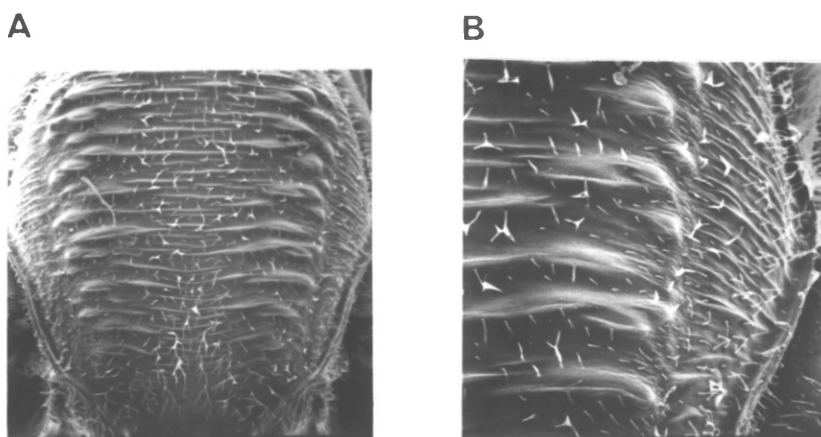


Fig 3.18. (a) Dorsal view of mesoscutum of *Rhyssa persuasoria*. X 50. (b) Higher magnification view of mesoscutum showing absence of punctate line. X 200.

remnants of the attachment of the dorsoventral indirect flight muscles in the pupa (Gibson, 1985). In the Ichneumonoidea as a whole, they occur uncommonly. They are not present in the braconid subfamilies, the Spathiinae and the Braconinae, which often show otherwise relatively underderived thoracic features. In the Ichneumonidae they are very rarely present, perhaps being visible as faint lines in various Xoridines (such as various species in the genus *Xorides*). The only subfamily where they occur obviously and consistently is the Labeninae, where parapsidal lines are clearly marked on the mesoscutum in many genera. Within the pimelines, only *Pseudorhyssa* shows any sign of possessing these features. Here, there is a punctate area bounding the mesoscutal ridges laterally which may indicate the position of the parapsidal lines. Its absence is clearly apomorphic. As only one taxon in the study OTUs shows the plesiomorphic condition, which is rare throughout the Ichneumonidae in any case, this character is of no phylogenetic significance.

A carina or suture runs laterally across the mesoscutum (the transscutal articulation) in several sawfly groups. The transscutal articulation is usually present on the side of the mesoscutum in ichneumonids, but in very few genera of pimelines does the suture extend further than the junction of the three axilla-associated carina (see below) and on to the top of the mesoscutum. It is faintly present laterally in *Afrephialtes*, and quite strong in *Dreisbachia* and *Pseudorhyssa*. Its loss seems to be apomorphic within the Ichneumonoidea. The Xoridinae are possibly the only ichneumonids where most species have the transscutal articulation present laterally and medially, at times forming a complete carina running across the mesoscutum, although the Anomaloninae clearly have this feature secondarily (Gauld, 1976). Other ichneumonids seem to have it present only laterally or, most commonly, it is entirely absent. In other primitive parasitica groups a complete transscutal articulation is, with a few exceptions, always present (Evaniioidea; Stephanoidea; Megalyridae). When present in ichneumonids it is always found close to the scutellum. as it is in Evaniids - in other groups it is usually distant from the scutellum. *Character 46. Transscutal articulation present as a short lateral carina reaching*

up onto the dorsal part of the mesoscutum (0); transscutal articulation either present only as a stub, not reaching up onto the dorsal part of the mesoscutum, or not present (1).

The transscutal articulation joins laterally with two other carinae; one running along the lateral edge of the mesoscutum (the parascutal carina) and the other delimiting the axillar surfaces (see below) (the axillar carina *sensu* Gibson). In nearly all pimplines the transscutal articulation runs up to the parascutal carina so that there is an equal angle between each of the three carinae. Comparing this with the outgroups it seems likely that this is the primitive condition. Xoridines seems to have the least derived mesothorax amongst ichneumonoids and they have the character as above. Spathiine braconids also possess equal angled junctions. The variations from this condition are listed below.

The axillar carina is often raised into a crest or ridge in the study OTUs. As the outgroups often have the axillar carina raised as a ridge its absence is apomorphic. *Character 47. Axillar carina present as a strong ridge like structure (0); axillar carina present as raised or punctate line (1).*

In several OTU's the axillar carina is obsolescent toward the junction and above the junction the parascutal carina forms a crest (fig 3.15). This is the apomorphic state. *Character 48. Parascutal carina formed into a crest (1); parascutal carina not formed into a crest (0)*

In *Podoschistus* the axillar carina meets the parascutal carina above the junction of parascutal carina and transscutal articulation. This is the case also in *Lytarmes* and *Epirhyssa* where the axillar carina is very weak. This is the apomorphic state. *Character 49. Axillar carina as above (1); axillar carina meets the parascutal carina at the junction of the parascutal carina and transscutal articulation (0).*

The axillar carina delineates two surfaces that make up the axilla

(the dorsal axillar surface and the lateral axillar surface). The axilla is bounded anteriorly by the transscutal articulation, and posteriorly by the scutellum. In most Ichneumonoidea it consists of the two surfaces at roughly right angles to each other with the axillar carina forming the immovable "hinge". This is the state in xoridines and doryctiine braconids, and other primitive apocritans. Amongst pimelines the surfaces are sometimes at greater angles than this, and sometimes they form an almost flat plate (*Theronia*) with a very weak axillar carina. In *Lytarmes* and *Epirhyssa* the axillar plate protrudes above the mesoscutum to form a ridge on the parascutal carina. This also occurs in the outgroup genus *Certonotus*. In this case, though, the plate is without a carina, and is much longer and broader running contiguously down to the forewing base. *Character 50. Axillary surfaces contiguous forming an angle of less than 40° with respect to each other (1); axillary surfaces forming an angle of greater than 40° with respect to each other (0).*

#### 3.3.4. Thoracic musculature

Thoracic musculature is conservative throughout the Ichneumonoidea. Within the pimelines and rhyssines there is very little variation in the only structure they possess which might be of phylogenetic significance (Gibson, 1985) - the mesotrochanteral depressor, which is the muscle originating from the posterior part of the mesoscutum and running down to the mesotrochanter. It consists plesiomorphically, in non-tenthredinoid sawflies, of two elements (the mesotergal-trochanteral depressor and the mesofurcal-trochanteral depressor). In ichneumonoids it consists only of the mesofurcal element, which is the condition found in all pimelines studied. The study OTUs show no variation and this character is therefore of no use in phylogenetic reconstruction.

### 3.3.5. Wings

Fore and hind-wing venation is similar in most groups which have been studied. The shape of the cell in the forewing bounded by veins 2rs-m, 2r-rs, M and 3rs-m (the areolet) appears to be very different in some groups of pimelines than others. However, this structure of the areolet is related to a general pattern of reduction in the vein 3rs-m, which seems plesiomorphically to intercept 2r-rs (or Rs) (fig 3.19) and during evolutionary history seems to have, in several independent lines, tended to move down onto 2rs-m (fig 3.20) before disappearing altogether (fig 3.21). As the same evolutionary sequence has occurred in several lines outside the Pimplinae (Richards, 1977; Gauld & Bolton, 1988) it does not seem to be a good phylogenetic character at this level. This is borne out by the high level of homoplasy in character 20 of the Townes data set.

In nearly all pimelines there are two folds in the forewing that lead to the presence of two fenestrae (or bullae) in vein 2m-cu. In a few genera, however, the folds converge to give the appearance of there being only one fenestra in the vein. The presence of two fenestrae is universal amongst the outgroups, indicating that the presence of one fenestra is apomorphic. *Character 51. One fenestra in vein 2m-cu of the forewing (0); two fenestrae in vein 2m-cu of the forewing (1)*

The number of hamuli in the hind-wing is very variable within the pimelines. Richards (1949) shows that there is a correlation between hamuli number and body size in aculeates. Clearly this character is size-related and therefore of no phylogenetic significance.

### 3.3.6. Legs

The tarsal claw tooth character as described in chapter 1 seems to be an expression of an analagous and not homologous state in the pimpline and poemeniine groups. In poemeniines it forms a clearly square peg-like structure, while in pimelines the tooth is a large

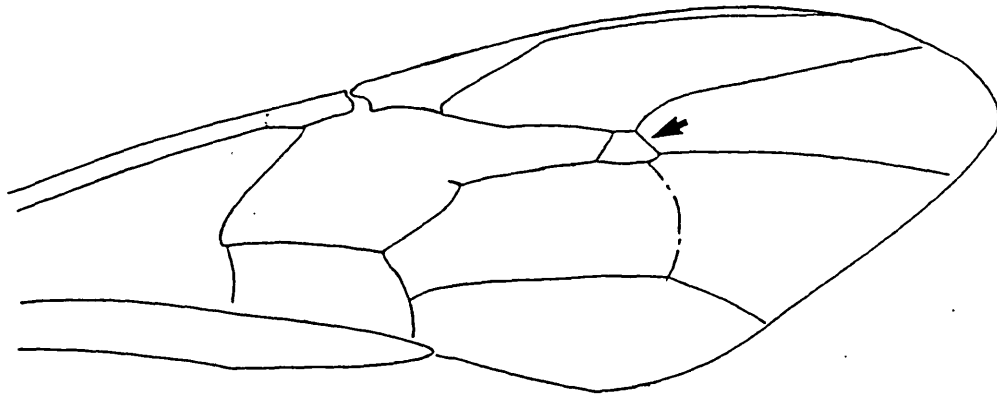


Fig 3.19. Forewing of *Dolichomitus imperator*. Arrow shows position of vein 3rs-m.

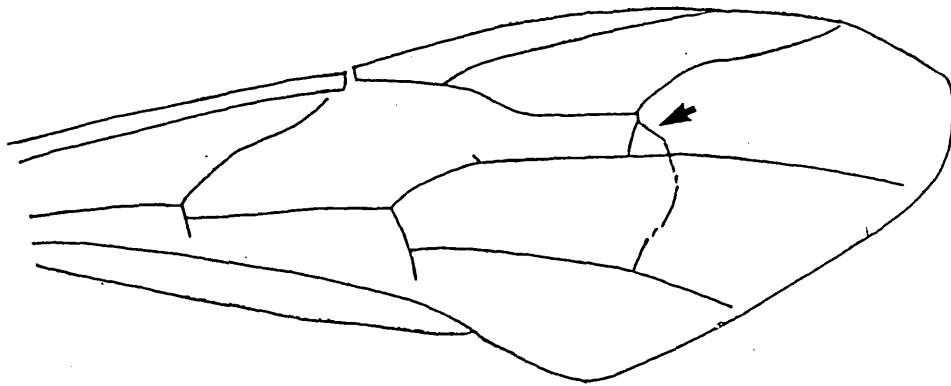


Fig 3.20. Forewing of *Rhyssella approximator*. Arrow shows position of vein 3rs-m.

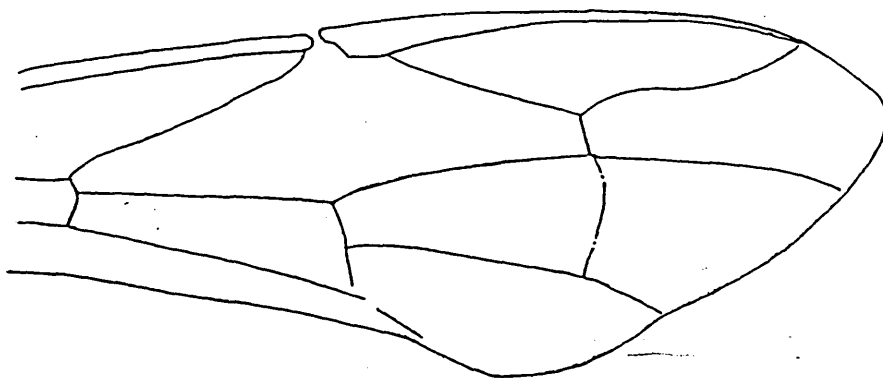


Fig 3.21. Forewing of *Epirhyssa flavopictum*. Note lack of vein 3rs-m.

rounded structure. *Revised characters 18.1 and 18.2. Female tarsal claw with rounded tooth (1,0); female tarsal claw with peg-like tooth (0,1).*

### 3.4. Abdomen

#### 3.4.1. Propodeal carination

As noted in chapter 2, propodeal carination tends to be reduced over evolutionary time across all the Hymenoptera. This leads to the recognition of rather homoplastic reduction characters except when the pattern of carination can clearly be seen to be derived from some unique conformation. One such case seems to be the retention of the posterior transverse carina in certain pimpline genera (fig 3.16). No closely related taxon seems to show this particular pattern of propodeal carination. *Character 52. Transverse posterior carina of propodeum strong, while the rest of the propodeum is unareolated (1); transverse carina weak, or strong but with a strongly areolated propodeum (0).*

#### 3.4.2. Attachment of gaster to propodeum

In all the study OTUs this is fairly low down and by means of a sturdy non-cylindrical fused or unfused tergite and sternite 1. Other groups share this type of attachment, including acaenitines, oxytorines, and orthocentrines. This is undoubtedly a plesiomorphic character state and of no information content as all pimplines have it.

#### 3.4.3 (Gastral tergites

The junction between tergite 1 and tergite 2 is very characteristic in various large pimplines, especially *Dolichomitus* and *Pseudorhyssa* forming a hinge like-structure. However, this character is very common

amongst the Ichneumonoidea, especially in the large wood-associated taxa (doryctines, some labenines, some acaenitines) and is undoubtedly plesiomorphic.

Tergite 9 is extended some distance beyond the insertion of the ovipositor in several of the studied taxa. In some groups where this occurs the tergite ends in a horn and is usually dorsally distinctly bipartite (fig 3.22) and in others there is no segmentation and no horn (fig 3.23). It is clear that these states are not homologous but outgroup comparison shows both states to be apomorphic. This requires the Townes set character 30 to be redefined. *Revised character 28. Tergite 9 extended apically, forming one continuous structure (1); tergite 9 extended apically and split into two parts, with an apical horn or boss or not extended apically (0,0).*

### 3.5. Ovipositor complex

#### 3.5.1. Tergite 9

In ichneumonids tergite 9 is covered almost completely posteriorly by the preceding tergites, and is much reduced and only lightly sclerotised. Tergite 9 probably moves gonocoxite 8 rather than acting as an immovable base, as is the case in the ovipositor complexes of more primitive Symphyta. One set of muscles attach to the gonopophysis 9 hook, which is fused to form a single structure. Tergite 9 is split into two except at the posterior end. Tergite 10 and tergite 11 are usually much reduced or absent (Smith, 1970; Fergusson, 1988).

It is usual for there to be a distinct phragmata on the dorsal edge of tergite 9 in Ichneumonidae (fig 3.25). In the study OTUs this tergite 9 phragmata is present in almost all groups but there are some OTU's where it is not present. It represents the attachment site for the lateral internal dorsal muscle (Smith, 1969) and its presence and size is probably dependent on how rigidly the ovipositor

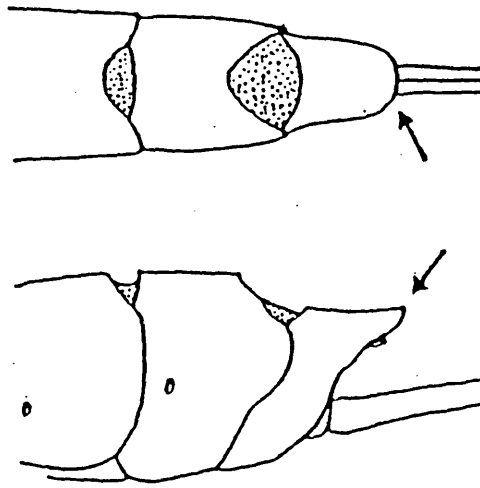


Fig 3.22. Posterior gastral tergites of *Pseudorhyssa alpestris*, arrows point to extended tergite 9. (From Fitton et al 1988)

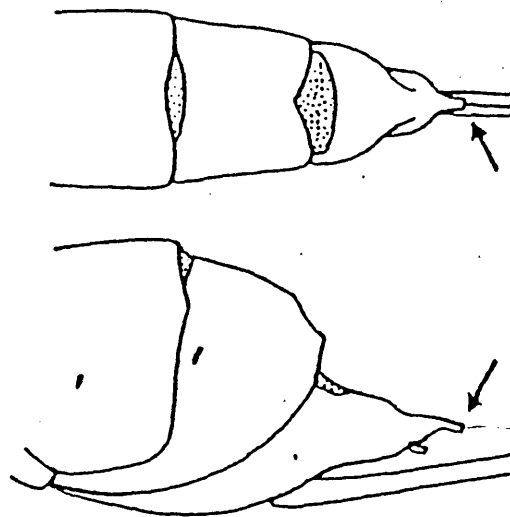


Fig 3.23. Posterior gastral tergites of *Rhyssella approximator*, arrows point to extended tergite 9. (From Fitton et al, 1988)

complex is held during oviposition. In the presently recognised tribe Pimplini and *Theronia* ("stabbers") it is a very large and robust structure, while in the other genera it is often small as in *Pseudorhyssa* or only lightly sclerotised as in *Scambus* and *Endromopoda* (both groups being "probers"). Outgroups universally show the presence of a tergite 9 phragmata. Character 53. Phragmata of tergite 9 present (0); phragmata of tergite 9 absent (1).

### 3.5.2. Ovipositor

The ovipositor is of varying lengths amongst the pimplines (see character 32 of the Townes set). The end of the ovipositor may be hooked (in *Apechthis* and some *Xanthopimpla*); complete with very strong teeth (as in most rhyssines); or sinuate (as in *Hybomischus* and *Myllenyxis*). These characters, at most, provide autapomorphies for single genera. The ovipositor also shows a great difference in thickness, between 'stabbers' where it is relatively robust (the Pimplini); 'drillers' where it is thinner (the Rhyssini); and 'probers' where it is long and often extremely thin (many of the Ephialtini and *Pseudorhyssa*). As these variations often occur within a single genus (*Xanthopimpla*, for example) and in no easily phylogenetically explicable way they have been rejected as a possible source of characters.

### 3.5.3. Gonostylus 9 (ovipositor sheath)

This structure covers the ovipositor at rest. It is supplied, in the plesiomorphic state, with three muscles: the dorsal tergogonostylar muscle; the lateral tergogonostylar muscle; and the gonocoxostylar muscle (Smith, 1969, 1970). All three muscles are present in most ichneumonids.

In pimplines the gonocoxostylar muscle is usually inserted into the top of the gonostylus via a simple flat apodeme. The only variant of this is <sup>where</sup> there is a bulging out of the top-surface of the gonostylus

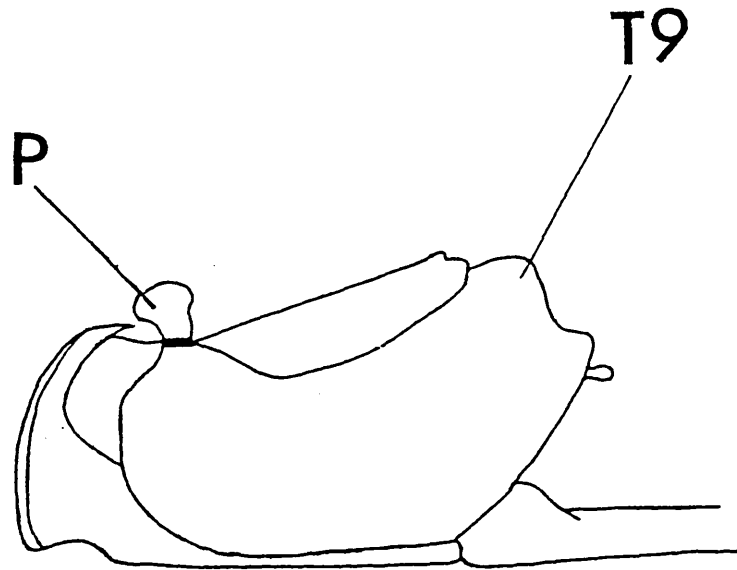


Fig 3.24. Diagram of ovipositor complex of *Exeristes roborator*, showing phragmata (P) on tergite 9 (T9).

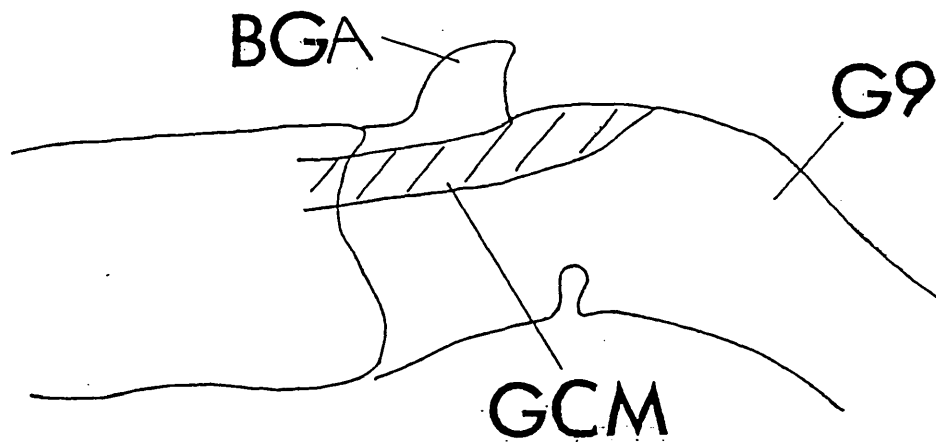


Fig 3.25. Diagram of Gonostylus 9 (G9: ovipositor sheath) of *Pimpla hypochondriaca* showing bulbous gonocoxostylar apodeme (BGA) and the large gonocoxostylar muscle (GCM)

27

to form a large muscle attachment site (called here the **bulbous gonocoxostylar apodeme**) Distal and ventral to this apodeme there is a constricted area (fig 3.24). This apodeme has a large gonocoxostylar muscle running into it and slightly distal to it. This allows the characteristic flick of the gonostylus away from the ovipositor seen in the group. In other pimelines with long ovipositors the apodeme is often very small, and the gonostylus relatively immobile. *Character 54. Bulbous apodeme of gonostylus 9 present only as a small cavity (0); large and forming a plate-like structure externally followed by a constriction posteriorly(1).*

### 3.6. Larval structures

The character which has been used as an autapomorphy of the pimelines - the hypostomal spur nearly meeting the stipital sclerite in the final instar larva, was discussed in chapter 2 where it was concluded that it was a plesiomorphy (cf. Wahl, in press). The only departure from this state seems to occur in *Neoxorides* where the hypostomal spur and stipital sclerite are fused. Although this state must be apomorphic, there is not enough information about other pimline final instar larvae available to conclude if this is an autapomorphy of the genus or more widely, and more phylogenetically informatively, distributed.

### 3.7. Results

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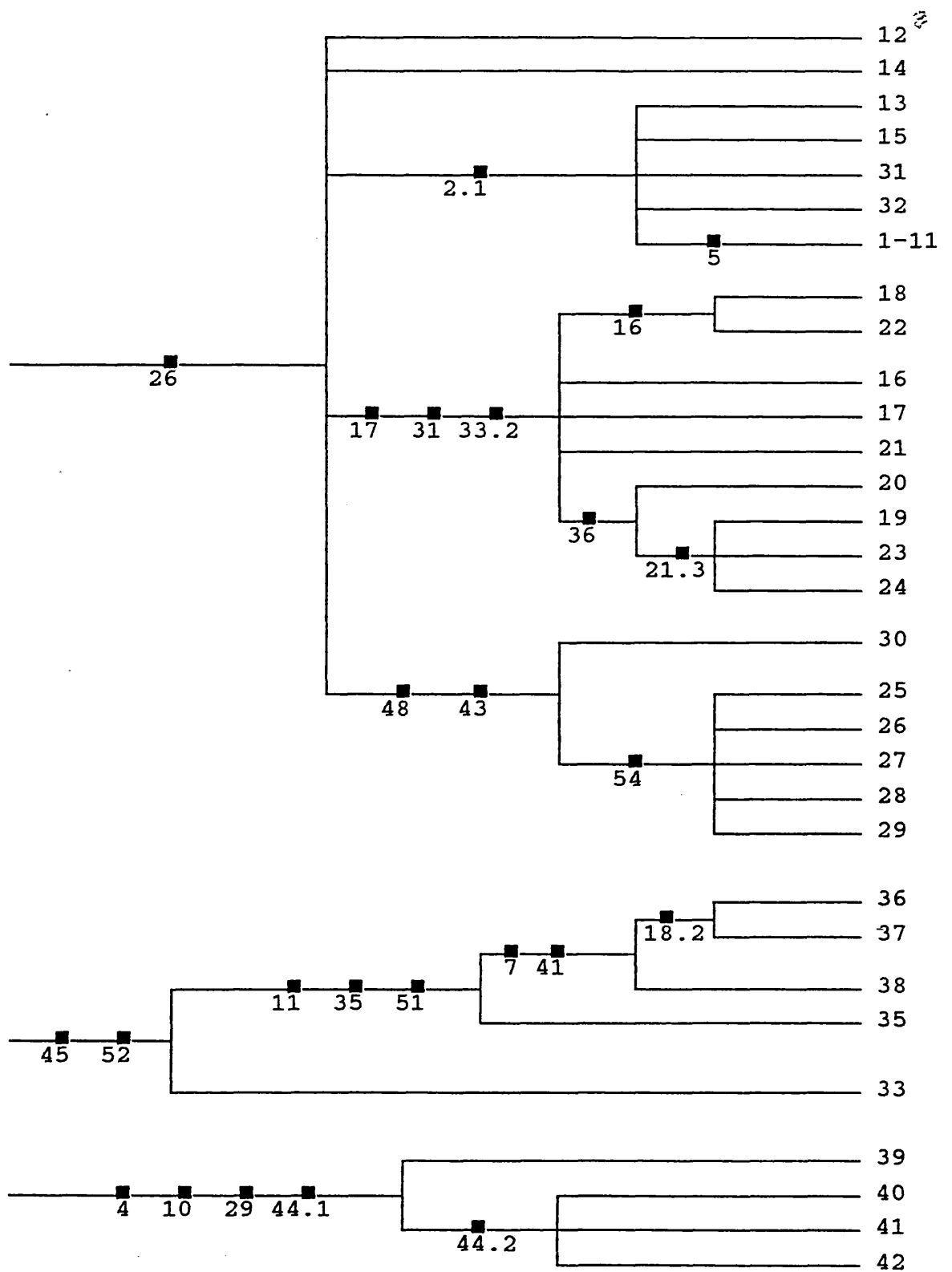
The overall Randomness Ratio for this data set is 0.68. This is significantly smaller than the RR for the Townes data set. One character (42) which ends up in the cliques shows 10 polar incompatibilities. However, it is not polar incompatible with any of the other characters in the final clique.

#### 3.7.1. Cladograms: initial analyses

The initial cladogram for this data set is shown in fig 3.26. This is the LEQU cladogram and it shows a much clearer grouping of the taxa than those in chapter 2. Four main, and unconnected lines, can be observed; first, the rhyssines; second, the poemenines and *Pseudorhyssa*; third, the remaining pimelines; and fourth, *Diacritus* on its own and with no obvious close relatives. This seems to be a reasonable representation of relationship, and the three groups, although holophyletic themselves are, at best, paraphyletic in relation to one other. The O'NOMOD cladogram differs from the LEQU only in the last character that is rejected from the analysis, character 33.1, and this is discussed in the section below. The LEQU cladogram is presented here as it is the unweighted analysis and therefore the more objective. Even without considerations of homoplasy a number of new groupings can be discerned within the pimelines they are listed below.

(b) *Pseudorhyssa* is placed along with the Poemenines in a clade, and this grouping is supported by two characters (45 and 52). This clade shares no synapomorphies with other clades produced by the analysis.

(c) *Theronia* and the Pimplini are grouped together in a clade supported by two characters (48 and 43).



Key: ■ - apomorphy.

Fig 3.26. LEQU/PROB Cladogram for the pimpline data set.

(d) The tribe Delomeristini is not supported by the cladogram. Its constituent parts are split between the 'poemenine-group' ((a) above), the 'pimpline-group' ((b) above), and the 'ephialtine-group' where *Delomerista* (taxon 32) and *Perithous* (taxon 31) are placed.

(d) The Rhyssini are clearly delineated by a number of characters (4, 10, 29, 44.1). This clade shares no synapomorphies with other clades produced by the analysis.

Trees can now be constructed from the cladogram by consideration of characters rejected late in the LEQU boil-down analysis.

### 3.7.2. Trees: phylogenetic hypotheses

By reintroducing the last few characters to be thrown out in the boil down it is possible to postulate reversals and parallelisms that would make rejected characters fit into the clique (Gauld & Underwood, 1986). These are listed and discussed below. The diagram resulting from this discussion is a hypothetical tree as discussed in chapter 1 (Tattersall & Eldredge, 1978).

(a) Character 33.1. This character can be fitted into the clique in two ways: first, a parallelism in taxon 13 for character 2.1; second, a reversal in the clade delineated by character 33.1. Although the first is the most parsimonious solution it is rejected for a variety of reasons. The primary reason lies in the nature of character 2.1. It is a character which seems to delineate the basal group of the ephialtine genera (i.e. the old Ephialtini and Polysphinctini), and under these circumstances reversals seem much more likely events than parallelisms, see chapter 1. Considerations of the evolution of biological characters also suggest that taxon 13 should be placed within the clade suggested by character 33.1 (see chapter 4). In addition, within the genus *Tromatobia* (taxon 12) character 2.1 can be either present or absent, showing that the reduction of the bilobed clypeus to its plesiomorphic state has certainly occurred in related taxa.

(b) Character 40. This character can be fitted into the clique by postulating a reversal in taxa 28 and 29. This character now becomes an autapomorphy of *Theronia* and the old tribe Pimplini.

(c) Character 2.2. This character can be fitted into the clique by postulating one reversal in taxon 33. This character originally grouped taxon 33 (*Pseudorhyssa*) with the Rhyssini. However, there is now evidence to support taxon 33 as part of the poemeniine-group of taxa, and so a parallelism is postulated here. This character seems to form part of a suite of related wood-associated characters which are discussed in some detail below (chapter 4).

(d) Character 18.1. This character requires 6 reversals to enter the clique (in taxa 31, 32, 30, 27, 28, 29 - although only 4 if a single loss in taxa 27, 28 and 29 is accepted, but I have not indicated this relationship in the tree diagram). However, the general comments for character 2.1 also apply here as this character is right at the base of the pimpline groups excepting the poemeniine-group and the rhyssines.

(e) Character 37. This links taxon 35, 36 and 37. One reversal in taxon 38 places this in the clique.

A subset analysis of some of the holophyletic groups in the analysis is now performed with the initial study OTUs.

### 3.7.3. Subset analyses

The following holophyletic subsets were re-analysed, using the methods outlined in chapter 1:

1. The ephialtine, polysphinctine and pimpline genera (1-32)
2. The poemeniine genera (33, 35-38)
3. The ephialtine and polysphinctine genera (1-24, 31-32)

#### 4. The pimpline genera (25-30)

#### 5. The rhyssine genera (39-42)

The five analyses produced only one character which was incompatible overall but compatible within a subset. This was character 12 which is the old autapomorphic character for the Pimplini (without *Theronia*) which had not previously entered the clique due to a parallelism with the rhyssines (see chapter 2). Two of the subset analyses (2 and 5) were upon such small numbers of taxa that a large number of homoplastic characters were included in the cliques that would require a unacceptable level of parallelism with other groups in order to be accepted. This tends to occur with all very small subset analyses. For this reason they have not been allowed into the cliques.

The final hypothetical tree for the study OTUs is shown in fig 3.27. These are the conjectured evolutionary relationships that will be used for a consideration of the evolution of host-preferences in chapter 4. A detailed cladistic analysis of the rhyssines is postponed until chapter 5.

The various groupings will now be examined in more detail, with genera outside the study group being examined to see how they might fit into the hypothetical tree. A rigorous cladistic method has not been used for the next section, and these comments must be considered provisional.

### 3.8. The Holophyletic Groups

#### 3.8.1. The poemeniine group

Three genera of this group were not included in the study OTUs: two Oriental genera - *Euglata* and *Cnastis*; and one Neotropical one - *Ganodes*. All three seem to be close to *Neoxorides*, in that they have

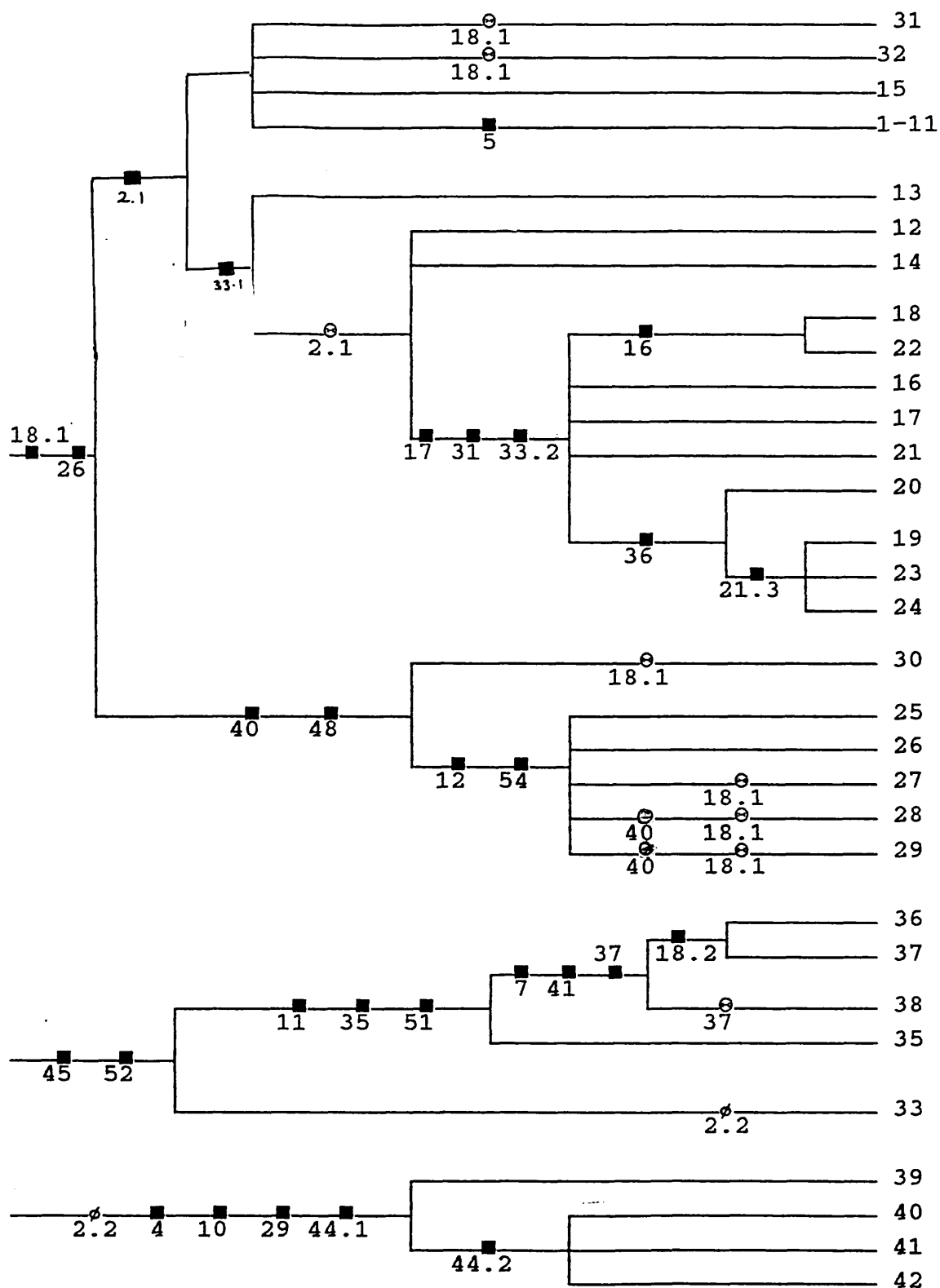


Fig 3.27. Final hypothetical tree for the pimpline data set.

8

a characteristic bending back of the last few antennal segments so that a highly specialised series of antennal sensilla (fig 3.10) can come into contact with the substrate. This bending can also be seen in *Podoschistus*, although it is less pronounced.

Both *Deuteroxoides* and *Poemenia* lack the specialisation of the antennae found in the other groups. In addition they have much less pronounced (*Deuteroxoides*) or absent (*Poemenia*) scabrous areas on the dorsal part of the temple. These changes clearly indicate an evolutionary sequence but its polarity is somewhat in doubt. For the time being it is assumed that *Poemenia* is the least specialised of the higher poemenines and that *Deuteroxoides* is intermediate between *Poemenia* and the *Neoxorides*-group. Unfortunately, *Poemenia*, which has a very different biology from the other, reasonably well studied, genera, may have secondarily lost the various features related to wood-boring in the other groups (see chapter 4), and its phylogenetic position could be very different from that conjectured in the hypothetical tree diagram.

It is clear that *Pseudorhyssa* is best placed within this clade. In the past it has been classified as a rhyssine (Morley, 1913; Kazmierczak, 1981), or as a delomeristine (Townes, 1969). The rhyssine-like characters have all been shown to be parallelisms (and see chapter 4 for the biological significance of this); and it is quite clear that the Delomeristini is a polyphyletic group. This leaves two characters supporting *Pseudorhyssa*'s membership of the poemenine clade - the structure of the epomia and the pattern of the propodeal carinae. *Pseudorhyssa* is undoubtedly the most primitive known poemenine.

The original hypothetical tree diagram supports these conclusions, except concerning the position of *Deuteroxoides* which is probably closer to *Poemenia* than to *Podoschistus*. It is clear that further taxonomic and phylogenetic work is needed to sort out both the generic classification of this group and its phylogenetic history. It is probable that a clearer idea about the relationships of the group will come about through the investigation of the immature forms

- especially the final instar larvae. Perhaps equally importantly, a great deal more needs to be discovered about the biology of the group.

It is recommended that the tribe Poemeniini be redefined as a subfamily: the Poemeniinae.

### 3.8.2. The Ephialtini

Townes (1969) splits the Ephialtini up into four groups; two of which have been included in the study OTUs: the *Ephialtes*-group, the (including the *Ephialtes*-subgroup (taxa 1-8); and the *Tromatobia*-subgroup (taxa 9-14)); and the *Pseudopimpla*-group (taxon 15). The other two groups outside the study OTUs are the *Alophosternum*-group (*Pachymelos* and *Alophosternum*) and the *Camptotypus*-group (5 genera in the Old and New World tropics).

The *Ephialtes*-group, corresponds roughly to the clade delineated by character 5; along with the clearly related taxa - 12,13 and 14. This seems to constitute a paraphyletic group. Within this group, the two subgroups that Townes recognises are supported uniquely only by characters which are either in the Townes test data set and did not enter the final clique or were rejected before the analysis as being too variable. Townes' based his groupings, in addition, upon biological characters which do delineate two separate groups (see chapter 4). The relationship seems to be that of a biologically specialised group (the *Tromatobia*-group *sensu* Townes - parasitoids of cocooned hosts) which has arisen from a biologically generalised group (the *Ephialtes*-group *sensu* Townes - parasitoids of organisms within softish plant tissue). The morphological changes associated with this shift seem to have been relatively small and difficult to identify as apomorphies (see chapter 4). In addition, the *Tromatobia*-group *sensu* Townes is itself paraphyletic, as the polysphinctines clearly arose from within it. For these reasons, a more broad unsplit *Ephialtes*-group is recognised here consisting of all species with dipped occipital carina. However, Townes' subgroups are used as

2

non-phylogenetic categories as they clearly refer to biologically homogenous groups. The three spider egg-sac parasitoids (*Tromatobia*, *Iseropus* and *Zagylptus*; the *Tromatobia*-group *sensu* Eggleton) are close to the polysphinctine clade, biologically, but for pragmatic reasons are recognised as a separate genus-group of the tribe Ephialtini. To summarise groups and characters:

(1) The *Ephialtes*-group. Characterised by the presence of a dipped occipital carina. This group consists of: OTU's 1-8 along with the following genera not included in the analysis: *Calliephialtes*, *Holcopimpla*, *Flavopimpla*, *Leptopimpla*, *Xanthophenax*, *Anastelgis*, *Pimplateus* and *Xanthephialtes* (the *Ephialtes*-subgroup *sensu* Townes 1969); and OTU's 9-11 along with *Sericopimpla* (part of the *Tromatobia*-group *sensu* Townes, which will be referred to here as the *Acropimpla*-subgroup, to separate it from the *Tromatobia*-group *sensu* Eggleton; the spider egg sac parasitoids mentioned above, which are closer to the Polysphinctini)

The remaining three groups have the occipital carina absent, at least at the mid-line. They do not seem to be phylogenetically very close to each other.

(2) *Pseudopimpla* is a very specialised ephialtine genus. Its affinities are uncertain.

(3) The *Alophosternum* group. Characterised by the presence of a rather densely hairy mesoscutum and an incomplete occipital carina. This is a very poorly defined group. This group consists of the genera *Alophosternum* and *Pachymelos*. Both genera are associated with leaf-mining larvae, and are probably not close to *Pseudopimpla*, the occipital carina being lost in parallel.

(4) The *Camptotypus*-group is distinctive in having the occipital carina almost entirely effaced. It is undoubtedly a specialised offshoot of the *Ephialtes*-group. This group consists of: *Camptotypus*, *Zonopimpla*, *Cenodontis*, *Odontopimpla* and *Clydonium*.

(5) The *Tromatobia*-group, discussed above.

Clearly, groups 2, 3 and 4 are derived from the *Ephialtes*-group. However, it is not clear which group of genera form the sister group of any of them.

Two genera (*Delomerista*, *Perithous* (and its sister group genus *Hybomischos*)) that were placed originally in the Delomeristini are probably best placed within the Ephialtini. Their possession of a medially notched clypeus fits them into this clade but they do not fit into any of the above groups. It is probable that they should be in the *Ephialtes*-group, but there are no obvious synapomorphies.

This ordering of taxa leaves the Ephialtini as a paraphyletic group, within which evolutionary relationships remain uncertain.

### 3.8.3. The Polysphinctini

Of the genera not used in the analysis *Zabrachypus* is rare and no specimen was available for study. *Afrosphincta* was placed by Townes as a genus close to *Schizopyga*, but examination of the holotype has shown that this is not the case (although it may be close to, or a synonym of, *Dreisbachia* (Gauld, 1984b)). *Millironia*, which Townes placed near *Eriostethus*, has been synonymised within *Eriostethus* (Gauld, 1984b). The affinities of the other genera are discussed below.

The polysphinctines can be split up into three natural groups:

(1) The *Schizopyga* group. This group is characterised by having the suture between the face clypeus weak or absent, the eyes sparsely to moderately hairy and the mesoscutum rather flattened. It comprises *Schizopyga* and *Dreisbachia*.

(2) The *Polysphincta*-group. This group is characterised by the having the submetapleural carina weak or not present. It consists of the largest polysphinctines with longish ovipositors. It comprises,

along with *Polysphincta*, of the two closely related Neotropical genera *Hymenoepimecis* and *Acrotaphus*.

(3) The *Acrodactyla*-group. This group is characterised by the possession of a three-segmented labial palp. It consists of *Piogaster* (which seems to be the least derived genus - see hypothetical tree diagram below), *Eriostethus*, *Sinarachna*, *Eruga*, *Zatypota* and *Acrodactyla*. The last three genera also seem to form a holophyletic subgroup.

Apomorphic character states used in the hypothetical tree diagram:

A. Suture line between face and clypeus weak or absent.

B. Eyes sparsely to moderately hairy.

C. Submetapleural carina weak or absent.

D. Labial palps 3-segmented.

E. Vein Cu of hindwing absent.

F. Vein M-Cu1 of hindwing strongly bent proximally.

G. Pronotal collar raised and rounded.

H. Pronotum greatly flattened and extended

Fig 3.28. shows the hypothetical tree diagram for the polysphinctines. (Characters that are in the original character set are referred to by their number, otherwise they are lettered).

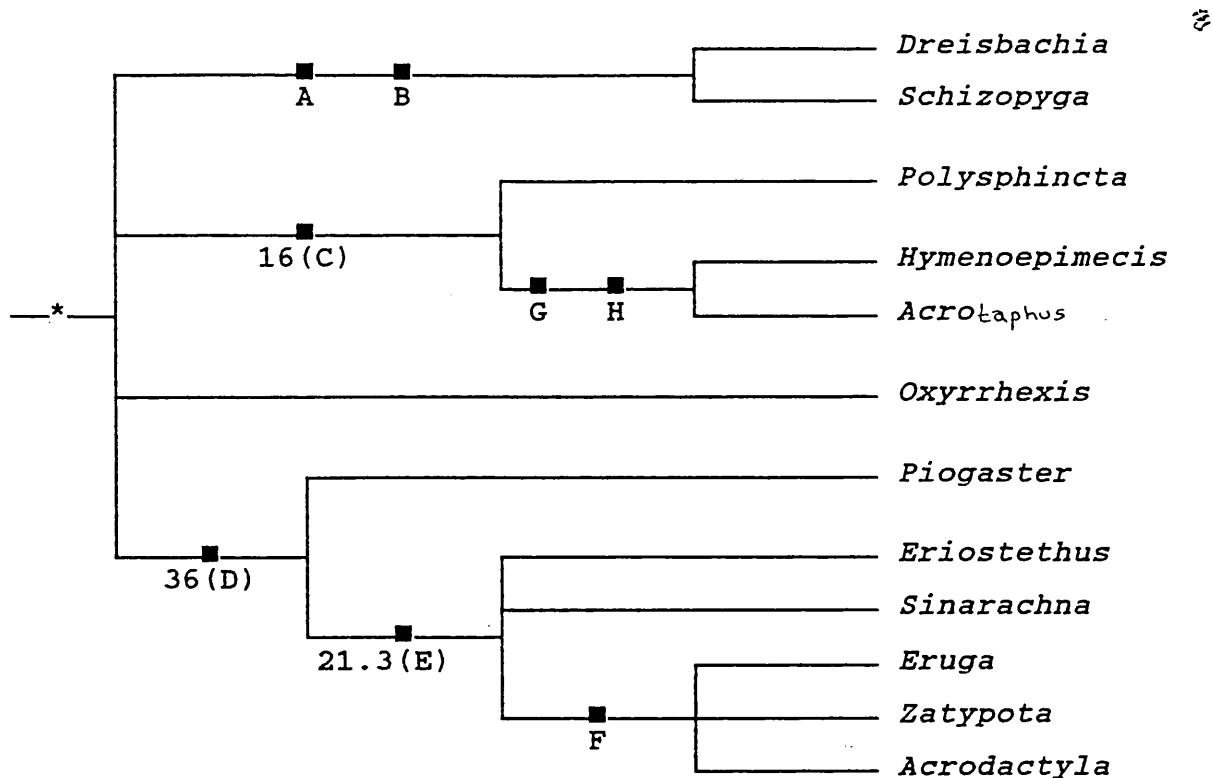
The three groups are clearly delineated, but it must be pointed out that this grouping is contradicted by a number of character states that would seem to link the three tropical forest genera *Eriostethus*, *Acrotaphus* and *Hymenoepimecis*. These character-states are: *occipital carina formed into a strong collar; extended pronota lacking the*

epomia and longer ovipositors than most polysphinctines (the last two of these characters discussed in Gauld, 1984b). These are probably parallelisms, but equally well the reduction characters which link together the *Acrodactyla* group may be related to size. The majority of species of the *Acrodactyla* group have fore-wing lengths less than 6mm, and reduction in palpar segment number (and the related character wing-veination reduction) is often an accompaniment of small size (Gauld & Bolton, 1988). If this is the case then there are two sets of incompatible character-states both of which may be of dubious value for phylogenetic reconstruction.

Fortunately, the size distributions of species within the genera cast some light on this problem. The genus with the smallest species in the *Polysphincta*-group is *Polysphincta* itself, which in *P. boops* has an average forewing length (n=12) of 4.8mm. *Zatypota*, one of the smaller *Acrodactyla*-group genera has, in *Zatypota percontaria* an average forewing length (n=12) of 3.6mm. *Eriostethus* has an average fore-wing length (in *E. pulcherrimus*) of 9.9 mm (n=12). *Eriostethus* is therefore much larger than the rest of its presumed group and the larger than the smallest members of the group competing for its membership. Its lack of a nervellus and 3-segmented labial palps is therefore most probably not size related. It seems that *Eriostethus* is a specialised genus that has arisen out of the smaller polysphinctines and that the grouping is indeed holophyletic.

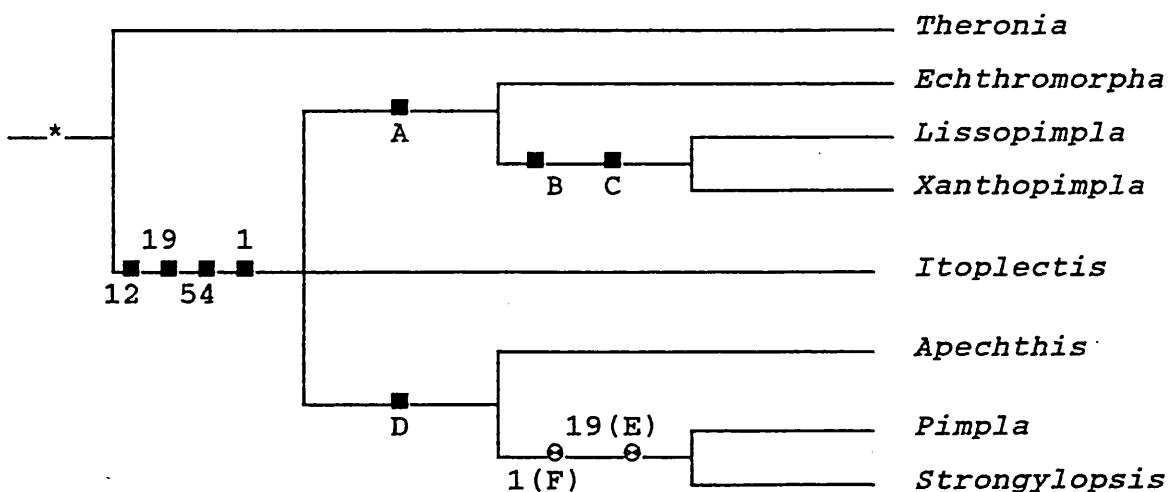
#### 3.8.4. The Pimplini

There are 2 important genera that were not dealt with in the initial analysis: *Echthromorpha* and *Lissopimpla*. These seem close to *Xanthopimpla* in that both have twisted mandibles and a divided clypeus (Townes, 1969). However, Gauld (pers comm) has pointed out that in *Echthromorpha* what appears to be a bipartite structure is, in fact, a single structure, beneath which the labrum protrudes. This makes two clades - one consisting of *Xanthopimpla*+*Lissopimpla* and the other consisting of that group and *Echthromorpha*. This predominantly tropical group seems to be separated from a group consisting of



Key: ■ - apomorphic. \* - autapomorphies of the Polysphinctini.

Fig 3.28. Unanalysed hypothetical tree for the Polysphinctini. For characters, see text.



Key: ■ - apomorphy; ○ - reversal; \* - Pimplini autapomorphies (see fig 3.27).

Fig 3.29. Unanalysed hypothetical tree for the Pimplini. For characters, see text.

*Apechthis*, *Pimpla* and *Strongyloopsis*. The position of *Itoplectis* is rather uncertain. It is a rather unspecialised genus, and does not seem to share any unambiguous apomorphies with either of the two groups (the *Xanthopimpla*-group and the *Pimpla* group).

Apomorphic character states used in the hypothetical tree diagram: (characters that are in the original character set are referred to by their number, otherwise they are lettered).

A. Mandibles modified: some torsion; lower tooth smaller than upper tooth.

B. Subgenital plate reduced to thin strip either side of the ovipositor complex (in female).

C. Clypeus clearly split into 2 parts

D. Strong, distinctive "warning" odour produced

E. Tarsal claw poison gland lost, often (in tropical species) replaced by defensive bristles

F. Compound eye not emarginate at level of antennal sockets. This is character 1 with the polarity reversed

The tree diagram for this group is shown in fig 3.29.

Several interesting points come out of this. The first is that poison glands of the type described by Gauld (1987b) are found in all tropical Pimplini, except for *Pimpla*. They are, when present, not particularly well developed in tropical *Apechthis*, although clearly visible; and well developed in certain tropical species of *Itoplectis*. This suggests that the tarsal claw poison gland-complex has been lost predominantly in the temperate species, due to the absence of predator pressure, and indeed is replaced in tropical *Pimpla* species by stout defensive bristles, presumably as a secondary

2

response to predator pressure (see figs 3 and 4 in Gauld, 1987b).

The scenario this suggests is that the Pimplini may have evolved as a *Theronia*-type ancestor in the tropics, and only later invaded temperate regions; in the process losing the tarsal claw poison-gland complex. In one case a genus has reinvaded (*Pimpla*) and evolved a totally new defensive structure. It may be that *Pimpla* is the only genus that has evolved in temperate regions, and that the loss of the poison-gland in *Apechthis* and *Itoplectis* has occurred several times; that is, once per invasion into the temperate region and as a response to the reduction in predator pressure. The comments about *Pimpla* apply also to the deserticolous *Stronglyopsis*. The tree-diagram places this genus close to *Pimpla* as suggested by Townes (1969) - although it is very highly modified, especially in the female sex, in response to arid environments.

The obtained diagram has many clades delineated by only one synapomorphy. For this reason it must be considered purely as a speculative exercise and not as a statement about how the groups should be classified. However, there must be some doubt about the status of the genus *Itoplectis* which may be definable only by plesiomorphic characters. The autapomorphies of the group as a whole, however, are very strong, and the erection of a newly defined Pimplini is recommended.

### 3.9. The Relative position of the Groups

It seems most likely that the the Pimplinae as presently recognised is not holophyletic and can be split into several groups - the relationships of which are not those of a single holophyletic subfamily. Leaving out *Diacritus* - about which not enough is known, the following holophyletic groups are recognised:

- (1) The Rhyssini group
- (2) The Pimplinii/Ephialtini/Polysphinctini group

2

(3) The Poemen<sup>i</sup>ini / *Pseudorhyssa* group

Table 3.2. summarises these changes and the proposed new taxonomic groupings.

The relationships between the groups are now considered, and how they fit into the clade Acaenitinae+Diplazontinae+Orthocentrinae+Collytrinae (Wahl, 1989). Fig 3.30 shows the possible relationships of the groups. The characters at the nodes are listed below and are a mixture of my characters and Wahl's (see chapter 2 for more details of Wahl's tree; the clades beyond the Acaenitines have been left as a single branch).

1. *Hypostomal spur close to stipial sclerite*<sup>in final instar larvae</sup>
2. *Presence of horn on tergite 9 of female.*
3. *Mesocutal ridges present but not bounded by punctate lines.*
4. *Anteriorly-dipping pronotal collar.*
5. *No phragmata on tergite 9 of female.*
6. *Notch on post-occiput*
7. *Posteriorly-dipping collar, usually with reflexed collar.*
8. *Raised epomial ridge*
9. *Shallow epicnemium.*
10. *Strong posterior lateral carina pattern on propodeum.*
11. *Tarsal claw teeth.*
12. *Tubercles on tergites 2 to 4*

13. Hypostomal spur fused with stipial sclerite<sub>k</sub> <sup>in final instar larvae.</sup>
14. Extended tergite 9, not split into two parts and with no horn
15. Large, stout bristles on the fore femur
16. Presence of a large convex sub-genital plate

The resulting tree diagram is shown in fig 3.30. It shows the rhyssines as a clearly holophyletic group distinct from the rest of the pimelines. In addition, the poemenine genera seem to be a separate holophyletic group (confirming the results of the whole analysis). This result tends to suggest that three newly defined subfamilies should be erected ( and it seems most sensible to place the Diacritini in a separate subfamily until more is known about their probable systematic position).

The tree diagram shows the Rhyssinae as the most primitive group amongst the "pimpliformes", and the Poemeninae and Pimplinae (*sensu stricto*) are then paraphyletic with respect to the rest of the clade. It remains to be seen whether the Poemeninae are really closer to the higher groups than the Pimplinae. In addition, there was some doubt about the correct subfamilial position of *Coleocentrus* (usually placed within the Acaenitinae). At first it was thought that *Coleocentrus* might be better placed in the Poemeninae, due to similarities in the structure of the pronotum. However, the structure of the larvae (Shaw & Wahl, 1989) and the presence of a very large female subgenital plate in *Coleocentrus* suggest that it is, indeed, an acaenitine.

Table 3.2 summarises the taxonomic changes recommended in this chapter, and these nomenclatural changes (although not formally advised) will be used for the rest of the thesis. To reduce confusion the pimelines (*sensu* Townes) will be referred to as the Pimplinae (*sensu lato*) and the pimelines (*sensu* Eggleton) will be referred to as the Pimplinae (*sensu stricto*).

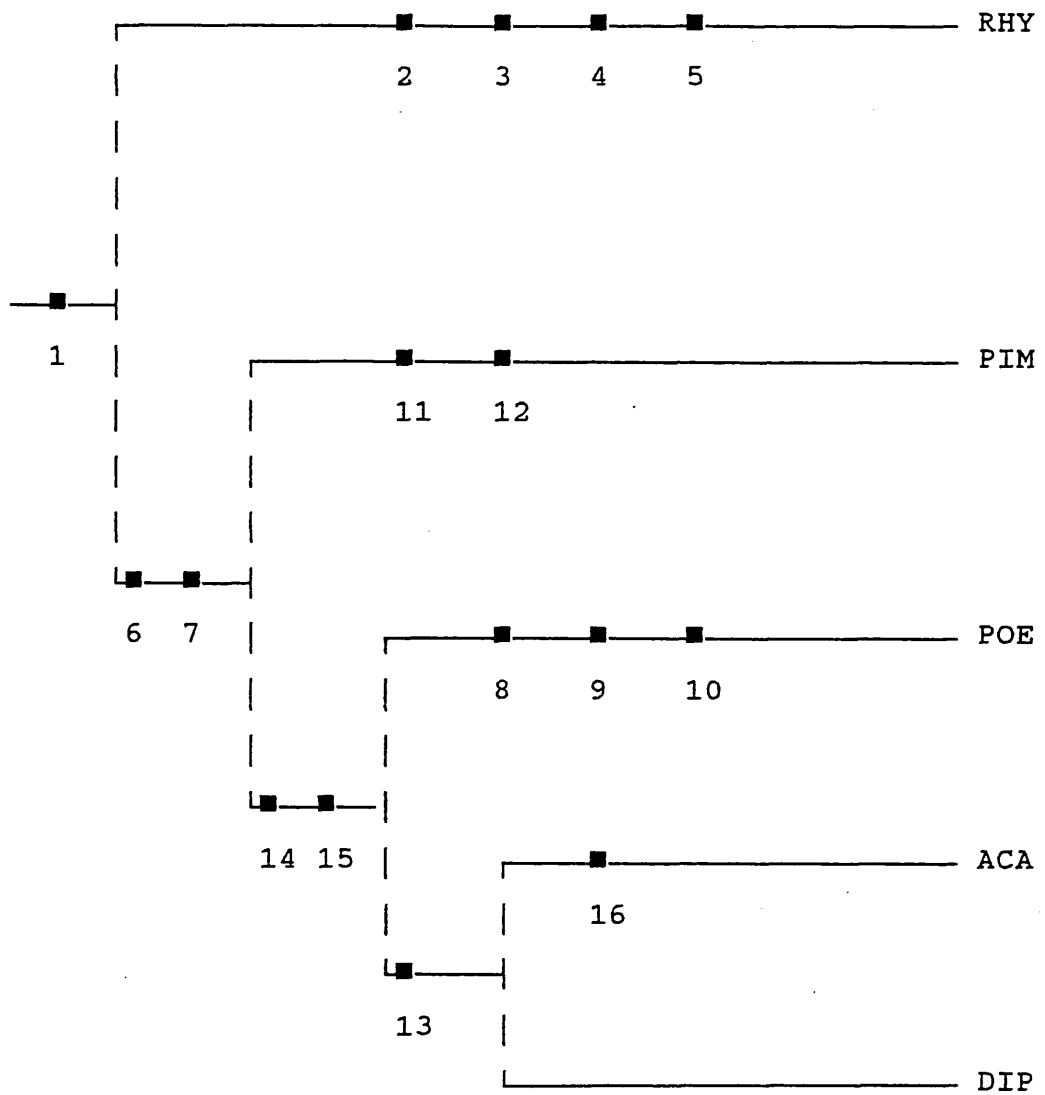


Fig 3.30. Hypothetical tree showing possible phylogenetic relationships within the lower "pimpliformes" groups. RHY = rhyssines; PIM = pimplines; POE = poemeniines; ACA = acaenitines; DIP = diplazontines and other "higher" pimpliformes (Wahl, 1989). ■ = apomorphy.

Table 3.2. Summary of proposed taxonomic changes amongst the "pimplines"

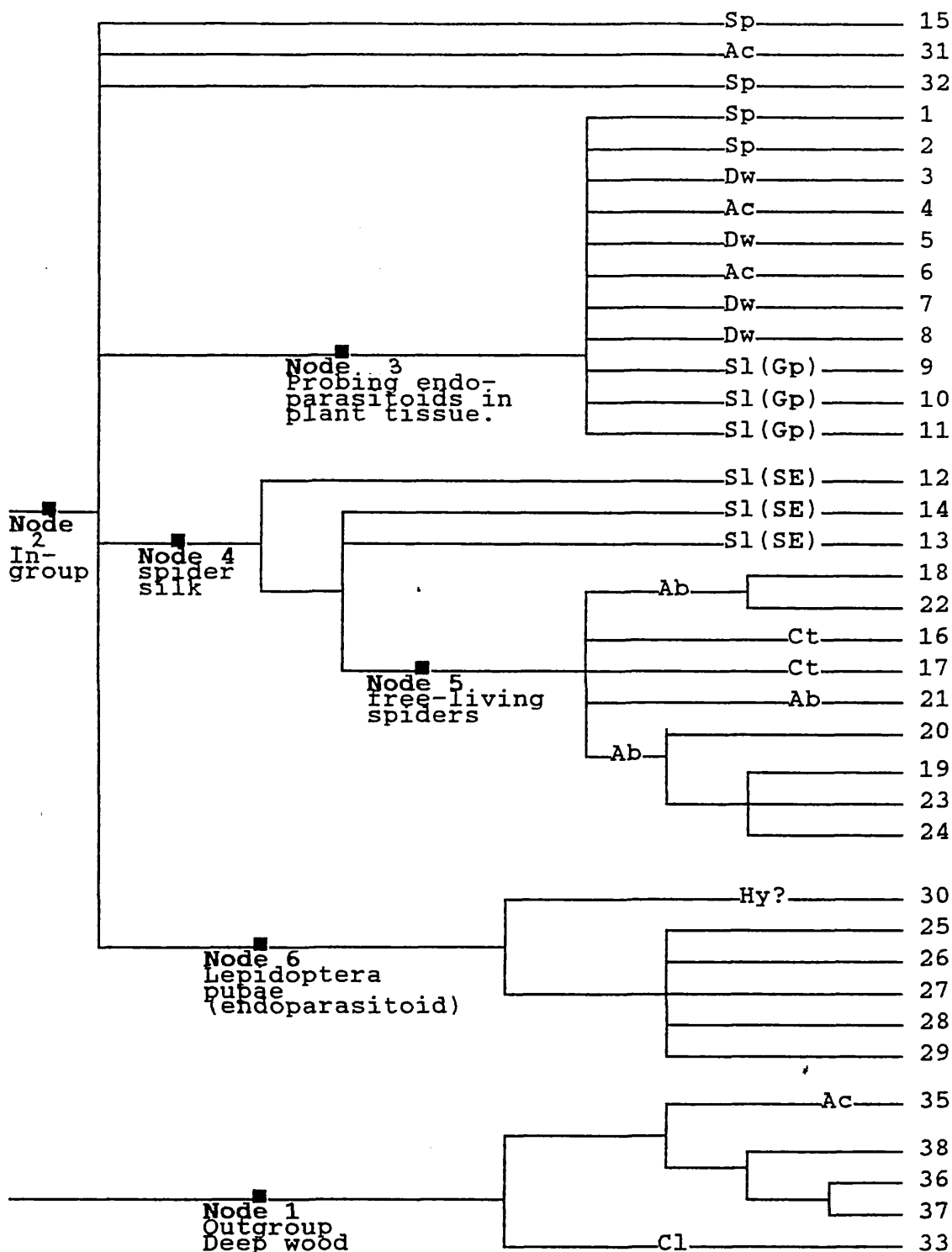
| Old grouping   | New grouping             | Taxa involved                                                                                                                                |
|----------------|--------------------------|----------------------------------------------------------------------------------------------------------------------------------------------|
| Pimplinae      | Pimplinae                | Pimplinae<br>(=Ephialtinae<br><i>sensu</i> Townes)<br>without the<br>Rhyssini,<br>Poemeniini<br><i>Pseudorhyssa</i><br>or <i>Diacritus</i> . |
| Ephialtini     | Ephialtini               | Ephialtini<br>(=Pimplini<br><i>sensu</i> Townes)<br>with<br><i>Perithous</i> ,<br><i>Hybomischos</i><br>and<br><i>Delomerista</i>            |
| Delomerstini   | not accepted             | proven to be<br>a<br>polyphyletic<br>group.                                                                                                  |
| Pimplini       | Pimplini                 | Pimplini<br>(=Ephialtini<br><i>sensu</i> Townes)<br>with<br><i>Theronia</i> .                                                                |
| Polysphinctini | Polysphinctini           | As before.                                                                                                                                   |
| Poemeniini     | Poemen <sup>i</sup> inae | Poemeniini,<br>with<br><i>Pseudorhyssa</i> .                                                                                                 |
| Rhyssini       | Rhyssinae                | Rhyssini.                                                                                                                                    |
| Diacritini     | Diacritinae              | Diacritini.                                                                                                                                  |

#### 4.1. Introduction

Biologically the Pimplinae (as recognised in this chapter, excluding the rhyssines and the poemeniines) are extremely diverse (Fitton, Shaw & Gauld 1988; Gauld 1984b).. A number of biological elements are treated here especially with regard to how host-preferences may have evolved. The intention is twofold: first, to use the tree obtained in chapter 3 (fig 3.27) to construct hypotheses about biological changes during evolutionary history; second, to use biological traits to shed some light on the phylogenetic reconstruction of the group.

Table 4.1 gives a brief summary of the host-associated biologies of the group. These biologies will then be considered in detail from an evolutionary perspective and scenarios constructed. The poemeniines are included as the outgroup in these discussions, and the rhyssines are mentioned briefly. A full discussion of rhyssine biology is postponed until chapter 5.

Fig 4.1 shows the phylogeny of the group with host-preference and other lifeway information superimposed on the nodes of the hypothetical tree. Each node will be discussed in turn, and hypotheses made about how host-preferences and host microhabitat preferences might have evolved. The majority of pimplines are idiobionts and are not normally associated with one particular host-group, but with what is best termed "host microhabitat". For this reason, the discussion will centre around microhabitat changes rather than host-associations.



Ac = associated with aculeates in old wood-burrows; Dw = associated with deeply concealed hosts in dead wood; Sp = associated with deeply concealed hosts in soft plant tissue; Sl = hosts associated with silk; Gp = gregarious ectoparasitoids of Lepidoptera pupae; SE = associated spider egg sacs; Ct = places egg on cephalothorax of spider; Ab = places egg on abdomen of spider; Hy? = predominantly hyperparasitoids?; Cl = cleptoparasitic on rhyssines.

Fig 4.1. Host and microhabitat associations superimposed on tree of pimpline data set.

Table 4.1. Host preference summaries

All the genera have the following basic host relations unless otherwise stated: *solitary idiobiont ectoparasitoids of immature endopterygote insects.*

|                     |                                                                                                                                                       |                                                              |
|---------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------|
| <i>Exeristes</i>    | Principally Lepidoptera larvae in soft plant tissue; especially Tortricidae producing resin-exudations in pines. Recorded as hyperparasitoid.         | Thorpe & Caudle (1938); Juilliet (1959); Fitton et al (1988) |
| <i>Endromopoda</i>  | Stem-inhabiting or gall-making hosts associated with monocotyledons (especially Graminae). Cephidae, Noctuidae, Chloropidae.                          | Fitton et al (1988)                                          |
| <i>Afrephialtes</i> | Sesiidae in sallow.                                                                                                                                   | Fitton et al (1988)                                          |
| <i>Ephialtes</i>    | Predominantly aculeate Hymenoptera in old tunnels of wood-boring insects.                                                                             | Fitton et al (1988)                                          |
| <i>Liotryphon</i>   | Hosts in thin plant tissue (galls, twigs, bark, nuts, fruit) and old workings of wood-boring insects. (Tortricidae, Cossidae, Sesiidae, Geometridae). | Barrett (1932); Fitton et al (1988)                          |

|                      |                                                                                                                                                |                                                                            |
|----------------------|------------------------------------------------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------|
| <i>Townesia</i>      | Aculeates in fairly old timber. (Sphecidae, Megachilidae)                                                                                      | Jussila & Kapyla (1975); Fitton et al (1988)                               |
| <i>Paraperithous</i> | ?Beetles under loose bark (Cerambycidae?)                                                                                                      | Fitton et al (1988)                                                        |
| <i>Dolichomitus</i>  | Wood-boring insects. Some recorded from gall-formers in <i>Rosa</i> . Recorded as highly polyphagous. Cerambycidae, Scolytidae, Curculionidae. | Kishi (1970a, 1970b); Vollger (1972); Gregoire (1976); Fitton et al (1988) |
| <i>Acropimpla</i>    | Gregarious parasitoids of Lepidoptera pupae and prepupae in large flimsy cocoons. Lasiocampidae.                                               | Fitton et al (1988)                                                        |
| <i>Gregopimpla</i>   | As <i>Acropimpla</i> .                                                                                                                         | Fitton et al (1988)                                                        |
| <i>Iseropus</i>      | As <i>Acropimpla</i>                                                                                                                           | Fitton et al (1988)                                                        |
| <i>Tromatobia</i>    | Pseudoparasitoids (predators) on successive eggs in more or less exposed spider egg sacs. Spider is not stung.                                 | Fitton et al (1987); Nielsen (1923); Fitton et al (1988)                   |

Philodromidae, Araneidae,  
Tetragnathiidae, Linyphiidae.

|                     |                                                                                                                                      |                                                                        |
|---------------------|--------------------------------------------------------------------------------------------------------------------------------------|------------------------------------------------------------------------|
| <i>Zaglyptus</i>    | Pseudoparasitoids on egg sacs and mature spiders. Spider may be stung. Especially on spider egg sacs in rolled leaves. Clubioniidae. | Fitton <i>et al</i> (1987); Nielsen (1935); Fitton <i>et al</i> (1988) |
| <i>Clistopyga</i>   | Pseudoparasitoids of deeply concealed spider egg cocoons. Spider is probably not stung. Segrestriidae, Clubioniidae.                 | Fitton <i>et al</i> (1987); Fitton <i>et al</i> (1988); Nielsen (1929) |
| <i>Pseudopimpla</i> | Hartigiine sawflies within canes of <i>Rubus</i> .                                                                                   | Bruzzese (1982)                                                        |
| <i>Dreisbachia</i>  | Koinobiont parasitoids of immature spiders in concealed habitats. Lays egg on the cephalothorax. Clubioniidae.                       | Fitton <i>et al</i> (1987); Fitton <i>et al</i> (1988)                 |
| <i>Schizopyga</i>   | Koinobiont parasitoids of sub-adults, adults and immature spiders in concealed habitats. Lays egg on cephalothorax. Clubioniidae.    | Fitton <i>et al</i> (1987); Fitton <i>et al</i> (1988)                 |
| <i>Acrotaphus</i>   | Koinobiont parasitoids?<br>Reared from a Tetragnathid spider in Costa Rica (Gauld,                                                   | Gauld (pers comm)                                                      |

pers comm).

|                     |                                                                                                                                            |                                                                                      |
|---------------------|--------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------|
| <i>Acrodactyla</i>  | Koinobiont parasitoids of adult and immature web-spinning spiders. Lays egg on abdomen. Linyphiidae, Mettidae, Dictynidae, Tetragnathidae. | Fitton et al (1987), Nielsen (1937), Howell & Pienkowski (1972); Fitton et al (1988) |
| <i>Piogaster</i>    | No host records.                                                                                                                           |                                                                                      |
| <i>Oxyrrhexis</i>   | Koinobiont parasitoids. Only reliable record from a Theridiid spider.                                                                      | Fitton et al (1987); Fitton et al (1988)                                             |
| <i>Polysphincta</i> | Koinobiont parasitoids of adult and immature araneid spiders. Lays egg on abdomen.                                                         | Fitton et al (1987); Fitton (1988); Nielsen (1928).                                  |
| <i>Sinarachna</i>   | Koinobiont parasitoids of adult and immature araneid spiders. Lays egg on abdomen. Araneidae, (Dictyniidae).                               | Fitton et al (1987); Vincent (1979); Fitton et al (1988)                             |
| <i>Zatypota</i>     | Koinobiont parasitoids of adult (commonly) and immature Theridiid spiders.                                                                 | Fitton et al (1987); Fitton et al (1988)                                             |

|                      |                                                                                                                                                                                                                                                                                                              |                                                                                                                                                  |
|----------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------|
| <i>Itoplectis</i>    | Endoparasitoids of easily accesible but weakly concealed or cocooned small Lepidoptera pupae (broadly "microlepidoptera"). Also pseudohyperparasitoid developing upon ichneumonoids in Lepidoptera pupae. Other endopterygote pupae are also attacked (Diprionidae, Chrysomelidae). Host feeding.            | Cole (1959, 1967); Horn (1974); Hard (1976); Leius (1960); Glowacki (1966); Togashi (1974); Ward & Pienkowski (1978); Fitton <i>et al</i> (1988) |
| <i>Apechthis</i>     | Endoparasitoids of somewhat wriggly exposed or poorly concealed Lepidoptera pupae. Host feeding.                                                                                                                                                                                                             | Cole (1967); Fitton <i>et al</i> (1988)                                                                                                          |
| <i>Pimpla</i>        | Endoparasitoids of Lepidoptera pupae, often those concealed in moss or soil. Oviposits into hard cocoons or pupae. Places egg carefully in 2-3 segment of host abdomen. Other endopterygote pupae are also attacked (Cerambycidae; Syrphidae). Occasionally recorded as pseudohyperparasitoid. Host feeding. | Carton (1971,1973); Graham (1946); Osman (1978); Sándlan (1979) Fitton <i>et al</i> (1988)                                                       |
| <i>Strongylopsis</i> | No host records.                                                                                                                                                                                                                                                                                             |                                                                                                                                                  |
| <i>Xanthopimpla</i>  | Endoparasitoids of Lepidoptera                                                                                                                                                                                                                                                                               | Gupta (1987);                                                                                                                                    |

|                     |                                                                                                                                                                                     |                                                                          |
|---------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------|
|                     | pupae in exposed or semi-exposed situations. many attack exposed pupae attached to trees and shrubs.                                                                                | Gauld (pers comm)                                                        |
| <i>Theronia</i>     | Endoparasitoids and hyperparasitoids of medium to large cocooned or naked Lepidoptera, situated more or less in the field or shrub layer. One subgenus is a parasitoid of sphecids. | Short (1978);<br>Gupta (1987);<br>Glowacki (1966)                        |
| <i>Perithous</i>    | Aculeate Hymenoptera in excavations made by wood-boring insects.                                                                                                                    | Danks (1971);<br>Van Lith (1974)<br>; Fitton <i>et al</i> (1988)         |
| <i>Delomerista</i>  | Cocoons of sawflies in plant tissue. Pseudohyperparasitoid of Ichneumonoidea.                                                                                                       | Morris <i>et al</i> (1937); Fitton <i>et al</i> (1988)                   |
| <i>Pseudorhyssa</i> | Cleptoparasitoids of rhyssine icneumonids.                                                                                                                                          | Spradbery (1969, 1970a); Skinner & Thompson (1960); Thompson (pers comm) |
| <i>Poemenia</i>     | Parasitoids of sphecids in dead wood.                                                                                                                                               | Westrich (1980);<br>Fitton <i>et al</i> (1988)                           |

|                      |                                                              |                                           |
|----------------------|--------------------------------------------------------------|-------------------------------------------|
| <i>Deuteroxoides</i> | Wood-boring beetles in hard wood. Cerambycidae.              | Fitton <i>et al</i> (1988); Aubert (1969) |
| <i>Podoschistus</i>  | Wood-boring beetles in hard wood. Cerambycidae.              | Fitton <i>et al</i> (1988)                |
| <i>Neoxorides</i>    | Wood-boring beetles in hard wood. Cerambycidae, Buprestidae. | Townes (1969)                             |

#### 4.2. NODE 1: (outgroups), the Poemeninae and Rhyssinae

*Holophyletic groups characterised by this node:* The poemeniines as a holophyletic group are in this category, as are the rhyssines and labenines. Doryctine braconids and xoridines are also rather more distant outgroups, but are probably best placed here. All the discussions below, therefore, concentrate on the poemeniines as the probable sister group of the pimelines. There are two microhabitats in this group.

##### 4.2.1. Microhabitat 1: Hard, dead wood

This host microhabitat consists of newly-fallen or relatively uncolonised trees, logs and large twigs that have no excavations or extensive cracking. The hosts are wood-boring or wood-probing insects living deep below the bark.

*Adaptive character suite:* The widely observed adaptations in parasitoids whose hosts live in this microhabitat are related to two separate but connected physical problems caused by the hardness of the substrate: First, how to get an egg onto the host - this is a drilling problem; second, how to get offspring out of the substrate - this is an egress problem. The resulting adaptive character suite is pervasive both within and outside the ichneumonids and is shown below (Table 4.2.).

Table 4.2. Adaptive character suite in deep wood associated parasitoids.

| Character                    | Poe. | Col. | Xor. | Rhy. | Dor. | Ste. | Lio. | Lab. |
|------------------------------|------|------|------|------|------|------|------|------|
| 1. ovipositor<br>teeth       | +    | +    | +    | +    | +    | +    | +    | +    |
| 2. long, stout<br>ovipositor | +    | +    | +    | +    | +    | +    | +    | +    |
| 3. long thin<br>legs         | +    | +    | +    | +    | +    | +    | (+)  | +    |
| 4. Extended<br>tergite       | +    | +    | +    | +    | -    | +    | (+)  | +    |
| 5. Clypeal<br>tooth          | -    | +    | (-)  | +    | (-)  | +    | (-)  | -    |
| 6. Small<br>clypeus          | +    | +    | +    | +    | +    | +    | -    | +    |
| 7. Flattened<br>thorax       | +    | -    | (-)  | -    | +    | +    | -    | (-)  |
| 8. Post-genal<br>bridge      | +    | +    | +    | +    | +    | +    | +    | +    |
| 9. Expanded<br>wide heads    | +    | +    | +    | +    | +    | +    | +    | +    |
| 10. Mesoscutal<br>ridges     | (+)  | -    | -    | +    | (+)  | (+)  | +    | +    |

Key: Poe. - Poemeniinae (including *Pseudorhyssa*); Col.- *Coleocentrus*;  
 Xor. - Xoridinae; Rhy. - Rhyssinae; Dor. - doryctine Braconidae; Ste.  
 - Stephanidae; Lio. - Liopteridae and Ibalidae; Lab.- Labeninae.

Characters 1-3 are known to be related to oviposition, while characters 3-10 are presumed to relate to enabling easy escape from the substrate. It is interesting to note how the parallel types of adaptation take different forms in different groups (table 4.2, above). Doryctine braconids, for example, never seem to possess an elongate tergite 9 (Huddleston pers comm), while liopterids and ibaliids have an extended tergite 9 that is associated with a differently highly specialised ovipositor complex (Fergusson 1988).

Mandibles of all the groups seem to show a broadening (a correlate of character 9). Most groups have greatly increased head widths and post-genal bridges - these character-states are related to the development of large muscles for the mandibles.

Structures that are presumably involved in anchoring the head during the excavation of an exit tunnel (characters 5 and 10) are quite variable. For example, neither doryctines, liopterids nor ibaliids possess a clypeal tooth, a structure which is found in several ichenumonid groups; in its place all three groups have a clypeal notch. In stephanids a ring of stout spines on the head seem to perform an analagous head-steadying function. The species of the braconid genus *Ascogaster*, which are parasitoids of exposed lepidoptera eggs often also have a clypeal tooth even though they do not appear to be emrging through a hard substrate (Huddleston 1984). This perhaps sounds a warning note about extrapolating too far from apparently analagous structures; they may often have evolved to perform entirely different tasks.

Mesoscutal ridges (character 10) are found throughout the groups (and in another deep wood-associated group, the aulacids). The head and propodeal regions of doryctines are often raised into ridges but the mesoscutum is rarely fully ridged, a particularly good example of this being in the Neotropical species *Bohartiellus cornutus* (Marsh 1983) where all but the anterior end of the mesoscutum is clear of sculpture while there is extensive sculpturing on the head and propodeum. This is also true of various helconine braconids (see the drawing of *Helcon tardator* in van Achterberg (1987)). This pattern

difference between ichneumonids and braconids implies that there is a phylogenetically related aspect of these adaptations. Different taxonomic groupings are responding with different morphological solutions to the same general physical problem.

A flattened thorax (character 7) is commonly present amongst wood-associated groups. It is not clear then why rhyssines, most xoridines and *Coleocentrus* should not have this modification. It may be related to the sizes of individuals in the various groups. This adaptation has been shown, in several Hymenoptera groups, to be an adaptation for wriggling out under bark and other substrates laid down as horizontal planes (Day, pers comm). Large insects might simply be unable to wriggle between the bark and the wood itself however dorso-ventrally flattened their thoraces became. Some indirect evidence for this is given by consideration of the Xoridinae; there, only the genus with the smallest species (*Aplomerus*) shows the flattened condition.

The general taxonomic distribution of the states in the above ichneumonid and braconid taxa; that is, in groups close to the base of the ichneumonoid stock, suggests that a deep wood-associated habit as a whole is plesiomorphic. Looking at the pimelines, this is borne out by a consideration of biologies in the outgroups. The Labeninae, Rhyssinae, Xoridinae and Acaenitinae are all groups whose most primitive members are associated with hosts deeply concealed within dead wood. It should be emphasised that not all of these groups are wood-borers, but all are associated with wood, as borers or probers. The only outgroup that is not predominantly associated with wood is the Tryphoninae, and even here the genus that is assumed to be most primitive - *Idiogramma* is a parasitoid of deeply concealed xylophagous hosts: xyelids in the male cones of Pinaceae (Burdick, 1961).

*Evolutionary significance:* This sheds some light on the evolution of the Pimplinae. The ancestral pimpline is likely to have been an ectoparasitoid idiobiont associated with deep living larvae, probably Hymenoptera. If this is so the poemenines and coleocentrines are showing the primitive biological condition from which the pimelines

(as defined holophyletically in chapter 3) are derived. The position of the wood-associated groups in the final hypothetical tree diagram (fig 4.1) strongly supports this.

One important point must be made to avoid confusion. Wood-boring in its strictest sense is undoubtedly a specialised lifeway that has evolved several times (as shown by the different ways that wood borers have evolved complex boring mechanisms). The primitive ancestor may have been boring some way into wood or probing through existing oviposition tunnels of the host. It is not suggested that wood-borers which are drilling through several inches of wood are exhibiting the ancestral lifeway. In fact, the ovipositional mechanism is of secondary evolutionary importance - the really important factor is that, however easy it may be to get deep into the wood (by exploiting the hosts oviposition tunnel for example) getting out of the wood is the real problem. An insect developing deep in wood will have to exit near vertically (and rhyssines at least clearly do) - this means that they need to anchor their bodies inside the emergence tunnel. The adaptations associated with this anchoring are fundamental to the wood-associated habit.

Two related, logical scenarios can now be proposed for the evolution of the cleptoparasitic *Pseudorhyssa* from a poemenine close to this ancestral form, given what is now supposed about the phylogeny of the group (chapter 3).

(1) Pre-adapted as a wood-borer and so able to gain egress from deeply concealed situations, its evolution can be considered as the exploitation of another similarly adapted species' oviposition behaviour. This would lead to the present situation where *Pseudorhyssa* species have developed much thinner ovipositors and a probing oviposition behaviour which is secondarily derived. From the point of view of energetics it seems more economical to let another individual do your drilling for you, especially as this process may take over 30 minutes to complete (see chapter 6).

(2) Pre-adapted as a deep wood prober and able to gain egress from deeply concealed situations; and also pre-adapted to the use of a host's oviposition tunnel. The swap from host to parasitoid is envisaged as a simple step from xylophagous host to parasitoid, but retaining essentially the same lifeway.

It is difficult to decide which of these possibilities may actually have occurred. One way to look at this would be to examine the ovipositional behaviour of a parasitoid in the poemeniine clade which is less derived than *Pseudorhyssa*. Unfortunately, *Pseudorhyssa* is the least derived poemeniine, and therefore it is not possible to tell whether its ancestor is likely to have been a prober or a borer.

#### 4.2.2. Microhabitat 2a: Aculeates in pre-existing workings

This host microhabitat consists of aculeates that build nests in old excavations of wood-boring insects. The hosts are usually Sphecidae, Megachilidae or Vespidae. One genus amongst the poemenines (*Poemenia*) exploits this microhabitat, and so do several of the ingroup taxa. The microhabitat will be discussed here as an advanced feature of the poemeniines and then referred to as each clade is discussed.

*Functional adaptations:* The three most striking adaptations are: first, the development of unequal lengths of mandibular teeth; second, the twisting of the end of the ovipositor; third, a general reduction in sculpture on the thorax. Essentially, this is a specialised offshoot of the soft woody plant tissue microhabitat (microhabitat 3).

*Evolutionary significance:* As will be shown later, several groups of the ingroup (pimplines) exploit this microhabitat and show one or more of the adaptations above. This is also true of the more distant outgroup lineage - the Labeninae (Gauld, 1983, 1988). In all groups the lifeway has clearly evolved from a deep wood-associated ancestor, and is apomorphic.

#### 4.3. NODE 2: The Pimplinae (*sensu stricto*)

*Holophyletic group in this category:* The Pimplinae *sensu stricto*, as redefined in chapter 3.

This node does not characterise a particular microhabitat, but a class of microhabitats ( 2 to 8). This class leads away gradually from deep hosts in newly fallen timber to more exposed hosts. In essence, the shift away from deep wood-associations is apomorphic (biologically) for the whole of the pimelines, and that apomorphy is one of a replacement of wood specialisations with those dealing with hosts away from wood. The primitive members of this clade, especially *Dolichomitous* are clearly deep wood probers; but, except for the presence of rather stout mandibles, this group does not possess the other deep wood inhabiting egress characters.

#### 4.4. NODE 3: The *Ephialtes*-group

*Holophyletic groups in this category:* All the Ephialtini with dipped occipital carinae (taxa 1-11 in the study OTUs).

This clade does not form a homogenous group biologically. In fact, 3 separate microhabitats are embraced within the clade. These may be indicative of real holophyletic groups, but they are not easily distinguishable by the phylogenetic analysis. The reasons for this are touched on below.

##### **4.4.1. Microhabitat 3: soft wood and bark**

This host microhabitat consists of fallen trees in an advanced state of decay (and often with existing wood-boring insect burrows) or the bark of trees at various stages of decay. The hosts of these parasitoids are usually Coleoptera (Scolytidae; some Curculionidae), Lepidoptera (Sesiidae).

*Functional Adaptations:* The main difference between this and microhabitat 1 is that the parasitoids concerned are all probers - that is they do not excavate a significant amount of the substrate in order to reach their hosts. The main morphological specialisations are (a) a long thin ovipositor (b) lack of sculpturing on the thorax; (c) mandibles with pointed apices, moderately well supplied with muscles. (d) large clypei without a median tooth. All of these characters are apomorphies for the group, but none can easily be used since they are predominantly loss characters which are very likely to be homoplastic.

*Groups within this microhabitat:* A large proportion of the ephialtine genera with long ovipositors can be included in this category (*Dolichomitus*, *Afrieptialtes*, *Liotryphon*, *Paraperithous*). However, they do not form a clearly holophyletic group within the *Ephialtes*-group - it is most likely that they are paraphyletic. *Dolichomitus* belongs in this group because it does not have deep wood exiting characters, but it is, in at least some species, a deep wood prober.

*Evolutionary significance:* the phylogenetic distribution of deep wood-associated groups at the bases of each lineage (in the Poemeninae, Xoridinae, Rhyssinae and Acaenitinae) leads to the conclusion that a wood association is plesiomorphic. However, the possibility does exist that this is a sampling artefact brought about by extinctions, and that each deep wood associated group has evolved independently. This would make it appear as if all primitive ichneumonoids are wood associated, although all it would really indicate is that the only extant members of these primitive groups are the highly specialised wood-associated ones. It may be that wood associations are energetically so expensive that they have only rarely been evolved, and the groups that have succeeded in colonising this microhabitat have not been ousted by more recently evolved groups. If this were the case then the presently discussed microhabitat would represent the apomorphic condition. However, there seems to be a strong argument against this supposition.

24

A necessary corollary of the above theory is that the wood-association in ichneumonids has evolved several times. The problem with this idea is, that although it is easy enough to envisage a soft-tissue probing parasitoid laying an egg onto a wood-boring host larvae through the host's oviposition tunnel, it is quite clear that the emerging adult would be totally unfitted for emergence from that deeply concealed situation. This would seem potentially to make the evolutionary sequence one way - getting into deeply concealed wood microhabitats will be easy, getting out of them will be very difficult. Perhaps the most parsimonious solution is to assume that the primitive apocritan parasitoids were deep wood-associated and that the least derived ichneumonoids have never left that habitat. The evidence that lends this overall hypothesis most weight is that there are very few if any examples of presumed advanced groups going back into deep wood microhabitats during their evolutionary history - in the Labeninae, for example, no reversals of this kind have been postulated (Gauld, 1983); and the same seems to apply to the Acaenitinae and Poemeniinae, although there is much more limited biological information for them.

The lack of sculpture on thorax and propodeum found in this microhabitat group, and the absence of most of the wood egress characters suggests that these characters are apomorphic, and the general difficulty of phylogenetic placement of this clade (see chapter 3) may be due to this derived loss.

#### 4.4.2. Microhabitat 4: Soft non-woody plant tissue

This microhabitat consists of areas of plant tissue such as stems, leaf petioles and fruits. Galls represent an intermediate position as some are relatively soft and some are definitely woody. Typical hosts are certain Lepidoptera (Noctuidae, Tortricidae, Cossidae) and Diptera (Chloropidae).

*Functional adaptations:* The characteristic adaptation is a stout,

short ovipositor which is used to probe or puncture. The ovipositor often has strong teeth at the tip. This is also associated with a rather more robust and less elongate gaster.

*Groups in this category:* Another group of ephialtine genera can be included in this category, and once again they do not form a holophyletic group (*Exeristes*, *Pseudopimpla*, *Endromopoda*, *Scambus*, *Fredegunda*).

*Evolutionary significance:* This group may have arisen out of the timber-inhabiting genera, but the only positive evidence lies in the shape of the gaster, as mentioned above. If possession of a long thin abdomen is plesiomorphic, as seems likely from consideration of the Poemeninae and Rhyssinae, then the state found in this group must be apomorphic. However, this is certainly not a strong enough character to delineate a robust clade.

Probing ovipositors can, with little modification, be used to puncture or cut holes in soft plant structures such as fruit. Within the genus *Liotryphon*, for example, some species are associated with bark dwelling organisms while others are parasitoids of such insects as the apple- and walnut-inhabiting codling moth. It seems likely that this type of microhabitat association could be derived easily from parasitoid groups with a probing ovipositor complex. To a certain extent this microhabitat blurs into the previous one.

#### 4.4.3. Microhabitat 5: Exposed or lightly concealed pupae

This microhabitat consists of pupae in leaf-rolls or in more exposed situations. Typical hosts include lasiocampid Lepidoptera. The parasitoids are all gregarious.

*Groups in this category:* As with the previous two microhabitats the genera in this class (the *Acropimpla*-subgroup: *Gregopimpla*, *Iseropus*,

2

*Acropimpla*, *Sericopimpla*, see chapter 3) do not clearly form a holophyletic group from morphological evidence, although this time they form a much more close-knit biological unit.

*Functional adaptations:* smaller size, a shorter ovipositor and a much less elongate gaster. However, these these difference grade into the microhabitat 4 adaptations and therefore are not stable enough markers to delineate the *Acropimpla*-subgroup as holophyletic.

*Evolutionary significance:* It seems likely that the relatively exposed condition of the new hosts meant that the silk-cocoons they had spun became important locatory cues for the parasitoids. It may be that a two stage process is occurring - the parasitoid may respond to the host-plant first and then focus on the detection of cocoons (Gauld, 1988). Once again this microhabitat blurs into the previous one - especially in such genera as *Scambus*.

#### 4.5. NODE 4: Polysphinctini and allies

*Holophyletic group defined at this node:* All of the Polysphinctini and the *Tromatobia*-group of ephialtines.

##### 4.5.1. Microhabitat 6: Spider egg-sacs

This microhabitat consists of the spider egg-sacs of exposed to deeply concealed spiders. This parasitoid lifeway is of a pseudoparasitoid eating either just the eggs or the eggs and the dead or immobilised guarding spider. One genus at least, *Zaglyptus*, stings the spider (Nielsen, 1935).

*Groups in this category:* the group defined in this work as the *Tromatobia*-group is the only one that shows this host association. As discussed in chapter 3, this grouping is undoubtedly paraphyletic. However, it does represent the transitional stage between the *Acropimpla*-subgroup and the polysphinctines, through the association with silk.

23

*Functional adaptations:* the most important functional adaptation is the presence of larval median dorsal tubercles, one per segment (Short, 1978; character 33.1). Each tubercle has a cluster of hooks associated with it, and it is presumed to allow the larvae to move around inside the spider egg sac silk. Interestingly, *Sericopimpla* a tropical genus in the *Acropimpla*-subgroup, has a rather less well developed version of these holdfast spines, which are used for an analogous purpose within Lepidoptera pupal cocoons (Smithers, 1956). *Sericopimpla*, therefore, seems to represent a transitional form.

*Evolutionary significance:* The evolution of this association can clearly be derived from the *Acropimpla*-type lifeway. It involves a shift from Lepidoptera silk to spider silk which has been discussed by several workers in the past (Townes, 1969; Gauld, 1984a, 1984b, 1988; Austin, 1985). The biologies of the three genera involved show a gradual change in the level of interaction with the guarding spider (when present) which seems to imply that they or their close ancestors are the forerunners of the polysphinctines (Townes, 1969).

#### 4.6. NODE 5: the Polysphinctini

*Holophyletic groups defined at this node:* The tribe Polysphinctini, as redefined in this work.

##### 4.6.1. Microhabitat 7: Free-living spiders

This microhabitat consists of spiders, especially those which make relatively extensive webs or live in concealed retreats. The parasitoid life-way is that of a koinobiont ectoparasitoid; the spider being temporarily paralysed, an egg being laid and then the spider recovering temporarily while the parasitoid develops. The details of spider taxonomy are taken from Merrett, Locket & Millidge (1985).

*Functional adaptations:* As with the *Tromatobia*-group the

2

polysphinctine larvae have holdfast organs on their body segments - however, this time they tend to be paired. Larvae also have very distinctive holdfast organs consisting of finger-like processes which enable them to attach to the spider (Nielsen, 1923, 1928, 1935, 1937). Adults have tapering ovipositors which enable them to sting the spiders effectively, and enlarged final tarsal segments probably to facilitate running over silk. All these adaptations are related to dealing with active spider hosts.

*Groups in this category:* One holophyletic group - the tribe Polysphinctini, consisting of four separate holophyletic lineages (see chapter 3). This is clearly a lifeway that has evolved only once amongst the pimelines.

The evolution of this association follows on from a *Zaglyptus*-type lifeway, except that the timing of events is changed so that a search for an egg-guarding spider is replaced by, primitively, a concealed sub-adult spider. The koinobiont lifeway has enabled the parasitoids to attack smaller spiders which presumably pose less of a physical threat. Beyond this evolutionary step several additional shifts can be seen.

(1) The *Dreisbachia*-group. This consists of the two apparently most biologically primitive genera *Dreisbachia* and *Schizopyga*. These species are attacking predominantly immature spiders in concealed situations, which would seem to be a microhabitat preference inherited from the spider egg sac parasitoids. In addition both genera place their eggs on the cephalothorax of their hosts. In contrast, all the other spider parasitoids show a tendency to attack more mature spiders in webs of various kinds (especially orb webs), and place their eggs on the abdomen of the host.

(2) The *Oxyrrhexis* group. This group consists of a single genus (which may be close to *Polysphincta*) and has only been reared from a theridiid spider.

(3) The *Polysphincta*-group. This consists of the cosmopolitan

2

genus *Polysphincta* and 2 Neotropical genera *Acrotaphus* and *Hymenoepimecis*. *Polysphincta* seems to be almost exclusively associated with Araneidae, and the other two genera have only been reared from araneid and tetragnathid spiders (Gauld, pers comm). Both of these spider groups consist of relatively large spiders which construct webs as large as, or larger, than their bodies.

(4) the *Acrodactyla* group. Analysis has shown that this group probably consists of 6 genera; *Piogaster*, *Eriostethus*, *Sinarachna*, *Eruga*, *Zatypota* and *Acrodactyla*. The last three genera clearly form a holophyletic group, while the other three seem to be paraphyletic with respect to that grouping. The whole group consists of small parasitoids excepting those of the Old World tropical rainforest genus *Eriostethus*, which are much larger (see chapter 3). This reduced size of parasitoid leads to a reduced size in the hosts which are attacked: mature Linyphiidae and Theridiidae (apparently the only hosts for *Zatypota*); immatures of Araneidae, Tetragnathidae, (and on occasions Dictynidae and Mettidae). All of these spin conspicuous webs of several shapes and sizes.

*Evolutionary significance:* The evolutionary sequences in this group seem to be quite clear. The primitive polysphinctines are attacking concealed hosts within silk tunnels or within silken retreats on vegetation, and place the egg on the cephalothorax of the host. The two main groups that have radiated from these underived genera have switched to web-spinning spiders, and place the egg somewhere on the abdomen; one group specialising on a wide range of smaller immature to mature spiders (the *Acrodactyla*-group) and the other on sub-adults and adults of a more restricted group of larger spiders (the *Polysphincta*-group).

#### 4.7. NODE 6: the Pimplini (including the *Theronia*-group)

*Holophyletic group defined at this node:* The tribe Pimplini (including *Theronia*).

#### 4.7.1. Microhabitat 8: Exposed or weakly concealed Lepidoptera pupae

This microhabitat consists of all pupae that are accessible to relatively short stabbing ovipositors. The parasitoid lifeway is that of a solitary idiobiont endoparasitoid. Adults often stab pupae which are not going to be oviposited within and feed from the wound (host feeding; Cole, 1959, 1967). As any suitable accessible pupa will suffice, some have evolved as pseudohyperparasitoids on ichneumonid pupae in their own cocoons.

*Functional adaptations:* All this group have stout gasters and thoraces, and the "higher" pimelines (the *Xanthopimpla*-group, the *Pimpla*-group and *Itoplectis*) have extremely stout stabbing ovipositors. The larvae of the "higher" Pimplini also have only a vestigial hypostoma and (usually) a well developed epistomal arch. These are characters normally associated with endoparasitoids.

*Subgroups:* The whole of the redefined Pimplini have this lifeway - that is the *Theronia*-group, the *Xanthopimpla*-group, the *Pimpla*-group and *Itoplectis* (of uncertain phylogenetic affinities, - see chapter 3).

The four groups have the following host-associations:

(1) the *Theronia*-group. Not all this group fit into the category described above. Species of the genus *Nomosphaeria* are parasitoids of vespids. The remaining genera seem to show a range of biologies from ectoparasitoids of Lepidoptera to secondary endoparasitoids of tachinids or ichneumonids in Lepidoptera pupae (Gupta, 1962, 1987; Short 1978, Gauld, 1984b). This group, then, is clearly in an intermediate position between an *Acropimpla*-type ancestor and the rest of the Pimplini; as is confirmed by its position in the hypothetical tree.

(2) *Itoplectis*. This genus stands alone phylogenetically, but is clearly correctly placed in this lifeway category. Both primary and hyper- endoparasitoids of small Lepidoptera pupae are known. This may be the plesiomorphic state in the "higher" Pimplini.

(3) The *Xanthopimpla*-group. *Xanthopimpla* dominates within this group. It is a tropical rain forest genus with a wide range of ovipositor modifications (Townes & Chiu, 1970) which suggest that the genus attacks a very wide range of hosts. The same comments apply to *Echthromorpha* and *Lissopimpla*, excepting that there are many more species of *Xanthopimpla* than of the other two genera. Host records (collected in Gupta, 1987) indicate that this group parasitises a very wide range of hosts, ranging from concealed to exposed. Some of this group have ovipositors very similar to those found in the *Pimpla*-group genus, *Apechthis* although this is clearly a parallelism. The distinctive mandibular structure of this group may relate to the need to escape from particularly hard pupae, although there is, as yet, no evidence for this.

(4) The *Pimpla*-group. Broadly speaking the same comments apply to this group as to the *Xanthopimpla*-group, although the host-ranges are more clearly demarcated, and with the exception of *Apechthis* the ovipositors are not as variable between the species. *Strongylopsis* is a deserticolous genus for which there are no host-records.

*Evolutionary significance:* This lifeway can again be easily derived from a *Acropimpla*-type ancestor. A shift to a more exposed and more vulnerable host has led to the egg being laid inside the host, where it is safe from abrasion (Gauld 1984a, 1988).

The Pimplini have a host-associated biology which allows of a very wide exploitation of Lepidoptera pupae. Within each apparently holophyletic group, however, there are no obvious host specialisations. The group, as discussed in chapter 3, seems to be split more along biogeographical lines, with the *Xanthopimpla*-group predominantly tropical and the *Pimpla*-group in the north temperate

region.

#### 4.8. General Trends

The evolution of host-associated biology in the Pimplinae (*sensu stricto*) can be considered to have three main components. The first, as recognised by Gauld (1988) is from concealed hosts, through semi-concealed, to exposed hosts. This results in a shift from host-habitat finding to host finding; and from ectoparasitoid idiobiont to endoparasitoid idiobiont pupal parasitoids, on the one hand, and to koinobiont ectoparasitoids of spiders, on the other.

The second is from deep wood probing (or limited boring) to deep boring. Relatively few ichneumonids have reached the level of boring ability of the rhyssines, where species of *Megarhyssa* have developed extremely complex ovipositor handling adaptations (Abbot, 1934; Heatwole et al, 1964). Amongst the pimplines as defined from the cladistic analysis no groups seem to have developed these adaptations. Within the pimpliformes (*sensu Wahl*) as a whole, the wood-boring groups are found at the base of the Poemeninae, the Acaenitinae and the Rhyssinae.

The third is from newly fallen timber to decaying timber. This seems to result from a cue shift from symbiotic fungi associated with hosts (Madden, 1969), to fungi indicative of timber age. It represents a shift from idiobiont ectoparasitoid borers to idiobiont ectoparasitoid probers, and, possibly, finally to koinobiont endoparasitoids of diptera associated with fungi in very old timber, in groups which may have been derived from the Pimplinae (*sensu lato*).

These three tendencies can be traced to relatively minor changes in the cues that are used to locate either host microhabitat or the host itself. One leads the parasitoid line out of wood and into other, living, green plants; one leads the parasitoid line further into the wood, perhaps in pursuit of hosts that are boring deeper; the final

one leads on toward the decaying plant and the saphrophytic organisms that feed off it, directly or indirectly. The three pathways are discussed in more detail below.

#### 4.8.1. From concealed to exposed hosts

The host-preferences of the Pimplinae (*sensu stricto*) shift gradually from a primitive association with deeply concealed wood-boring hosts, then with concealed, semi-exposed and finally to one with exposed hosts. A majority of the changes in pimpline biology discussed above can be explained as responses to dealing with a more and more exposed host. Gauld has summarised this (1988: pp. 356, 357, 359, 363) in an evolutionary sequence which follows very closely that indicated by the hypothetical tree with biologies superimposed (fig 4.1). The only major difference between Gauld's ideas and those presented here is that he postulates that the ancestral ichneuemonoid was a parasitoid in "relatively soft plant tissue". This seems unlikely given the phylogenetic distribution of the wood-associated habit and the difficulties of returning to the wood-boring habit from a probing one.

Buried hosts are simply pieces of meat that must be reached and then, after development, escaped from. As such, the nature of meat is unimportant - adults will do as well as larvae if they are caught before they escape from the wood (Hanson, 1939); and Cerambycids will do as well as Siricids if they happen to lie where other cues suggest an egg should be laid (Aubert, 1969). The problems are predominantly physical. This condition has been shown to be primitive and is characterised by solitary idiobiont ectoparasitoids with wide host ranges, although it is questionable whether the idea of a host range is very meaningful in this case. The main advantage of this microhabitat preference is that the immature stages are as safe as the host from predators.

The subsequent evolution poses two problems : the first, how to oviposit efficiently on or into a new host; and second, how to protect

offspring from predators which can reach the now more vulnerable host.

The first problem only arises when a shift away from probing occurs. The stabbing ovipositor is easy to derive as the action of stabbing is intrinsic to the action of puncturing the host to paralyse it. A shortening of the ovipositor and an increase in the amount of musculature within the ovipositor complex are the main morphological changes that are required.

The more exposed nature of the host has led to biologically diverse ways of ensuring the safety of offspring. Both the evolution of the endophagous habit in the Pimplini and the koinobiont habit in the Polysphinctini are related to ensuring that parasitoid larvae are as safe as the hosts they are in. The koinobiont lifeway enables free-living, i.e. adult, stages of arthropods to be parasitised. However, the only group which have been exploited by any pimelines are spiders. This can be explained by the evolutionary route which pimelines have taken to spiders: that via the environmental cue of silk. This has formed a bridge across to an adult arthropod, but has also constrained the parasitoids to hosts which can be found by searching for silk.

These shifts from one host microhabitat to another are highly characteristic of idiobiont ectoparasitoids (Gauld, 1988), which are unconstrained by the need to respond to a host's immune system. One of the most interesting aspects of the evolution of biology mentioned above is the small size of each individual step that needs to be conjectured. No great saltatory event appears to have occurred and there seems to have been no extinctions of intermediate lifeways.

#### 4.8.2 from concealed hosts to very deeply concealed hosts

This second evolutionary pathway has occurred independently in several groups of the Ichneumonidae, and always at the base of lineages. Each lineage shows very different modifications for the task of boring into wood (Gauld, 1984a), and it seems that a number of groups

have developed this lifeway independently. It is likely that these groups have evolved in response to their hosts burrowing deeper and deeper, either because the hosts are <sup>a</sup>searching for richer and richer plant tissue, or because they are attempting to escape the parasitoids. In either case it can be imagined that the primitive wood-boring host and parasitoid were less deeply concealed early on in their evolutionary development, and that co-evolution has taken them deeper and deeper into the wood.

#### 4.8.2. From newly fallen to rotting timber

This second evolutionary tendency is less well documented than the first one. It represents, not an evolutionary escape from the newly fallen log by moving outwards to more and more exposed microhabitats, but a change in the age of fallen log that is searched for. The stages in this pathway most probably relate to how fungal cues are used.

(A) Recently fallen new wood. The timber is still relatively free of fungi. Insects that exploit this microhabitat need to introduce fungi into the wood in order to begin the breakdown process (Francke-Grossman, 1939, 1967; Madden & Coutts, 1979) and produce digestable material. The wood-boring parasitoids often use these fungal symbionts of their hosts as host-locatory cues (for instance rhyssines (Spradbery, 1970b), see chapter 5).

(B) Decaying wood. By this stage fungi may have entered into the wood which are toxic to the original arthropod colonisers (*Armillaria mellea*, for instance, kills siricoid larvae (Madden & Coutts, 1979)). From this point on the wood is so permeated with fungi that the location of a particular host using its symbiotic fungi may become increasingly difficult. At this stage parasitoids may be searching for a log which has the right fungal volatiles that indicate a certain state of decay necessary for colonisation of the host type they are attacking.

(C) Decaying wood with fungal fruiting bodies. The final stage of this process is the reduction of the timber to a mass of fungal hyphae, from which basidiomycete and ascomycete fruiting bodies emerge. A wide range of arthropods feed off these structures, and additionally they form a cue for various parasitoids (Gilbertson, 1984; Shaw & Askew, 1978). In the pimphiiformes (Wahl, in press) most of the advanced groups attack Diptera. It may be the case that a decaying-wood probing parasitoid shifted from one cue of highly fungus infested wood to another of the fruiting body of the fungus. This could mean a switch to a Dipteran host - possibly to mycetophilids (fungus-midges) that are associated with polyphore bracket fungi (Oldroyd, 1964). Certainly, within the pimphiiformes both the Orthocentrinae and Oxytorinae have species that are parasitoids of mycetophilids (Shaw & Askew, 1978).

#### 4.9. Conclusions

The evolution of the pimpline lifeways has been constrained by the initial host substrate, dead wood. The whole of the evolutionary biology of the group can be traced as small steps from this original, evolutionarily stable, host microhabitat. No groups appear to have returned to this association once they have left the wood, and it seems possible that the parasitoids in wood have never been anywhere else, and that they have evolved from some symphytan ancestor that was xylophagous. This would mean that they represent the ancestral condition for all the apocrita. Consideration of the difficulties of evolving wood-boring adaptations *de novo* (see above) suggest that this is the case, as do considerations of the taxonomic distribution of the lifeway (at the base of braconid, ichneumonid and cynipoid lineages).

Fig 4.2. shows diagrammatically the evolutionary steps discussed in this section - concentrating on microhabitat, cue type and hosts. Further work on oviposition behaviour, fungal associations, and larval biology and morphology will fill in the many gaps and show that the story is far more complicated than that outlined here.

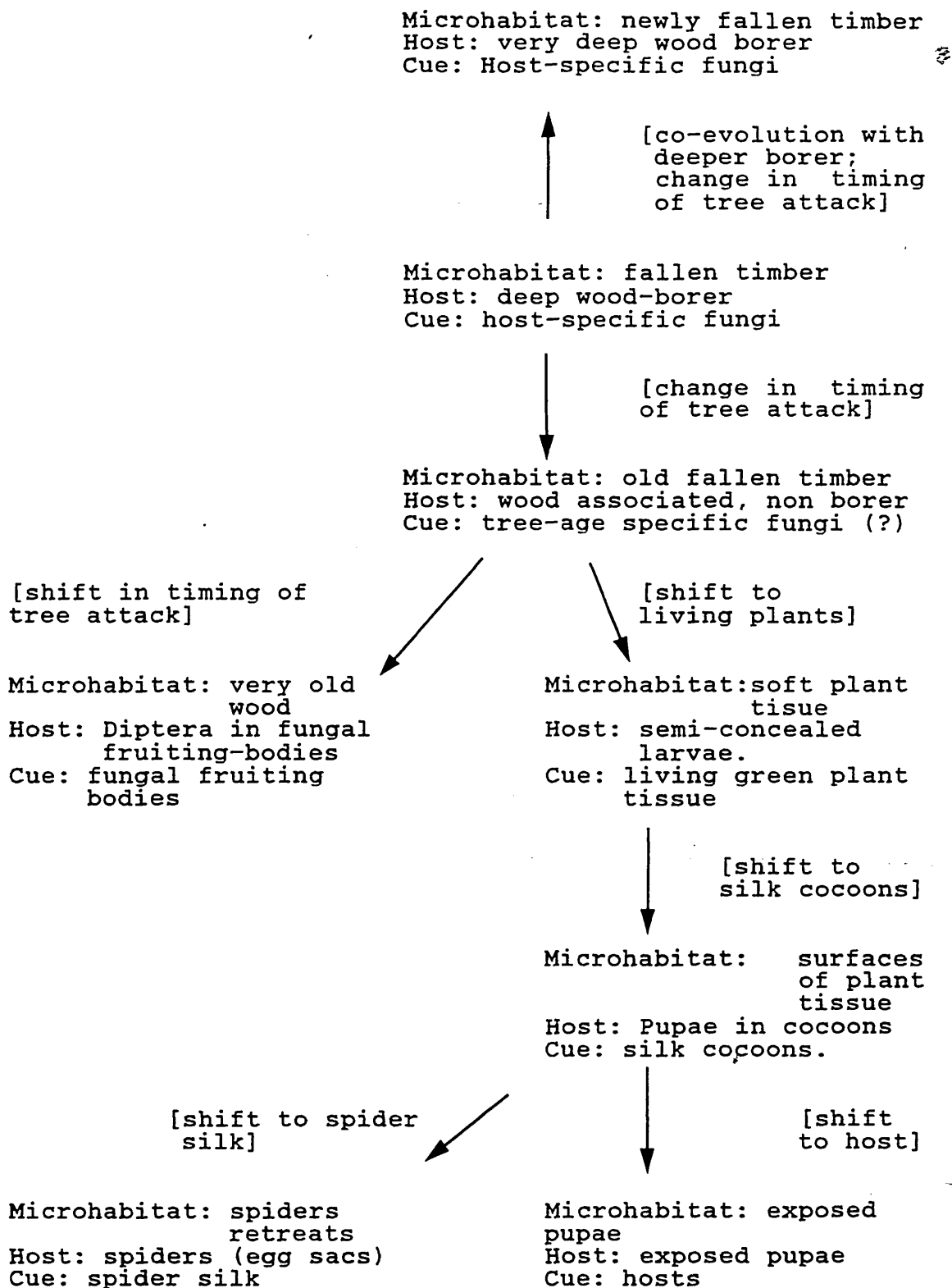
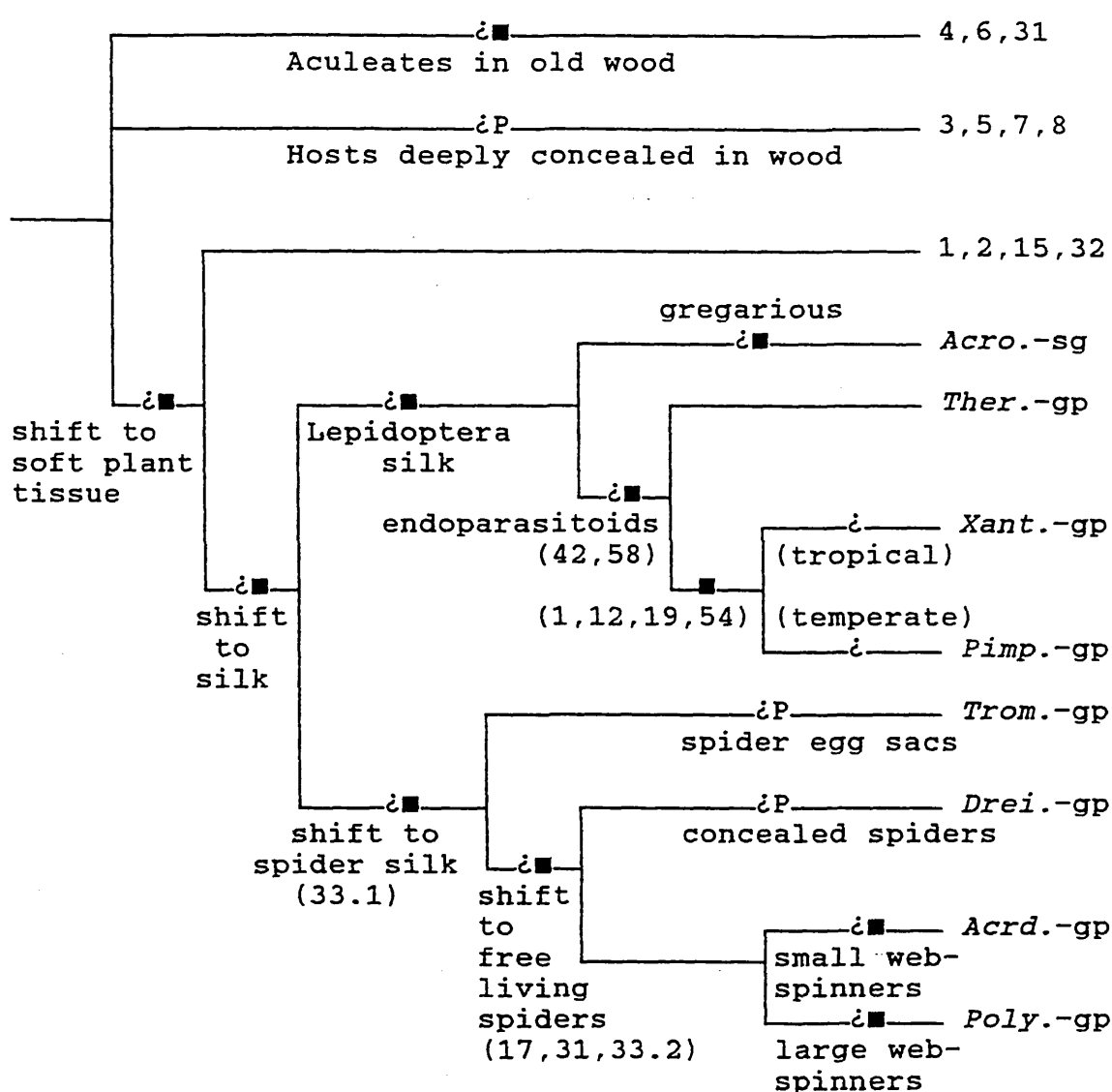


Fig 4.2. Diagram showing possible pathways of biological evolution at the base of the "pimpliformes" clade.

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The collation of all the available information on pimelines - both biological and morphological now enables a full scenario diagram to be constructed. This is shown in fig 4.3. It shows a very clear hennigian-comb type structure, which is indicative of the biological steps from concealed to exposed hosts. In addition it shows the clade consisting of the *Acropimpla*-subgroup and the Pimplini as the sister group to the Polysphinctini and the *Tromatobia*-group, due to the association with silk found in all the taxa.

It is interesting to note how several of the presumed biological "apomorphies" have no morphological apomorphies, for example those related to the shift to a soft plant tissue cue and the shift to a silk cue. In addition the Ephialtini are split into five separate groups, suggesting that they may be paraphyletic. The scenario diagram cannot be considered to give a real indication of relationships and will not be used to suggest the rearrangement of taxonomic groups, but it does give an insight into the possible pathways of biological evolution in the group, and to where relationships may exist not shown by a morphological analysis.



Key:  $\square$  - presumed biological "apomorphy";  $\circ$  - presumed biological plesiomorphy; Acro.-sg - Acropimpla subgroup; Ther. - Theronia; Xant. - Xanthopimpla; Pimp. - Pimpla; Zagl. - Zaglyptus; Drei. - Dreisbachia; Acrd. - Acrodactyla; Poly. - Polysphincta. Several groups of uncertain affinities are not included. Supporting morphological apomorphies are shown in brackets.

Fig 4.3. Simplified scenario diagram for the biological evolution of the Pimplinae.

### 5.1. Introduction

Rhyssines are found in wet forests throughout the world (except for *Rhyssa* species which inhabit dry boreal pine forests). The main activities of the adults are centred around the detection of suitable fallen trees both for host and mate searching. A great predominance of recorded hosts of rhyssines are Siricoidea found in angiosperm and gymnosperm wood. The hosts of tropical rain forest rhyssines are unknown, although it seems likely that they are not woodwasps. One dubious host record exists for tropical rhyssines (on a noctuid moth).

Rhyssines are one of the few ichneumonids groups which have been the focus of detailed, if taxonomically patchy, biological study. There are two main reasons for this. First, they are amongst the most conspicuous of the parasitic Hymenoptera, and can be common in certain places. For example the three sympatric species of *Megarhyssa* in North America not only include the largest known ichneumonid (*Megarhyssa atrata*) but are also collectible in large numbers in early summer. Second, the accidental introduction of pest siricids to Australia and New Zealand concentrated much work on potential control agents - the foremost of which were *Rhyssa* and *Megarhyssa* (Chrystal, 1928; Chrystal & Myers, 1928; Kirk, 1974, 1975; Miller & Clarke, 1935; Morgan & Stuart, 1966; Nuttall, 1973, 1980; Spradbery, 1970a, 1970b; Spradbery & Kirk, 1978; Spradbery & Ratkowsky, 1974; Taylor, 1976, 1978; Zondag & Nuttall, 1961). *Rhyssa persuasoria* has even been cultured for biological control purposes (Spradbery, 1968).

### 5.2. Distribution

Rhyssines are a basically tropicopolitan group with outliers in temperate regions. A biogeographical survey of the group is

postponed until the cladistic analysis has been performed. However, table 5.1 shows the number of described species from each biogeographical region.

### 5.3. Sexual dimorphism

Casual inspection suggests strongly that rhyssines females tend to be larger than males. This is in keeping with evidence for other ichneumonids (Gauld & Fitton, 1987). This dimorphism in size is confirmed by a t-test performed on reared material of *Rhyssella approximator*. The mean forewing lengths were significantly different (n=60, male mean 45mm, female mean 58.5 mm,  $t = 5.15$ ,  $p < 0.001$ ). It is not known whether this difference is genetically controlled, or comes about by females laying unfertilised eggs on small hosts. The latter condition is common amongst some ichneumonids (Arthur & Wylie, 1959) but has never been shown to occur in wood-associated parasitoids.

### 5.4. General Adult Behaviour

Adult rhyssines are strong-flying insects but seem to spend much of their time resting under leaves of their host's food-plant. Like many ichneumonids they prefer warm, moist conditions; Heatwole & Davis (1965) have shown (in *Megarhyssa*) that there is a depression in the activity of the adults during the driest part of the day, and during dry, hot parts of the year. In the tropics rhyssines seem to be active only in the lushest parts of rain-forests where there is a great deal of canopy cover (Porter, 1978). However, rhyssines have also been collected from secondary forest (Porter, 1978; Eggleton, unpublished).

It is not known whether adult rhyssines feed from flowers. However, they can be kept alive for some time in the laboratory. Thompson (pers comm) kept adults of *Rhyssella approximator* and fed them on a diet of sugar solution, under which conditions they lived for an average of 41 days (males, n=7, mean longevity 41 days;

Table 5.1. Numbers of valid species in each biogeographical region.

| Region           | Number of described species |          |
|------------------|-----------------------------|----------|
|                  | Total                       | Endemics |
| Palaearctic      | 21                          | 17       |
| East Palaearctic | (17)                        | (12)     |
| West Palaearctic | ( 8)                        | ( 4)     |
| Nearctic         | 14                          | 12       |
| Neotropical      | 38                          | 36       |
| Oriental         | 118                         | 115      |
| Australasian     | 1                           | 0        |
| Pacific          | 0                           | 0        |
| Ethiopian        | 7                           | 7        |
| Malagasy         | ( 1)                        | ( 1)     |
| TOTALS           | 194                         | 187      |

Information for the table above comes from: (a) for the Palearctic region - Aubert (1969), Townes, Monoi & Townes (1965); (b) for the Nearctic region - Townes & Townes (1960); (c) for the Neotropical region - Muesebeck et al, 1951; Townes & Townes (1966), Porter (1978); (d) for the Oriental region - Gupta (1987); (e) for the Australasian region - Gauld (1985); (f) for the Ethiopian region - Townes & Townes (1973).

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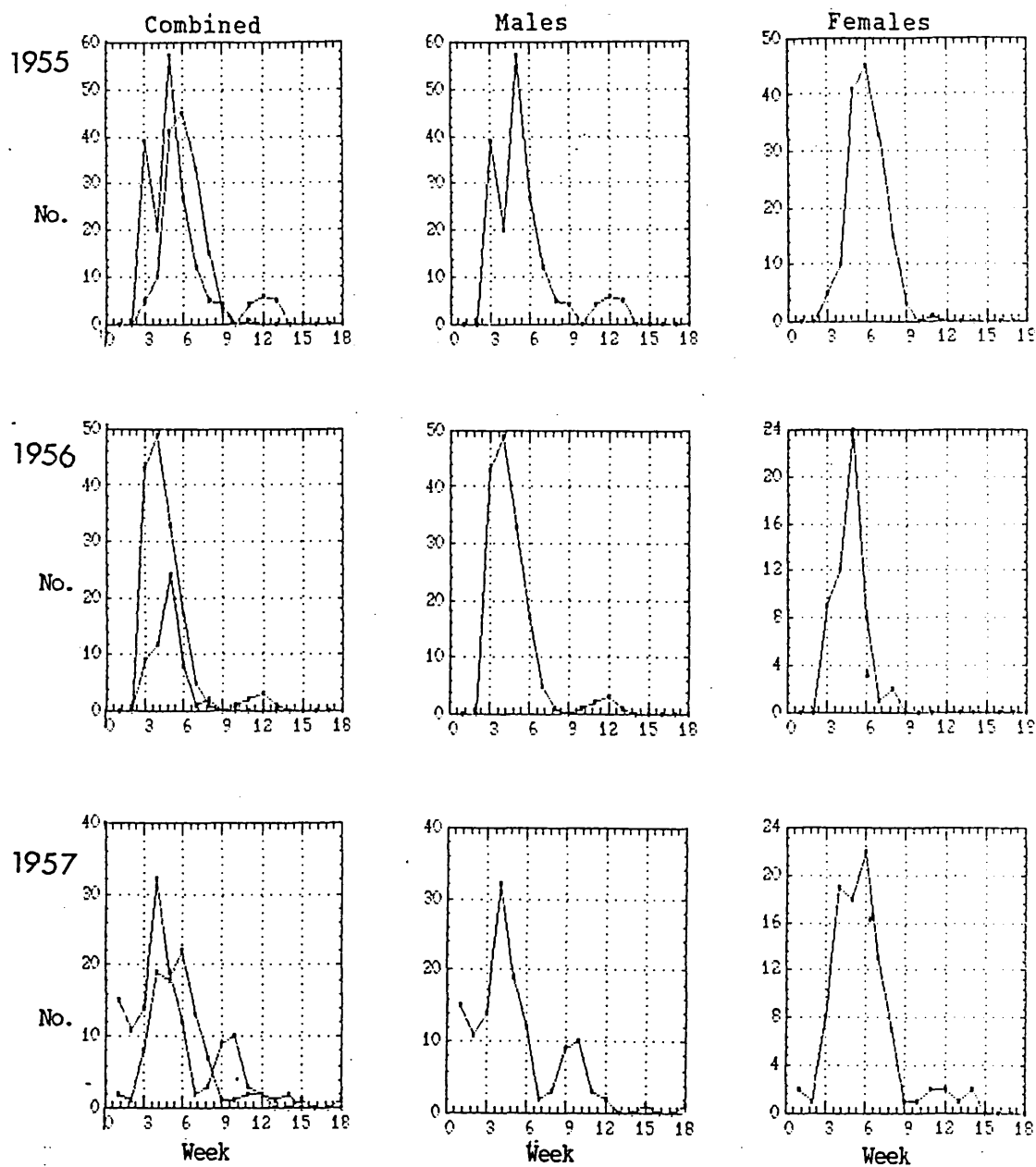
females n=4, mean longevity 41 days); on water only for an average of 15.5 days (males, n=3, mean longevity 18 days, females n=1, mean longevity 8 days); and when not fed at all for an average of 11.8 days (males, n=8, mean longevity 11 days; females, n=5, mean longevity 13 days). Three female specimens of *Lytarmes maculipennis* were kept alive for periods of 18, 24 and 26 days on sugar solution in a crude laboratory setting in Sabah (Eggleton, unpublished data). This is circumstantial evidence for the presence of some adult feeding (or at least for the need for water). Heatwole & Davis (1965) report no competition either for resting sites (under leaves) or for food in *Megarhyssa*.

#### 5.4.1. Emergence timings

The most comprehensive data relating to emergence timings in both sexes was collected by G. H. Thompson between the years of 1955 and 1960, for *Rhyssella approximata*. Dr. Thompson has kindly let me analyse his data and present the results here. The emergences are plotted in figs 5.1 and 5.2, year by year with the sexes separate. Week 1 is 22-29th April in each year. The plots show a number of interesting features.

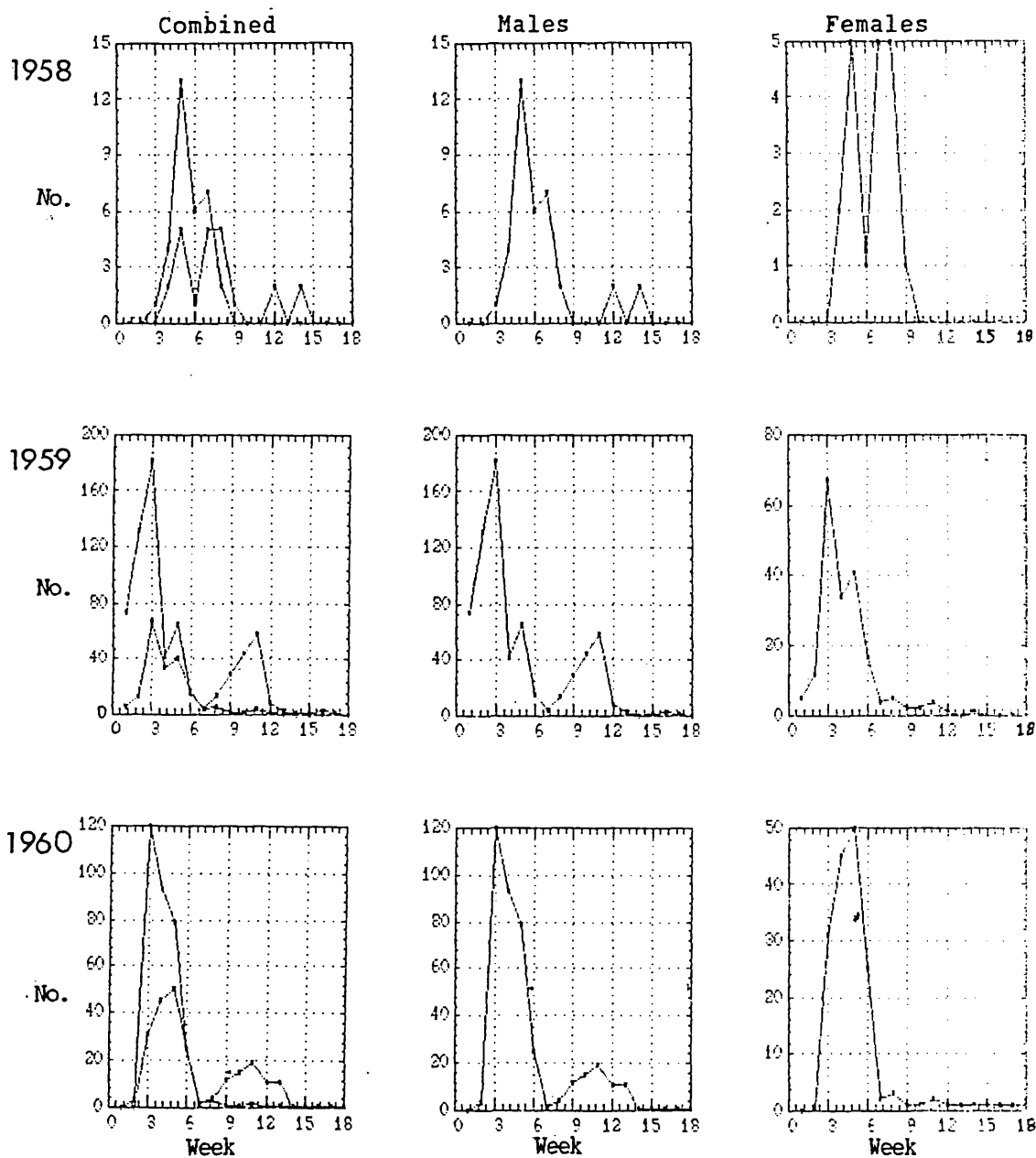
(a) As males mate with females at the time of female emergence (see next section) it might be expected that males should emerge before females. Do the results obtained by Thompson suggest that this is so? As the emergence frequencies clearly do not show a normal distribution a non-parametric median-test has been performed producing a 2X2 contingency table to produce a  $\chi^2$  test statistic (Fryer, 1966). This is a one-tailed test as only results in the direction of earlier male emergence are of interest. The results are shown in table 5.2.

Table 5.2 shows that, in all cases but the 1958 one, the median of male emergences occurred significantly before the median in female emergences. This means that there is a tendency for males to emerge



Key: week 1 = 22-29th April

Fig 5.1. Plots of emergence times for male and female *Rhyssella approximator* specimens, 1955-1957. (Data from Gerald Thompson).



Key: week 1 = 22-29th April.

Fig 5.2. Plots of emergence times for male and female *Rhysella approximator* specimens, 1958-1960. (Data from Gerald Thompson).

Table 5.2. Median tests for earlier male emergence of *Rhyssella approximator*, 1955-1960.

| Year | chi <sup>2</sup> | prob.  | Significance    |
|------|------------------|--------|-----------------|
| 1955 | 43.20            | <0.001 | Significant     |
| 1956 | 15.22            | <0.001 | Significant     |
| 1957 | 6.86             | <0.05  | Significant     |
| 1958 | 1.28             | >0.25  | Not significant |
| 1959 | 56.22            | <0.001 | Significant     |
| 1960 | 32.3             | <0.001 | Significant     |

Table 5.3. Sex ratio of emergences of *Rhyssella approximator*, 1955-1960.

| Year | ratio | chi <sup>2</sup> | P     | result          |
|------|-------|------------------|-------|-----------------|
| 1955 | 1.17  | 2.05             | 0.15  | not significant |
| 1956 | 2.77  | 59.56            | <0.01 | significant     |
| 1957 | 1.33  | 4.73             | <0.05 | significant     |
| 1958 | 1.95  | 6.45             | <0.05 | significant     |
| 1959 | 3.48  | 385.11           | <0.01 | significant     |
| 1960 | 2.42  | 119.76           | <0.01 | significant     |

before females, and thus be in a position to mate at the female emergence sites. The one year where the result is not highly significant was a year of low overall emergence (1958).

(b) Male emergence frequencies show a secondary peak in late summer. This secondary peak is not easy to explain, as by the time these males are emerging very few females are still left to emerge (i.e. there is no secondary female peak). Two possibilities present themselves. First, males which emerge later may be smaller, and represent males with an alternative mating strategy (see chapter 6). Inspection of reared material in the collection gives no indication that late emerging males are smaller than early emerging ones. Second, the late emerging males may be hibernating to ensure that they are the first to encounter emerging females next spring. No male *Rhyssella* specimens appear to have been collected in the winter months. Hibernation is relatively well documented amongst ichneumonids, however, especially in the Pimplini (references in Fitton *et al*, 1988), although it does not seem to occur in *Megarhyssa macurus* and *M. atrata* (Duffield & Nordin, 1970).

(c) The sex ratio differs markedly from year to year (table 5.3), and in all but 1955 it is significantly male biased. Whether this is due to an artifact of sampling is difficult to judge. The ratios may show such striking differences for a variety of reasons. It may be that different sizes of branches were chosen in each year, and this might bias the result either way (probably toward the males if relatively thin branches were collected, and toward the females if relatively thick branches were collected). However, Thompson (pers comm) collected branches of equal thickness in each year, and an attempt was made to standardise rearing conditions from year to year. Alternatively, it may represent a response by ovipositing females in the previous year - it may be that females lay a female biased sex ratio when resources are low, as females are the limiting resource in terms of offspring produced, and a male biased ratio when resources are low. This is difficult to test as there is no easy way of assessing resource levels - as this is influenced by several factors,

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including meteorological conditions, availability of suitable moribund branches for hosts, and the mortality of the hosts in the previous year.

#### 5.4.3. Meteorological effects on emergence

In an attempt to examine at least the meteorological effects on male emergence, four weather variables (mean temperature, number of days with air frost, sunlight hours, rainfall) have been collected month by month for 1954-1960. The information was obtained from *Weather* (1954-60); the data all refer to meteorological conditions at Kew Observatory (taken to be indicative of the overall weather conditions in the south of England - exact locality data were not available). The following possible effects were investigated: (a) mean monthly temperature, sunshine hours and rainfall in the previous summer (defined as April to June, in the year previous to the emergences); a poor summer might mean that ovipositing females were less active and fewer eggs were laid. This might be expected to result in fewer emergences in the following year. (b) mean monthly temperature, sunshine hours and rainfall during the emergence period (defined as April to June, during the emergence period) ; this might be expected to have an effect on the activity of the insects and their ability to successfully emerge. (c) mean monthly temperature, number of air frosts, sunshine hours and rainfall in the previous winter (defined as December to March of the previous winter): very cold weather might kill the developing parasitoids within the wood.

Of these possibilities only the sunshine hours in the summer of the emergence was significantly correlated with the emergence records ( $n=6$ ,  $r=0.8251$ ,  $p = 0.02 - 0.05$  for the combined male and female data;  $n=6$ ,  $r=0.80528$ ,  $p= 0.02-0.05$  for the male data;  $n=6$ ,  $r=0.8492$ ,  $p < 0.02$  for the female data). If this correlation really means anything at all, it is perhaps that in summers with very little sunshine, logs may not be able to heat up enough to provide the ectothermic insects inside with a suitable thermal environment for emergence. The effect might be expected to be greater for males than

females, as males are smaller and therefore have a less advantageous surface area to volume ratio. If this is the case there ought to be a correlation between sex ratio and sunshine hours. However, in this case it is not statistically significant ( $n=6$ ,  $r=0.3645$ ,  $p > 0.1$ ; however, it is marginally significant for air temperature:  $n=6$ ,  $r=0.7460$ ,  $p=0.1-0.05$ ).

Zondag & Nuttall (1961) present emergence records for *Rhyssa lineolata* and *Rhyssa persuasoria* in New Zealand. The results show a similar pattern of male emergence occurring before female emergence, and a biased sex ratio, but no secondary peak in male numbers in late summer. Heatwole & Davis (1965), looking at museum specimens of *Megarhyssa*, noted the sex of the first recorded captures over a number of years and concluded that there was no significant difference in the pooled sex ratio. This is, of course, not a direct measure of emergence times. It is also probable that more females are captured, due to their conspicuousness, at all times of year, and this may be a major factor biasing the results.

### 5.5. Male reproductive behaviour

#### 5.5.1. Male reproductive behaviour in *Rhyssa* and *Megarhyssa*

Once emerged the males immediately begin hunting for female emergence sites. A suitable log is located and the searching insects walk up and down the log or circle it flying with their abdomens at right angles to the bole of the tree and the individuals thorax, which is parallel with the bark (Crankshaw & Matthews, 1981). Heatwole & Davis (1965) have shown by marking experiments that both males and females habitually return to the logs that they emerged from. It is not stated whether individuals return to the log they emerged from more often than they visited other suitable logs. How these particular logs are identified is unknown. However, we have some idea of how emergence sites in general are located.

Fungal cues seem to be especially important. Madden (1968) and

Davies & Madden (1985) have shown that *Megarhyssa nortoni* males respond to the siricid symbiont (Parker, 1942), *Amylostereum* sp. (a basidiomycete fungus), whether presented on filter paper, in agar culture or in the host frass. The response is one of attraction leading to greatly increased recruitment of males to a site. This effect is dependent on culture age. This attraction may be due to the localised increase in concentration of fungal volatiles associated with moisture changes occurring during adult eclosion. Certainly, water introduced into frass filled emergence burrows will result in male aggregative behaviour 1-2 days later (Madden & Davies, 1985) . The same effect has been observed in *Rhyssa persuasoria*, but at different threshold response levels (*op. cit.*).

In addition, Heatwole *et al* (1964) have suggested that males may find the position of emergents by chewing noises made by them while making their way to the surface of the log. He recorded the sound made by emerging females and elicited pre-copulatory responses from males when these were played back under laboratory conditions.

Male rhyssines around future emergence sites form into characteristic aggregations (Barlow, 1921; Champlain 1921; Yasumatsu, 1937, 1938). These may partially be due to a group of individuals all reacting to emergent stimuli at the same time. It is also probably associated with pheromones produced by the waiting males themselves. Males of *Megarhyssa nortoni* and *Rhyssa persuasoria* have been shown to produce various mandibular secretions (Davies & Madden, 1985) which may partially act as an aggregative cue. These seem to be species-specific pheromones and are probably also involved in recognition of conspecific females when an emerging insect breaks through to the surface of a log (see below).

In all groups aggregative behaviour itself is associated with intense antennation. Males tap the substrate and each other with the distal parts of their antennae. In other respects, however, there is a fair amount of variation, especially in the density of males at a site and their reactions to each other.

*Megarhyssa* species form the densest and largest aggregations yet recorded (Chrystal & Skinner, 1932; Heatwole et al, 1964; Crankshaw and Matthews, 1981). In one case Three Nearctic species (*Megarhyssa atrata*, *Megarhyssa greeni* and *Megarhyssa macurus*) may occur in enormous aggregations together at the same time (sometimes over thirty individuals). Much of the behaviour at these places is related to the peculiar abdominal modifications of *Megarhyssa* and the presence of anal glands (Matthews et al, 1979; see chapter 6). These behaviours include abdominal tipping, tergal stroking and attempts at abdominal insertion into cracks in the bark. These are described below:

(1) Abdominal tipping. The abdomen is bent forward between the legs, and left motionless. This is possibly a 'ready' position prior to inserting. (2) Tergal stroking. A very similar attitude is taken up as in (1) but here the final tergite (complete with anal gland) is rubbed against the substrate parallel to the orientation of the body. (3) Abdominal insertion. Here the male attempts to insert its long abdomen into cracks in the bark which are not necessarily related to emergence sites. (2) and (3) may be examples of displacement activities (Matthews et al, 1979).

At the same time as all these activities are going on there is a period of jostling and intense effort to keep abdomens tipped over the future site of emergence. It was also found that as the emerging female got closer to the surface the proportion of non-conspecific males in a group dropped (Crankshaw & Matthews, 1981). If the emergent turned out to be a male or an emerging host then the aggregation speedily dispersed.

Aggregations are reported to be much looser in *Rhyssa* (Spradbery, 1970b; Davies & Madden, 1985; but cf. Champion, 1929) and intermediate in density in *Rhyssella* (Skinner & Thompson, 1960; Thompson, pers comm; Eggleton, unpublished data). There were no proper aggregations in *Lytarmes maculipennis* (see below). None of the characteristic *Megarhyssa* gastral-bending behaviour has been recorded in *Rhyssa*, but it certainly does occur in *Rhyssella* and *Lytarmes* (see

below). Two studies (Myers, 1928; Davies & Madden, 1985) suggest that *Rhyssa* may be incapable of bending its abdomen between its legs, due to its abdominal morphology, and that this may explain the lack of a *Megarhyssa*-like response.

The labenine, *Certonotus tasmanensis* also shows a similar aggregative response to *Megarhyssa* (Davies & Madden, 1985). In fact a number of labenines have similar abdominal modifications in males as those in rhyssines.

Surprisingly there is little evidence of territoriality or dominance hierarchies within aggregations (see below). Heatwole *et al* (1964) and Nuttall (1973) report no such behaviour, and Crankshaw & Matthews (1981) and Davies & Madden (1985) have observed mutual aggression but with no apparent dominance structure between males. In *Megarhyssa nortoni* and *Rhyssa persuasoria* the mandibular gland secretions have been found to contain 6-methylhept-5-ene-2-one which has been identified in other groups as a repellent (and alarm) pheromone (Davies & Madden, 1985), and all though this may act as a general anti-male substance no trace of a hierarchy based on this has been described. Matthews *et al* (1982) however do report some sort of dominance hierarchy in one aspect of *Megarhyssa* behaviour. They found that it was nearly always the same one or two individuals, at any one aggregation site which did the majority of the tergal stroking.

The moment that the female's head is visible a group of species-specific chemicals produced by the mandibular glands can be detected by males at the surface and incite conspecific males to attempt to copulate with her. This may be especially important where there is sympatry between rhyssines and mixed-species aggregations are formed. In *Megarhyssa nortoni* these secretions appear to be a group of closely related spiroacetals, and in *Rhyssa persuasoria* they seem to be predominantly 3-OH-3-methyl butan-2-one. (Madden & Davies, 1985).

In *Megarhyssa* once the female has made an opening to the surface

the surrounding males attempt to insert their abdomens into the hole. This activity is associated with two main behavioural activities: (1) Tergal stroking, and (2) pre-emergence copulation. These are described below:

(1) Tergal-stroking. As discussed elsewhere (chapter 6) most rhyssine species have males which possess anal glands situated around the opening of the anus just posterior to the 9th (abdominal) tergite. The characteristic use of this gland in pre-insertion tergal-stroking is described above. Matthews *et al* (1979) suggest that cells of the hind gut may be involved in producing secretions which act in some way as a markant. It is possible that this markant is secreted onto the setae of the anal gland (see fig. 6.17) and rubbed against the emergent. The function of this supposed substance is unknown, although it may be that tergal-stroking of the substrate may increase the likelihood that a male will return to the same tree.

(2) Pre-emergence copulation. The possibility that *Megarhyssa* males might mate with emerging females before they leave their exit tunnels has been discussed for many years (Gade, 1834; Harrington 1887). Some earlier authors (Gade, 1834; Abbott, 1936) discounted this possibility because they did not believe that many of the males would be able reach down to the female's genital opening through the emergence tunnel and inseminate her. However, Nuttall (1973) seemed to show that it was possible for a male to insert deeply enough into the hole to mate. Crankshaw and Matthews (1981) found sperm in the spermatheca of a female that had been allowed to encounter only inserting males, providing strong evidence for the existence of pre-emergence fertilisation. Yasumatsu's (1937) excellent drawings of inserting males of *Megarhyssa praezellens* are reproduced in figs 5.3 and 5.4.

The details of the above process have been most closely studied in the three sympatric *Megarhyssa* species (Matthews *et al*, 1979; Crankshaw & Matthews, 1981). Here, up to 8 males may insert at any one time, and there may be inserters of all 3 species. In all cases, though, males conspecific to the emerging female are the most common

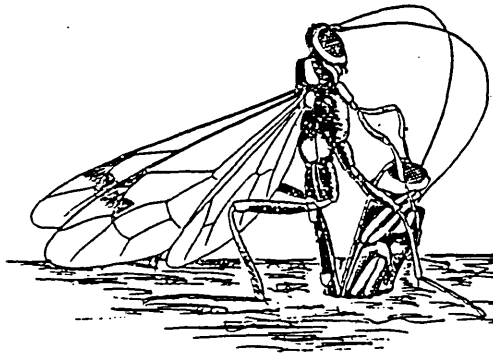


Fig 5.3. Partial male insertion in *Megarhyssa praecellens*, prior to female emergence. (From Yasumatsu, 1937).

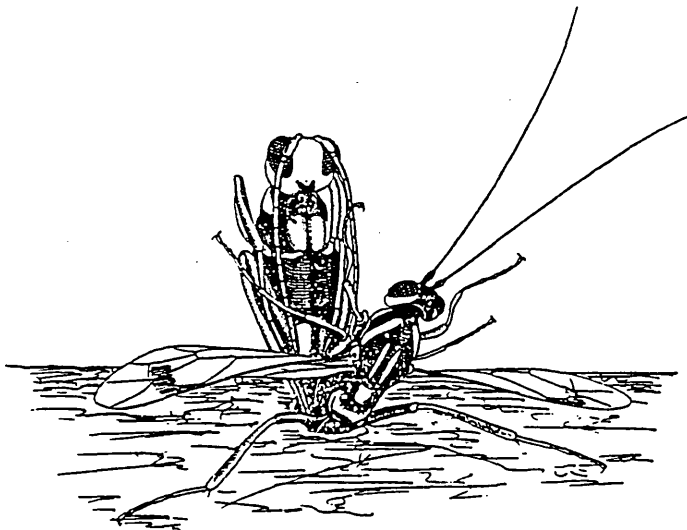


Fig 5.4. Full male insertion in *Megarhyssa praecellens*, as female emerges. (From Yasumatsu, 1937).

inserters. It is not known if the female has any mechanism for preventing non-conspecifics from mating with her or for choosing particular conspecific males to mate with. As the female enlarges the emergence hole the males are able to get more and more of their abdomens down the tunnel, up to the point when some were inserted up to the metathorax. Males remained inserting for a very variable length of time (2-410 minutes). The average size of first inserters did not differ significantly from the average size of males in all aggregations. In addition, there was no correlation between the order of arrival at the site and the order of insertion. In 90% of all cases males would leave the aggregation after full insertion.

Once emerged the female *Megarhyssa* walks away from the emergence hole with males following her and attempting to copulate with her. These females either did not respond to this behaviour or attempted to shrug off the males. Post-emergence copulation followed 33% of emergences where the female remained undisturbed. It is probable that females are not always receptive after emergence, and also that they remain receptive for only a short time after in any case. This may be the general rule in parasitic Hymenoptera (Gauld & Bolton, 1988).

In *Rhyssa* mating always takes place after emergence. Myers (1928) conducted an experiment to show that males of *Rhyssa persuasoria* were unreceptive to emerging females, although the number of replicates was very low.

#### 5.5.2. Male reproductive behaviour in *Rhyssella*

During the making of Skinner & Thompson (1960), G. H. Thompson took a number of photographs of male reproductive behaviour in *Rhyssella approximata*. He has kindly given permission for some of them to be used here. Although there are no written observations that go with the photographs, the general pattern of reproductive behaviour can be deduced.

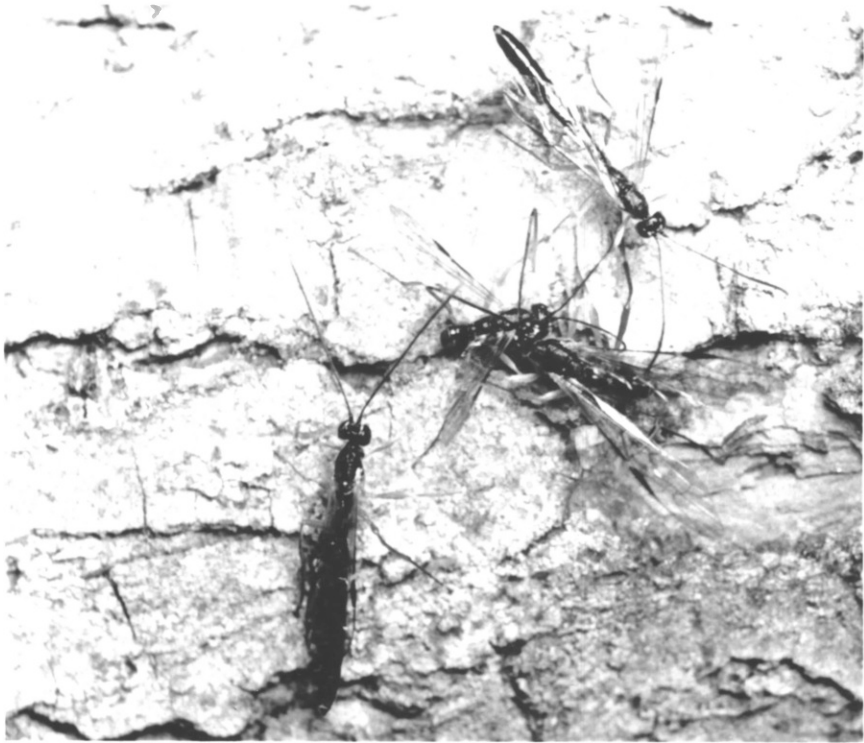


Fig 5.5. Male aggregation in *Rhyssella approximator*, prior to female emergence. (Photograph courtesy of Gerald Thompson).

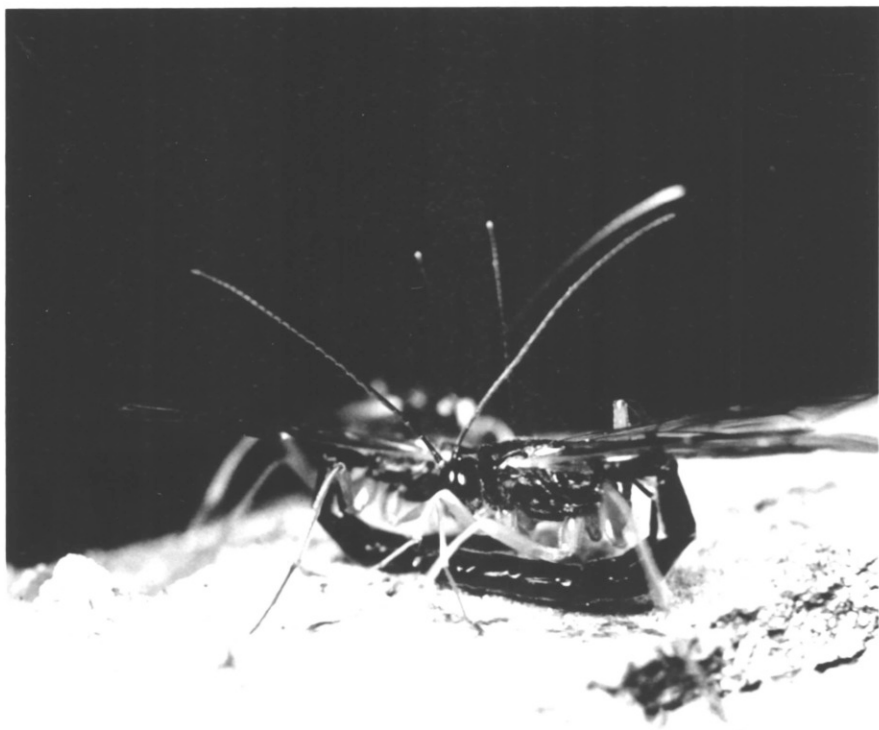


Fig 5.6. Male aggregation in *Rhyssella approximator*, showing characteristic abdomen-bending behaviour. (Photograph courtesy of Gerald Thompson).

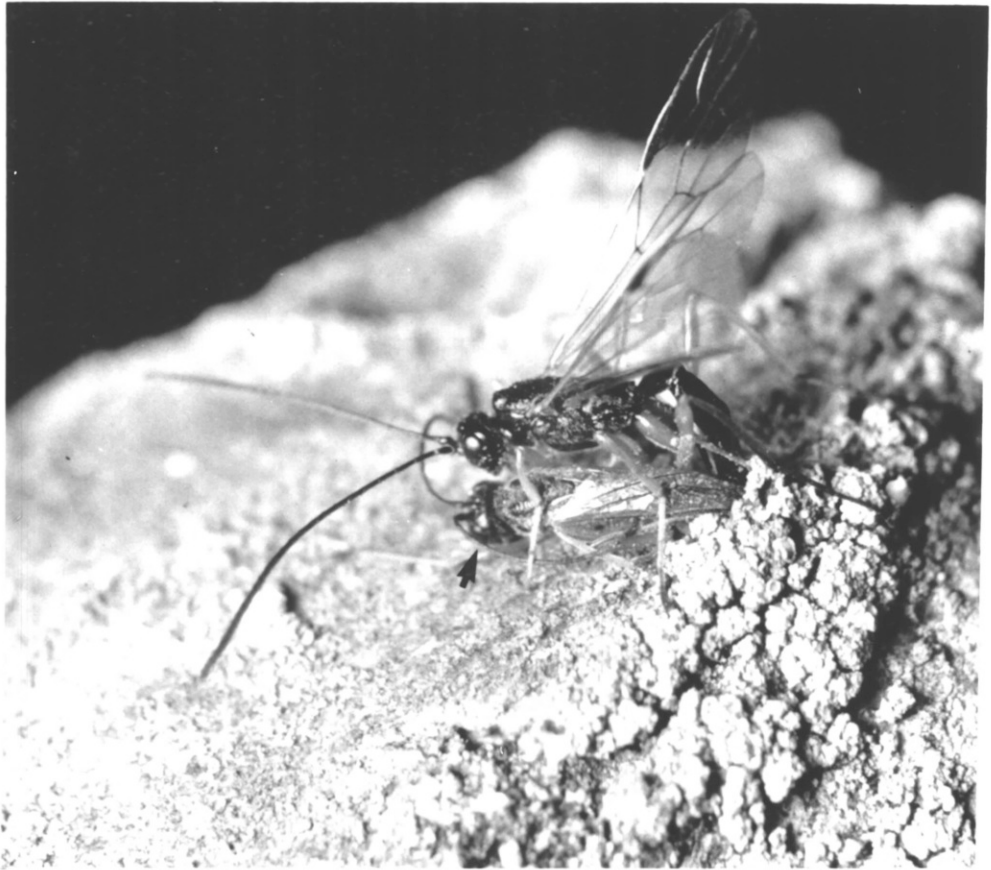


Fig 5.7. Male insertion in *Rhyssella approximator*. Arrow points to emerging female. (Photograph courtesy of Gerald Thompson).

Fig 5.5 shows a characteristic aggregation around a female emergence site. There are two males showing abdominal bending behaviour, and another two males close by. This aggregation is much more compact than that found in *Lytarmes maculipennis* (see below), more like that found in *Megarhyssa* (above). The abdomen bending behaviour is shown in fig 5.6, the way the abdomen is held is very similar to that found in *Megarhyssa* (Yasumatsu, 1937, 1938; Crankshaw & Matthews, 1981) and *Lytarmes maculipennis* (see below).

Fig 5.7 shows a pre-emergence insertion by a male. this is very similar to that found in *Megarhyssa*. Additional photographs and Thompson's anecdotal descriptions (pers comm) suggest strongly that *Rhyssella* males are showing a pre-emergence scramble competition system.

#### 5.5.3. Male reproductive behaviour in *Lytarmes*

The reproductive behaviour of only one species of tropical rhyssines has ever been observed. This was a single observation at the Danum Valley Field Studies Centre on *Lytarmes maculipennis*. The details of this are given below (and also in Eggleton, in press).

Males of *Lytarmes maculipennis* were first observed at 11:30 hrs 13th December 1986 [just past E11 on the Danum Valley Field Centre trail system]. They were flying round a group of 7 fallen logs all apparently part of the same fallen tree. At this stage two sorts of behaviour were observed: (a) searching behaviour; where males were vigorously tapping the substrate with their antennae. This occurred either as they flew up and down logs with their gasters held at roughly 90 degrees away from the surface of the wood, or while they walked on the surface of the log. (b) Resting behaviour; remaining motionless on the shaded parts of logs or under nearby leaves. There was no clustering of the males at any one point. Females were occasionally seen flying around but they did not show any characteristic searching behaviour. During the observation periods there were only two occasions when there was interaction between the

sexes. On both occasions a male approached a female and tapped her with his antennae but the female flew away immediately after.

On approaching the study site on the third day of observation (at 06:00) it was noticed that one large log had a group of males clustered loosely around its end. This group consisted, at any one time, of between 4 and 6 individuals (Fig 5.8). From 08:20 onwards, and at irregular intervals, a noise could clearly be heard (from a distance of up to 2 metres) coming from the log. It resembled the sound of chewing and scratching and was caused by the female enlarging the emergence tunnel she was making beneath the wood. These noises had an immediate effect on the males; they tapped more rapidly with their antennae and began to interact with each other more frequently.

The male interactions began soon after the noises of emergence were first heard. One large male [forewing length 11.2 mm] flew on to the log close to the source of the noises. The lack of a large portion of his left hindwing clearly identified this male and his movements throughout were easy to observe. From then on smaller males would repeatedly approach the large male by crawling toward him over the surface of the log or by flying above him. In either case the smaller males seemed to be attempting to bite at the wings and gaster of the large male, which invariably repulsed them by biting at an approaching crawling male or shaking off a flying one. The larger male would always return to within 10mm of the emergence site (which was marked with chalk) and at no time was any other male within this area (Fig 5.9). If the males were disturbed from the log at any time, either deliberately by the investigator or accidentally by extraneous noise, the large male would fly a few metres away and return to the marked area within 20 seconds.

At 12:10 the jaws of the emerging female could clearly be seen through the wood (Fig 5.9). At this stage the large male brought his gaster forward between his legs so that its tip was in contact with the bark of the tree, about level with his head (Fig 5.10). At no time was there the rapid movement of the gaster tip across the



Fig 5.8. Loose male aggregation in *Lytarmes maculipennis*, prior to female emergence.



Fig 5.9. Magnified view of large *Lytarmes maculipennis* male guarding emergence site. Arrow points to the head of the emerging female.

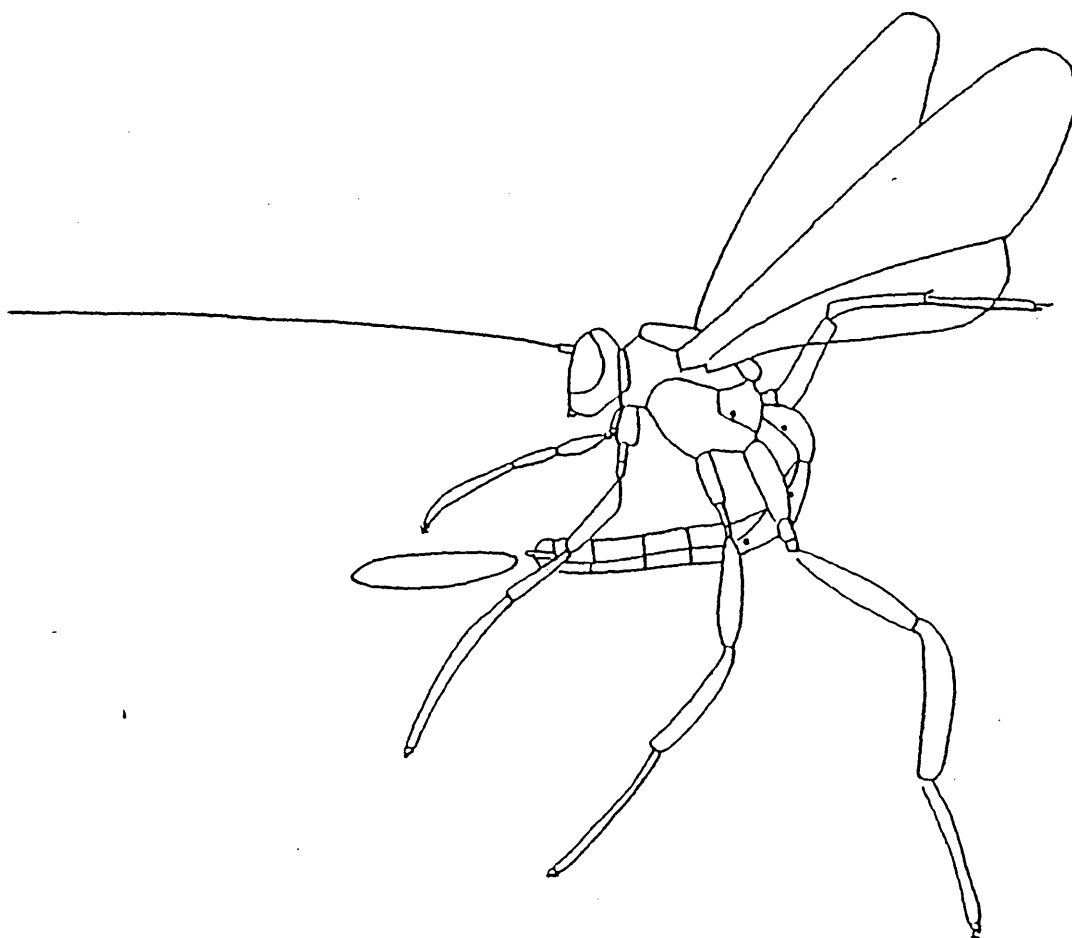


Fig 5.10. Guarding male of *Lytarmes maculipennis*, showing abdomen-bending behaviour close to female emergence hole.

substrate seen in *Megarhyssa* and known as tergal stroking (see above). Subsequent dissection has shown, however, that an anal gland is present in this species similar to that found in *Megarhyssa*. None of the small males showed this abdomen-bending behaviour.

The emerging female continued to enlarge the emergence hole by chewing off pieces from around its periphery. On 12 occasions the male drew the tip of his gaster across the hole apparently over the head of the female. On 4 occasions the female pulled herself some way out of the hole but was unable to emerge completely, because it was not yet large enough. Each time the large male inserted his gaster under the thorax of the female before she retreated into the hole. Finally, she emerged completely out of the hole (at 14:10). As she did so the large male inserted his gaster for about 2 seconds, following which 3 of the smaller males flew to the site and clung on to the female's thorax and gaster. The female was not arrested in her movement out of the log and once she had completely emerged she flew off apparently with the smaller males still attached. The smaller males were attached for less than 2 seconds before the female left the log. The large male remained at the emergence site for 7 more minutes but there was no further antennal tapping or abdomen-bending. At this point the large male and 3 remaining smaller males were captured. No other males were observed subsequently around the emergence site.

#### 5.5.4. Mating systems

The presence of emerging females which have a clumped distribution in time and space should provide an opportunity for males to compete amongst themselves for the opportunity to be first to inseminate emerging females. This could lead to the type of behavioural strategy known as *Female Defence Polygyny* (Thornhill & Alcock, 1983) where males defend an area in which females are prevalent and exclude other males from mating. The evidence for this occurring in rhyssines is presented in chapter 6. In the well documented examples of *Megarhyssa* species where there is pre-emergence fertilisation this

does not seem to occur. No obvious territoriality or other kind of dominance system have been noted between males and a *scramble* type system seems to have evolved. Here there is a premium on being at the right place at the right time (Crankshaw and Matthews 1981). The strategy seems to consist of racing to be the first male to fertilise an emerging female. However if (due to reasons of being too small or timing the attempt wrongly) that is not possible then a 'Conditional' response of post-emergence fertilisation is attempted (see chapter 6).

#### 5.5.5. Conclusions

Three different mating strategies can be recognised within the rhyssines. (1) Scramble competition/ post-emergence mating. This is the system recorded in *Rhyssa persuasoria*, where males cannot bend their abdomens beneath their legs and therefore neither possess an anal gland nor can insert their gasters into the female's emergence tunnel. It is not certain that this is a scramble system, but the descriptions of aggregations (such as Champion, 1929) suggest that this is the case. (2) Scramble competition/ pre-emergence mating. This is the system recorded in the North American species of *Megarhyssa*, and presumed, from rather more anecdotal evidence, to be the case in the Palaearctic *Rhyssella approximator*. (3) Female defence/ at emergence mating. This is the system recorded in *Lytarmes maculipennis*.

Both (2) and (3) involve gastral bending behaviour, and it seems likely that this behaviour is present in all rhyssines except *Rhyssa* species. there are 2 pieces of evidence to support this. First, all male rhyssines, except *Rhyssa* species, have anal glands on the dorsal surface of the final gastral tergite. If the glands function is in marking the emergence site, then it would need to be bent beneath the legs. Second, material of males collected in alcohol invariably show a bending of the abdomen beneath the legs, which makes removing rhyssine males from such samples very easy. The only rhyssine males that do not look like this in alcohol are *Rhyssa* species.

### 5.6. Host Searching and Oviposition Behaviour

As with most parasitoid groups, published host records of rhyssines are often unreliable. Often these records are the result of rearings from logs which contain potential recorded hosts but without definite associations having been made between parasitoid and host. For example Aubert (1969) records *Rhyssa persuasoria* as a parasitoid of 5 species of cerambycid beetles, and 8 species of siricid. More recent records tend to suggest that this species is only parasitic on Siricids, although cerambycids may very occasionally be parasitised if they too are present in the decaying logs (indeed, Hanson, 1939, has recorded *Rhyssa persuasoria* as a parasitoid of *Ibalia* species, another parasitoid of siricoids). However, the primary hosts of all Holarctic rhyssines seem to be siricoids, and the hosts seem to split up into three taxonomic groupings. (The host records are collected in Townes *et al* (1965); Aubert (1969); Carlson (1979), and; Kazmierczack (1979)).

(a) Siricinae. All recorded host for *Rhyssa* species are siricine siricoids on Pineaceae. Two species of *Megarhyssa*; *M. nortoni* and *M. emarginatoria* are also associated with these hosts.

(b) Tremecinae. Most *Megarhyssa* species are associated with angiosperm trees (usually *Acer*) and tremecine siricoids.

(c) Xiphydriidae. All *Rhyssella* species are associated with xiphydriid siricoids in *Alnus*, *Betula* and *Salix*.

All these species are temperate and represent a very small proportion of the rhyssine fauna. There is only one host record for the whole of the tropical rhyssines. This is for *Sychnostigma hyblaeana* from the Lepidoptera *Hybalea purpurea*; which is a pest of teak (Sonan, 1933). This is likely to be a dubious record, given the many adaptations associated with wood-boring hosts (*Hybalea purpurea* is not found in deep wood microhabitats).

Larvae and pupae are regularly parasitised (Hanson, 1939). However, even unemerged adults are sometimes parasitised (Cheesman, 1921; Hanson, 1939; Hocking, 1968).

The host-searching behaviour of female rhyssines seems to be superficially similar to that of males searching for females. Fungus infested wood seems to stimulate female rhyssines to oviposit (Spradbery, 1968). Madden (1968) showed that females would tap cultures of certain ages of *Amnylostereum* with their antennae.

Oviposition behaviour has been described a large number of times but with varying accuracy. The best accounts are Heatwole, Davies and Wenner (1962) for *Megarhyssa* and Spradbery (1970b) and Gardiner (1966) for *Rhyssa*.

Heatwole et al (1964) suggest that the ovipositor must always be introduced fully into the log. Spradbery (1970b) did not find this for *Rhyssa*. There is a spectrum of oviposition behaviours and morphological modifications associated with them. The most extreme cases are in the three species of North American sympatric *Megarhyssa* where oviposition only occurs after a long period of searching and exploratory behaviour. The first stage (in *Megarhyssa*) consists of the raising of the abdomen vertically and then a bending of the tip so that the ovipositor swings forward. In the case of *M. atrata*, especially, the ovipositor is too long for it to be manoeuvrable just by this lifting of the abdomen, so the distal part of the ovipositor is passed up into a membranous structure between the 7th and 8th tergite (the 'ovipository membranes' of Heatwole, Davies & Wenner 1963). This is achieved by the rotation of the 9th tergite through 360° forcing the ovipositor up into the membranous sac. This movement is combined with a forward movement of the abdomen, pushing the ovipositor against the substrate. This may help inflate the membranous region.

When the membrane has expanded far enough for the tip of the ovipositor to be just raised above the substrate, the ovipositor is fitted into a series of grooves along the midline of the abdominal

sternites - the ovipositor guides (see fig 6.1). Muscles in the ovipositor complex contract rhythmically forcing first one half and then the other half of the ovipositor into the wood. Teeth on the end of the ovipositor assist in gripping the substrate during this process, and the two parts working together, along with flexions of the whole abdomen, help pull the other into the wood. The ovipositor guides hold the ovipositor in place and prevent buckling. At no time does the ovipositor sheath enter the wood. This can mean introducing the ovipositor up to 10 cm into the wood.

During this process tergite nine of the ovipositor complex rotates back until it is in its normal position. Once the ovipositor has reached the host tunnel, the host is stung and paralysed. The egg is then laid near or on it.

Removing the ovipositor is the reverse of the above, except that the ovipositor guides are not used. At the end of the withdrawal the abdomen is rapidly swung back over the head and tergite 9 returns to its normal resting position.

In other studied rhyssines the ovipository membranes are always smaller than in *Megarhyssa atrata*. *M. atrata* also has the longest recorded oviposition times, ranging from 22 minutes to 5 hours 33 minutes. In comparison the two *Megarhyssa* species sympatric with *M. atrata*, *M. macurus* and *M. greenei* take between 4 and 19 minutes to complete oviposition. Other studies on *Megarhyssa*, *Rhyssella*, *Epirhyssa* and *Rhyssa* show a very similar basic pattern to that described above (Gardiner 1966; Myers, 1928; Heatwole *et al* 1964; Porter, 1978).

Oviposition does not seem to be very efficient. Often drills are made where there are no hosts (Cheesman, 1921; Hanson, 1939; Hocking, 1967). Kazmierczack (1981) gives some data on percentage successful oviposition attempts. He records figures of 12% (n=83) for *Rhyssa persuasoria*; of 11% (n=66) for *Rhyssa amoena*; and of 9% (n=56) for *Megarhyssa emarginatoria*. These all suggest a very inefficient system given the length of time taken for each oviposition attempt; which

ranges from 22-333 minutes in *Megarhyssa atrata* (Heatwole, Davies and Wenner, 1962) to 7-15 minutes in *Rhyssella approximator* (Kazmierczack, 1981).

### 5.7. Larval Biology

The majority of the work on this topic has been on *Rhyssa persuasoria*, as part of CSIRO's *Sirex* project. The discussion, therefore, refers to *R. persuasoria* unless otherwise stated.

Rhyssine eggs are elongate, so that the egg can pass easily along the ovipositor (Iwata, 1958; Spradbery, 1970a). They are laid near the host, but do not travel a great distance to reach it (Chrystal & Myers, 1928). The first instar larva has a large head capsule and mandibles, both for piercing the host and dealing with supernumerary larvae (Spradbery, 1970a). Once the host is paralysed it does not move further within the burrow (Hocking, 1968).

Spradbery (1970a) figures the successive instars of the larvae of *Rhyssa persuasoria*, *Rhyssa amoena*, and *Megarhyssa emarginatoria*. By the final (5th) larval instar the siricoid is usually completely consumed. The rhyssine then spins a rather diaphanous cocoon (Chrystal & Myers, 1928). This thinness may have led Morgan & Stewart (1966) to conclude that no cocoon was spun. Pupal morphology is similar throughout the group, except in the size of the ovipositor (Spradbery, 1970a). Once the adult has left the pupal case it chews its way up to the surface (Hocking, 1968).

## CHAPTER 6. THE PHYLOGENY OF THE RHYSSINAE, AND THE EVOLUTION OF THEIR MALE MATING SYSTEMS

### 6.1. Historical review

The taxonomic history of the Rhyssini is tied up very closely with that of the rest of the Pimplinae (see chapter 2). Gravenhorst in his *Ichneumonologica europaea* (1829) placed *Rhyssa* as a subgenus of *Pimpla*. Holmgren (1860) placed *Rhyssa* and *Thalessa* (= *Megarhyssa*) in his subfamily Pimplariae. Later Ashmead (1900) placed *Rhyssa*, *Megarhyssa*, *Lytarmes* and *Epirhyssa* in the tribe Pimplini of the subfamily Pimplinae.

Morley (1913) was the first to realise that the accumulated specimens of the above genera formed a similar group morphologically and united them into a tribe - the Rhyssides. The tribe Rhyssini was accepted by some (eg. Cushman & Rower, 1920), but not all workers. Townes retained this classification (1944) although later he changed the subfamily limits.

Townes & Townes (1960) excluded several Oriental species from the genus *Epirhyssa* and transferred them to a new genus *Hierax* (= *Sychnostigma*) and to some undescribed genera. Later Baltazar (1961) established three new genera: *Triancyra*, *Cyrtorhyssa* and *Myllenyxis*. Townes et al (1961) rearranged all the species from the Oriental region so that the classification was more natural. This work was consolidated in Townes (1969). Kamath & Gupta (1972) have revised the Oriental Rhyssini, and it is their classification, which is based on Townes, which is discussed here.

### 6.2. The present classification

At present there are nine genera recognised worldwide:

*Rhyssa* Gravenhorst  
*Lytares* Cameron  
*Rhyssella* Rohwer  
*Megarhyssa* Ashmead  
*Triancyra* Baltazar  
*Sychnostigma* Baltazar  
*Epirhyssa* Cresson  
*Cyrtorhyssa* Baltazar  
*Myllenyxis* Baltazar

The most recent definitions of these genera are those of Kamath & Gupta (1972). Table 6.1 shows their diagnostic characters for the genera. Kamath & Gupta (1972) included only those genera found in the Indo-Oriental area. The table also includes the characters of the two remaining genera, *Rhyssella* and *Epirhyssa*, which are not found in the Indo-Oriental area, and are taken from Townes (1969) and Porter (1975, 1978).

### 6.3. Outgroups

Taking into account the conclusions reached in chapter 3 the following groups have been used for outgroup comparisons: Pimplinae (*sensu stricto*), Poemeniinae, Acaenitinae, Labeninae, Xoridinae and Tryphoninae. All these groups are paraphyletic with respect to the rhyssines, and therefore fulfil the criterion of Underwood (1982) for outgroup suitability (see sections 1.3 and 2.4.1).

### 6.4. The holophyly of the group

All rhyssine species have the following adult autapomorphy:

- (1) An anteriorly dipping pronotal collar (fig 3.14).

In addition the group can be defined polythetically (Gauld & Mound, 1982) and membership recognised by the presence of at least two of these character states:

(2) No phragmata on gastral tergite 8 (abdominal tergite 9, see chapter 3) of female.

(3) Tubercles on gastral sternites 2-4 (fig 6.1)

(4) Longitudinal carina on trochantellus of mid-leg (fig 6.2).

(5) Horn or hollow rounded apex to gastral tergite 8 of female (fig 3.23).

(6) Radial hamuli of hind-wing grouped into two, three or four proximally, subsequent hamuli singly spaced (figs 6.3-6.5).

These character states confirm the holophyly of the group. The genus *Pseudorhyssa* which has often been grouped with the rhyssines (Kazmierczak 1979, 1980, 1981; Constantineanu & Pisica, 1977) has been shown to belong in the Poemeniinae (see chapter 3) and is therefore specifically excluded.

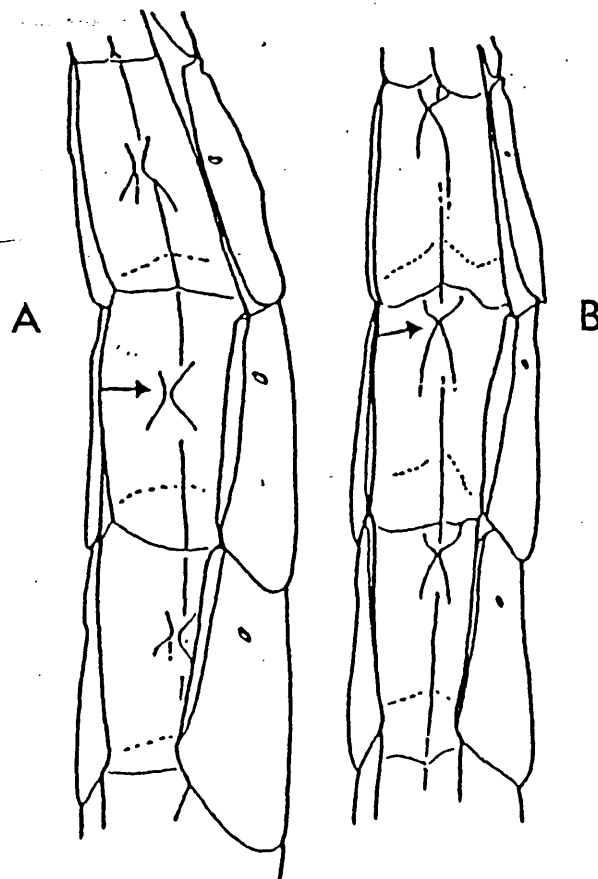


Fig 6.1. Tubercles on sternites 2-4 (ovipositor guides) of  
A. *Rhyssa persuasoria*; B. *Rhyssella approximator*.  
(from Fitton et al, 1988)

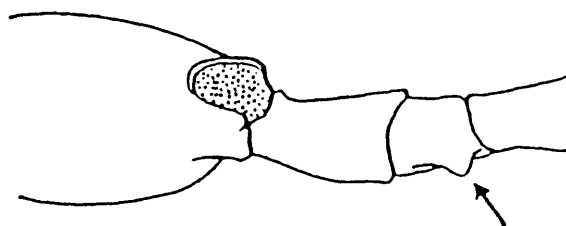


Fig 6.2. Longitudinal carina on trochantellus of mid leg  
of *Rhyssella approximator*. (From Fitton et al,  
1988)

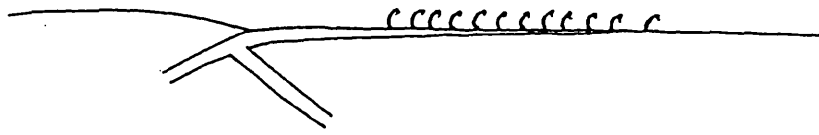


Fig 6.3 Pattern of radial hamuli on hind wing of *Rhyssa persuasoria*.

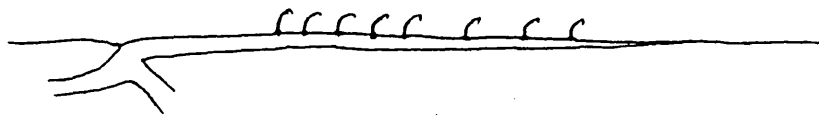


Fig 6.4.. Pattern of radial hamuli on hind wing of *Rhyssella approximator*.

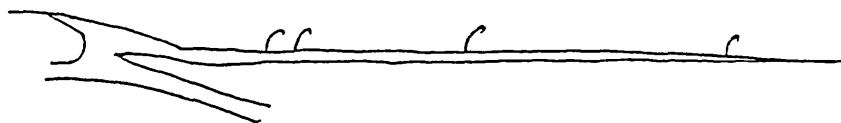


Fig 6.5. Pattern of radial hamuli on hind wing of *Epirhyssa flavopictum*.

Table 6.1. Defining characters of the presently recognised rhyssine genera. (Throughout "hamuli" refers to the *Radial hamuli*; "tergites" and "sternites" to gastral structures.)

| Genus                                                                                                                                                                                     | Defining characters                                                                                                                                                                                                                 |
|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| <i>Rhyssa</i>                                                                                                                                                                             | Sternite and tergite 1 unfused.<br>Tubercles on sternites 2-4 in middle.<br>Glymma present. Radial hamuli in continuous series, not divided.<br>Ventral longitudinal carina on trochantellus of mid-leg absent.<br>Areolet present. |
| The remaining genera all have: sternite 1 and 2 fused; tubercles on sternite 2-4 at the anterior end; the glymma absent; ventral longitudinal carina on trochantellus of mid-leg present. |                                                                                                                                                                                                                                     |
| <i>Rhyssella</i>                                                                                                                                                                          | Hamuli state not defined. Areolet present. Male gaster with weakly developed modifications.                                                                                                                                         |
| <i>Megarhyssa</i>                                                                                                                                                                         | Hamuli with a proximal group of 2 hooks followed by singly placed hooks in Indo-Australian species. Areolet present. Male gaster with strongly developed modifications.                                                             |
| <i>Lytarmes</i>                                                                                                                                                                           | Hamuli with proximal group of 2 hooks followed by singly placed hooks. Junction of occipital and hypostomal carina at or very close to base of mandible. Areolet present. Frontal orbits raised.                                    |
| <i>Triancyra</i>                                                                                                                                                                          | Hamuli with proximal group of 3 hooks followed by singly placed hooks. Mandibles with lower tooth wider than upper tooth. Areolet absent. Frontal orbits raised.                                                                    |
| <i>Sychnostigma</i>                                                                                                                                                                       | Hamuli with proximal group of 2 hooks followed by singly placed hooks. Areolet absent. Frontal orbits raised or not raised.                                                                                                         |
| <i>Epirhyssa</i>                                                                                                                                                                          | Hamuli state not defined. 2rs-m basad of vein 2m-cu by 0.2 to 1.0 its length.<br>Tergite 1 without a basal dorso-lateral carina.<br>Aerolet absent.                                                                                 |
| <i>Cyrtorhyssa</i>                                                                                                                                                                        | Hamuli with proximal group of 2 hooks followed by singly placed hooks. Areolet present or absent. Pterostigma merging imperceptibly with vein Sc+R+Rs.<br>Tergite 1 at base terete.                                                 |
| <i>Myllenyx</i>                                                                                                                                                                           | Hamuli with proximal group of 2 hooks followed by singly placed hooks.<br>Mandibles with upper tooth wider than lower tooth and with notch in upper tooth. Areolet absent. Ovipositor tip sinuate.                                  |

### 6.5. Material examined

The majority of the material used in this work is from the collections of the British Museum (Natural History), London (= BMNH). These collections are extensive and contain rhyssines from all biogeographical regions. Its one limitation is that many of the tropical species are only represented by a few specimens. European and American species associated with pine are well represented due to the presence in the collection of the CSIRO *Sirex* Project material.

In addition the work has benefited from several recent Museum expeditions in the tropics, which have yielded much larger numbers of some species. the most important of these additions are:

(a) In the Indo-Australian region. The Royal Entomological Society's Project Wallace in Sulawesi, Indonesia has produced a great bulk of rhyssine specimens, although in a fairly small number of species (around 12). Collecting undertaken at the Danum Valley Field Centre, Sabah, East Malaysia between July 1986 and March 1987 has produced around 50 species of rhyssines. Four species of rhyssines were collected from Ceram in 1988.

(b) The Afrotropical region. New material has been obtained from the Cameroon (3 species).

(c) The Neotropical region. A continuing study of the Costa Rican insect fauna has produced 7 species from this area.

In addition to all the old and recently collected BMNH material, specimens have been examined from the following institutions: Hope Department, Oxford; American Entomological Institute, Gainesville, Florida, USA; Museum fur Naturkunde zu Berlin, DDR; CNC, Biosystematics Research Institute, Ottawa, Canada; RMNH, Lieden, Holland; Bishop Museum, Honolulu, Hawaii, USA.

The OTUs are listed in appendix 2.

## 6.6. Character States

Characters for the preliminary analyses are taken from females and non-gastral parts of males. The reason for this relates to one of the purposes of the study - which is to look at the evolutionary patterns in male reproductive behaviour. This information is being derived from studies of male abdominal morphology, and as such is not admissible as evidence for evolution (to avoid *a priori* reasoning). Along with the characters of abdominal morphology also excluded are characters of the male genitalia. This has been done because there is some uncertainty about the relationship between male reproductive strategies (which may be very plastic) and the morphology of the male genitalia. This relationship is discussed in some detail later in this chapter, where the possible phylogenetic and adaptive significance of the enormous variation in male abdominal structure is indicated.

Certain other characters have been deliberately excluded from the analyses. There is a great deal of variation in colour pattern, gastral tergite punctation and size within the group. These characters have been generally avoided, for the following reasons:

First, they often vary intraspecifically. A good example of this is the species *Sychnostigma flavopictum* which is separated from *Sychnostigma sinuatum* in Kamath & Gupta (1972) by the extent of puncturing on the third gastral tergite. However, new specimens from Sulawesi key out as *S. flavopictum* for the male specimens and *S. sinuatum* for the females, indicating that they are most probably conspecific. This sort of intra-specific variation in a character makes it clearly unsuitable for phylogenetic analysis.

Second, they are exceedingly homoplastic characters. Characters of colour pattern and sculpture have clearly arisen several times in many different lineages. For example, most tropical rhyssines form part of mimicry complexes, and a wide range of parallel colour changes have occurred in many species. These characters are used repeatedly in keys

(Kamath & Gupta, 1972; Porter, 1975,1978) to separate off two species from each other; which is clear, if indirect, evidence for their high level of homoplasy.

One character state which is listed in table 6.1. (the stigma merging imperceptibly with the vein Sc+R+Irs), was not used in the analysis, as no difference could be ascertained between OTUs that should have shown the character state and those that should not (Baltazar, 1961; Kamath & Gupta, 1972).

The character states are described below (for coding see section 2.4.3):

1. 'Occipital carina complete (1), or centrally interrupted (0). The outgroups all show a predominantly complete occipital carina. However preliminary analysis showed a very high polar incompatibility score and so in subsequent analysis the polarities have been reversed.
2. Genal carina not reaching the hypostomal carina (1), meeting the hypostomal carina at some point (0). Nearly all the outgroups have a genal carina meeting the hypostomal carina at some point.
3. Genal carina meeting the hypostomal carina less than 0.3 the width of the mandible away from the mandible (1); meeting the hypostomal carina more than 0.3 the width of the mandible away from the mandible(0)
4. Strongly raised hypostomal carina (1); weak hypostomal carina (0).
5. Clypeus carinate (1); smooth or punctate (0).
6. Clypeus formed into central point (0); flat with no obvious point (1). As discussed earlier the clypeus is raised into a point in the genus *Pseudorhyssa*, but this is undoubtedly due to convergence, otherwise the point would appear to be apomorphic. However, this character has a high polar incompatibility score in the preliminary analysis and so in subsequent analyses the polarity was reversed.

7. Apex of clypeus raised (1); apex flat (0).
8. Clypeus margin concave (fig 6.6) (1); truncate (0).
9. Frons with strong longitudinal carina (1); without or with weak longitudinal carina (0).
10. Frontal orbits strongly convex (1); frontal orbits flat (0).
- 11.1, 11.2. Mandibles tridentate (0,1) (fig 6.7A), bidentate with upper tooth narrower than lower tooth (1,0) (fig 6.7b), with upper tooth wider than lower tooth (fig 6.6) (0,0)
12. Lower face strongly bulged (1), lower face flat or slightly concave (0).
- 13.1, 13.2. Lower face smooth (1,0), wrinkled (0,1), punctate (0,0).
14. Trochantellus of mid-leg with a longitudinal ridge (fig 6.2) (1), trochantellus of mid-leg flat and without ridge (0).
15. Proximal part of vein Rs of fore-wing strongly curved (1), not strongly curved (0).
16. Vein 3rs-m of forewing (areolet) absent (1), Vein 3rs-m of forewing (areolet) present (0).
17. Vein 2m-cu of forewing interstitial with 2rs-m (1), Vein 2m-cu of forewing distad of 2rs-m (0).
- 18.1, 18.2, 18.3. radial hamuli evenly spaced along distal part of hind wing (fig 6.3) (0,0,0); hamuli increasingly distantly spaced along the distal part of hind wing (fig 6.4) (1,0,0), hamuli grouped into two, three or four closely associated hooks with a series of hooks behind it - the space between the proximal group and the next hook less than the distance between that hook and the next hook after

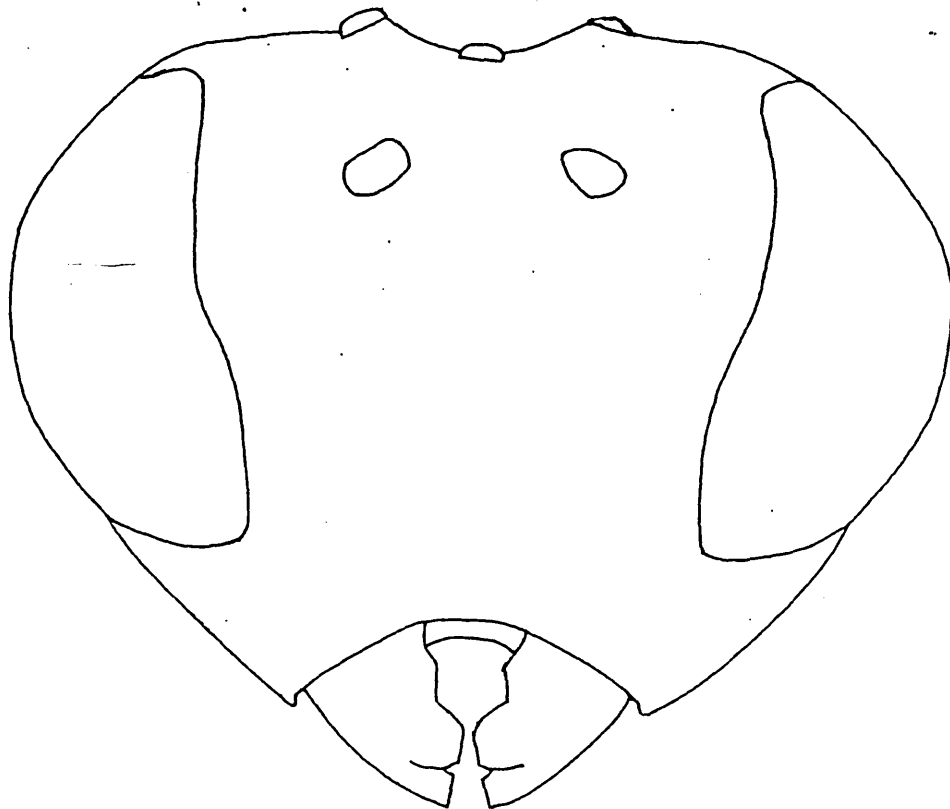


Fig 6.6. Front of head of *Megarhyssa emarginatoria* male showing mandible with wide flat upper tooth.

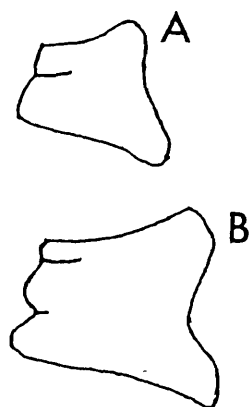


Fig 6.7. Mandibles of (a) *Triancyra scabra*; (b) *Myllynyxis bernsteinii*. (Redrawn from Kamath & Gupta, 1972)

(1,1,0) (fig 6.5), hamuli grouped into two, three or four closely associated hooks with a series of hooks behind it - the space between the group and the next hook greater than that between the hook and its following one (1,1,1).

19. 2m-cu of forewing strongly curved outwards (1), weakly curved (0).

20. Wings hyaline (1), wings clear (0).

21. Forewing with stigmal spot (1), forewing with no stigmal spot (0).

23. Central lobe of mesoscutum jutting well over the pronotum (1), central lobe of mesoscutum not jutting over the pronotum (0).

24.1, 24.2, 24.3. Epicnemial carina not present (1,1,0), epicnemial carina present but not reaching up to level of mesopleural scroll (1,0,0) (fig 6.8C), epicnemial carina extending up past the mesopleural scroll (0,0,0) (fig 6.8A), epicnemial carina reaching up past the mesopleural scroll and reflexed onto the mesopleural edge (0,0,1) (fig 6.8B).

25.1, 25.2. Subtegular tubercle (homologous with the sub alar prominence *sensu* Fitton *et al*, 1988) hollowed at its posterior end as a cleft (1,0), subtegular tubercle hollowed as a hole (0,1), not hollowed (0,0).

26. Subtegular tubercle evenly curved at its outer edge (1), strongly curved at its outer edge (0).

27.1, 27.2. Ventral margin of epicnemium with median pair of strong ventrolateral crests (1,1), with weak carina near ventral margin of epicnemium (1,0), with no carina (0,0).

28. Propodeum with median longitudinal groove on basal 0.3-0.5 (1), no groove (0).

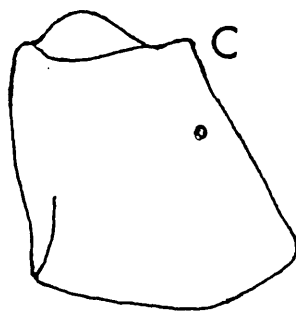
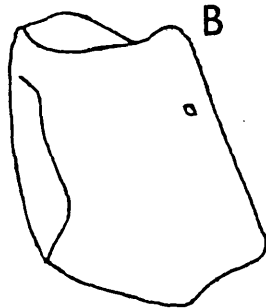
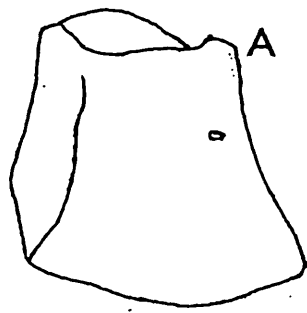


Fig 6.8 Epicnemium and epicnemial carina of (a) *Sychnostigma validum*; (b) *Sychnostigma flavopictum*; (c) *Cyrtorhyssa mesopyrrha*.  
(Redrawn from Kamath & Gupta, 1972)

29.1, 29.2. Propodeum smooth and impunctate except on the sides (0,1); strongly rugose-striate (1,0); punctate throughout (0)<sup>0</sup>.

30. Distance between the pleural carina and the propodeal spiracle greater than the length of the spiracular opening (1), distance less than the length of the spiracular opening (0).

31.1, 31.2. Pronotal collar strongly dipped so that bottom of the collar is close to base of pronotum (1,1), pronotal collar definitely but only slightly dipped (1,0), pronotum not dipped (0,0).

32.1, 32.2. Gastral tergite 2 smooth (1,0), wrinkled (0,1), punctate (0,0).

33. First gastral sternite fused to gastral tergite (1), first gastral tergite free of gastral sternite (0).

34. First gastral tergite without a glymma (1), first gastral tergite with a glymma (0).

35. First gastral tergite without short dorso-lateral carina (1), with short dorso-lateral carina (0).

36.1, 36.2. First gastral tergite over 1.6 times as wide as long at apex (1,0), less than 0.6 times as long as wide at apex (0,1), between 1.6 and 0.6 times as long as wide at apex (0,0).

38. Gastral sternite 1 ends posterior of spiracle of gastral tergite 1 (1), gastral sternite 1 ends basad of spiracle of gastral tergite 1 (0).

39. Gastral tergite 1 spiracle situated within or greater than 0.36 of basad part of gastral tergite 1 (1), gastral tergite 1 situated less than 0.36 basad of gastral tergite 1 (0).

40.1, 40.2. Gastral sternite 1 with a pair of flat tubercles (1,0), gastral sternite 1 with a pair of sharp tubercles (0,1), gastral sternite 1 without tubercles (0,0).

41. Gastral tergites 3-5 with strong transverse furrows (1), gastral tergites 3-5 without transverse furrows or present only very weakly (0).

42.1, 42.2. Gastral sternites 2-4 with tubercles at mid-point (fig 6.1A) (1,0), gastral sternites 2-4 with tubercles near anterior border (fig 6.1B) (0,1), sternites 2-4 with no tubercles (1,1).

43.1, 43.2. Tubercles on gastral sternite 3 limited to a ridge on the edge of the gastral sternite, not projecting ventrally below the gastral sternite (0,0), tubercles raised up above the level of the gastral sternite (1,0), tubercles projecting from the bottom of the gastral sternite and curved inwards (0,1).

47.1. Gastral tergite 5 apico-lateral angle less than 125 degrees (1); greater than 125 degrees (0).

48.1, 48.2. Gastral tergite 8 horn clearly visible dorsally and with a hollow centre (0,0), horn not present but edge of gastral tergite 8 hollow (1,0), horn not present and edge of gastral tergite 8 not hollow (1,1).

49. Ovipositor sinuate and compressed just behind apex (1), ovipositor tip straight and unflattened (0).

50.1, 50.2. Forewing length of largest specimens over 20 mm (1,0), forewing length under 8 mm (0,1), forewing length between 8 mm and 20 mm (0,0).

## 6.7. Preliminary Results

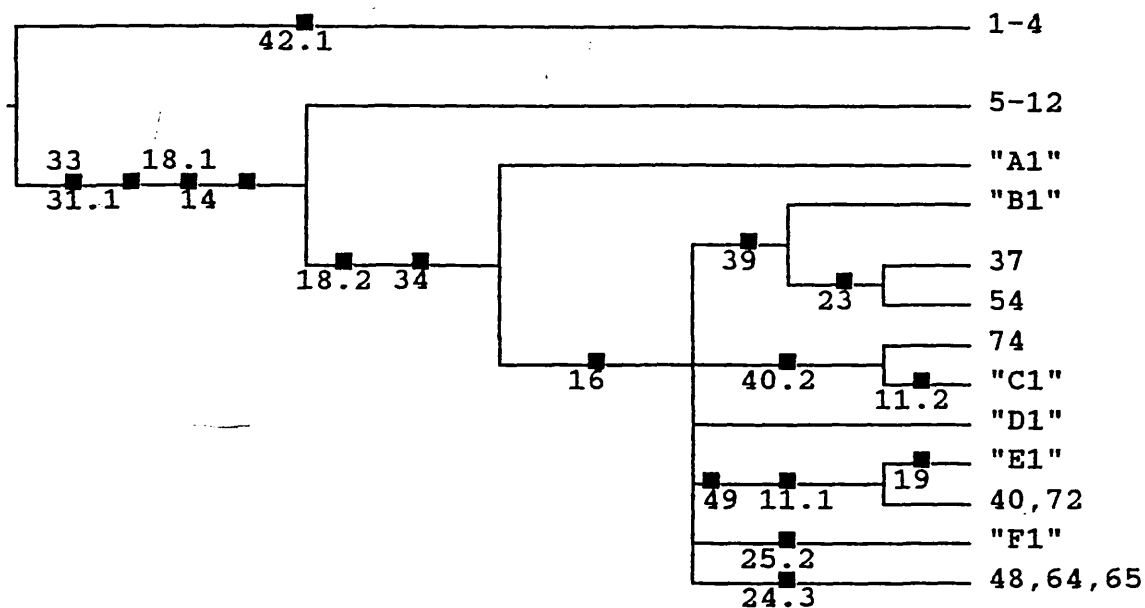
The overall randomness ratio for the data set was 0.7, indicating a high level of homoplasy, just lower than that found in the Townes data set (chapter 2), but higher than the final pipeline data set (chapter 3). The polar incompatibilities are discussed below.

### 6.7.1. Cladograms: initial results

Figs 6.9 and 6.10 show the results of the LEQUB/PROBS and O'NOMOD analyses. These cladograms are very interesting as they show the same basic structure except in two characters that are in the O'NOMOD analysis (characters 25.1 and 4) and not in the LEQU; and two that are in the LEQU but not in the O'NOMOD - (19 and 25.2). Therefore, the two cliques are of identical size. However, character 19 which is thrown out late in the O'NOMOD analysis is, in fact, compatible with the final clique, but was lost due to incompatibility with the character thrown out last in the O'NOMOD analysis (character 12).

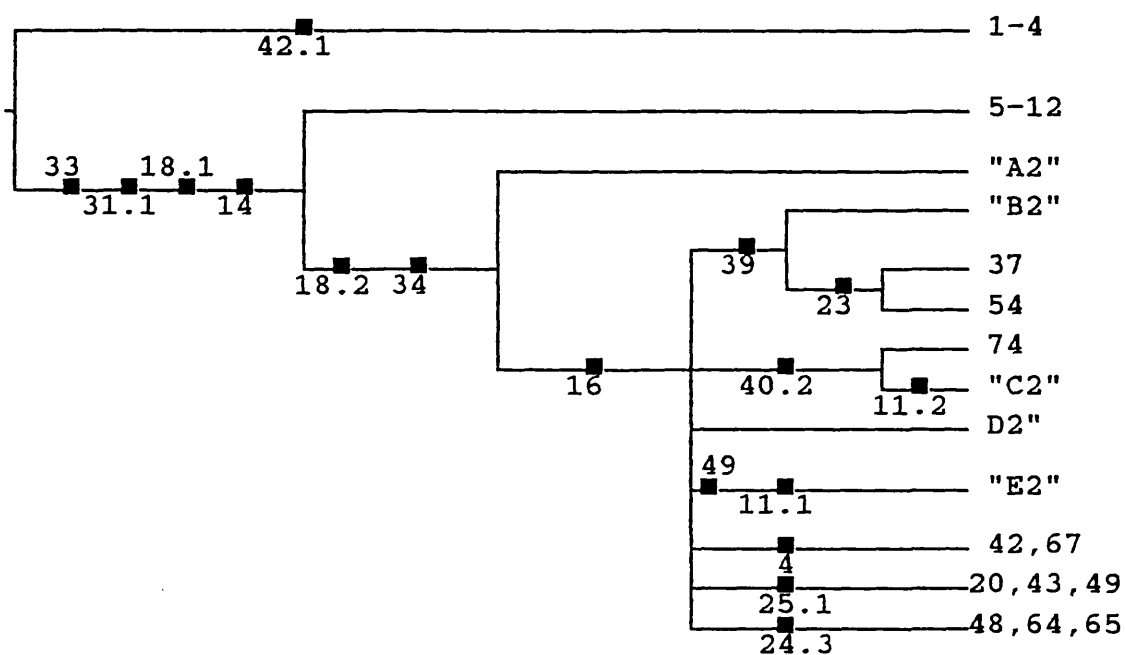
The results show a basically similar pattern of apomorphies. There is one very strong element in the cladogram (the four characters that separate taxa 1-4 from the rest), and 2 fairly robust groupings (the grouping supported by characters 18.2 and 34; and the grouping supported by characters 49 and 11.1). However, beyond that all the groupings are delineated by a single apomorphy. These must be considered unsubstantiated links.

Several of the genera which are presently recognised (Townes 1969, Kamath & Gupta 1971) are not delineated as holophyletic groups. *Megarhyssa* (group "A": 13-15, 25-28 and 71, along with 8-12) is split into two paraphyletic groups; *Rhyssella*, and *Lytarmes* have no autapomorphies; and *Sychnostigma* is shown as a paraphyletic grade-group from which *Epirhyssa*, *Triancyra* and *Myllenyxis* have arisen. Both *Epirhyssa* and *Triancyra* are supported by one character, and in addition two groups normally in *Sychnostigma* are delineated by one character. The only genera that are strongly supported are *Rhyssa* (which is clearly right at the base of the rhyssines) and *Myllenyxis* (which is clearly the most derived rhyssine). The position of the genus *Cyrtorhyssa* is uncertain. One species of this genus is described as possessing vein 3rs-m in the forewing, that is the plesiomorphic state of character 16 (*C. mesopyrrha*, taxon 28) (Kamath & Gupta, 1971) and the other as not possessing vein 3rs-m in the forewing, that is the apomorphic state of character 16. As character



Key: ■ - apomorphy. "A1" = 13-15, 25-28, 71; "B1" = 32-6, 55-7, 78; "C" = 30, 31, 60, 68, 69; "D1" = 16-17, 19-24, 29, 38, 39, 43-46, 49, 50, 53, 58, 59, 61, 63, 66, 67, 71, 75, 77; "E1" = 41, 51, 70, 73, 79, 80; "F1" = 18, 42, 52, 62.

Fig. 6.9. LEQU/PROB Cladogram for the rhyssine data set, without male gastral characters.



Key: ■ - apomorphy. "A2" = 13-15, 25-28, 71; "B2" = 32-6, 55-7, 78; "C2" = 30, 31, 60, 68, 69; "D2" = 16-19, 22-24, 29, 38, 39, 44-46, 50, 52, 53, 58, 59, 61-3, 66, 71, 75, 77; "E2" = 40, 41, 51, 70, 72, 73, 79, 80.

Fig. 6.10. O'NOMOD Cladogram for the rhyssine data set, without male gastral characters.

16 enters the final clique this implies that the genus is at best paraphyletic. However, no specimens of the second and only other species in the genus, *C. muelleri* were available for study.

Table 6.3. Summary of initial results.

| Genus               | Apparent Status |
|---------------------|-----------------|
| <i>Rhyssa</i>       | Holophyletic    |
| <i>Rhyssella</i>    | Paraphyletic    |
| <i>Megarhyssa</i>   | Paraphyletic    |
| <i>Lytarmes</i>     | Paraphyletic    |
| <i>Cyrtorhyssa</i>  | Polyphyletic    |
| <i>Sychnostigma</i> | Paraphyletic    |
| <i>Epirhyssa</i>    | Holophyletic    |
| <i>Triancyra</i>    | Holophyletic    |
| <i>Myllenyxis</i>   | Holophyletic    |

#### 6.7.2. Trees: phylogenetic hypotheses

Although the two cladograms are similar, the characters just outside the clique are quite different. Of the last five characters to be thrown out of the two analyses there is only one common to both: character 2. The other characters form a mutually incompatible set, except for character 25.2 in the O'NOMOD set which is in the original LEQU clique. The last characters to be thrown out from both analyses will now be reintroduced.

### 6.7.3. The PROBS/LEQUB analysis

The following characters are just outside the clique:

(a) Character 2. Enters the clique if two parallelisms are postulated: the first in taxa 35,36,57,78 ("A"); and the second in 67.

(b) Character 36.1. Enters the clique if four parallelisms are postulated: one in taxa 26,27,28; one in the clade delineated by character 39; one in taxa "D3" <sup>and</sup> 24 (see fig 6.11) ; and one in taxon 79.

(c) Character 50.1. Enters the clique if 3 parallelisms are postulated: one in taxa 8-12; <sup>and</sup> one in taxa 13 and 14.

(d) Character 42.2. Enters the clique if a reversal is postulated in the clade defined by characters 11.1 and 49.

(e) Character 24.2. Enters the clique if four parallelisms are postulated: one in taxa 35 and 78; one in taxon 54; one in taxon 57; and one in taxon 24.

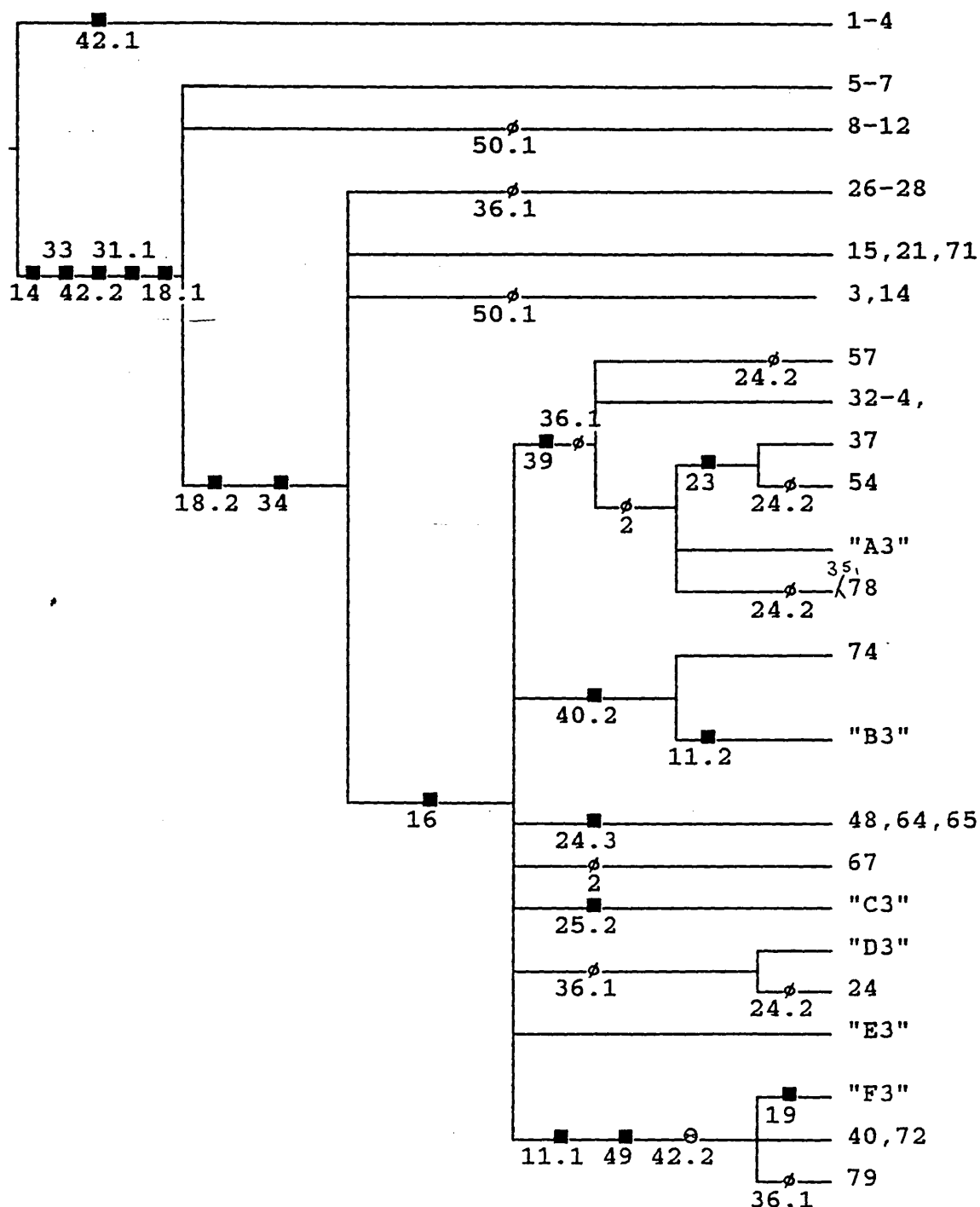
With these homoplastic characters added the resulting hypothetical tree is as shown in fig 6.11.

### 6.7.4. The O'NOMOD analysis

The following characters are just outside the clique:

(a) Character 12. Enters the clique if a parallelism is postulated between taxa 72 and 73. As this produces two single taxon autapomorphies and therefore has no real information content, it has not been indicated on the hypothetical tree diagram.

(b) Character 30. This enters the clique if a parallelism is



Key: ■ - apomorphy; ∅ - parallelism; ⊖ - reversal;  
 "A3" - taxa 36, 55, 56; "B3" - 30, 31, 60, 68, 69;  
 "C3" - 18, 42, 62, 52; "D3" - 16-19, 21, 29, 39, 63, 66, 46; "E3"  
 - 17, 18, 22, 23, 25, 38, 44, 45, 50, 53, 58, 59, 61, 71, 20, 43, 49, 75  
 , 77; "F3" - 51, 70, 73, 41, 79, 80.

Fig 6.11. Hypothetical tree without male gastral characters for the rhyssine data set. LEQUB/PROBS analysis.

postulated between taxa 35 and 37. Once again this produces two single taxon apomorphies and has not been indicated on the diagram.

(c) Character 25.2. Enters the clique if two parallelisms are postulated: one in taxa 18, 52 and 62; the other in taxon 42.

(d) Character 2. Enters the clique if two parallelisms are postulated: one in taxa 54, 37, 35, 36, 78, 57; the other in taxon 67.

(e) Character 29.1. Enters the clique if two parallelisms are postulated: one in taxa 19, 22, 63 and 77; the other in taxon 40.

(f) Character 3. Enters the clique if two parallelisms are postulated: one in taxa 26, 27 and 28; the other in taxon 32.

The resulting hypothetical tree is shown in fig 6.12.

#### 6.7.5. Subset analyses

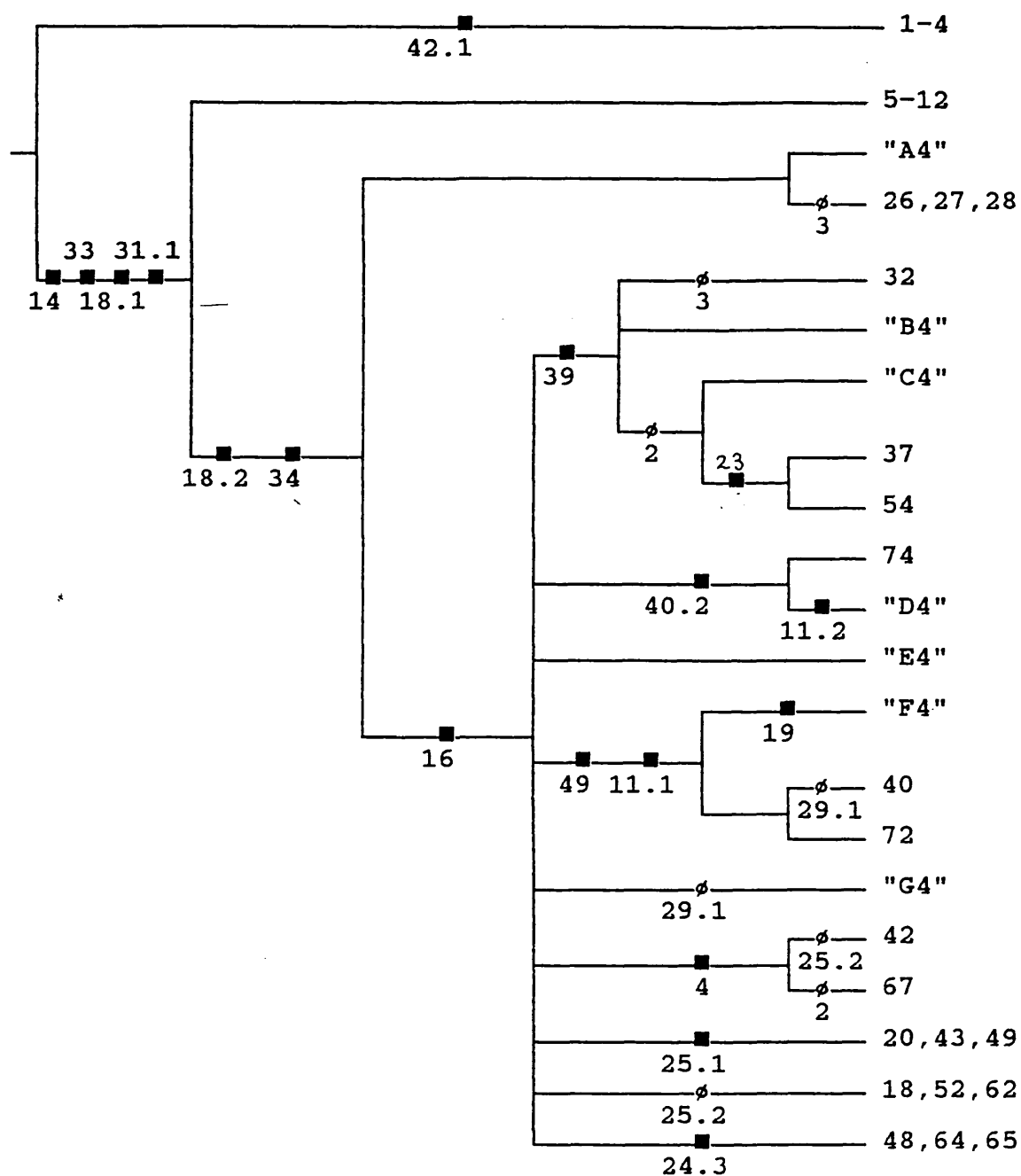
Subset analyses were only performed where there was strong evidence

for a grouping. This was decided upon because of the confusion that would be caused by picking groups that are defined by highly homoplastic characters and performing an analysis on them. The criterion used for this was where both analyses showed at least two characters supporting the presumed clade. This left the following subsets:

(1) taking out taxa 1-4; leaving the clade defined by characters 14, 18.1, 31.1 and 33. This produced the same set of results in each case.

(2) taking out taxa 1-12; leaving the clade defined by characters 18.2 and 34. This produced the same set of results in each case.

(3) taking out all taxa except for those grouped by characters 11.1 and 49. There were too few taxa for this analysis to be meaningful.



Key: ■ - apomorphy; ∅ - parallelism; θ - reversal; "A4" - taxa 13,14,15,71; "B4" - 32-36,55-57; "C4" - 35,36,57;  
 "D4" - 30,31,60,68,69; "E4" - 16,17,19,21,23,24,25,29,38,39,44,45,46,50,53,58,59,61,66,75; "F4" - 51,70,73,41,79,80; "G4" - 22,77,63,19.

Fig 6.12. Hypothetical tree, without male gaster data for the rhyssine data set. O'NOMOD analysis.

As was the case for the poemeniine subset analysis in chapter 3, the results give a large number of apomorphies at each node all of which would require an unlikely number of reversals in the group as a whole.

#### 6.7.6. Comments on the two trees

The two tree diagrams obtained by the two compatibility methods have various elements in common and several major differences. It is interesting to note that the sections which are in common are usually those supported by more than one character, suggesting that they may be more robust indicators of relationship than those lines supported by a single character. These sections are:

(1) Characters 14, 18.1, 31.1, and 33 separating taxa 1-4 from 5-80.

(2) Characters 18.2 and 34 separating taxa 5-12 from 13-80.

(3) Character 16 splitting the group into one clade consisting of taxa 13-15, 26-28 and 71 and another of taxa 16-25, 29-70 and 72-80.

(4) Character 39 splitting off taxa 32-37 <sup>and 78</sup> 54-57. Within this clade both analyses have taxa 35, 36, 56, 54 and 37 linked by character 2, and characters 54 and 37 linked by character 23.

(5) Character 40.2 splitting off taxa 30-31, 60, 68, 69, and 74. Within this clade taxa 30, 31, 60, 68, <sup>and</sup> 69 are characterised by character 11.2.

(6) Characters 11.1 and 49 separate off taxa 40, 72, 70, 73, 41, 51, 79 and 80. The character 19 then takes off all the taxa within this group excepting 40 and 72.

It can be seen that the only additional character that is common to both trees and is not in an initial cladogram is character 2. This

indicates, as discussed above, that the remaining taxa show conflicting character states which tend to cause clades defined by single apomorphies to shuffle around according to the order in which characters are removed within the analyses. This implies that the resulting groupings are not particularly strong.

In the next section of the thesis male gastral characters will be introduced. Of special interest will be whether *Megarhyssa*, which appears to be a paraphyletic group in the initial analysis, but apparently has autapomorphies which are gastral characters, is defined by those characters or whether the gastral characters are highly homoplastic. From the initial analysis it must be assumed that the latter is true, and that the *Megarhyssa* gastral characters have evolved at least twice.

## 6.8. Male gasters and mating systems

One of the most striking things about rhyssines is the wide range of gastral shape found in the males (Townes, 1969; Kamath & Gupta, 1972; Porter, 1978). While females show a range of modifications associated with manipulating the ovipositor, their basic body plan remains essentially the same. For example, *Megarhyssa* has a membranous region between gastral tergites 7 and 8 into which part of the ovipositor passes during oviposition (see chapter 5). Species of other genera show a similar structure but which is much less well developed, simply because the ovipositor is not as long. The similarity of female morphology is reflected in the tree derived from predominantly female morphology (see above). This section will try to explain why males are so variable and whether the patterns of male gaster shape have phylogenetic significance, or are simply rather short-term adaptive responses to environmental factors.

Another interesting feature of male rhyssines is that in certain species there is a strong tendency for small males to have a different gastral shape from large ones (Abbott, 1935; Townes, 1969). Along with this change in shape, small *Megarhyssa* species lose the defining characters of the genus (Townes, 1969: defined as characters 51 and 52 in section 6.9). This shape change is shown for *Megarhyssa emarginatoria* in fig 6.13. The difference is very obvious, and it is manifested even more clearly in the density of hairs in large and small males. Figs 6.14 and 6.15 show this: large males have almost completely smooth gastral tergites while small males have extremely hairy gastral tergites. That large male *Megarhyssas* are smooth is easy to explain - they are inserting into female emergence tunnels, and having a hairy abdomen would make this a difficult process. As for small hairy males, it is clear that they cannot be inserting, and they may be hairy for reasons of thermal regulation, as they will have a unfavourable surface area to volume ratio.

In addition to these intra-specific variations, one other major inter-specific morphological difference occurs amongst the

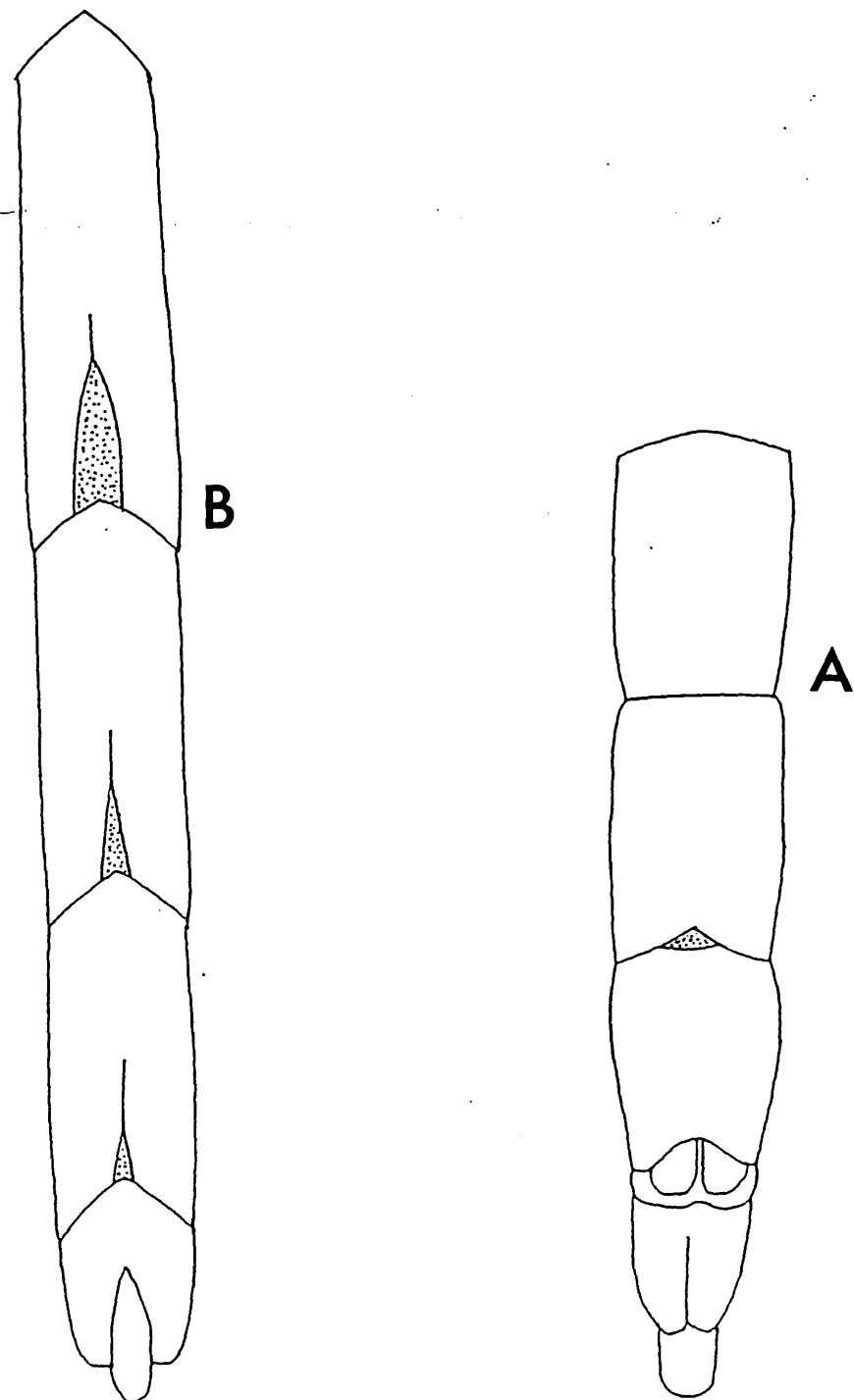


Fig 6.13. Final gastral segments of males of *Megarhyssa emarginatoria*. A. Small male (fore wing length 10.5mm). B. Large male (fore wing length 21.4 mm).

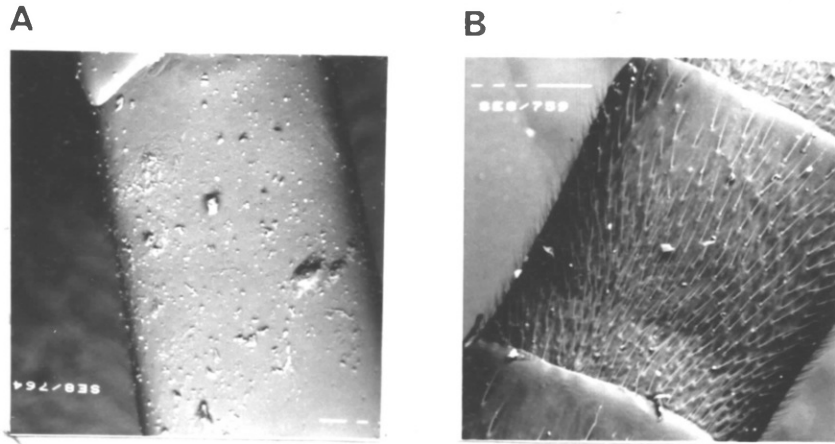


Fig 6.14. Dorsal view of gastral tergite 5 of *Rhyssella approximator*:  
 (a) large male; (b) small male. Note difference in shape.

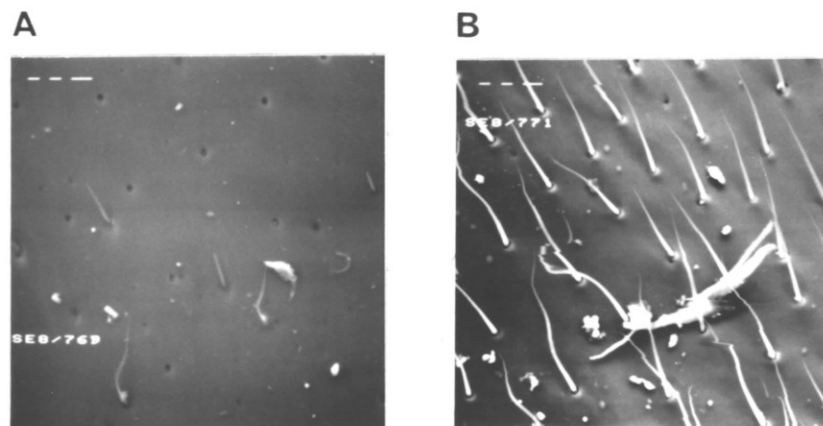


Fig 6.15. High magnification view (X 800) of gastral tergite 5 of  
*Rhyssella approximator*: (a) large male; (b) small male.  
 Note difference in density of hairs.

rhyssines; that is the presence or absence of the anal gland (Matthews *et al*, 1979) in males. This paired brush-like structure is found at the posterior end of the final gastral tergite (fig 6.17) in all examined species of rhyssines, except *Rhyssa* species (fig 6.16). This is presumed to relate to differences in mating systems that are discussed in chapter 5, and below.

The emphasis of this section is on male mating systems, leading on from the descriptions in chapter 5. One of the main problems that it will seek to solve is that of the apparently closely related genera *Megarhyssa* and *Rhyssella* which can only be defined by male abdominal characters. It is the discovery of what these abdominal characters mean in a biological sense, and whether they have evolved once or several times, that will lead to a clarification of the phylogenetic and taxonomic status of the group.

#### 6.8.1. Mating strategies in the Rhyssinae

In chapter 5 the mating systems found in the Rhyssinae were described. The taxonomic distribution of the observations is very patchy, referring to around half-a-dozen species. The conclusions can be summarised:

1. Post-emergence mating. Males waits until female is fully emerged before mating with her. Recorded in *Rhyssa persuasoria*. (This is probably a scramble competition system).
2. Pre-emergence mating. Males mate with females before they are fully emerged. This can be split into two sub-sections: (a) Female Defence Polygny: Males guard emergence sites - recorded in *Lytarmes maculipennis*. (b) Scramble competition polygyny - recorded in several species of *Megarhyssa*.

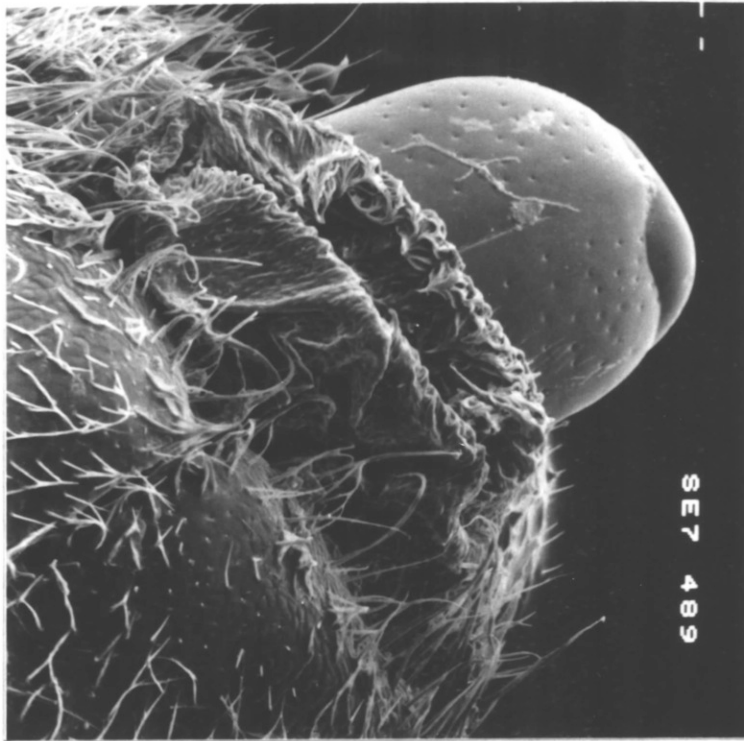


Fig 6.16. Final gastral tergite of *Rhyssa* showing absence of strongly developed anal gland. X 35.



Fig 6.17. Final gastral tergite of *Epirhyssa flavopictum* showing the strongly developed brush-like anal gland. X 40.

There are two main indicators of the mating system of rhyssines. One of these ways is direct and the other relies on assumptions about male gastral shape and mating strategies.

#### 6.8.2. Direct evidence

The various mating systems found throughout the rhyssines were discussed in chapter 5. The table below summarises this information:

Table 6.3. Summary of known male mating systems in the Rhyssinae

| Species                       | Mating System  | Reference                                                                            |
|-------------------------------|----------------|--------------------------------------------------------------------------------------|
| <i>Rhyssa persuasoria</i>     | Post-emergence | Myers (1928)                                                                         |
| <i>Megarhyssa citrata</i>     |                |                                                                                      |
| <i>Megarhyssa praecellens</i> | Scramble comp. | Yasumatsu (1937,1938)                                                                |
| <i>Megarhyssa greeniei</i>    | Scramble comp. | Heatwole et al,<br>1962, 1964; Matthews<br>et al 1979;Crankshaw<br>& Matthews, 1981. |
| <i>Megarhyssa macurus</i>     | Scramble comp. |                                                                                      |
| <i>Megarhyssa atrata</i>      | Scramble comp. |                                                                                      |
| <i>Megarhyssa nortoni</i>     | Scramble comp. | Madden,1968;<br>Davies & Madden, 1985.                                               |
| <i>Rhyssella approximator</i> | Scramble comp. | Thompson, pers comm                                                                  |
| <i>Lytarmes maculipennis</i>  | Female defence | Eggleton, in this thesis<br>(chapter 5, in<br>press)                                 |

### 6.8.3. Indirect evidence

It has been noted by several workers (Townes, 1969 especially), that small males of *Megarhyssa* species tend to lack the extreme abdominal specialisations of their larger conspecifics. They have often been referred to as "dwarf males" and they lack the defining characters of *Megarhyssa* (see below). Upon casual inspection it seems that this effect is one of a gradual shift between the smallest and largest males in any sample. It would be interesting to see whether this effect is a statistically real one and whether it applies across all the rhyssines. The problem can be seen in terms of shape changes in the gaster of the organisms - do all rhyssines show size-related shape changes or is the effect only seen in one group of species? - whether they be a taxonomic or ecological grouping.

In order to investigate this, the species where the mating system is known were examined. The length of the forewing was used as a measure of the body size of individual males (Gauld & Fitton, 1987) and the ratio of length:width of tergite 5 of the gaster was chosen to represent the shape of the abdomen. This measure was chosen as it was found to be difficult to measure the entire length of the gaster accurately due to the effects of telescoping of the posterior gastral segments (an effect common to most ichneumonids). The fifth segment is not normally significantly telescoped into its posterior or anterior neighbours, yet it does vary in shape in species that exhibit the phenomenon.

For the species with known mating strategy the tergite 5 length:width ratios have been plotted against the fore-wing length to see if there are any correlations. Unfortunately, there were too few specimens of *Megarhyssa nortoni*, *M. atrata*, *M. citrata* and *M. praecellens* available to enable them to be included. The plots are shown in figs 6.18 and 6.19A-B , and the associated correlation coefficients and probabilities of these correlations being statistically significant<sup>are presented in table 6.4</sup>. As a correlation is expected only in

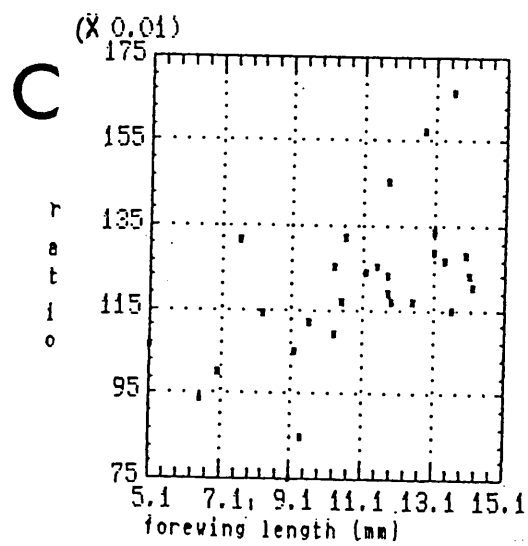
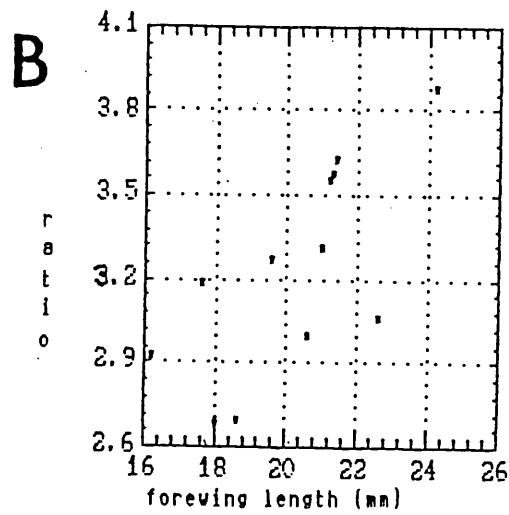
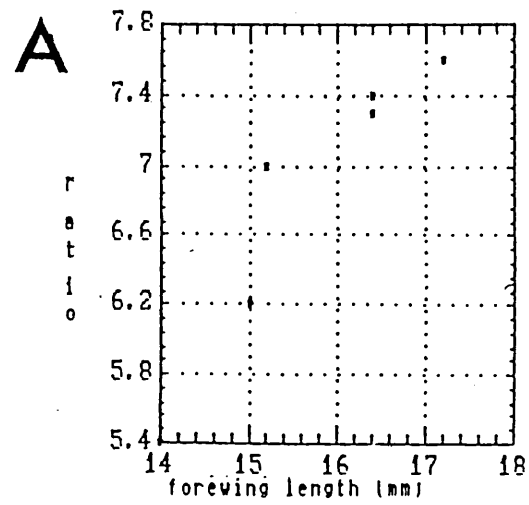


Fig 6.18. Graphs of male gastral tergite 5 length:width v. forewing length for: A. *Megarhyssa greenei*; B. *Megarhyssa macurus*; C. *Rhyssella approximator*.

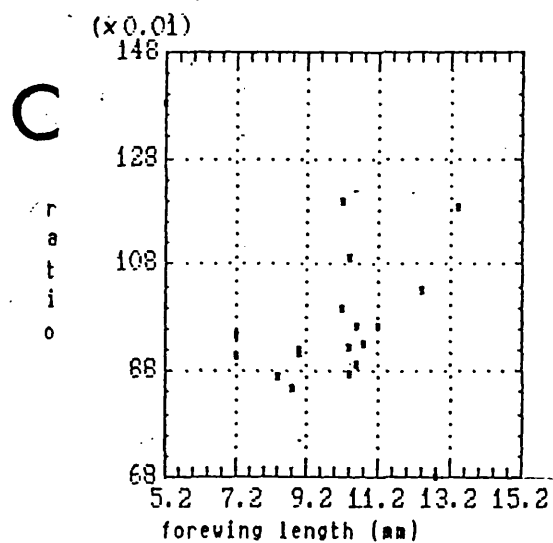
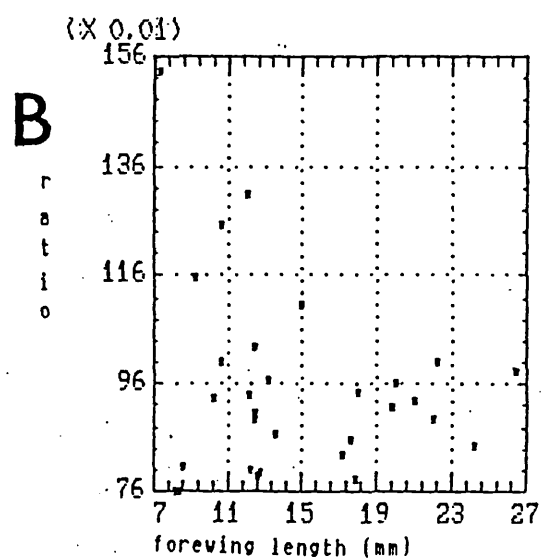
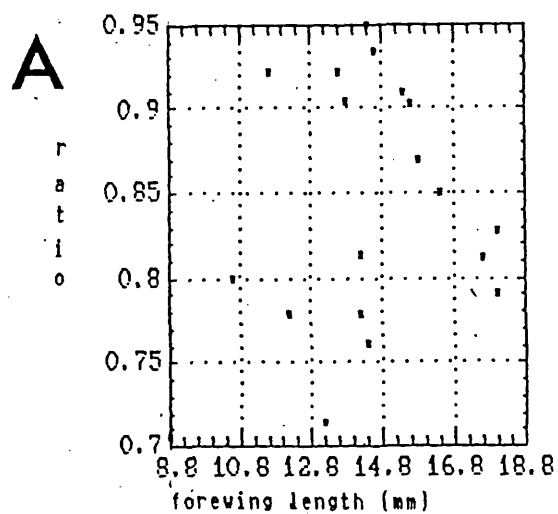


Fig 6.19. Plots of male gastral tergite 5 length:width v. forewing length for: A. *Lytarmes maculipennis*; B. *Rhyssa persuasoria*; C. *Rhyssa amoena*.

the one direction (toward thinner gasters with greater size) a one-tailed significance test was employed (Sokal & Rohlf, 1969). The results are summarised in table 6.4.

Table 6.4. Correlations for species with known mating strategies.

| Species            | n  | mating sys. | corr.  | prob.        |
|--------------------|----|-------------|--------|--------------|
| <i>M. greenei</i>  | 6  | SC          | 0.809  | <i>0.051</i> |
| <i>M. macurus</i>  | 12 | SC          | 0.711  | <i>0.009</i> |
| <i>R. approx.</i>  | 30 | SC          | 0.568  | <i>0.001</i> |
| <i>L. maculip.</i> | 19 | FD          | 0.101  | 0.322        |
| <i>R. persua.</i>  | 30 | Pre-em      | -0.201 | 0.286        |

(Probabilities in italics reject the null-hypothesis of no correlation in a one-tailed test.)

Clearly the mating systems are separated here by differences in shape change with size. The three scramble competition species show increasing narrowing and lengthening of gastral tergite 5 with increased forewing length. This is exactly what has been reported when workers (Townes, 1969; Kamath & Gupta, 1972) have referred to "dwarf males", specimens in the lowest size class of males with stout gasters that are apparently not equipped for insertion. The biological significance of the unmodified males found in the scramble competition species is discussed in section 6..

If all the results for species where the mating system is known are pooled and plotted together, a very clear discontinuity can be seen (fig 6.23A). Some points about this graph are worth noting.

(a) There are no specimens in the study group with a small relative body size and a narrow tergite 5 of the gaster. This clearly relates to the problem of being a small male in a scramble competition species, where the chance of successful

insertion can be inferred to drop off with decreasing gastral length (Crankshaw & Matthews, 1981). Essentially, all small rhyssine males can be inferred to have the same body plan - hence the large cluster of points around a forewing length of 5 mm and a gastral 5 ratio of 1.

(b) There is a discontinuity between large males with thin gastral t5 segments and large males with wide gastral t5 segments. This suggests that shape changes do not apply across the board, but are only found in pre-emergence scramble competition species.

From these observations, it should be possible to infer whether a species is showing a <sup>pre-emergence</sup> scramble competition system by whether it shows a, size-related, gastral shape change. More species from the BM (NH) collections, and from other sources have been examined as above, and the results are shown in figs 6.19C, 6.20, 6.21 and 6.22; and table 6.5.

Table 6.5. Correlations for species with unknown mating systems.

| Species                 | n  | corr.  | prob.        | inferred |
|-------------------------|----|--------|--------------|----------|
| <i>R. amoena</i>        | 19 | -0.231 | 0.340        | not SC   |
| <i>R. lineolata</i>     | 16 | -0.040 | 0.881        | not SC   |
| <i>R. obliterator</i>   | 10 | 0.724  | <i>0.018</i> | SC       |
| <i>L. fasciatus</i>     | 16 | 0.060  | 0.824        | not SC   |
| <i>E. cruciatum</i>     | 9  | 0.207  | 0.207        | not SC   |
| <i>M. emarginatoria</i> | 12 | 0.812  | <i>0.001</i> | SC       |
| <i>E. flavopictum</i>   | 13 | 0.077  | 0.803        | not SC   |
| Species 29              | 8  | 0.283  | 0.496        | not SC   |
| <i>E. mexicana</i>      | 9  | 0.071  | 0.545        | not SC   |
| <i>E. phoenix</i>       | 8  | 0.090  | 0.832        | not SC   |

(Probabilities in italics reject the null hypothesis of no correlation in a one-tailed test.)

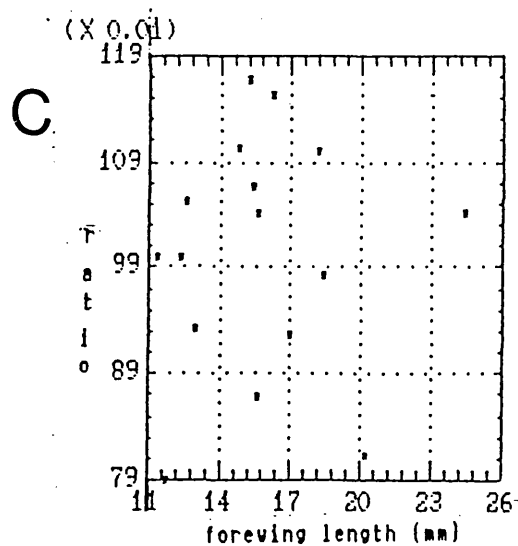
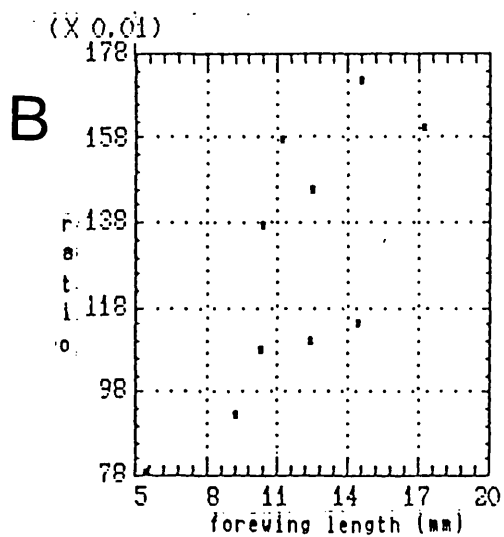
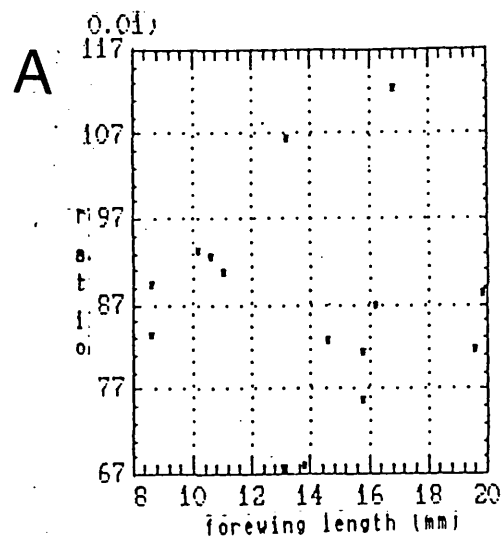


Fig 6.20. Plots of male gastral tergite 5 length:width v. forewing length for: A. *Rhyssa lineolata*; B. *Rhyssella obliterator*; C. *Lytarmes fasciatus*.

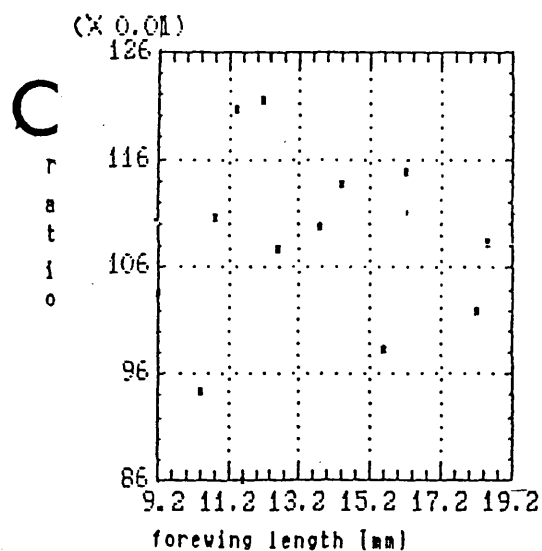
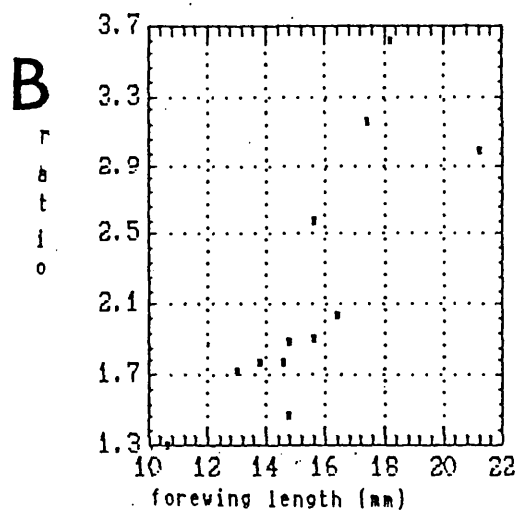
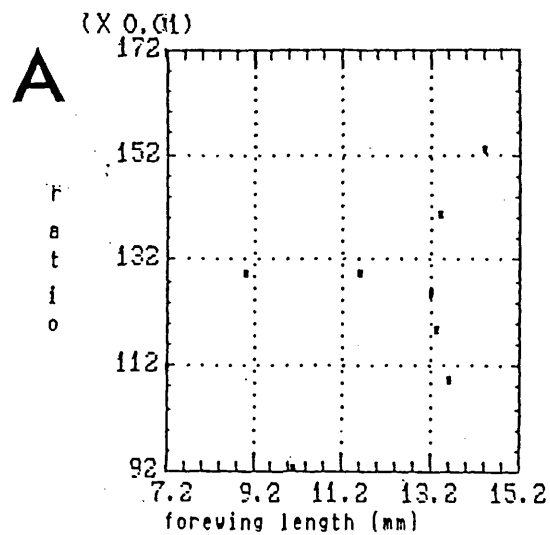


Fig 6.21. Plots of male gastral tergite 5 length:width v. forewing length for: A. *Epirhyssa cruciatum*; B. *Megarhyssa emarginatoria*; C. *Epirhyssa flavopictum*.

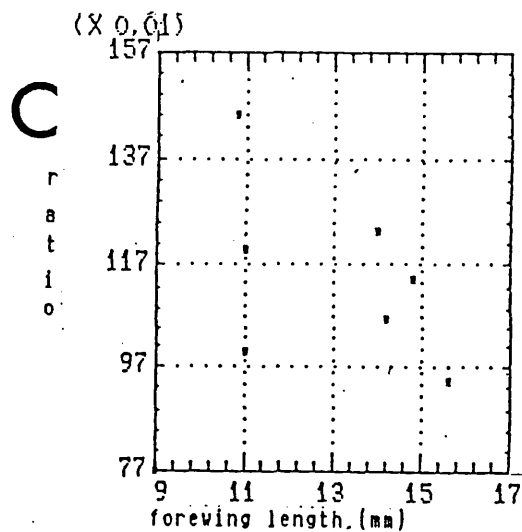
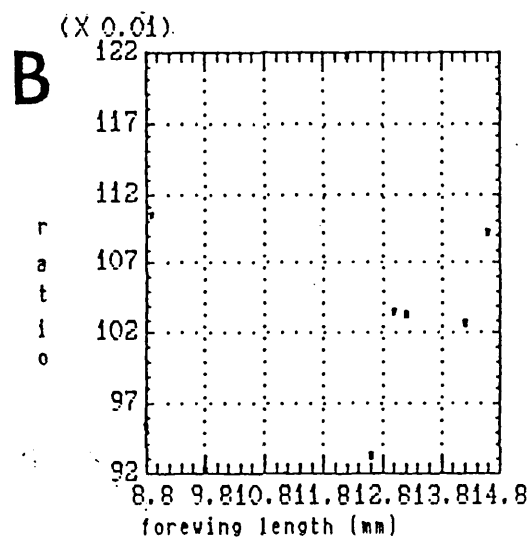
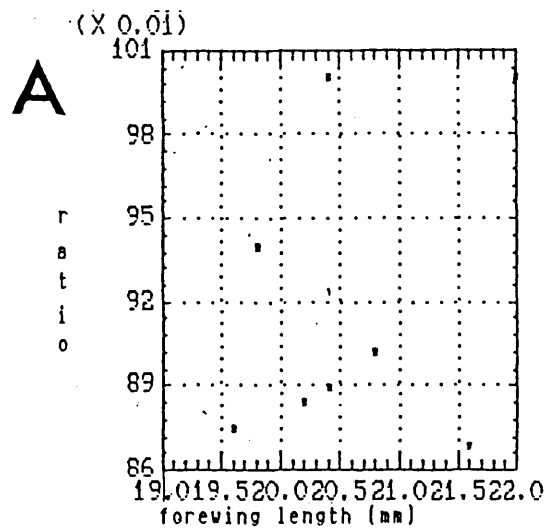


Fig 6.22. Plots of male gastral tergite 5 length:width v. forewing length for: A. *Epirhyssa* sp. 29 ; B. *Epirhyssa mexicana*; C. *Epirhyssa phoenix*.

These results demonstrate that *Rhyssella obliterata*, which is clearly taxonomically close to *Rhyssella approximata*, is showing a very similar change in gastral tergite 5 shape with increasing fore-wing length. All the other species show no such changes, and can be assumed not to be showing a <sup>pre-emergence</sup> scramble competition system. Once again, if the species with known and unknown mating systems are plotted together a very similar pattern arises (6.23B), with no specimens in either of the two areas of discontinuity. This supports the original conclusions.

These conclusions have been based on only a few species of rhyssines. It will be interesting to observe if this discontinuity is found in a much wider range of species, where there are only one or two specimens available. To investigate this a number of individual specimens from all species which have been examined during the study were measured. These were added to the plot above (fig 6.23B). The plot is clearly biased by the species where a large number of species were available, but the pattern remains the same (fig 6.23C). None of the new species fall outside the general shape of the other two plots.

What causes this discontinuity? It is argued that it is a result of a dichotomy in mating systems, between pre-emergence and post-emergence copulation. This dichotomy runs entirely along presently constituted taxonomic lines. If the genera *Rhyssella* and *Megarhyssa* are removed from the analysis, the resulting diagram shows an extreme clustering and clearly no correlation (fig 6.24B). The specimens that have been taken out show no clustering, except at low body sizes, and an obviously significant correlation (fig 6.24A). The discontinuity is therefore a real phenomenon, assuredly related to differences in male mating systems and is linked to one particular taxonomic grouping. However, as discussed in chapter 4, the taxonomic grouping is defined by characters which are size-related and clearly linked to the observations made here. So, two questions need to be asked: first, where and why are discontinuities occurring?; and, second, is *Megarhyssa* defined

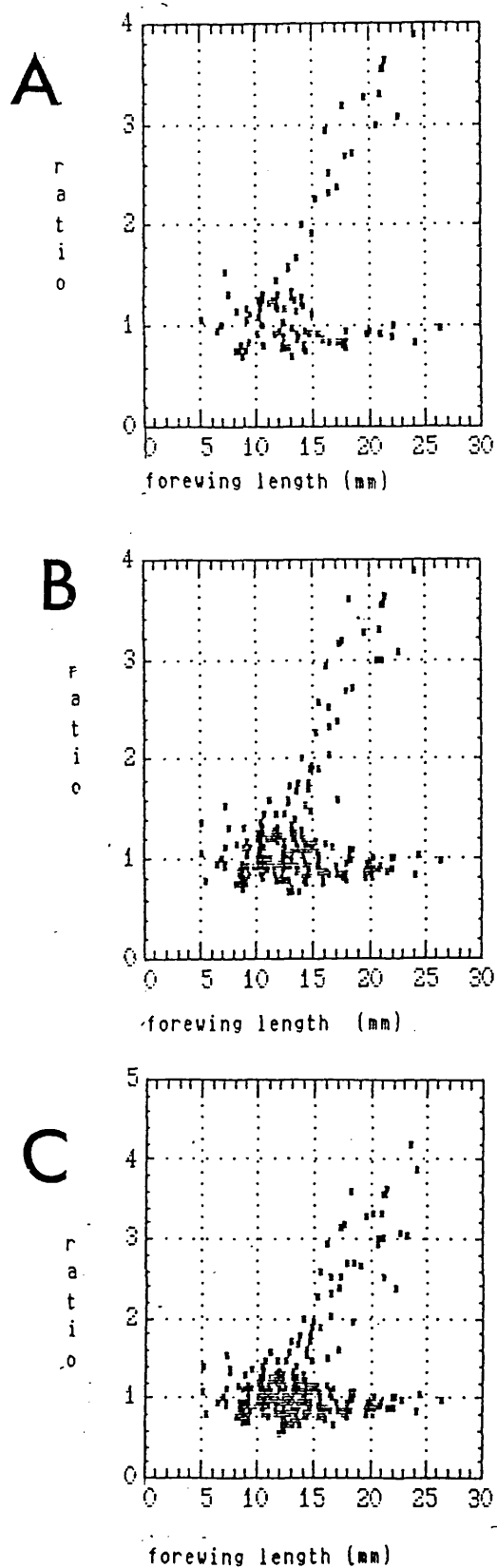


Fig 6.23. Pooled plots of male gastral tergite 5 length:width v. forewing length for: A. species with known mating systems; B. A. + species with unknown mating systems; C. B + species with fewer than 6 specimens available.

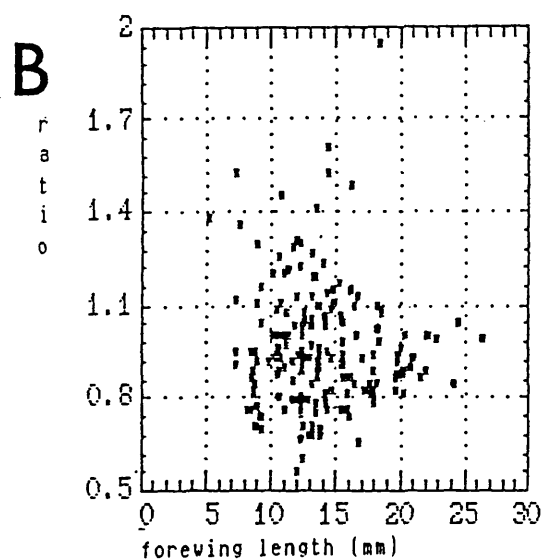
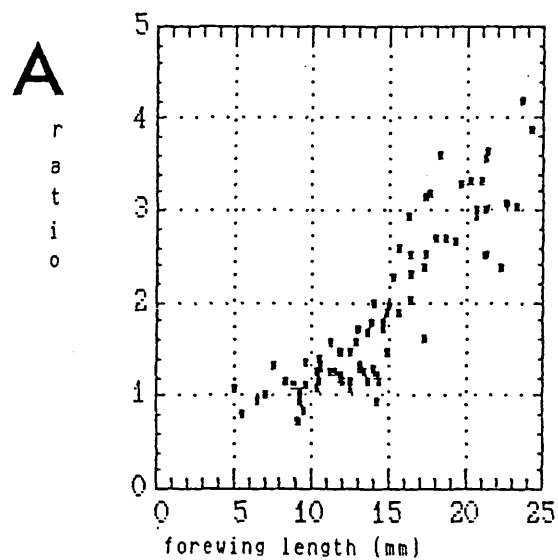


Fig 6.24. Pooled plots of male gastral tergite 5 length:width v forewing length for: A. *Megarhyssa* and *Rhyssella* species only; B. All species except *Megarhyssa* and *Rhyssella*.

because the species in it all have similar mating systems, although these systems have been acquired independently?, or is *Megarhyssa* defined by a mating system that has evolved only once in the group and therefore defines it?

#### 6.9. Is *Megarhyssa* a holophyletic group?

Having concluded that the species belonging to the genera *Megarhyssa* and *Rhyssella* show a very characteristic size related shape change, it now remains to see whether characters related to this size-related shape change are compatible or incompatible with the original rhyssine data set. These characters are (Townes, 1969):

51. *Tergites 3-6 of male strongly concave apically and with a median apical or subapical longitudinal submembranous area*

52. *Male clasper with a strong setiferous groove close to and paralleling the apical  $0.7\pm$  of its lower inner edge, and with a short longitudinal setiferous groove apico-laterally.*

Both these characters vary with body size and it is very likely that the size related nature of these characters are obvious morphological manifestations of the processes described above. As such they are convenient to use, as characters, here. A more precise way of expressing the phenomenon might be by measurements of correlation between gastral shape and overall body size; or by some measure of increasing density of hairs on the last few segments of the gaster, with body size. However, they would both require a large number of specimens in each species to ascertain clearly, and so to avoid a large number of missing values they have been avoided. *Rhyssella* specimens have been coded as apomorphic for character 51, as it is clear that larger specimens show vestiges of this condition, especially on the apex of the last tergite.

#### 6.9.1. Cladograms and trees

The overall randomness ratio of the data set is 0.68, slightly lower than that of the data set without male gastral characters. This indicates that the male gastral characters have a below average level of homoplasy for the data set.

The cladograms produced by the addition of these characters related to mating systems are shown in fig 6.25 (LEQUB/PROB) and fig 6.26. (O'NOMOD). Both analyses place character 51 and 52 within the clique.

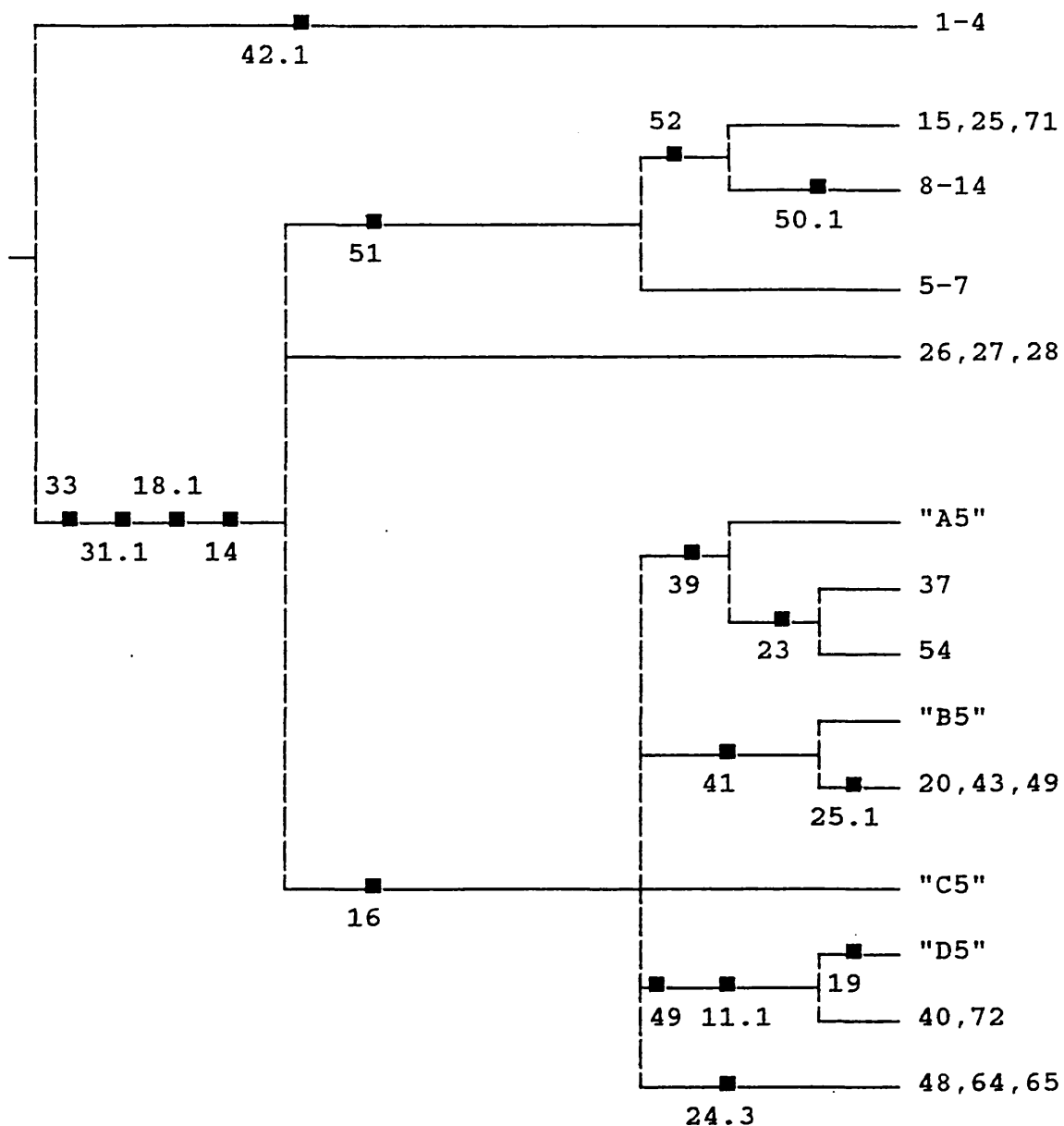
The LEQU/PROBS cladogram is essentially similar to the cladogram produced without the gastral characters. The most striking difference is the inclusion of character 41 as part of the clique. This character prevents characters 40.2 and 11.2 entering the clique and so does not show *Triancyra* as a holophyletic group. *Rhyssella* and *Megarhyssa* are shown as holophyletic, with *Rhyssella* as the paraphyletic sister-group of *Megarhyssa*. *Myllenyx* and *Epirhyssa* are delineated as before. The hypothetical tree can be constructed as follows:

(a) Character 42.2 enters the clique if a reversal is postulated in the *Myllenyx* clade. This is the same situation as the initial analyses.

(b) Character 1 enters the clique only if 6 parallelisms are postulated - in taxa 30,31 and 68; in the taxa 20,43,49 and the taxa marked "A7"; in taxon 73; in taxon 70; in taxa 72,79 and 80; and in the taxa marked "D7". This is rather uninformative as a character.

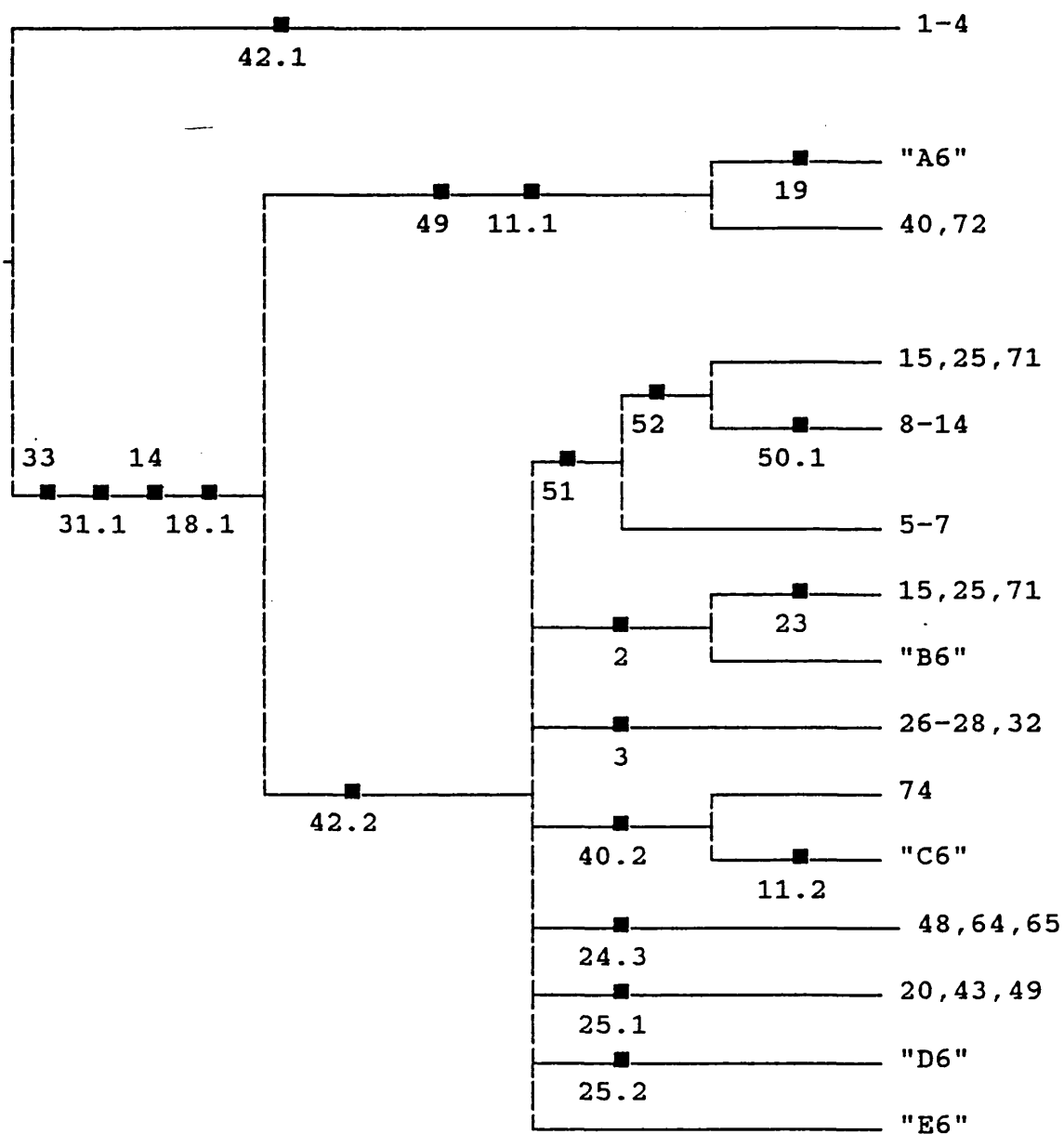
(c) Character 24.2 enters the clique if two parallelisms are postulated: in taxa 35, 57 and 78; and in taxon 24.

(d) Character 40.1 enters the clique without homoplasy if two



Key: ■ - apomorphy; "A5" - 32-36, 55-7, 78. "B5" - 16, 18, 19, 22, 23, 29, 44-46, 50, 59, 63, 66-69, 74, 75; "C5" - 17, 21, 24, 30, 31, 38, 39, 42, 52, 53, 58, 60, 61, 62, 75, 77; "D5" - 41, 51, 70, 73, 79, 80;

Fig. 6.25. LEQU/PROBS Cladogram for the rhyssine data set with gastral characters added.



Key: ■ - apomorphy; "A6" - 41,51,70,73, "B6" - 35,36,57,67,78; "C6" - 30,31,60,68,69; 79,80."D6" - 18,42,52,62; "E6" - 16-19,21-24,29,33,34,37,38,39, 44,45,46,50,53,54,55,56,58,59,61, 63,66,74,75,77.

Fig. 6.26. O'NOMOD Cladogram for the rhyssine data set with male gastral characters added.

parallelisms are postulated in character 41: in taxon 68; and in the rest of the group delineated by character 41.

(e) Character 12 enters the clique if two parallelisms are postulated - one in taxon 72 and one in taxon 73.

(f) Character 18.2 enters the clique if three parallelisms are postulated: one in taxa 13, 14, 15, 25 and 71; one in taxa 26, 27 and 28; and one in the whole clade delineated by character 16.

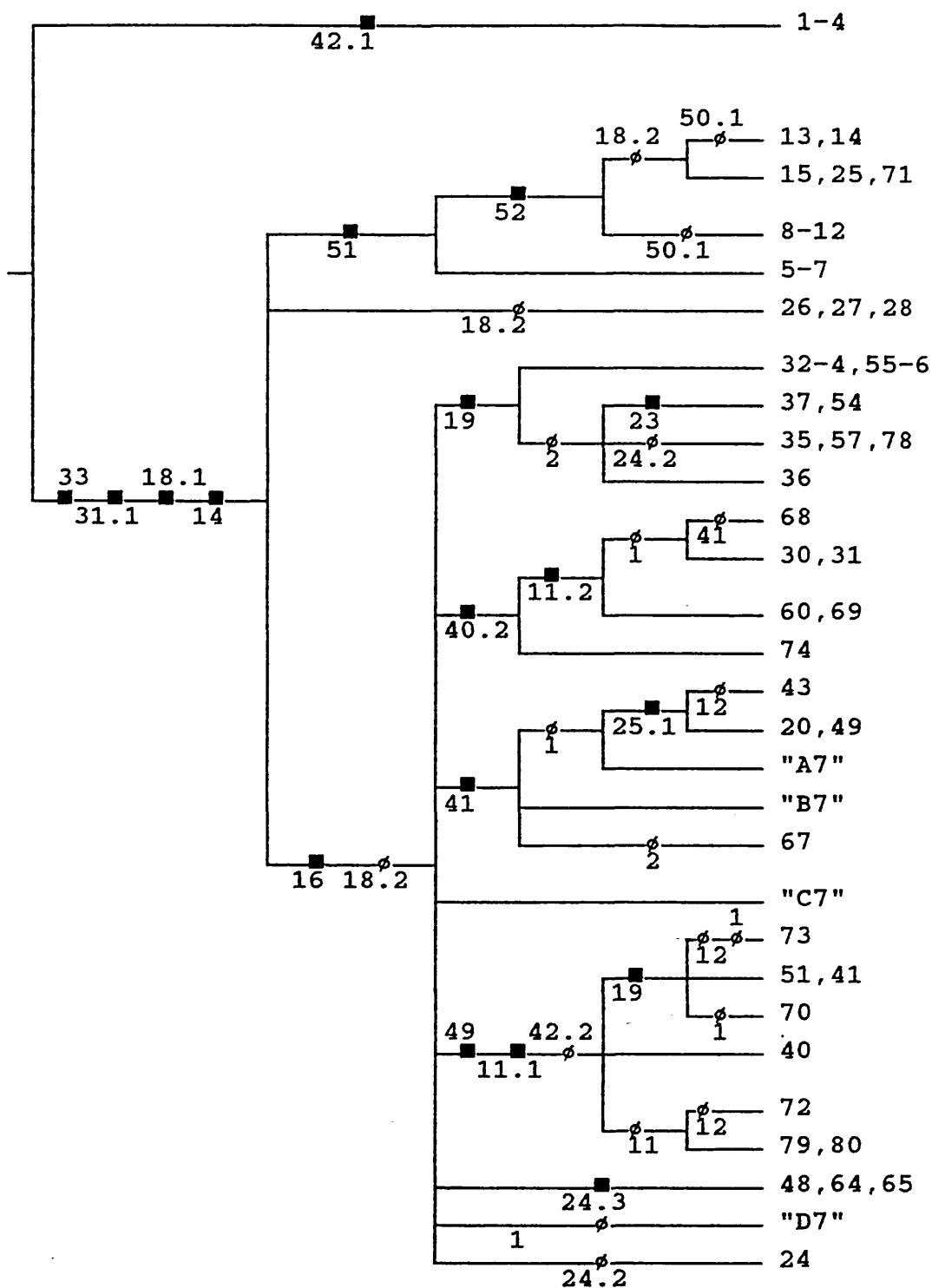
(g) Character 2 enters the clique if 2 parallelisms are postulated. One in taxon 67 and one in taxa 35, 36, 37, 54, 57 and 78.

The resulting hypothetical tree is shown in fig 6.27. Subset analyses were, as before, only performed where there were at least two supporting characters for a clade. This meant only one subset analysis (leaving out the *Myllenyxis* clade which is too small for unambiguous results, see above) for all the taxa minus taxa 1-4. This analysis placed no new characters in the clique.

The final tree differs in relatively small ways from the "without gaster characters" tree. The presence of characters 1 and 41 prevent several groupings which appeared in the initial tree, from being part of this one.

The O'NOMOD tree (fig 6.28) shows one striking difference in topology. Character 16 is not in the final clique and this leaves *Myllenyxis* sharing no apomorphies with the "higher rhyssines", and *Megarhyssa* as more apomorphic than *Myllenyxis*. This has meant a swap in position for the two groups, as compared with the LEQU analysis. In other respects the analysis gives similar grouping to the earlier ones in the most apomorphic branches. The hypothetical tree is constructed as follows:

(a) Character 30 enters the clique if two parallelisms are postulated: one in taxon 37 and one in taxa 36, 57 and 78.



Key: ■ - apomorphy; ø - parallelism; ⊖ - reversal; "A7" - 16, 18, 19, 29, 44-46, 49, 75; "B7" - 22, 23, 50, 59, 63, 66; "C7" - 17, 38, 39, 42, 52, 53, 58, 61, 62, 77; "D7" - 21, 38, 39.

Fig 6.27. LEQU/PROBS hypothetical tree for the rhyssin data set with male gastral characters added.

(b) Character 12 enters the clique without parallelisms, but was thrown out due to one parallelism with character 19.

(c) Character 19 enters the clique if two parallelisms are postulated in taxon 73 and taxa 41, 51 and 70.

(d) Character 16 enters the clique if two parallelisms are postulated: one in the *Myllenyxis* clade and one in the other "higher rhyssines"<sup>along with a reversal in taxa 26-28.</sup>

(e) Character 39 enters the clique without homoplasy if two reversals are postulated in character 2: one in taxon 67 and one in taxa 35, 36, 37, 54, 57 and 78.

This hypothetical tree (fig 6.28) recognises the same basic groupings as the "without male gaster" trees. The difference lies only in the position of *Myllenyxis* with respect to *Megarhyssa*, and a few minor differences in the least certain parts of the tree.

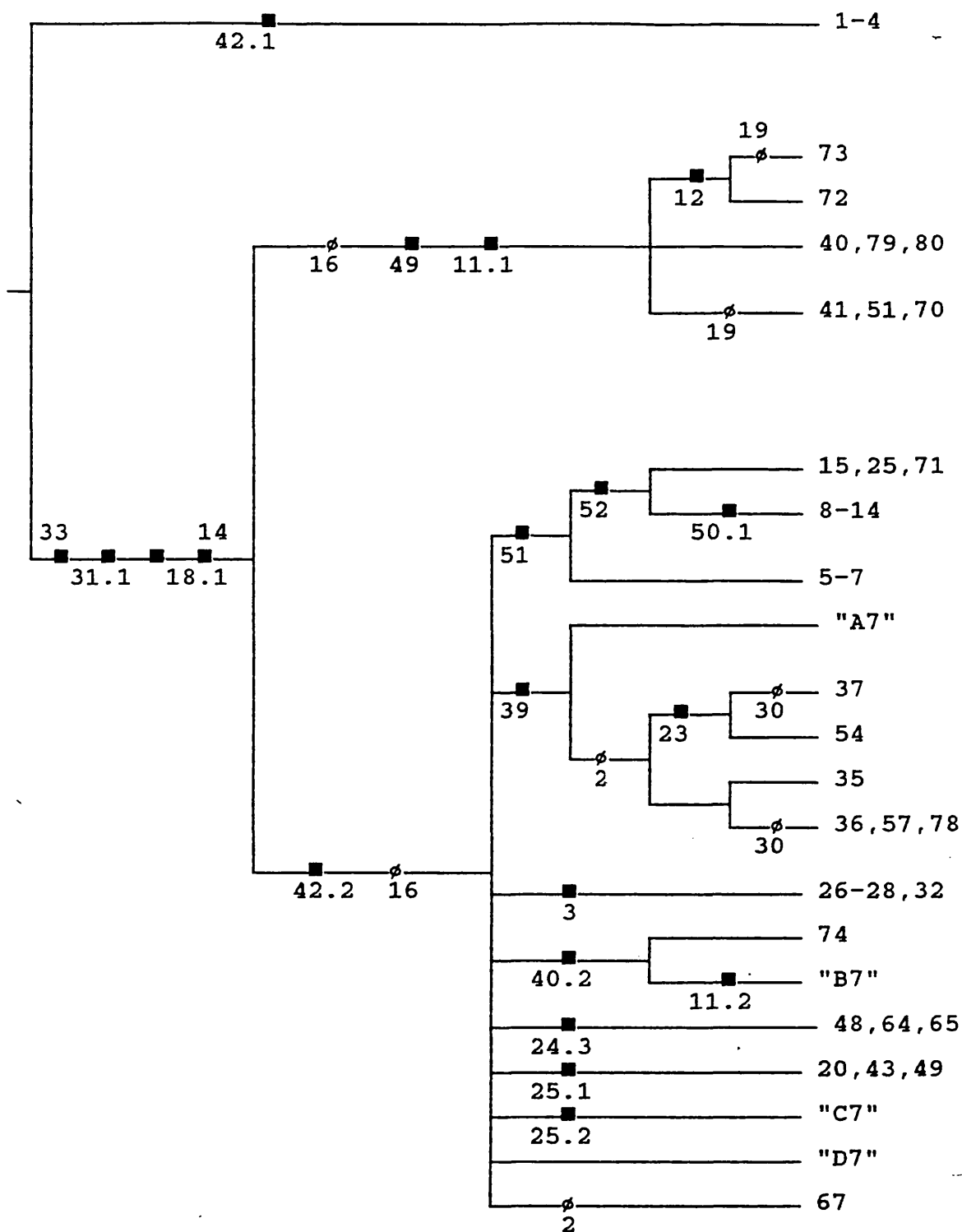
#### 6.9.2. *Megarhyssa* - phylogenetic conclusions

The possible resolution of the problem of the four obtained trees for rhyssine phylogeny is discussed below. The main interesting result here, however, is that characters 51 and 52 are shown as delineating a holophyletic group, and that by doing so they change the overall topology of both cladograms and hypothetical tree. What characters, then, do characters 51 and 52 throw out of the tree? And are these characters really less reliable and open to homoplasy than the male gastral ones?

The two characters thrown out of the cliques are characters 18.2 and 34. Character 18.2 is a character relating to the pattern of distribution of the radial hamuli. At first sight this character seems to be very good - there seems to be a gradual change from having the hamuli evenly spaced, through becoming clustered loosely at the base, to having them obviously grouped in twos, threes or fours. This original coding split *Megarhyssa* into two paraphyletic

groups. This is, however, a common evolutionary sequence amongst the Hymenoptera (Gauld & Bolton, 1988) and as such is a familiar example of a potentially homoplastic loss character. The second character (34) relates to the presence or absence of the glymma. Some *Megarhyssa* and *Rhyssella* species seem to have a vestige of the glymma remaining. However, it is a somewhat arbitrary choice of dividing line between presence and absence.

Against these two characters are 2 presence characters which delineate groups showing biological similarities - as far as is known all the group are parasitoids of Siricoidea (although, of course, the hosts of the tropical groups are unknown; but, as discussed above, they are unlikely to be woodwasps). These two characters are clearly more compatible with the data set than the other two, and seem on purely morphological grounds to be more acceptable. However, these characters are clearly indicative of a particular male mating system and would normally be considered highly homoplastic. Here, they appear not to be, and it is conceivable that a pre-emergence scramble competition system has evolved only once amongst the rhyssines. The possible explanations for this are discussed in section 6.11, after a final tree diagram for the rhyssines has been constructed and discussed.



Key: ■ - apomorphy; ○ - parallelism; θ - reversal "A7" = 33, 34, 55, 56; "B7" = 30, 31, 60, 68, 69. "C7" = 18, 42, 52, 62; "D7" = 16, 17, 19, 21-24, 29, 38, 39, 44-46, 50, 53, 58, 59, 61, 63, 66, 72, 75, 77;

Fig. 6.28. O'NOMOD hypothetical tree for the rhyssine data set with male gastral characters added.

#### 6.10. Phylogeny - overall conclusions

There are four trees which result from the analysis of the rhyssine data set. Two of these consist only of female and non-gastral male characters, and two have gastral characters added. From this mass of contradictory conclusions, can any overall phylogenetic hypothesis be constructed?

The first thing to consider is what groupings all four trees have in common. These similarities are listed below:

(a) *Rhyssa* (taxa 1-4) is taken off at the first branch of all the trees as the least apomorphic taxa. It is also defined as a holophyletic group by one autapomorphy (the presence of gastral sternite tubercles at the midline of the sternite mid-line (fig 6.1A). The separation of this group from the other rhyssines is the strongest dichotomy of all.

(b) *Myllenyxis* (taxa 40, 41, 51, 70, 79 and 80) is defined in all trees as a holophyletic group. The position of the group differs between the last two trees, however.

(c) *Epirhyssa* (referred to later as the *speciosa* species-group: taxa 32-37, 54-57, 78) is defined in all trees (but not the final PROBS/LEQU cladogram) as a holophyletic group.

(d) *Triancyra* (taxa 30, 31, 60, 68, 69, 74) is defined in all trees (but not the final PROBS/LEQU cladogram) as a holophyletic group.

(e) the *flavopictum* species-group (taxa 20, 43, 49) is defined in all cladograms and all trees.

(f) *Megarhyssa* and *Rhyssella* are defined as a holophyletic group together. The reasons for this are discussed above.

Beyond this, there are two main sources of incompatibility which make the trees incongruous. These are:

(a) The incompatibility between character 16 (absence of vein 3rs-m in the fore wing) and character 42.2 (absence of sternal (ovipositor) guides). The resolution of this incompatibility will decide the position of *Myllenyxis* in the tree. Other characters that support the two competing characters are as follows:

(1) Characters 18.2 (presence of grouped radial hamuli) and 34 (absence of a glymma) support character 16, if a total of two parallelisms are accepted in each.

(2) Character 16 supports character 42.2 if two parallelisms and two reversals are postulated.

So, character 42.2 is supported by one other character which requires 4 state changes to enter the clique, while character 16 is supported by two characters which require 3 state changes each. The most parsimonious solution is therefore to support the clade delineated by character 16.

In addition *Myllenyxis* is unlikely to be boring through wood. Although *Megarhyssa* species have ingenious methods of increasing the effective length of their gasters, *Myllenyxis* seems to have only a vestige of the adaptations associated with this (a highly membranous region between gastral tergites 5 and 6, see chapter 5) and the ovipositor is sometimes three times as long as the body (in *Myllenyxis longiterebra*, for example). Also, the apical region of the ovipositor is sinuate, so that a *Myllenyxis* species would not be able to oviposit as other rhyssines do, as the effect would be like trying to drill through wood with an immobilised corkscrew. It is more likely that *Myllenyxis* is ovipositing in a manner similar to that described by van Achterberg (1986) for a braconine braconid. As a non-borer the species would have no sternal guides (the apparently plesiomorphic state of character 42.2) - and this is the sort of

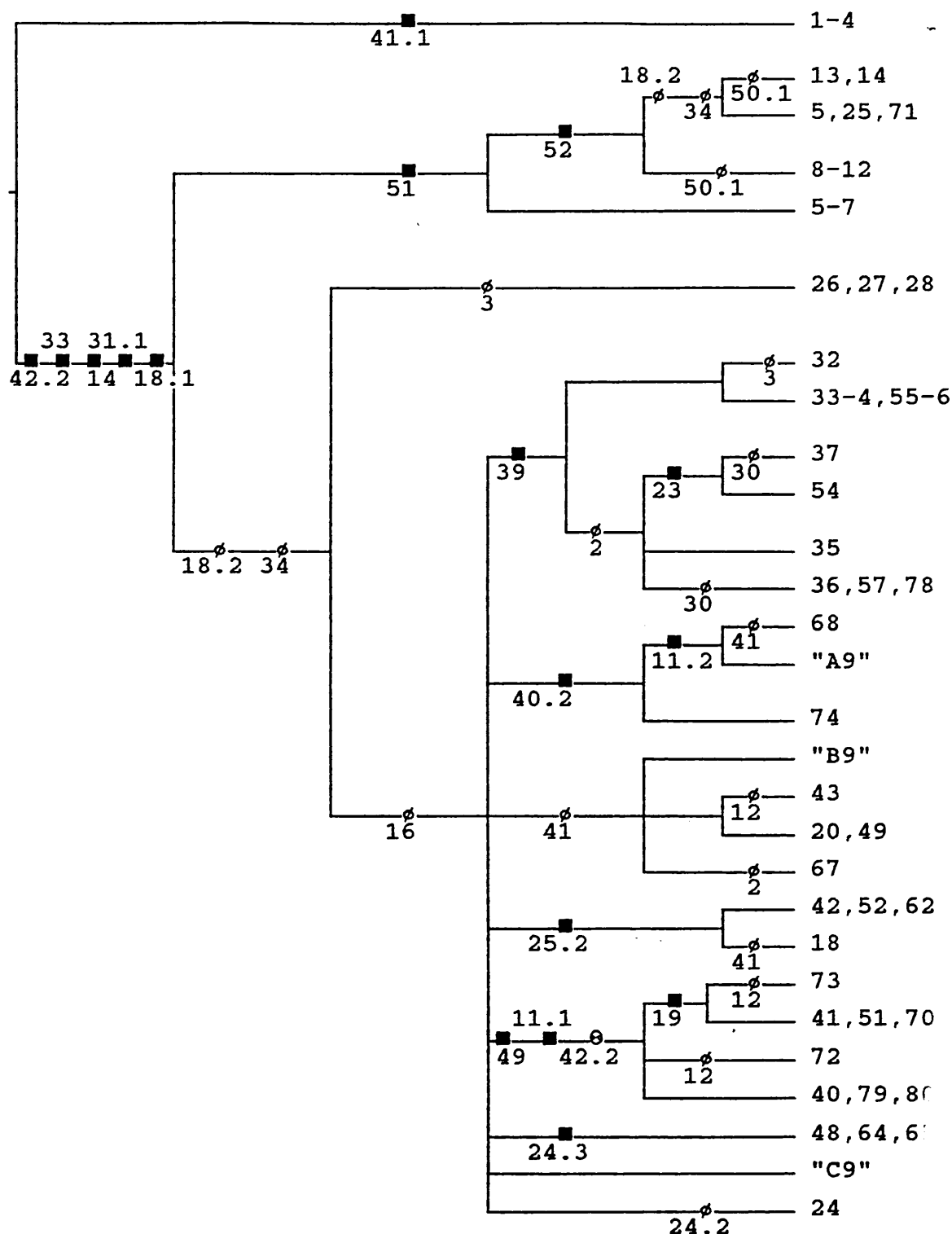
absence character which is always difficult to recognise as apomorphic or plesiomorphic. The alternative character, which involves the loss of a vein, is clearly an apomorphic condition even if it has been identified as homoplastic in other ichneumonid groups (see chapter 3).

Additionally, the wood-boring habit appears to be primitive in rhyssines. The outgroup of the higher rhyssines (those defined by characters 33, 31.1, 14 and 18.1) is clearly *Rhyssa*, and this taxon is a wood-borer. Any loss of the specialisations associated with wood-boring then become apomorphic, and so the loss of the sternal tubercles would be apomorphic. This is, of course, not strictly an out-group comparison at all, and would not be enough to justify the grouping without supporting characters.

Overall, character 16, supported by characters 18.2 and 34, is a stronger character than character 42.2, which may be polarised incorrectly. Character 42.2 is placed as double apomorphic in the *Myllenyxis* clade, and *Myllenyxis* is placed as the most derived rhyssine.

(b) Characters <sup>25.1</sup>25.2 and character 41/1. Character 1 is a very odd character. It was originally coded as: *absence of occipital carina, apomorphic; presence of occipital carina, plesiomorphic*. However, in all the analyses this character was strongly polar incompatible. This is because only a small number of Indo-Australian species have a complete occipital carina. The reversal of the polarity makes the character enter one clique (the "with male gaster data" LEQU clique, fig 6.27) but only if 6 parallelisms are postulated. Because of its high homoplasy and its uncertain polarity, it is rejected from the final tree. Character 41 can be made compatible with characters 25.1 and 25.2 by postulating two additional parallelisms in taxon 18, and taxon 68. The resulting combined tree diagram is shown in fig 6.29.

The final groupings at the most derived branches of the tree are to be considered very uncertain. However, the tree can stand as a hypothesis which will be modified as more characters from immature



Key: ■ - apomorphy; ∅ - parallelism; ⊖ - reversal; "A9" - 30, 31, 60, 69; "B9" - 16, 18, 19, 20, 22, 23, 29, 44, 45, 46, 49, 50, 59, 63, 66, 75; "C9" - 17, 21, 38, 39, 53, 58, 61, 77;

Table 6.29. Final combined hypothetical tree for rhyssine data set.

stages and internal anatomy are discovered. Overall, though, it will probably be the biological characters that will turn out to be the most important clues to the evolutionary relationships of the group. As more data are collected it will be interesting to see how far these tenuous groupings have solid biological foundations.

#### 6.10.1. Comments on the final tree

The cladograms and trees above show that the relationships within the rhyssines are unclear, especially within the relatively diverse tropical rainforest species. However, from just a consideration of the evolution of morphological characters, some groupings and evolutionary relationships can be postulated. In the discussion below where a grouping coincides with a presently accepted (Townes, 1969; Kamath & Gupta, 1971) one it is referred to by name. In addition, groups that do not appear as natural are discussed when they have been given taxonomic significance in the past. It is the combined tree (fig 6.29) that is referred to throughout this discussion.

(a) the *Rhyssa*-group. This taxa is clearly marked off as the most primitive member of the subfamily. It has a single autapomorphy (the position of the sternite 2-4 tubercles) but is so different morphologically from the rest of the rhyssines that it merits its present generic status. The biological, biogeographical and behavioural peculiarities associated with its underived state are discussed later in this chapter.

(b) the genus *Megarhyssa*. The gastral modifications associated with this group have been shown to be compatible within all the cliques produced. The conclusion that must be reached, therefore, is that the group is holophyletic. The consequences of this are discussed below.

(c) *Rhyssella*. The species placed at present in this genus are not easily distinguishable from *Megarhyssa*, even if male abdominal structures are considered. It has already been shown that the relative reduction in specialisation of the gaster is due to a size-

related shape change which applies both inter- and intra-specifically. Townes (1969) as much as says this when he comments in the key to pimpline genera: "abnormally small males (of *Megarhyssa*) have the characters stated for *Rhyssella*". This genus can confidently be placed within *Megarhyssa*. It seems that *Rhyssella* species are just small *Megarhyssa* species specialised for a slightly different host - xiphydriid siricoids rather than siricid siricoids. The differences between the two groups may indeed be only a consequence of the fact that xiphydriids are generally smaller than siricids.

(d) *Lytarmes*. This genus is supported by its presently accepted unique character (the genal carina reaching the occipital carina near the base of the mandible, see table 6.1), if one species in the presently recognised genus *Cyrtorhyssa* is included in it, and with the acceptance of one parallel acquisition in a Neotropical *Epirhyssa* species. It is clearly separated from *Megarhyssa* by its gastral morphology, and presumably by differences in mating systems (*Lytarmes* species probably all have female defence systems).

(e) *Cyrtorhyssa*. As commented above, one species (*C. mesophyrra*) of this genus is best placed within *Lytarmes*, while the other (*C. muelleri*, which has not been seen during this study) appears, from the description to be a rather aberrant *Epirhyssa* species. It is clearly not a holophyletic genus.

(f) The *Epirhyssa*-group. The cladograms and trees indicate that a large number (indeed a great majority) of rhyssine species come out in a rather homogeneous, poorly defined grouping at the top of the tree. These are all medium sized insects associated with tropical rainforests, although details of their biology are unknown (see chapter 5). Within this grouping *Myllenyxis* is obviously rather distant from the presumed ancestral form. The difficulty which has been encountered in analysing relationships is not only due to the rather unvarying structures in the animals, but also to the high levels of homoplasy (as indicated by the differences between the four trees). This combination, of single apomorphies and high homoplasy, has led to uncertainty about relationships which suggests strongly

that all these species are very close to each other. It is proposed that the species presently in *Sychnostigma*, *Epirhyssa*, *Triancyra* and part of *Cyrtorhyssa* should be synonymised under *Epirhyssa* (as the oldest name). Within this group a number of subgroups can be recognised, and these are discussed below. However, none of them seem strongly enough defined to warrant a separate generic status. The presently recognised genera within this group are only as well defined as the other subgroups that have never been given generic status. Indeed, using the existing limits for genera, each of the described subgroups would have to be raised to generic level. For example, the genus *Epirhyssa* is defined by one autapomorphy which seems to be less stable than the epicnemial character which is used to characterise the *flavopictum* species-group; it seems to be only the biogeographical separation of the Neotropical fauna from the Palaeotropic one that has led to its description as a separate genus. As the species-groups are so poorly defined it seems best to keep the whole group, except *Myllenyxis*, together in a presumably paraphyletic genus *Epirhyssa*, rather than raising the species-groups to generic level. Within this genus the following groupings are recognised:

(i) The *speciosa* species-group (the genus *Epirhyssa* sensu Porter 1978). The Neotropical rhyssines are separated on the structure of the 1st tergite of the gaster, but not by the other characters used in the past (see table 6.1, Townes, 1969; Porter, 1978). The group is possibly paraphyletic. It is undoubtedly an undercollected group (for example, in the rather rhyssine depauperate dry tropical forests of Costa Rica, Ian Gauld (pers comm.) has collected 4 new species, more than doubling the total number of species). When a wider range of specimens is collected it may be that the defining character will turn out to be an artificial autapomorphy based on a sampling error. Porter (1978) has split the genus up into species groups, but these groups are not clearly delineated in the analysis.

(ii) The *scabra* species-group (*Triancyra* sensu Kamath & Gupta, 1972). This group seems to be somewhat better characterised: by the presence of a clearly much wider lower than upper tooth to the mandible, which<sup>is a</sup> generic characters in table 6.1. The other two

characters mentioned in table 6.1 do not come out in the analysis. It was discovered that a grouping of 3 hamuli as found in this group is often present in species of *Megarhyssa* and some species of the *speciosa* species-group - for this reason it did not define *Triancyra* in the analysis. Additionally the presence of raised frontal orbits did not come out as an autapomorphy, and so does not define the group. The group is also defined by the presence of flat rounded tubercles on sternite 1 of the gaster of both sexes (character 40.2), if *Sychnostigma japonica* (taxon 74) is included with it.

(iii) The *flavopictum* species-group (part of *Sychnostigma* sensu Kamath & Gupta, 1972). Defined as having an epicnemial carina which is reflexed onto the anterior edge of the mesopleuron. Within the analysis *Sychnostigma flavopictum*, *S. atrum* and *S. cinctum* all belong within this group. In Kamath & Gupta (1971) *S. masoni* and *S. persicum* would also seem to belong here, but the former has not been seen and the latter (the holotype being in the BMNH) does not appear to have a reflexed epicnemial carina, and so has not been included in the group.

(iv) The *bimaculatum* species-group, characterised by having a cleft in the subtegular tubercle. This delineates *S. bimaculatum*, *S. pumilum* and the undescribed species taxon 43. This group may be close to the *cruciatum* species group.

(v) The *cruciatum* species-group. This is characterised by having a rounded hole in the subtegular tubercle. The species in this group are *S. cruciatum*, *S. kerrichi*, and *S. binarium*. This subgroup may be part of the *flavobalteatum* species group.

Other species which have not been studied but which from descriptions seem to belong either in the *bimaculatum* species-group or the *cruciatum* species-group are *S. simile*, *S. masoni*, *S. orientale*, *S. sarawakense* and *S. confractum*, although it is not clear from the description how their subtegular tubercles are developed, so they cannot be confidently placed in either group. Although, there is a clear morphological difference between the *cruciatum* and

*bimaculatum* species-groups, they are probably very close.

Note: the species referred to and keyed by Kamath and Gupta (1971) as *cruciatum* is not conspecific with the holotype in the BMNH. The species represented by the holotype clearly belongs in the above species group, and being the senior name within the group has been chosen for the informal taxonomic grouping. Kamath & Gupta's *cruciatum* is dealt with as a separate OTU (no. 61), and it does not have a hollowed subtegular tubercle.

(vi) The *flavobalteatum* species-group (part of *Sychnostigma* sensu Kamath & Gupta, 1972). This group is defined by the gastral tergites 3-5 having lateral depressions and a submedian lateral humps on gastral tergites 4 and 5. the species within the study group belonging here are *S. biroi*, *S. malayanum*, *S. perspicuum*, *S. validum*, *S. silvaticum*, *S. maculiceps*, *S. flavobalteatum*, and two undescribed species: taxa 46 and 50.

(viii) This grouping consists of the majority of the rest of the *Epirhyssa*-group, and it has not been assigned a species-group name, as it is a paraphyletic grouping. It is a very homogenous group, but its only possible autapomorphy is the rather polished impunctate to slightly punctate propodeum. It is analogous to the polysphinctine genus *Acrotaphus* from which *Hymenoepimecis* has been derived, but which in itself has no autapomorphies (Gauld, pers comm; cf. section 3.8.3).

(g) *Myllenyxis*. This presently recognised genus is clearly a holophyletic group and the most divergent from the generalised rhyssine ground-plan. Its generic status is justified.

### 6.11. Possible explanations for the taxonomic distribution of gaster shape

Now that some of the phylogenetic relationships within the rhyssines have been investigated, the problem posed earlier can be attended to. That problem was concerned with the concentration of one mating system and associated abdominal adaptations within a single holophyletic group: *Megarhyssa* including *Rhyssella*. In this section the possible explanations are discussed, and consideration is given to the biological significance of "dwarf males". There are four main possibilities:

#### 6.11.1. Size factors

Only species with large males may be showing pre-emergence scramble competition. This would be due to the simple physical constraints of small size; an small individual would not be able to reach down to an emerging female. If this were the case then all small rhyssine species would have short stout abdomens, and all large species would have long thin abdomens. Although *Megarhyssa* species are often large, the pooled plot of fore-wing length versus gastral shape (fig 6.23C) shows several large species with stout gasters. In any case, the ability of a male to reach down into an egress tunnel does not just depend on his body size, but also on the body size of the emerging female. A small male could inseminate a small female and *Rhyssella*, as a relatively small species with relatively small largest males, bears this out - it still shows a scramble competition system.

#### 6.11.2. Intruder male numbers

The clearest explanation of the differences observed in these polygynous mating systems relate to the number of competing males at an emergence site (*intruder males* see Thornhill & Alcock, 1983). If the females are easily locatable but patchily distributed in space (Orians, 1969) then the following ought to apply:

(a) intruder male numbers high, therefore operational sex ratio high. Large males unable to monopolise emerging females. Males race to be first to an emerging female. *Scramble competition system*. (Emlen & Oring, 1977; Thornhill & Alcock, 1983)

(b) intruder male numbers low. Large males able to monopolise emerging females. Males guard emergence sites. *Female defence system* (Thornhill & Alcock, 1983).

This may tie in with some ecological factors relating to the differences between temperate and tropical ecosystems. In the tropics conspecific host tree species are present at very low densities (Whitmore 1975), and therefore a rhyssine's hosts (assuming they are host specific or oligophytophagous) will be at low densities. This implies that both males and female rhyssines will be at low operational frequencies, assuming, as was found in *Megarhyssa* (Heatwole & Davies, 1965) that the species have a roughly defined home range. As so few males are about within the specific home range of any individual male, it will be possible to defend each female emergence, without being swamped by intruders.

In the temperate regions, trees are far more often distributed as monospecific stands. Rhyssine hosts are therefore much more clumped in distribution and so will be rhyssine parasitoids. In addition, temperate regions are strongly seasonal, meaning that all emergences will be concentrated over a fairly short period, annually, and male and female parasitoids will be at higher densities over that period. This should mean that intruder male numbers are greater than in tropical regions (although this oversimplifies the situation in tropical ecosystems somewhat; where there may be a highly complex seasonality in arthropod numbers (Maclure, 1978)). The observations made on *Lytarmes maculipennis*, however, showed an intruder male number only a little under the average for the three sympatric American *Megarhyssa* species (*Lytarmes* numbers, 4-6; average number from Crankshaw & Matthews (1981) for *Megarhyssa*, 6.6). From one observation it is not possible to judge whether this is a usual

number of males. However, it may not be the average number of males in an aggregation that is important but the maximum number.

The presence of single species stands and seasonal peaks in numbers of emerging adults may lead to the presence of large numbers of intruder males. The important thing here may not be the number of intruder males at any one site but the time factor. If females are emerging over a long period of time and are very patchily distributed then it may pay a male to concentrate on one particular log and guard that, as (a) there will be relatively few intruder males about at any one time; and, (b) searching for another source of emerging females will be unprofitable, as the transit times may become uneconomical.

If this is the case then there should be a clear partitioning of mating systems between temperate and tropical zones. Fig 6.30 shows the distributions of gastral shapes in the two zones. This is based upon measurements of the largest males of each species as they will be the specimens which show the size-related shape changes most clearly. It can be seen that there is some tendency for the temperate region species to have longer and thinner gasters than tropical ones. However, there are some problems with this interpretation. First, *Rhyssa* species do not have long thin gasters, and they are predominantly temperate species. This is probably explained by the fact that they are all species using *post*-emergence scramble competition systems. Hence, although they do not show the characteristic abdominal modifications they may still be responding to similar environmental influences. Second, there are several species of *Megarhyssa* with long thin gasters in the tropics. However, the hosts of tropical rhyssines are not known, let alone their relative densities in a forest.

The most likely explanation is that *Megarhyssa* is a holophyletic group that has specialised on hosts that are at fairly high densities, <sup>wh-</sup>ether they be in polyphagous hosts in the tropics or oligophagous hosts (siricids) in temperate regions. Under these circumstances the evolution of a pre-emergence scramble system has been selectively favoured. In contrast, the tropical rhyssine groups

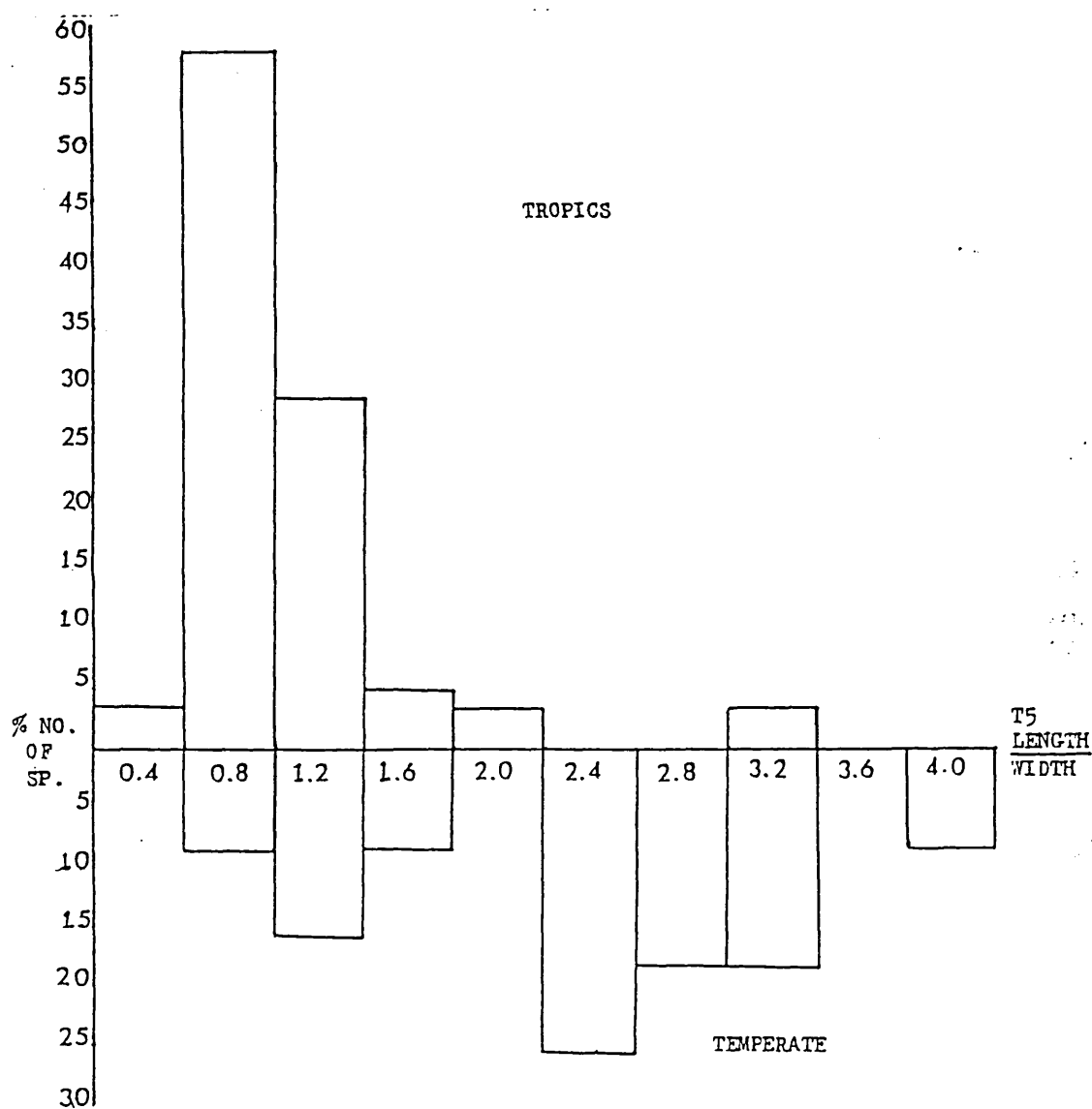


Fig 6.30. Histogram of largest male gastral tergite 5 shape, for tropical ( $0^{\circ}$ - $30^{\circ}$  N & S) and north temperate ( $> 30^{\circ}$  N) latitudes.

may have specialised upon hosts that are at a fairly low density, and there has been no strong selective pressure to develop pre-emergence scramble competition systems. It is presumed that they will be adopting female defence systems under these circumstances. Hopefully, as more data are collected about these insects' host preferences, these questions will be answered.

### 6.11.3. Mimicry complexes

Another factor which could be important in shaping mating system evolution is differences in predator pressure between temperate and tropical regions. In the tropics predators are much more common than in temperate regions (Gauld 1987b), and mimicry complexes are very common. There are reasons to believe that there may be strong selective pressure on rhyssines to be involved in mimicry complexes. This is due to the peculiarly vulnerable position of ovipositing female and aggregating males. Females may take hours to oviposit (see chapter 5) and males move only reluctantly when in aggregations (as observed in *Lytarmes maculipennis*). If this is the case then rhyssines may be somewhat limited in the shapes and sizes they take up by the need to be part of a mimicry complex. This limitation in size and shape may then lead to a limitation in terms of adopted mating strategies. How does the evidence fit this idea?

Most tropical rhyssines are, indeed, part of mimicry complexes. Nearly all Oriental *Sychnostigma* species are mimics of polistine vespids; and Neotropical *Epirhyssas* are almost all polistine vespid mimics, or mimics of odiferous braconids (Porter, 1978). In contrast most tropical *Megarhyssa* species are braconine mimics, while *Myllenyxis* species tend to be rather drab, often black, insects, although they are occasionally vespid mimics.

Temperate rhyssines tend to be comparatively drabber although they often have yellow spots or bands on the gastral tergites, especially on the sides of the tergites. They do not form part of clear mimicry complexes as do many tropical rhyssines (Porter, 1978).

These observations do not necessarily support the theory. First, it is not obvious which groups are really part of mimicry complexes. Although temperate rhyssines are often black with no markings, some are quite strikingly marked, and it is not clear whether this some form of flash colouration, or due to mimicry. Being unable to decide exactly when the effect might be taking place is unfortunate. Second, although the observations are somewhat in agreement with the theory, there is no way of testing it. Long thin rhyssines are mimics of long thin models (tropical *Megarhyssa* species and tropical braconines), and short stout rhyssines are mimics of short stout models (*Sychnostigma* and *Epirhyssa* and polistine wasps). So, which came first, the mating system or the mimicry?

Although predator pressure may play a part in forcing animals to adopt particular shapes, sizes and colour patterns, it is probably not an important factor here. After all, social vespids are not the only possible unpalatable models that rhyssines have exploited. There is no real reason why a scramble competition *Epirhyssa* or *Sychnostigma* species should not use a long thin model. The fact that they do not is probably only another indicator that they do not have pre-emergence scramble competition mating systems.

#### 6.11.4. Phylogenetic constraints

It may be the case that the ancestral *Megarhyssa* species evolved a pre-emergence mating system that has, in subsequent descendant species, become an absorbing state, due either to a lack of genetic variability or a low mutation rate (Bull & Charnov, 1985). If this is the case then *Megarhyssa* species should show the same behavioural mating repertoire regardless of the number of intruder males present at each emergence site, as the mating system will be independent of ecological factors. This would mean that the evolution of a pre-emergence scramble competition system has become a phylogenetic constraint (or an example of *canalisation* (Waddington,

1957)), overriding the adaptive pull of changing ecological factors.

Recently, several authors have pointed out the importance of a species evolutionary history in constraining its subsequent evolution (Gould & Lewontin, 1979; Ridley, 1983, 1985). Several studies have also used cladistic analyses to locate where phylogenetic constraints may be acting (Clutton-Brock & Harvey, 1977, 1984; Ridley, 1983). It is worth looking at Ridley's methods in a little more detail. They involve superimposing biological data onto existing cladograms to see how many times a particular feature may have evolved. This provides an *ad hoc* method for deciding where whole holophyletic groups may have a particular biological feature in common, and thus to an indirect idea of where phylogenetic constraints may be occurring. Can these methods be used here?

Following Ridley's methods it would have to be assumed that the pre-emergence scramble system has evolved at least twice in rhyssines (see figs 6.11, 6.12, where species with the male abdominal modifications are separated into two parts of the tree). However, in this case, the male abdominal characters turned out to be more compatible with the other characters in the data set than the characters which split the species possessing them into two. Therefore the assumption must be made that the male gastral characters are good phylogenetic markers. By definition this means that they are postulated to have evolved only once. This indicates a flaw in Ridley's method. Unless the cladograms he has chosen are very well resolved there always exists the possibility that the biological feature he is investigating may be more compatible with the other characters in a character set than some of the characters which make up the cladogram he uses. Under these circumstances the estimate of the number of times a biological character state has evolved would be invalid.

Here, the evidence points towards the scramble competition system having evolved only once. Whether this is because it is correlated with a particular host-preference of *Megarhyssa* or due to an absorbing state is not clear. It is perhaps best to assume the former

is true until real evidence is accrued that shows *Megarhyssa* species adopting scramble competition systems under conditions where other rhyssines are adopting different systems.

#### 6.12. Alternative male strategies

Several workers (Yasumatsu, 1937; Crankshaw & Matthews, 1981; Thompson, unpublished data) have reported the existence of an alternative strategy by small *Megarhyssa* (including *Rhyssella*) males at emergence sites. They wait for females to emerge and attempt to copulate with them. Crankshaw & Matthews (1981) report that coupling followed 31% of aggregations where a female emerged undisturbed, although no figures are available for how successful these couplings are. The presence of this alternative strategy is interesting in that a body of literature has built up about these types of strategies (reviewed in: Thornhill & Alcock, 1983; Krebs & Davies 1981; Austad, 1984).

Most satellite strategies involve males that show "sneaky" mating. That is, they find a way to reach the female before a larger and more aggressive male can fertilise her. There are many examples of this, including, gobioid fish (Miller, 1979), bluegrass sunfish (Gross & Charnov, 1980), bees (Alcock *et al*, 1977; Severinghaus *et al*, 1981), frogs (Howard, 1978), chalcid wasps (King *et al*, 1969), and even large mammals such as elephant seals (Le Boeuf, 1974). Small males are normally at a disadvantage in interactions with larger males and therefore adopt these sorts of strategies.

One of the most important aspects of satellite strategies is that in order to persist within a population they must be *evolutionarily stable strategies* (Maynard Smith, 1974). This implies that they are normally under genetic control, and that the gene for the satellite strategy results in an identical fitness in satellite individuals as in ordinary individuals. The logic of this is simple - if a gene for the satellite strategy produces less fitness in an individual then it's frequency in the population will inevitably reduce generation by

generation, until it disappears altogether. At least one alternative mating strategy has been shown to be under genetic control (Cade, 1979). An alternative mating strategy is often assumed to be an evolutionarily stable strategy due to a trade off between the cost of aggressive interactions with other males, and the loss of mating opportunities caused by not being aggressive (Gadgil, 1972).

In the case of *Megarhyssa* species, however, this is unlikely to be the case. This is because there is a positive correlation between host size and resulting adult size in parasitic Hymenoptera (Gauld & Bolton, 1988). This means that size is, at best, only partially genetically controlled. In rhyssines this implies that a gene for a small male post-emergence mating strategy would be very unlikely to become established in a population. This is because any such gene would be shuffled at random between different sized males in different generations. If it arose in a small male then it might be effective in terms of the number of offspring that male produces, but in subsequent generations it stands as good a chance of ending up in a large male, where it would have a deleterious effect. This is especially true as post-emergence copulation is probably extremely difficult for a large male, and certainly small agile males would have a selective advantage (Crankshaw & Matthews, 1981) in a competition with a large male which had the gene for post-emergence mating. Hence, the disruptive effect of host-size related body lengths is likely to mean that the alternative strategy is not genetically controlled. It seems likely instead that males are employing a strategy based upon judging their ability to compete with other males. In this scheme large males would learn quickly that they can race for females, while small males find that they cannot. This sort of conditional strategy (Alcock, 1979) probably also occurs in the pompilid wasp *Cryptocheilus* (Day, 1984; pers comm) and in other species with runt (kleptogamous) males (reviewed in, Krebs & Davies, 1981).

One way to look indirectly at whether small size is genetically controlled is to look to see whether there is a bimodal frequency distribution in size. This is certainly the case with certain

chironomid and chaoborid midges (McLachlan 1986; McLachlan & Allen, 1987, McLachlan & Neems, 1989) where there is a definite secondary frequency peak in the smallest size class of males. However, there is no such secondary frequency peak in either of the two species where reared material (which seems the closest available approximation to a random sample) was available: *Rhyssa persuasoria* and *Rhyssella approximata*. In both cases the frequency histograms fitted a normal curve (for *R. approximata*  $p > 0.9$  in a Kolmogorov-Smirnov test of goodness of fit (Sokal & Rohlf, 1969); for *R. persuasoria*  $p > 0.25$  in a Kolmogorov-Smirnov test) and neither show a clumping of distribution at the smallest size classes.

The major factor influencing the production of small males is probably the inefficiency of female drilling (which seems to be around 10%; Kazmierczack, 1981, see chapter 5). Therefore, it is likely that an egg is laid whenever a host is encountered, whatever its size (Hanson, 1939). In this case very small males with extremely low fitness may result. These 'disposable males' may be adopting a conditional strategy simply to make the best of a bad thing. Females may be following a simple rule of - lay an egg if anything is there, lay a female if the host is above a certain size (and females do tend to be larger than males, see above). In certain Aculeate Hymenoptera it has been shown that the amount of provisioned host (in this case the parental investment) influences the mating system of the offspring (Alcock *et al*, 1977), and this seems to be an analogous situation to the rhyssine one. In the rhyssine case, however, the amount of provisioned host (so to speak) is unknown before the parental investment occurs (i.e. the drilling effort).

One of the features of this system which may have caused a size-linked size gene to evolve is an energetic one. McLachlan (1986) has shown that small males of chironomid midges have reduced energy reserves and flying ability. It may be that it is energetically cheaper to produce small males with short abdomens than small males with long, thin abdomens. It could be this limit in resources that is one of the factors that has led to the development of this size-variation.

### 6.13. Evolutionary Biology and Biogeography

With these insights into the evolution of the group some provisional comments can be made about how the group may have evolved its biological features and how it may have taken up its present distribution. The biological evidence, is at present rather flimsy, but hopefully these conjectures will provide a framework for future studies.

#### 6.13.1. Present day distribution of holophyletic groups

The distribution of the various holophyletic groups is shown in figs 6.31 to 6.35. Included with these is the distribution of the possibly paraphyletic grouping *Epirhyssa/Sychnostigma/Triancyra*. The following patterns emerge:

(a) *Rhyssa* has a alpine-boreal distribution with some populations at low altitudes further south (fig 6.31). All *Rhyssa* species are parasitoids of siricid woodwasps in Pineaceae. This would seem to be the primitive state. The distribution shown in the map is a rather poor representation of the actual range of the genus. In the literature its distribution has been rather poorly described, especially from the north of the USSR (Meier, 1934, for example, refers to its distribution as "east to Sakhalin"). Most of the distribution information comes from the BMNH collections, with some data from Spradbery & Ratkowsky (1974), Townes & Townes (1960), and Townes et al (1965).

(b) *Megarhyssa* (including *Rhyssella*) inhabits the whole of the northern temperate region, with outliers in tropical Africa and the Oriental region. It does not extend down into the Neotropical region (fig 6.32). Two species of *Megarhyssa* (*M. emarginatoria* and *M. nortoni*) are parasitoids of siricids in Pinaceae. The remaining temperate species are parasitoids of Siricoidea in angiosperm trees.

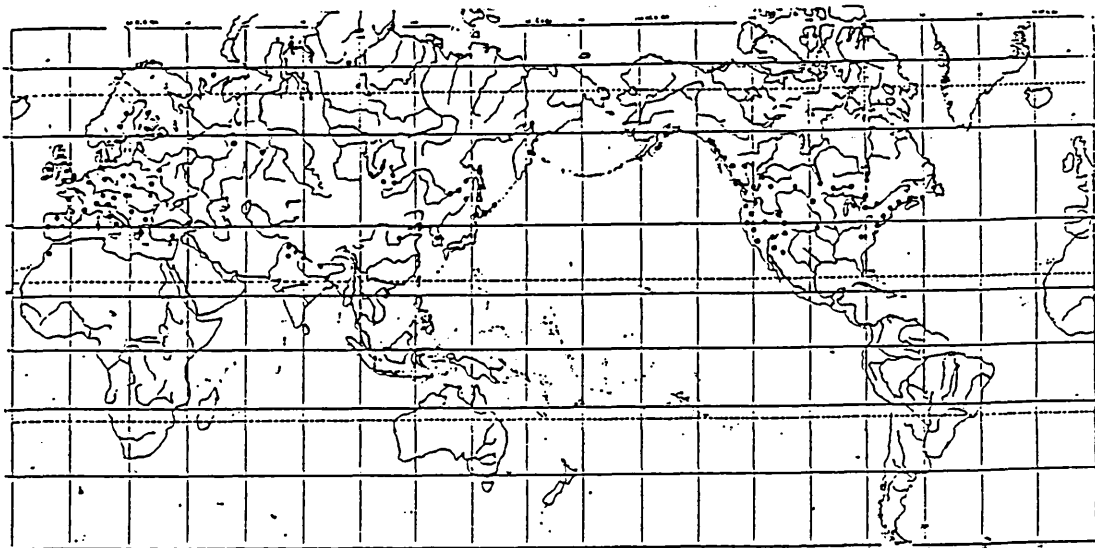


Fig 6.31. Distribution of *Rhyssa*.

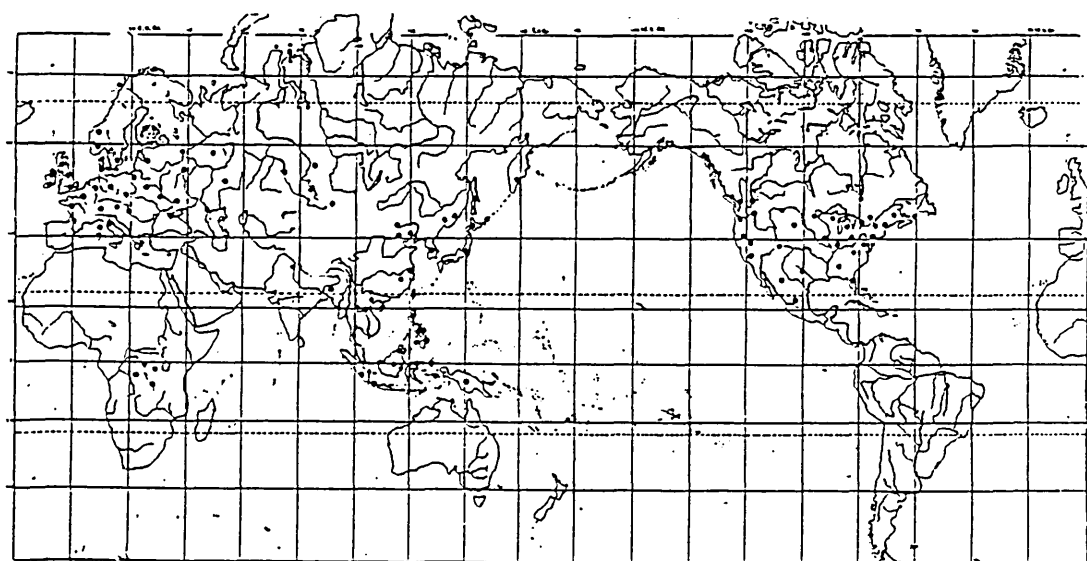


Fig 6.32. Distribution of *Megarhyssa*.

The hosts and host plant preferences of the tropical species are unknown. Much of the distribution information comes from the BMNH collections, with some data from Townes & Townes (1960), Townes *et al* (1965) and Deyrup (1985).

(c) *Lytarmes* (including *Cyrtorhyssa mesopyrrha*) is entirely Oriental in its distribution (fig 6.33), ranging from Burma in the north-west to The Solomon Islands in the south-east. Its hosts and host plant preferences are unknown. The distribution information comes from the BMNH collections and Kamath & Gupta (1972).

(d) The paraphyletic genus *Epirhyssa* (consisting of the genera *Sychnostigma*, *Epirhyssa*, *Triancyra* and *Cyrtorhyssa moellerii*) is pantropical in its distribution (fig 6.34). The distribution of the tentative species-groups have not been indicated, as any patterns produced are likely to be artifactual. The most strongly supported holophyletic group, the *scabra* species-group, is generally sympatric with the other Oriental *Epirhyssas* except that its westwards range extends to southern India and Sri Lanka. The *speciosa*-group is confined to the Neotropics, but there is a suspicion that it is partially defined by its geographical distribution. All the other species-groups are confined to the Oriental region, with the exception of a handful of species in equatorial Africa, South Africa and one species in Madagascar. The African species are very close to the Indo-Malesian species, and in the phylogenetic analysis were split into several of the putative species-groups. The distribution information comes from Seyrig (1927, 1932); Benoit (1951, 1952); Townes *et al* (1965); Kamath & Gupta (1972); Townes & Townes (1973); Porter (1978).

(e) *Myllenyxis* (fig 6.35). This highly derived rhyssine has a distribution almost identical to *Lytarmes*. It is not found outside the belt of ever-wet forest in Indo-Malesia.

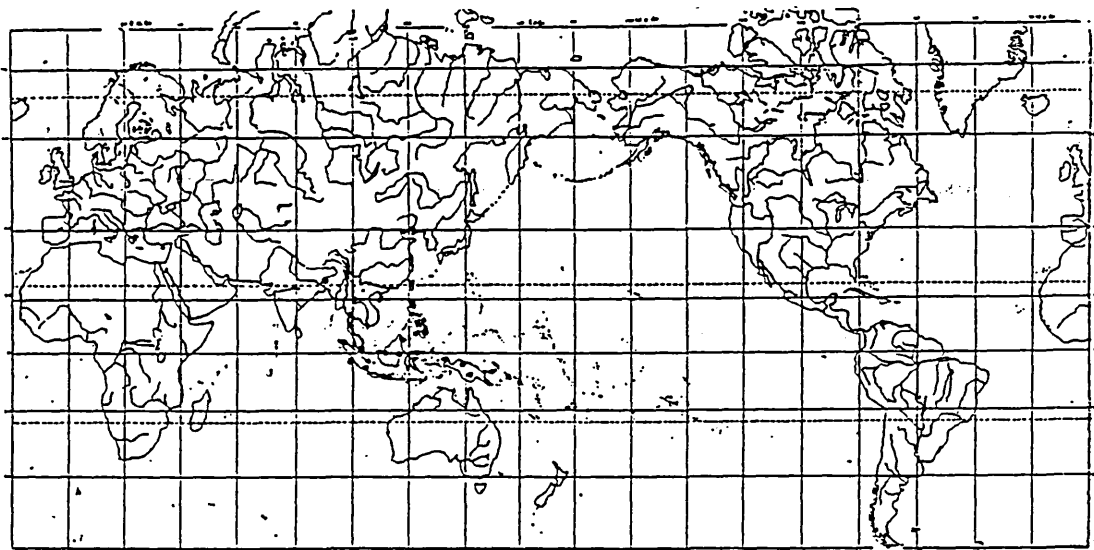


Fig 6.33. Distribution of *Lytarnes*.

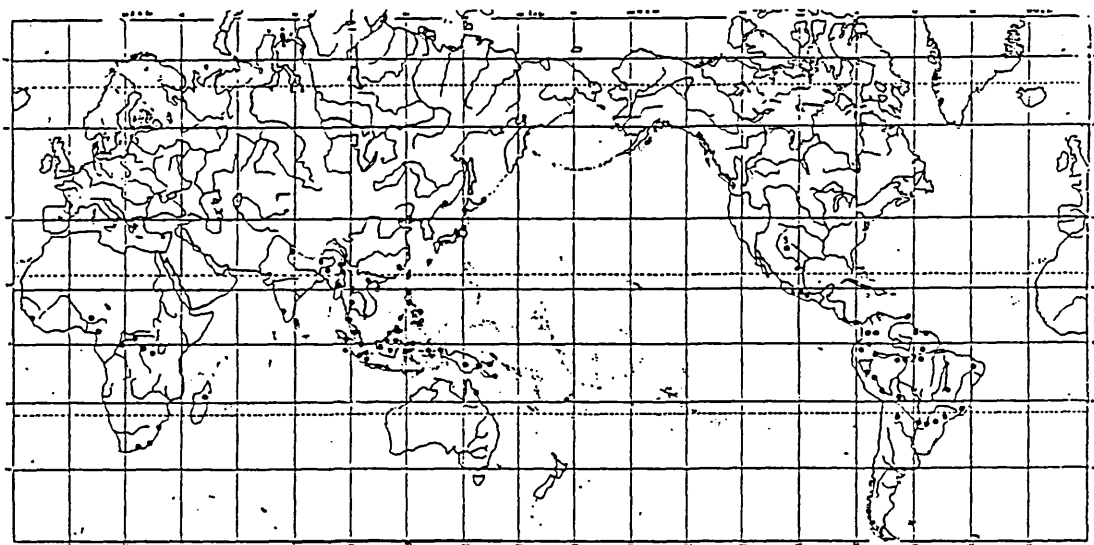


Fig 6.34. Distribution of *Epirhyssa*.

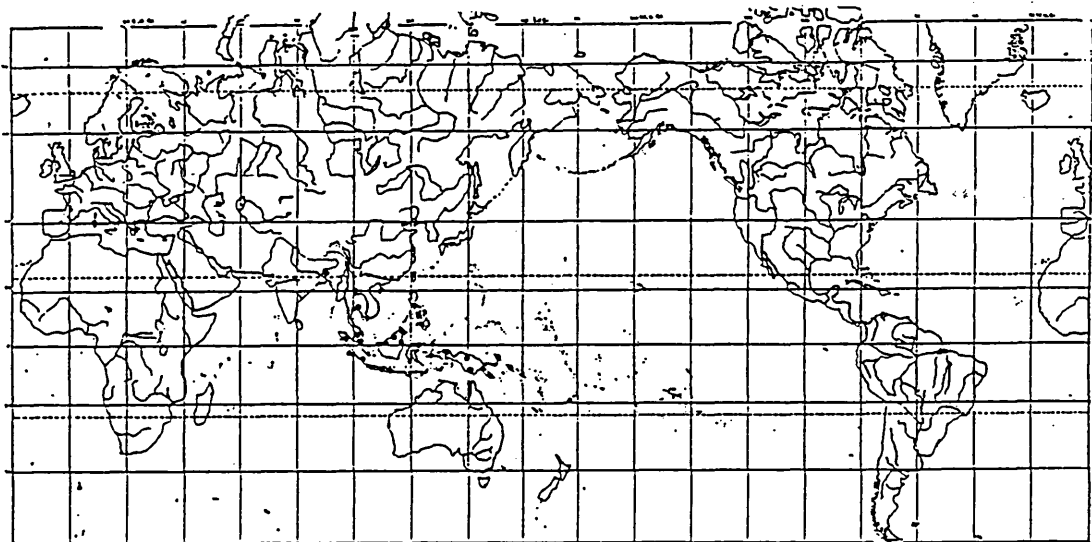


Fig 6.35. Distribution of *Mylennyxis*.

### 6.13.2. The evolution of the Rhyssinae: a speculative scenario

A few putative fossil rhyssines have been described (Scudder, 1890; Brues, 1906) but, from the descriptions, none, can confidently be assigned to the Rhyssinae. For this reason a consideration of their origins and biogeographical history must be from indirect sources. These sources are:

- (a) Phylogenetic analyses of the group (see above).
- (b) Biogeography and phylogeny of hosts.
- (c) Biogeography and phylogeny of host plants.
- (d) Plate tectonics and Palaeoclimateology.

### 6.13.3. Background

1. The earliest fossils of the only reliably recorded rhyssine host group, the Siricoidea, are from the Lower Jurassic (200 mya) (Rasnitsyn, 1980). They subsequently radiated widely, presumably upon arborescent gymnosperms. Some group ancestral to the Pineaceae seem likely to have been the probable host plant group, and it may very well have been the contemporaneously diverse family the Voltziaecae (Miller, 1982). The continents were at this time still joined together as a single land mass (Pangeae) (Howarth, 1981) and the siricoid and conifer distributions were probably pan-global (Miller, 1977).

2. The Pineaceae began their major radiation in the early Cretaceous (135mya), and are the most recently evolved of the Coniferales (Miller, 1976). Their present distribution and fossil record indicates that they must have appeared after the break-up of Pangeae, in the northern continent Laurasia. At this point one group of siricoids (the Siricinae) seem to have switched to this host plant group, where they have remained specialised to the present (Benson, 1942; Smith, 1978).

During the early Cretaceous pines were beginning to form a major part of the tree flora throughout the Northern Hemisphere (Miller, 1977).

3. During the mid-Cretaceous, angiosperms began their primary radiation, possibly as a response to change from a rather dry to a wetter climate (Upchurch & Wolfe, 1987). The angiosperms are likely to have evolved in low palaeolatitudes (Brenner, 1976; Hughes, 1976) and spread polewards (Axelrod, 1959). Flenley (1979) showed how angiosperm pollen diversified between the late Cretaceous (Senonian) and the Quaternary. The result of this was the very slow out-competition of Gymnosperms, and a reduction in the range of the Pineaceae into relict northern and high altitude habitats. Two separate lines of the *Siricoidea* are found on angiosperms - the *Tremicinae*, clearly close to the *Siricinae* (Benson, 1942); and the *Xiphydriidae*, which represent a rather divergent group of siricoids (Rasnitsyn, 1980).

4. At the beginning of the Eocene period the climate was isothermal and much warmer. Non-seasonal forests communities were present from palaeolatitudes 32°N to 32°S (Creber & Chaloner, 1985). Indeed, humid sub-tropical broad-leaf forests stretched up to high latitudes (Reid & Chandler, 1933; Dilcher, 1973) across the whole of Laurasia (Parrish, 1987). By this stage, North America was moving away from Eurasia, as the Atlantic expanded; South America was close to or in contact with North America; and the Gondwanic Australian plate (Sahul shelf) was approaching the Laurasian Indo-Malesian plate (the Sunda shelf) (Howarth, 1981). Subsequently the climate became colder and much less isothermal, this caused the shrinkage of the sub-tropical high latitude forests and their replacement by the typical low diversity broad-leaf forests of the present day (Upchurch & Wolfe, 1987).

This information allows some speculations to be made about the historical biogeography and palaeoecology of the rhyssines. The rhyssines are split into 5 groups, one of which (*Epirhyssa*) has not been proven to be holophyletic (see above).

Fig 6.36 shows a simplified area cladogram (tree) with distributions shown with the genera (defined above) on the cladogram.

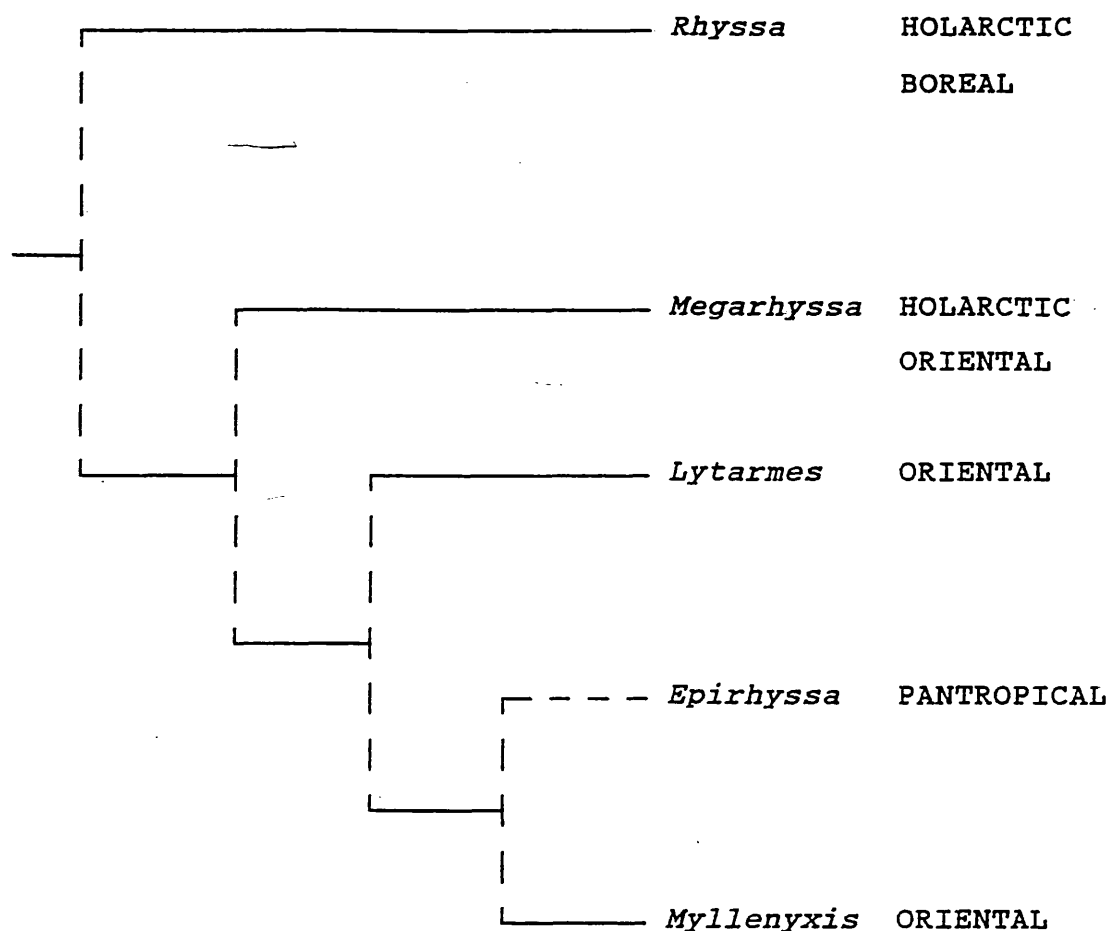


Fig 6.36. Simplified area tree diagram (area cladogram) for the Rhyssinae (genera as suggested in section 6.10.1). *Epirhyssa* is connected to the rest of the tree by a dotted line as it is probably a paraphyletic group.

#### 6.13.4. *Rhyssa*

*Rhyssa* is clearly the most primitive extant rhyssine group, and its species are all parasitoids of Siricinae on Pineaceae. This suggests, at the latest, an early Cretaceous origin for the rhyssines. Clearly, the Rhyssinae could be a much older group, and may have evolved in the Middle Jurassic fairly soon after the origin of the Siricoidea. However, it is probable that a *Rhyssa*-like ancestor was a parasitoid of siricines. The biogeographical history of *Rhyssa* can be imagined to be congruent with that of the Pineaceae. As the pines shrunk back to the alpine-boreal region so did *Rhyssa*, leaving a relict distribution (fig 6.31).

The present day *Rhyssa* species most probably all have male post-emergence scramble systems. This is likely to be due to the highly seasonal low diversity forests in which they live. Not enough is known about the community structure of Middle Cretaceous pine forests, to judge whether this mating system was secondarily derived after *Rhyssa* arrived in high boreal forests, or was derived within the primitive coniferous forests. Why *Rhyssa* has not evolved a pre-emergence scramble system while the two sympatric *Megarhyssa* species have, is unclear.

It is interesting to note that *Rhyssa* species are living in a fairly arid environment, and that the Cretaceous pine forests were probably much drier than the present broad-leaf forests. This tends to suggest that the normal habitat of the majority of rhyssines, humid forests, is a secondarily derived adaptation. This is the opposite conclusion to that reached by Porter (1978) who implies that *Rhyssa* is a rather advanced genus.

#### 6.13.5. *Megarhyssa*

*Megarhyssa* species (including *Rhyssella*) are parasitoids of the two angiosperm-associated siricoid lineages (xiphydriids and tremecines). They are associated with high density hosts in low diversity forests,

excepting the few species found in the Palaetropics, where the hosts are unknown. They are all presumed to show pre-emergence scramble competition systems in the reproductive behaviour<sup>a</sup> of the males. Two scenarios are postulated for their evolution:

(a) *Megarhyssa* species appeared early in the evolution of angiosperms, and followed tremecines or xiphydriids onto broad-leaf trees. The early angiosperm communities were not as diverse as the present ones (Upchurch & Wolfe, 1987), and it is possible that the distinctive abdominal morphology was evolved in this relatively depauperate environment, where early angiosperm trees were at much higher conspecific densities. In a similar way to *Rhyssa*, as angiosperm diversity increased *Megarhyssa* species would be pushed northwards, as their host resources became more partitioned. The populations in the Palaetropics can then be considered as relicts, possibly pre-adapted to rather polyphagous hosts.

(b) *Megarhyssa* species evolved as a response to the lower diversity North temperate forests that began to appear from the end of the Palaeocene. The lower diversity and seasonality of these forests would lead to large numbers of intruder males during the emergence season, and therefore selective pressure on males to develop scramble competition modifications. The present Palaetropical species are then considered as recent migrants, adapted to rather polyphagous host groups or to oligophagous host on a high conspecific density tree species. This is only a slight modification of Porter's (1978) hypothesis which suggests that *Megarhyssa* species evolved as a response to changing environmental conditions. It seems the most likely of the two hypotheses, especially given the present degree of uncertainty about the speed of diversification of early angiosperm evolution (Hughes, 1976). In addition, the absence of *Megarhyssa* species in South America tend to suggest a northern rather than an equatorial origin.

The morphological changes observable between a *Rhyssa*-type ancestor and the ancestral *Megarhyssa* were very great (see cladograms in earlier part of this chapter). This change may very well be due to a

change from gymnosperm to angiosperm wood. However, only two of the characters involved (position of the sternal ovipositor guides and fusion of gastral sternite 1 and tergite 1) even remotely suggest a difference in oviposition behaviour. And, if this is the case, then at least two *Megarhyssa* species have returned to pines (*M. emarginatoria* and *M. nortoni*).

Another problem which needs addressing relates to the hosts of tropical *Megarhyssa* species. They are unlikely to be tremicines or xiphydriids as these are relatively rare in the tropics (Benson, 1943, 1952). It seems most likely that they have switched to wood-boring beetles, and it would be interesting to discover what groups they now exploit and at what densities they occur.

#### 6.13.6. *Lytarmes*

This holophyletic group occupies an intermediate position between *Megarhyssa* and *Epirhyssa*. Interestingly, it has an almost identical distribution to *Myllenyxis* (see above). It may be a specialised *Megarhyssa* which has lost its male gastral modifications since dispersing to the Oriental tropics (supporting explanation (b) above), or it may be a separate lineage which has evolved fairly recently. The latter possibility fits in with the position of *Lytarmes* in the final tree. It seems likely that the group evolved in the South Laurasian area (which is now Indo-Malesia) and has not spread significantly since then.

#### 6.13.7. *Epirhyssa*

This paraphyletic group consists of a number of species-groups which are presumed to be among the most recently evolved in the subfamily. It is possible that they evolved in tropical palaeolatitudes in parallel with the greatest diversification of the angiosperms (perhaps as recently as the late Eocene). None of the studied species show the male abdominal modifications associated with a scramble competition mating system. This is compatible with the idea that they

have evolved in a very diverse tropical forest environment, where female emergences are very patchily distributed, and there is little seasonality. It is likely that the group spread across the Laurasian sub-tropical forest and formed a single faunal element in Eocene times. With the establishment of a connection between South and North America in the late Eocene-Oligocene (Parrish, 1987; Howarth, 1981) *Epirhyssa* will have dispersed into the southern continent. This would make the South American *Epirhyssa* species (the *speciosa* species-group) only around 25-30 million years old and probably only as old as the Bombini (Williams, 1985), a group which might intuitively be considered to be far more recent. Porter (1978) gives an account of the possible subsequent evolution of the group within South America while suggesting a somewhat earlier arrival of the group to South America.

The later biogeographical history of *Epirhyssa* can be seen as series of vicariance events (Nelson & Platnick, 1981). The gradual shrinking of the tropical forests, in response to the cooling of the climate, left the three Holocene tropical regions isolated. This isolation must be considered a fairly recent event, and this is supported by the closeness of the rhyssine taxa in the three regions. With the collision of the Laurasian Sunda and Gondwanic Sahul shelves (Whitmore, 1985) a dispersal route opened up into New Guinea and Australia; a route which has been followed by a few rhyssines.

Porter (1978) suggested that the *speciosa* species-group might originate in West Gondwanaland. This seems unlikely for the following reason. The most primitive extant rhyssine (*Rhyssa*) is associated with the Pinaceae, which implies, that the advanced rhyssines are polyphyletic, the *speciosa* species-group having evolved separately from the other rhyssines since the break-up of Pangeae (about 150 mya). This could only be accepted if: (a) *Epirhyssa* were very divergent from all the Laurasian rhyssines, which it clearly is not, or; (b) the reconstructed rhyssine tree is the wrong way up, and *Epirhyssa* is the least derived genus. In fact, Porter (1978) implies that the second of these possibilities is likely. However, the cladistic analysis performed in this study indicates that *Rhyssa* is

the most primitive genus and therefore it is reasonable to assume that the whole group is Laurasian in origin.

#### 6.13.8. *Myllenyxis*

*Myllenyxis* is the most derived rhyssine and is confined to the Oriental tropics. It may have evolved since the break up of the tropical forest masses in the Middle Tertiary. It seems again to have a male gastral shape associated with low density hosts, although some species have males with rather more elongate abdomens ( a specimen collected in New Guinea (probably close to *Myllenyxis bernsteinii*) shows an elongated gaster, although it does not have either of the two characters defining *Megarhyssa*).

#### 6.13.9. General Conclusions

The rhyssines appear to have evolved in Laurasia in early Cretaceous times as parasitoids of siricoid wood-wasps in pines. Their subsequent evolutionary history seems to have been characterised by 4 main events.

1. The evolution of angiosperm dominated plant communities and the shift from gymnosperm-associated to angiosperm-associated hosts.

2. The diversification and spread of non-seasonal high diversity angiosperm forests to high palaeolatitudes with a concomitant spread of rhyssines across Laurasia.

3. The gradual cooling of the climate leading to the shrinking of non-seasonal forests. Possible subsequent evolution of a group adapted to the newly emerging strongly seasonal, high density forests (*Megarhyssa*). Emergence in Oriental region of both *Lytarmes* and *Epirhyssa*.

4. The vicariance of the pan-Laurasian non-seasonal forest belt into three main parts. *Epirhyssa* species remaining in the three blocks. Radiation of *Myllenyxis* in the Oriental region.

## REFERENCES

- Abbott C.E. 1934. Anatomical modifications associated with the oviposition of *Megarhyssa lunator*. *Bulletin of the Brooklyn Entomological Society* 29:39-41
- Abbott C.E. 1935. Modifications in the genitalia of the male *Megarhyssa lunator*. *Bulletin of the Brooklyn Entomological Society* 30:11-13
- Abbott C.E. 1936. On the olfactory powers of *Megarhyssa lunator* (Hymenoptera; Ichneumonidae). *Entomological News* 47: 263-264
- van Achterberg C. 1986. The oviposition behaviour of parasitic Hymenoptera with very long ovipositors (Ichneumonidae: Braconidae). *Entomologische Berichten* 46: 113-115
- van Achterberg C. 1987. Revision of the European Helconini (Hymenoptera: Braconidae: Helconinae). *Zoologische Mededelingen*, 61(18): 263-285.
- Alcock J. 1979. The evolution of intraspecific diversity in male reproductive strategies in some bees and wasps. In, Blum M.S. & Blum N.A. *Sexual Selection and Reproductive Competition in Insects*:391-403. Academic Press, New York.
- Alcock J., Jones C.E. & Buchmann S.L. 1977. Male mating strategies in the bee, *Centris pallida* (Hymenoptera: Anthophoridae). *American Naturalist* 111:145-155.
- Arthur A.P. & Wiley H.G. 1959. Effects of host size on sex ratio, development time and size of *Pimpla turionellae* (L.) (Hymenoptera: Ichneumonidae). *Entomophaga*, 4:297-301
- Ashlock P.H. 1971. Monophyly and associated terms. *Systematic Zoology*, 20:63-69.

- Ashmead W.H. 1900. Classification of the ichneumon-flies, or the superfamily Ichneumonoidea. *Proceedings of the United States National Museum* 23: 1-220
- Aubert J.F. 1969. *Les ichneumonides ouest-palaearctiques et leurs hôtes. 1. Pimplinae, Xoridinae, Acaenitinae*. Paris.
- Austad S.N. 1984. A classification of alternative reproductive behaviours and methods for field-testing ESS models. *American Zoologist*, 24:309-319.
- Austin A.D. 1985. The function of spider egg sacs in relation to parasitoids and predators, with special reference to the Australian fauna. *Journal of Natural History*, 19:359-376.
- Axelrod D.I. 1959. Poleward migration of early Angiosperm flora. *Science* (New York), 130: 203-207.
- Baltazar C.R. 1961. The Philippine Pimplini, Poemeniini, Rhyssini and Xoridini (Hymenoptera, Ichneumonidae, Pimplinae). *Monograph of the National Institute of Science and Technology, Manila*. 7
- Barlin M.R. & Vinson S.B. 1981. Multiporous plate sensillae in antennae of the Chalcidoidea (Hymenoptera). *International Journal of Insect Morphology and Embryology* 10 (1): 29-42.
- Barlin M.R., Vinson S.B. & Piper G.L. 1981. Ultrastructure of the antennal sensilla of the cockroach-egg parasitoid, *Tetrastichus hagenowii* (Hymenoptera: Eulophidae). *Journal of Morphology*, 168:97-108
- Barlow J. 1921. The mating habits of *Megarhyssa*. *Entomological News* 32: 291.
- Barrett R.E. 1932. Notes on a new parasite of the codling moth. *Journal of Economic Entomology*, 25:1111.

- Beirne B.P. 1941. A consideration of the cephalic structures and spiracles of final instar larvae of Ichneumonidae. *Transactions of the Society for British Entomology*, 7:123-190.
- Benoit P.L.G. 1951. Les Rhyssini Ethiopiens (Pimplinae - Ichneumonidae). *Revue Zoologique Botanique Africaines* 44:382-385
- Benoit P.L.G. 1952. Notes Ichneumonologiques Africaines (II). *Revue Zoologique Botanique Africaines* 46:51-59
- Benson R.B. 1942. Studies in Siricidae, especially of Europe and Southern Asia (Hymenoptera, Symphyta). *Bulletin of Entomological Research*, 34(1):27-51.
- Benson R.B. 1953. Classification of the Xiphydriidae (Hymenoptera). *Transactions of the Royal Entomological Society of London*, 105(9):151-162.
- Bin F. & Vinson S.B. 1986. Morphology of the antennal sex gland in male *Trissolcus basalus* (WOLL) (Hymenoptera: Scelionidae), an egg parasite of the green stink bug *Nezara viridula* (Hemiptera: Pentatomidae). *International Journal of Insect Morphology and Embryology*, 15(3):129-138.
- Le Boeuf B.J. 1974. Male-male competition and reproductive success in elephant seals. *American Zoologist*, 14:163-176.
- Brenner G.J. 1976. Middle Cretaceous floral provinces and early migrations of angiosperms. in C.B. Beck (ed), *Origin and early Evolution of Angiosperms*:23-47. Columbia University Press, New York.
- Brooks R.W. & Wahl D.B. 1987. Biology and mature larva of *Hemipimpla pulchripennis* (SAUSSURE), a parasite of *Ropalidia* (Hymenoptera: Ichneumonidae: Vespidae). *Journal of the New York Entomological Society* 95: 547-552.

Brues C.T. 1906. Fossil parasitic and phytophagous Hymenoptera from Florissant, Colorado. *Bulletin of the American Museum of Natural History*, 22:491-498.

Bruzzese E. 1982. Observations on the biology of *Pseudopimpla pygidiator* Seyrig (Hymenoptera, Ichneumonidae), a parasite of the blackberry stem boring sawfly *Hartigia albomaculatus* (Stein) (Hymenoptera, Cephidae). *Entomologist's Monthly Magazine* 18:249-252.

Bull J.J. & Charnov E.L. 1985. On irreversible evolution. *Evolution* 39 (5):1149-1154.

Burdick D.J. 1961. A taxonomic and biological study of the genus *Xyela* Dalman in North America. *University of California Publications in Entomology*, 17:285-356.

Cade W.H. 1979. Alternative mating strategies: genetic differences in crickets. in Blum M.S. & Blum N.A. (eds) *Sexual Selection and Reproductive Competition in Insects*:343-379. Academic Press, New York.

Carlson R.W. 1979. Family Ichneumonidae. in Krombein K.V., Smith D.R. & Burks B.D (eds), *Catalogue of Hymenoptera North of Mexico*:1-1198. Washington.

Carton Y. 1971. Biologie de *Pimpla instigator* F. 1793. 1. - mode de perception de l'hôte. *Entomophaga*, 16:285-296.

Carton Y. 1973. Biologie de *Pimpla instigator* F. 1793. (Ichneumonidae: Pimplinae) 2. - choix d'un emplacement privilégié dans l'hôte pour le dépôt de ses oeufs; mode de localisation. *Entomophaga*, 18:25-39.

Champion H.G. 1929. Notes on the mating habits of *Rhyssa persuasoria* Linn. *Entomologist's Monthly Magazine* 65: 231-232

- Champlain A.B. 1921. The curious mating habits of *Megarhyssa atrata* (Fab.) (Hymenoptera: Ichneumonidae). *Entomological News* 32:241
- Charney T. 1947. Tertiary centres and migration routes. *Ecological Monographs*, 17:139-148.
- Cheesman L.E. 1921. *Rhyssa persuasoria*: its oviposition and larval habits. *The Proceedings of the South London Entomological and Natural History Society* (1921-1922):1-2
- Chrystal R.N. 1928. The sirex woodwasps and their parasites. *Empire Forest Journal* 7:145-154
- Chrystal R.N and Myers J.G. 1928. Natural enemies of *Sirex cyaneus* Fabr. in England and their life history. *Bulletin of Entomological Research* 19:67-77
- Chrystal R.N. & Skinner E.R. 1932. Studies in the biology of the woodwasp *Xiphydria prolongata* GEOFFR. (*dromedarius* F.) and its parasite *Thalessa curvipes* GRAV. *Scottish Forestry Journal (Edinburgh)* 46:36-51.
- Clutton-Brock T.P. & Harvey P.H. 1977. Primate ecology and social organisation. *Journal of Zoology*, 183:1-39.
- Clutton-Brock T.P. & Harvey P.H. 1984. Comparative approaches to investigating adaptation. In Krebs J. & Davies N. (eds), *Behavioural Ecology: an Evolutionary Approach* 2nd Edition:7-29. Sinauer, New York.
- Cole L.R. 1959. On the defences of the Lepidoptera pupae in relation to the oviposition behaviour of certain ichneumonidae. *Journal of the Lepidopterist's Society*, 13:1-10.

Cole L.R. 1967. A study of the life-cycle and hosts of some Ichneumonidae attacking pupae of the green oak-leaf roller moth, *Tortrix viridana* (L.) (Lepidoptera:Tortricidae) in England. *Transactions of the Royal Entomological Society of London*, 119:267-281.

Constantineau M.I. & Pisica C. 1977. Hymenoptera, familia Ichneumonidae. *Fauna Republicii Socialiste Romania: Insecta*, 9(7)

Crankshaw O.S and Matthews R.W. 1981. Sexual Behaviour amongst Parasitic *Megarhyssa* wasps (Hymenoptera: Ichneumonidae). *Behavioural Ecology and Sociobiology* 9:1-7

Creber G.T. & Chaloner W.G. 1985. Tree growth in the Mesozoic and early Tertiary and the reconstruction of palaeoclimates. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 52:35-60.

Croizat L., Nelson G. and Rosen D.E. 1974. Centers of origin and related concepts. *Systematic Zoology* 23:265-287

Curtis J. 1828. *British Entomology*, 5:plates 195-241. London.

Cushman R.A. & Rohwer S.A. 1920. Holarctic tribes of the ichneumon-flies of the subfamily Ichneumoninae (Pimplinae). *Proceedings of the United States National Museum* 57:379-396.

Danks H.V. 1971. Biology of some stem-nesting aculeate Hymenoptera. *Transactions of the Royal Entomological Society*, 122:323-399.

Davies N.W and Madden J.L. 1985. Mandibular gland secretions of two parasitoid wasps (Hymenoptera: Ichneumonidae). *Journal of Chemical Ecology* 11:1115-1127

Day M.C. 1984. Male polymorphism in some Old World species of *Cryptocheilus* Panzer (Hymenoptera: Pompilidae). *Zoological Journal of the Linnean Society*, 80:83-101.

Day W.H.E. 1983. Computationally difficult parsimony problems in phylogenetic systematics. *Journal of Theoretical Biology* 103:429-438

Day W.H.E & Sankoff D. 1988. Computational complexities of inferring phylogenies by compatibility. *Systematic Zoology* 35:224-229

Deyrup M.A. 1985. A Maple Wood Wasp, *Xiphydria maculata* and its Insect Enemies (Hymenoptera: Xiphydriidae). *Great Lakes Entomologist* 17:17-28

Dilcher S. 1973. A palaeoclimactic interpretation of the Eocene floras of South East North America. In, Graham A. (ed) *The Vegetation and Vegetational History of Northern Latin America*:36-59. Elsevier, Amsterdam and New York.

Duffield R.M. & Nordin J.H. 1970. Hibernation and the production of glycerol in the Ichneumonidae (Hymenoptera). *Nature*, 228:381.

Eggleton P. In press. The male reproductive behaviour of *Lytarmes maculipennis* (Smith) (Hymenoptera: Ichneumonidae). *Ecological Entomology*.

Eldredge N. 1979. Cladism and common sense. in Cracraft J. & Eldredge N. *Phylogenetic analysis and palaeontology*:165-198. New York. Columbia Press.

Emlen S.T. & Oring L.W. 1977. Ecology, sexual selection and the evolution of mating systems. *Science*, 197:215-233.

<sup>T.L.</sup>  
Erwin 1985. The taxon pulse: a general pattern of lineage radiation and extinction among carabid beetles. In Bull G.E. (ed.) *Taxonomy, Phylogeny and Zoogeography of Beetles and Ants*:437-472. Dr W. Junk, Dordrecht.

Estabrook G.F. 1978. Some concepts for the estimation of evolutionary relationships in Systematic Botany. *Systematic Botany*, 3:146-158.

Estabrook G.F. & Anderson W.R. 1978. An estimate of phylogenetic relationships within the genus *Crusea* (Rubiaceae) using character compatibility analysis. *Systematic Botany*, 3:179-196.

Estabrook G.F., Strauch J.G. & Fiala K.L. 1977. An application of compatibility analysis to the Blackith's data on orthopteroid insects. *Systematic Zoology*, 26:269-276.

Farris J.S. 1979. The information content of the phylogenetic system. *Systematic Zoology*, 28:483-519.

Felsenstein J. 1978. Cases in which parsimony or compatibility methods will be positively misleading. *Systematic Zoology* 27: 401-410.

Felsenstein J. 1981. A likelihood approach to character weighting and what it tells us about parsimony and compatibility. *Biological Journal of the Linnean Society* 16:183-196.

Felsenstein J. 1982. Numerical methods inferring evolutionary trees. *Quarterly Review of Biology* 57:381-404.

Fergusson N.D.M. 1988. A comparative study of the structures of phylogenetic importance of female genitalia of the Cynipoidea (Hymenoptera). *Systematic Entomology*, 13:13-30.

Fitton M.G. & Gauld I.D. 1976. The family group names of the Ichneumonidae (excluding Ichneumoninae) (Hymenoptera). *Systematic Entomology*, 1:247-258.

Fitton M.G., Shaw M.R. & Austin A.D. 1987. The Hymenoptera associated with spiders in Europe. *Zoological Journal of the Linnean Society*, 90(1):65-93.

- Fitton M.G., Shaw M.R. & Gauld I.D. 1988. Pimpline ichneumon- flies (Hymenoptera, Ichneumonidae, Pimplinae). *Royal Entomological Society Handbooks for the Identification of British Insects* 7 (1)
- Flenley J. 1979. *The Equatorial Rain Forest: a Geological History* Butterworths, London.
- Francke-Grosmann H. 1939. Ber das Zusammentleben van Holzwespen (Siricidae) mit Rilzen. *Zeitschrift für Angewandte Entomologie*, 25:674-680
- Francke-Grosmann H. 1967. Ectosymbiosis in Wood-inhabiting Insects. *Symbiosis* 6(2):142-205
- Fryer H.C. 1966. *Concepts and methods of experimental statistics*. Boston.
- Gade H. 1834. "Society News" (Sept 27th). *Bulletin of the Brooklyn Entomological Society*, 7:103-104
- Gadgil M. 1972. Male dimorphism as a consequence of natural selection. *American Naturalist*, 104:1-24.
- Gaffney E.S. 1979. An introduction to the logic of phylogeny reconstruction. In Cracraft J. & Eldredge N. (eds) *Phylogenetic Analysis and Palaentology*:79-111. Columbia University Press, New York.
- Gardiner L.M. 1966. A photographic record of oviposition by *Rhyssa lineolata* (Kirby) (Hymenoptera: Ichneumonidae). *Canadian Entomologist* 98:(95-97).
- Gauld I.D. 1976. The classification of the Anomaloninae (Hymenoptera: Ichneumonidae). *Bulletin of the British Museum (Natural History)*, 33(1):1-135.

Gauld I.D. 1983. The classification, evolution and distribution of the Labeninae, an ancient southern group of Ichneumonidae (Hymenoptera). *Systematic Entomology*. 8:167-178

Gauld I.D. 1984a. *An Introduction to the Ichneumonidae of Australia*. British Museum (Natural History), London.

Gauld I.D. 1984b. The Pimplinae, Xoridinae, Acaenitinae and Lycorininae (Hymenoptera:Ichneumonidae) of Australia. *Bulletin of the British Museum (Natural History), Entomology Series*, 49:235-339.

Gauld I.D. 1985. The phylogeny, classification and evolution of the subfamily Ophioninae (Ichneumonidae). *Bulletin of the British Museum of Natural History (Entomology)*, 51(2):61-185

Gauld I.D. 1987a. Taxonomy, its Limitations and its Role in Understanding Parasitoid Biology. In Waage J. & Greathead D. (eds) *Insect Parasitoids*:1-19. Academic Press, London.

Gauld I.D. 1987b. Some factors affecting the composition of tropical faunas. *Biological Journal of the Linnean Society*, 30:299-312.

Gauld I.D. 1988. Evolutionary patterns of host utilisation by ichneumonid parasitoids (Hymenoptera:Ichneumonidae:Braconidae). *Biological Journal of the Linnean Society*, 35:351-377.

Gauld I.D. & Bolton B. 1988. *The Hymenoptera*. British Museum (Natural History) and Oxford University Press.

Gauld I.D. & Fitton M.G. 1987. Sexual dimorphism in Ichneumonidae: a response to Hurlbutt. *Biological Journal of the Linnean Society*, 31:291-300.

Gauld I.D. & Mound L.A. 1982. Homoplasy and the delineation of holophyletic genera in some insect groups. *Systematic Entomology* 7:73-86

Gauld I.D. and Underwood G. 1986. Some applications of the LeQuesne compatibility test. *Biological Journal of the Linnean Society* 29:191-222

Gibson, G.A.P. 1985. Some pro- and mesothoracic structures important for phylogenetic analysis of Hymenoptera, with a review of terms used for the structures. *Canadian Entomologist*. 117:1395-1443

Gilbertson R.L. 1984. Relationships between insects and wood-rotting Basidiomycetes. In Wheeler Q. and Blackwell M. (eds) *Fungus-Insect relationships; perspectives in Ecology and Evolution* :130-165  
Columbia University Press.

Glowacki J. 1966. Notes on the secondary parasites amongst the ichneumon flies (Hymenoptera: Ichneumonidae) in the fauna of Poland. *Polskie Pismo Entomologiczne*, 36:377-382.

Gould S.J. & Lewontin R. 1979. The Spandrels of San Marco and the Panglossian paradigm; a critique of the adaptionists programme. *Proceedings of the Royal Society of London*, 205:581-598.

Graham A.R. 1946. Feeding of *Pimpla examinator* on host pupae exposed for parasitism. *Annual Report of the Entomological Society of Ontario*, 77:44-45.

Gravenhorst I.L.C. 1829. *Ichneumonologica europaea*. Vratislavia sum. Auct 1: 1-827; 2: 1939; 3: 1-1097

Gregoire J.C. 1976. Note sur deux ennemis naturels de *Dendroctonus micans* KUGELMANN en Belgique (Coleoptera: Scolytidae). *Bulletin et Annales de la Société Royale Entomologique Belgique*, 112:208-212.

Gross M.R. & Charnov E.L. 1980. Alternative male life histories in Bluegill Sunfish. *Proceedings of the National Academy of Science*, 77:6973-6940.

Gupta V.K. 1962. Taxonomy, zoogeography and evolution of Indo-Australian *Theronia* (Hymenoptera: Ichneumonidae). *Pacific Insects Monographs*, 1:1-142.

Gupta V.K. 1987. The Ichneumonidae of the Indo-Australian region (Hymenoptera). *Memoirs of the American Entomological Institute* 41(1)

Hanson H.S. 1939. Ecological notes on the *Sirex* wood wasps and their Parasites. *Bulletin of Entomological Research* 30(1):27-65.

Hard J.S. 1976. Natural control of the hemlock sawfly, *Neodiprion tsugae* (Hymenoptera: Diprionidae) populations of SE Alaska (USA). *Canadian Entomologist*, 108:485-498.

Harrington W.H. 1887. The nuptials of *Thalessa*. *Canadian Entomologist* 19:206-209

Heatwole H. and Davis D.M. 1965. Ecology of three Sympatric species of Parasitic Insects of the Genus *Megarhyssa* (Hymenoptera; Ichneumonidae). *Ecology* 46:140-150

Heatwole H., Davis D.M. and Wenner A.M. 1962. The behaviour of *Megarhyssa*, a genus of parasitic Hymenopterans (Ichneumonidae; Ephialtinae). *Zeitschrift für Tierpsychologie* 19:652-664

Heatwole H., Davis D.M. and Wenner A.M. 1964. Detection of mates and hosts by parasitic insects of the genus *Megarhyssa* (Hymenoptera: Ichneumonidae). *American Midland Naturalist* 71:374-381

Hecht M.K. & Edwards J.L. 1977. The methodology of phylogenetic inference above the species level. In Hecht M.K., Goody P.C. & Hecht B.M. (eds), *Major Patterns in Vertebrate Evolution*:3-51. Plenum Press, New York.

Hennig W. 1950. *Grundzüge einer Theorie der Phylogenetischen Systematik*. Deutsches Zentralverlag, Berlin.

1979.  
Hennig W. *Phylogenetic Systematics* (revised translation). University of Illinois Press, Urbana.

Hill L.R. 1975. Problems arising from some tests of LeQuesne's concept of uniquely derived characters. In Estabrook G.F. *Proceedings of the 8th International Conference of Numerical Taxonomy*:375-398. San Fransisco.

Hocking H. 1968. Studies on the biology of *Rhyssa persuasoria* (L.) (Hymenoptera: Ichneumonidae) incorporating an X-ray technique. *Journal of the Australian Entomological Society*. 7:1-5

Holmgren A.E. 1857. Förösk till uppställning och beskrifning af de i Sverige funna tryphonider. *Konig. Svenska. Vetensk. Akad. Handl.* 1: 93-246; 305-394

Holmgren A.E. 1860. Förösk till uppställning och beskrifning af de i Sverige funna pimplariae. *Konig. Svenska. Vetensk. Akad. Handl.*, 3:1-76.

Horn D.J. 1974. Observations on the primary and secondary parasitoids of the California Oakworm, *Phryganidia californica* (Lepidoptera: Dioptidae). *Pan Pacific Entomologist*, 50:53-59.

Howard R.D. 1978. the evolution of mating strategies in bullfrogs, *Rana catesbiana*. *Evolution*, 32:850-871.

Howarth M.K. 1981. Palaeography of the Mesozoic. in Cocks L.R.M., *The Evolving Earth*:197-220. British Museum (Natural History) and Cambridge University Press. London and Cambridge.

Howell J.O. & Pienkowski R.L. 1972. Notes on the biology of a spider parasitoid *Colpomeria kincaidii* Ashmead (Hymenoptera: Ichneumonidae). *Entomophaga*, 17:5-7

Huddleston T. 1984. The Palaearctic species of *Ascogaster* (Hymenoptera: Braconidae). *Bulletin of the British Museum (Natural History), Entomology series*, 49(5):341-392.

Hughes N.F. 1976. *Palaeobiology of Angiosperm Origins*. Cambridge University Press, Cambridge.

Iwata K. 1958. Ovarian eggs of 233 species of the Japanese Ichneumonidae. *Acta Hymenopterologia*, 1:63-74.

Juillet J.A. 1959. Morphology of immature stages, life-history, and behaviour of three hymenopterous parasites of the European Pine Shoot Moth, *Rhyaciona buoliana* (Schiff.) (Lepidoptera: Olethreutidae). *Canadian Entomologist* 91:709-719

Jussila R. & Kämpylä M. 1975. Observations on *Townesia tenuiventris* (Holmgren) (Hymenoptera: Ichneumonidae) and its hosts *Chelostoma maxillosum* (Hymenoptera: Megachilidae) and *Trypoxylon figulus* (Hymenoptera: Sphecidae). *Annales Entomologici Fennici*, 41:81-86.

Kamath, M.K and Gupta, V.K. 1972. The tribe Rhyssini. *Ichneumologica Orientalis*, 2

Kazmierczak T. 1979. Zglebce Rhyssini (Hymenoptera: Ichneumonidae) Pasożyty szkodników technicznych drewna drzew iglastych i liściastych oraz ich znaczenie w biocenozie lasu. *Acta Agraria et Silvestria* 18:121-137

Kazmierczak T. 1980. Rewizja stanowiska systematycznego rodzaju *Pseudorhyssa* Merrill (Hymenoptera: Ichneumonidae). *Acta Agraria et Silvestria* 19:41-55

Kazmierczek T. 1981. Polskie Zgtebce - Rhyssini (Hymenoptera: Ichneumonidae). *Monografie Fauny Polski* 12 :1-111.

King P.E., Askew R.R. & Sanger C. 1969. The detection of parasitised hosts by males of *Nasonia vitripennis* (Hymenoptera: Pteromalidae) and some possible implications. *Proceedings of the Royal Entomological Society of London*, 79: 399-407.

Kirk A.A. 1974. The distribution and ecology of woodwasps (Hymenoptera: Siricidae) and their parasitoid (*Rhyssa persuasoria*) in Ireland. *Entomologist's Monthly Magazine* 110:215-221.

Kirk A.A. 1975. Siricid woodwasps and their associated parasitoids in South-west United States (Hymenoptera: Siricidae). *Pan Pacific Entomologist* 51(1):57-61.

Kishi Y. 1970a. *Dolichomitus* sp. (Hymenoptera: Ichneumonidae) - a hymenopterous parasite of the pine bark weevil. *Japanese Journal of Applied Entomology and Zoology*, 14:122-126.

Kishi Y. 1970b. Differences in the sex ratio of the pine bark weevil parasite, *Dolichomitus* sp. (Hymenoptera: Ichneumonidae), emerging from different hosts species. *Applied Entomology and Zoology*, 5:126-132.

Krebs J. & Davies N. 1981. *An Introduction to Behavioural Ecology*. Blackwell Scientific Publications, Oxford.

Leius K. 1960. Attractiveness of different foods and flowers to the adults of some hymenopterous parasites. *Canadian Entomologist*, 92:369-376.

Le Quesne W. 1969. A method of selection of characters in numerical taxonomy. *Systematic Zoology* 8:201-205

Le Quesne W. 1982. Compatibility analysis and its applications. *Zoological Journal of the Linnean Society*. 74:267-275

van Lith J.P. 1974. Notes on Palaearctic Psenini V-VIII (Hymenoptera: Sphecidae). *Entomologische Berichten*, 34:323-399.

- McLachlan A. 1986. Survival of the smallest: advantages of and costs of small size in flying animals. *Ecological Entomology*, 11:237-240.
- McLachlan A. & Neems R. 1989. An alternative mating system in small male insects. *Ecological Entomology*, 14:85-91.
- Maclure H.E. 1978. some arthropods of of the dipterocarp forests in Malaya. *Malayan Nature Journal*, 32:31-52.
- Madden J.L. 1968. Behavioural responses of parasites to the symbiotic fungus associated with *Sirex noctilio* F. *Nature* 218:189-190
- Madden J.L. 1981. Egg and larval development in the woodwasp *Sirex noctilio*. *Australian Journal of Zoology* 29:493-506.
- Madden J.L. and Coutts M.P. 1979. The role of Fungi in the biology and ecology of woodwasps (Hymenoptera: Siricidae). in <sup>Batra L.R. (ed)</sup> *Insect-fungus Symbiosis*:165-174. John Wiley and sons
- Marsh P.M. *Bohartiellus*, a new genus of Doryctinae from South America (Hymenoptera: Braconidae). *Pan-Pacific Entomologist*, 59:1-4.
- Matthews R.M. 1975. Courtship in parasitic wasps. in Price P.W. *Evolutionary strategies of parasitic insects and mites*. University of Illinois at Urbana.
- Matthews R.W, Matthews J.O and Crankshaw O. 1979. Aggregation in male parasitic wasps of the genus *Megarhyssa*. I: sexual discrimination, tergal stroking, and description of associated anal structures behaviour. *Florida Entomologist*. 62:3-8
- Maynard Smith J. 1974. The theory of games and the evolution of animal conflicts. *Journal of Theoretical Biology*, 47:209-221.

Mayr E. 1942. *Systematics and the Origin of the Species*. Columbia University Press, New York.

Mayr E. 1963. *Animal species and Evolution*. Harvard University Press, Cambridge.

Mayr E. 1969. *Principles of Systematic Zoology*. McGraw-Hill, New York.

Meier N.F. 1934. *Tables systematiques des Hymenopteres parasites (famille Ichneumonidae) de l'URSS et des pays limitrophe*. 3(15).

Merrett P., Locket G.H. & Millidge A.F. 1985. A check list of British spiders. *Bulletin of the British Arachnological Society*, 6(9):381-403.

Miller C.N. 1976. Early evolution in the Pinaceae. *Review of Palaeobotany and Palynology*, 21:101-117.

Miller C.N. 1977. Mesozoic conifers. *Botanical Review*, 43:217-280.

Miller C.N. 1982. Current status of Paleozoic and Mesozoic conifers. *Review of Palaeobotany and Palynology*, 37: 99-114.

Miller D. and Clarke A.F. 1935. *Sirex noctilio* (Hymenoptera) and its parasites in New Zealand. *Bulletin of Entomological Research*, 26:149-154

Miller P.J. 1979. Adaptiveness and implications of small size in teleosts. In Miller P.J. (ed) *Fish Phenology: Anabolic Adaptiveness in Teleosts*:363-296. Symposia of Zoological Society of London, 44. Academic Press, London.

Moody S.M. & O'Nolan P. 1987. An *a priori* character weighting method for cladistic analysis. (American Society of Zoologists meeting , December 1987; handout).

- Morgan D. and Stewart N.C. 1966. The effects of *Rhyssa persuasoria* on a population of *Sirex noctilio* (Siricidae). *Transactions of the Royal Society of New Zealand*. 8:31-38
- Morley C. 1913a. A revision of the Ichneumonidae based on the collection in the British Museum (Natural History) with descriptions of new genera and species. Tribes Rhyssides, Echthromorphides, Anomalides and Paniscides. 2, London.
- Morris K.R.S., Cameron E. & Jepson W.F. 1937. The insect parasites of the spruce sawfly (*Diprion polytomum*, HTG.). *Bulletin of Entomological Research*, 360-361
- Muesebeck C.F.W; Krombein K.V and Townes H. 1951. Hymenoptera of America north of Mexico. *United States Department of Agriculture, Agricultural monograph 2*
- Myers J.G. 1928. Further notes on *Rhyssa* and *Ibalia*, parasitising *Sirex cyaneus* Fabr. *Bulletin of Entomological Research*, 19:317-323.
- Nelson G. 1979. Cladistic analysis and synthesis: principles and definitions with a historical note on Adanson's *Familles des Plantes* (1763-1764). *Systematic Zoology*, 28:1-21
- Nelson G. & Platnick N. 1981. *Systematics and Biogeography, Cladistics and Vicariance*. Columbia University Press, New York.
- Nielsen E. 1923. Contributions to the life history of the pimpline spider parasitoids (*Polysphincta*; *Zaglyptus*; *Tromatobia*). *Entomologiske Meddelelser*, 14:137-205.
- Nielsen E. 1928. A supplementary note on the life histories of the polysphinctas (Hymenoptera: Ichneumonidae). *Entomologiske Meddelelser* 16:162-165.
- Nielsen E. 1929. A second supplementary note on the life histories of the polysphinctas (Hymenoptera: Ichneumonidae). *Entomologiske Meddelelser* 16:366-368.

- Nielsen E. 1935. A third supplementary note on the life histories of the polysphinctas (Hymenoptera: Ichneumonidae). *Entomologiske Meddelelser* 19:191-215.
- Nielsen E. 1937. A fourth supplementary note on the life histories of the polysphinctas (Hymenoptera: Ichneumonidae). *Entomologiske Meddelelser* 20:25-28.
- Norton W.N. & Vinson S.B. 1974. Antennal sensillae of 3 parasitic Hymenoptera. *International Journal of Insect Morphology and Embryology* 3:305-316
- Noskiewicz J. 1957. Uwagi o slaskich gatunkach z grupy *Megarhyssa superba* SCHRK. *Polski Pismo Entomologiczne* 26:321-330
- Nuttall M.J. 1973. Pre-emergence fertilisation of *Megarhyssa nortoni nortoni* (Hymenoptera: Ichneumonidae). *New Zealand Entomologist* 5:112-117
- Nuttall M.J. 1980. Insect parasites of *Sirex*. *Forest and Timber Insects in New Zealand* 47.
- O'Nolan P. Unpublished manuscript. Character weighting in cladistic analysis. Unpublished MSc thesis, Ohio University.
- Oldroyd H. 1964. *The Natural History of Flies*. Weidenfeld and Nicholson, London.
- Orians G.H. 1969. On the evolution of mating systems in birds and mammals. *American Naturalist*, 103:589-603.
- Osman S.E. 1978. Der Einfluss der Imaginalernährung und der Begattung auf die Sekretproduktion der weiblichen Genitalanhangdrüsen und auf die Eirifung van *Pimpla turionellae* L. (Hymenoptera: Ichneumonidae). *Zeitschrift für angewandte Entomologie*, 85:113-122.

Panchen A.L. 1982. The use of parsimony in testing phylogenetic hypotheses. *Zoological Journal of the Linnean Society* 74:305- 328.

Parker E.A. 1942. Symbiosis and siricid woodwasps. *Annals of Applied Biology*, 29:268-274

Parrish J.T.—1987. Global palaeogeography and palaeoclimate of the Late Cretaceous and Early Tertiary. In, Friis E.M., Chaloner W.G. & Crane P.R. (eds), *The origins of angiosperms and their biological consequences*<sup>51-74</sup> Cambridge University Press, Cambridge.

Patterson C. 1980. Cladistics - pattern versus process in nature: a personal view of a method and a controversy. *Biologist*, 27:234-240

Platnick N.I. 1980. Philosophy and the transformation of cladism. *Systematic Zoology*, 26:360-365.

Porter C.C. 1975. A revision of the Argentine species of *Epirhyssa* (Hymenoptera: Ichneumonidae). *Acta Zoologica Lilloana* 31:125-158

Porter C.C. 1978. A Revision of the Genus *Epirhyssa* (Hymenoptera: Ichneumonidae). *Studia Entomologica* 20:297-411

Rasnitsyn A.P. 1980. The origin and evolution of hymenopteran insects. *Trudy Paleontologicheskogo Instituta. Akademiya Nauk SSSR*, 174:1-191. (English translation 1984. Agricultural Canada, Ottawa).

Reid E.M. & Chandler M.E.J. 1933. *The Flora of the London Clay*. British Museum (Natural History), London.

Richards O.W. 1949. The significance of the numbers of wing hooks in bees and wasps. *Proceedings of the Royal Entomological Society of London (Series A)*, 24:75-78

Richards O.W. 1977. Hymenoptera - introduction and key to families. *Royal Entomological Society Handbook for identification of British Insects* 6 (i)

Ridley M. 1983. *The Explanation of Organic Diversity; the Comparative Method and Adaptations for mating*. Clarendon Press, Oxford.

Ridley M. 1985. *The Problems of Evolution*. Oxford University Press, Oxford.

Ridley M. 1986. *Evolution and classification: the Reformation of Cladism*. Longman, London.

Sandlan K. 1979. Host-feeding and its effect on the physiology and behaviour of *Coccygomimus turionellae* L. (Hymenoptera: Ichneumonidae). *Physiological Entomology*, 4:383-392.

Schimitschek V.E. 1974. Beitrag zur Okologiew van Nadelbaum- und Laubbaums Holzwespen (Hymenoptera: Siricidae). *Zeitschrift angewandte Entomologie*, 75:225-247

Scudder S.H. 1890. *Tertiary Insects of North America*. New York.

Selvin H.C. & Stuart A. 1966. Data dredging procedures in survey analysis. *American Statistician*, 20:20-23.

Severinghaus L.L., Kurtak B.H. and Eickwort G.C. 1981. The reproductive behaviour of *Anthidium manicatum* (Hymenoptera: Megachilidae) and the significance of size for territorial males. *Behavioural Ecology and Sociobiology*, 9:51-58

Seyrig A. 1927. Captures d'Ichneumonides *Bulletin Societie Entomologique France*, 32:124-125, 133-137

Seyrig A. 1932. Les Ichneumonides de Madagascar. 1. Ichneumonidae; Pimplinae. *Mem. Acad. Malgache*, 11: 1-183

Shaw M.R. & Askew R.R. 1978. Hymenopterous parasites of Diptera (Hymenoptera Parasitica). In *The Dipterist's Handbook*. In, Stubbs A. & Chandler P. (eds) *The Amateur Entomologist*, 15:164-171.

- Shaw M.R. & Wahl D.B. 1989. The biology, egg and larvae of *Acaenitus dubiator* (Panzer) (Hymenoptera: Ichneumonidae: Acaenitinae). *Systematic Entomology*, 14(1):117-125.
- Short J.R.T. 1978. The Final Larval Instars of the Ichneumonidae. *Memoirs of the American Entomological Institute*, 25.
- Simpson G.G. 1944. *Tempo and Mode in Evolution*. Columbia University Press.
- Simpson G.G. 1953. *The Major Features of Evolution*. Columbia University Press.
- Simpson G.G. 1961. *Principles of Animal Taxonomy*. Columbia University Press.
- Skinner E.R. & Thompson G.H. 1960. FILM. *The Alder Wood Wasp and its Insect Enemies*.
- Slifer E. and Sekhon S. 1960. The fine structure of the plate organs on the antennae of the honey bee, *Apis mellifera* Linnaeus. *Experimental Cell Research*, 19:410-414
- Slifer E. and Sekhon S. 1961. Fine structure of the sense organs on the antennal flagellum of the honey bee, *Apis mellifera* Linnaeus. *Journal of Morphology*, 109:351-362
- Smith D.R. 1978. *Hymenopterum Catalogus, Pars 14. Sub-order Symphyta*. Dr W. Junk. B.V, The Hague, Holland.
- Smith E.L. 1969. Evolutionary morphology of the external insect genitalia. 1. Origins and relationships to other appendages. *Annals of the Entomological Society of America*, 62:1051-1079

Smith E.L. 1970. Evolutionary morphology of the external insect genitalia. 2. Hymenoptera. *Annals of the Entomological Society of America*, 63:1-27.

Smithers C.N. 1956. On *Philopsyche abdomalis* MORLEY (Hymenoptera: Ichneumonidae) a parasite of *Acanthopsyche junodi* Heylaerts (Lepidoptera: Psychidae). *Journal of the Entomological Society of South Africa*, 19:225-249.

Sneath P.H.A. & Sokal R.R. 1973. *Numerical Taxonomy*. W.H. Freeman, San Francisco.

Sokal R.R. & Rohlf F.J. 1969. *Biometry*. W.H. Freeman, San Francisco.

Spradbery J.P. 1968. A technique for artificially culturing ichneumonid parasites of woodwasps (Hymenoptera: Siricidae). *Entomologia Experimentalis et Applicata*, 11: 257- 260

Spradbery J.P. 1969. The biology of *Pseudorhyssa sternata*, a cleptoparasite of siricid wasps. *Bulletin of Entomological Research*. 59:291-297

Spradbery J.P. 1970a. The immature stages of European ichneumonid parasites of siricine woodwasps. *Proceedings of the Royal Entomological Society*, 45:14-28

Spradbery J.P. 1970b. Host-finding in *Rhyssa persuasoria*. *Animal Behaviour*, 18:103-114

Spradbery J.P. & Kirk A.A. 1978. Aspects of the biology of Siricid woodwasps (Hymenoptera: Siricidae) in Europe, North Africa and Turkey with special reference to the biological control of *Sirex noctilio* F. in Australia. *Bulletin of Entomological Research*, 68:341-359.

Spradbery J.P. & Ratkowsky D.A. 1974. An analysis of geographical variation in the parasitoid *Rhyssa persuasoria* L. (Hymenoptera: Ichneumonidae). *Bulletin of Entomological Research*, 64:653-668.

Strauch J.G. 1984. Use of homoplastic characters in compatibility analysis. *Systematic Zoology*, 33:167-177.

Tattersall P. & Eldredge N. 1978. Fact, theory and fantasy in human palentology. *American Scientist* 65:104-110

Taylor K.L. 1976. The introduction and establishment of insect parasitoids to control *Sirex noctilio* in Australia. *Entomophaga* 49:429-440

Taylor K.L. 1978. Evaluation of the insect parasitoids of *Sirex noctilio* (Hymenoptera: Siricidae) in Tasmania. *Oecologia*, 32:1-10

Thornhill R. & Alcock J. 1983. *The Evolution of Insect Mating Systems*. Harvard University Press.

Thorpe W.H. & Caudle H.B. 1938. A study of the olfactory responses of insect parasites to the food plant of their hosts. *Parasitology* 30:523-528.

Tinbergen N. 1963. On the aims and methods of ethology. *Zeitschrift für Tierpsychologie*, 20:410-433.

Togashi I. 1974. The hymenopterous parasites of *Outema oryzae* (Kuwayama) (Coleoptera:Chrysomelidae) in Ishikawa Prefecture (Japan). *Mushi*, 48(2):7-13.

Townes H. 1944. A Catalogue and reclassification of the Nearctic Ichneumonidae. *Memoirs of the American Entomological Society*, 11(1)

Townes H. 1969. The genera of Ichneumonidae. Part 1. *Memoirs of the American Entomological Institute*, 11

Townes H. & Chiu S. 1970. The Indo-Australian species of *Xanthopimpla* (Ichneumonidae). *Memoirs of the American Entomological Institute*, 14.

Townes H., Momoi S. & Townes M. 1965. A catalogue and reclassification of the eastern Palearctic Ichneumonidae. *Memoirs of the American Entomological Institute*, 5

Townes H. & Townes M. 1960. Ichneumon-flies of America north of Mexico: 2. Subfamilies Ephialtinae, Xoridinae and Acaenitinae. *United States National Museum Bulletin*, 216(2)

Townes H. & Townes M. 1966. A catalogue and reclassification of the Neotropical Ichneumonidae. *Memoirs of the American Entomological Institute*, 8

Townes H. & Townes M. 1973. A catalogue and reclassification of the Ethiopian Ichneumonidae. *Memoirs of the American Entomological Institute* 19

Townes H., Townes M., & Gupta V.K. 1961. A catalogue and reclassification of Indo-Australian ichneumonids. *Memoirs of the American Entomological Institute*, 1

Underwood G. 1982. Parallel evolution in the context of character analysis. *Zoological Journal of the Linnean Society* 74:245-266

Upchurch Jr. G.R. & Wolfe J.A. 1987. Mid-Cretaceous to Early Tertiary vegetation and climate: evidence from fossil leaves and woods. in, Friis E.M., Chaloner W.G. & Crane P.R. (eds), *The origins of angiosperms and their biological consequences*:75-106. Cambridge University Press, Cambridge.

Vincent L.S. 1979. A new record for *Sinarachna anomala* (Hymenoptera: Ichneumonidae), an external parasitoid of *Mallos pallidus* (Araneae: Dictynidae). *Pan Pacific Entomologist*, 55(3):192-194.

Völlger, E. 1972. Zum wirtsspektrum van *Dolichomitus mesocentrotus* Grav. und *D. imperator* Krb. (Hymenoptera: Ichneumonidae). *Entomologische Berichten, Berlin*, (1972):14

Waddington C.H. 1957. *The Strategy of the Genes; a Discussion of some Aspects of Theoretical Biology*. Allen & Unwin, London.

Wahl D.B. 1984. Larval structures of oxytorines and their significance for the higher classifications of some ichneumonids (Hymenoptera). *Systematic Entomology* 11:117-127

Wahl D.B. In press. A review of the mature larvae of Diplazontinae, with notes on larvae of Acaenitinae and Orthocentrinae, and the proposal of two new subfamilies (Insecta: Hymenoptera: Ichneumonidae). *Journal of Natural History*.

Ward R.H. & Pienkowski R.L. 1978. Mortality and parasitism of *Cassida rubiginosa*, a thistle feeding Shield Beetle accidentally introduced into North America. *Environmental Entomology*, 7(4):536-540

Walther J.R. 1979. Vergleichende morphologische Betrachtung der antennalen Sensillenfelder einiger ausgewählter Aculeata (Insecta, Hymenoptera). *Sonderdruck aus Zeitung für Zoologische Systematik und Evolutionsforschung*, 17(1):30-56.

Weather journal. Monthly meteorological data 1954 - 1960.

Wesmael C. 1844. Tentamen dispositionis methodicae Ichneumonum Belgii. *Nouvelles Mémoires d'Académie Science. Bruxelles.*, 18:1-238.

Westrich P. 1980. Die Stechimmen (Hymenoptera: Aculeata) des Tübinger Gebiets mit besonderer Berücksichtigung des Spitzberg. *Veröffentlichungen Naturschutz Bad.-Württ.*, 51/52:601-680.

Whitmore T.C. 1975. *Tropical Rainforests of the Far East*. Oxford Scientific Press.

Whitmore T.C. 1981. *Wallace's Line and Plate Tectonics*. Clarendon Press, Oxford.

Wiley E.O. 1981. *Phylogenetics: the Theory and Practice of Phylogenetic Systematics*. John Wiley and Sons, New York.

Wiley E.O. 1975. Karl R. Popper, systematics and classification: a reply to Walter Bock and other evolutionary taxonomists. *Systematic Zoology*, 24:233-242

Williams P.H. 1985. A preliminary cladistic investigation of relationships among the bumble bees (Hymenoptera, Apidae). *Systematic Entomology*, 10:239-255.

Wilson E.O. 1965. A consistency test for phylogenies based on contemporary species. *Systematic Zoology*, 14:214-220

Yasumatsu K. 1937. Some observations on *Thalessa citraria* (OLIVIER) and *Thalessa superbiens* MORLEY. *Akitu*, 1:33-43.

Yasumatsu K. 1938. Further considerations on the habits of *Thalessa* and its allied genera. *Akitu*, 1:71-76

Zondag R. & Nuttall M.J. 1961. *Rhyssa lineolata* (Kirby) (Hymenoptera: Ichneumonidae: Pimplinae). A species new to New Zealand. *New Zealand Entomologist*, 2(6):40-44.

## APPENDIX 1

### Operational taxonomic units for the pimpline analyses

1. *Exeristes roborator* (Fabricius)
2. *Endromopoda detritus* (Holmgren)
3. *Afrephialtes cicatricosa* (Ratzeburg)
4. *Ephialtes manifestator* (Linnaeus)
5. *Liotryphon cydiae* Perkins
6. *Townesia tenuiventris* (Holmgren)
7. *Paraperithous gnathaulaux* (Thompson)
8. *Dolichomitous imperator* (Kreichbaumer)
9. *Acropimpla didyma* (Gravenhorst)
10. *Gregopimpla santanas* Morley
11. *Iseropus stercorator* (Fabricius)
12. *Tromatobia oculatorius* (Fabricius)
13. *Zaglyptus varipes* (Gravenhorst)
14. *Clistopyga incitator* (Fabricius)
15. *Pseudopimpla pygidiator* Seyrig
16. *Dreisbachia pictifrons* (Thompson)
17. *Schizopyga frigida* Cresson
18. *Acrotaphus tibialis* (Cameron)
19. *Acrodactyla degener* (Haliday)
20. *Piogaster albina* Perkins
21. *Oxyrrhexis carbonator* (Gravenhorst)
22. *Polysphincta tuberosa* Gravenhorst
23. *Sinarachna pallipes* (Holmgren)
24. *Zatypota percontaria* (Müller)
25. *Itoplectis alternans* (Gravenhorst)
26. *Apechthis compunctor* (Linnaeus)
27. *Pimpla hypochondriaca* (Retzius)
28. *Strongylopsis belua* (Kuzin)
29. *Xanthopimpla regina* Morley
30. *Theronia lurida* Tosquinet
31. *Perithous scurra* (Panzer)
32. *Delomerista mandibularis* (Gravenhorst)
33. *Pseudorhyssa sternata* Merrill
34. *Diacritus aciculatus* (Vollenhoven)
35. *Poemenia notata* Holmgren
36. *Deuteroxoides elevator* (Panzer)
37. *Podoschistus scutellaris* (Desuignes)
38. *Neoxorides collaris* (Gravenhorst)
39. *Rhyssa persuasoria* (Linnaeus)
40. *Rhysella approximator* (Fabricius)
41. *Lytarmes maculipennis* (Smith)
42. *Epirhyssa flavopicta* (Smith)

## APPENDIX 2

### Operational taxonomic units for the rhyssine analyses

1. *Rhyssa amoena* Gravenhorst [Palaearctic]
2. *Rhyssa lineolata* Kirby [Nearctic]
3. *Rhyssa alaskensis* Ashmead [Nearctic]
4. *Rhyssa persuasoria* Linnaeus [Holarctic]
5. *Rhyssella approximata* (Fabricius) [Palaearctic]
6. *Rhyssella nitida* (Cresson) [Nearctic]
7. *Rhyssella humida* (Say) [Palaearctic]
8. *Megarhyssa emarginatoria* Thunberg [Palaearctic]
9. *Megarhyssa nortoni* (Cresson) [Holarctic]
10. *Megarhyssa perlata* (Christ) [Palaearctic]
11. *Megarhyssa superba* (Schrank) [Palaearctic]
12. *Megarhyssa atrata* (Fabricius) [Nearctic]
13. *Megarhyssa praecellens* (Tosquinet) [Palaearctic]
14. *Megarhyssa macurus* (Linnaeus) [Nearctic]
15. *Megarhyssa greeni* (Viereck) [Nearctic]
16. *Sychnostigma biroi* (Mocsáry) [Oriental]
17. *Sychnostigma vulgare* Baltazar [Oriental]
18. *Sychnostigma kerrichi* Kamath & Gupta [Oriental]
19. *Sychnostigma malayanum* Kamath & Gupta [Oriental]
20. *Sychnostigma bimaculatum* (Cameron) [Oriental]
21. *Sychnostigma spiloptera* (Cameron) [Oriental]
22. *Sychnostigma validum* Kamath & Gupta [Oriental]
23. *Sychnostigma silvaticum* Kamath & Gupta [Oriental]
24. *Sychnostigma migratoria* Seyrig [Madagascar]
25. *Megarhyssa laniaria* (Vollenhoven) [Oriental]
26. *Lytarmes maculipennis* (Smith) [Oriental]
27. *Lytarmes fasciatus* (Smith) [Oriental]
28. *Cyrtorhyssa mesophyrrha* (Mocsáry) [Oriental]
29. *Sychnostigma* sp. [Oriental]
30. *Triancyra sarojinae* Kamath & Gupta [Oriental]
31. *Triancyra* sp. [Oriental]
32. *Epirhyssa diatropis* Porter [Neotropical]
33. *Epirhyssa mexicana* Cresson [Neotropical]
34. *Epirhyssa phoenix* Porter [Neotropical]
35. *Epirhyssa isthmia* Porter [Neotropical]
36. *Epirhyssa braconoides* Porter [Neotropical]

37. *Epirhyssa tristis* (Kreichbaumer) [Neotropical]
38. *Sychnostigma* sp. [Ethiopian]
39. *Sychnostigma ghesquierei* Seyrig [Ethiopian]
40. *Myllenyxis muelleri* (Vollenhoven) [Oriental]
41. *Myllenyxis bernsteinii* (Vollenhoven) [Oriental]
42. *Sychnostigma velensis* Benoit [Ethiopian]
43. *Sychnostigma* sp. [Oriental]
44. *Sychnostigma* sp. [Oriental]
45. *Sychnostigma* sp. [Oriental]
46. *Sychnostigma* sp [Oriental]
48. *Sychnostigma flavopictum* (Smith) [Oriental]
49. *Sychnostigma pumilum* Kamath & Gupta [Oriental]
50. *Sychnostigma* sp. [Oriental]
51. *Myllenyxis kuchingensis* Kamath & Gupta [Oriental]
52. *Sychnostigma cruciatum* [as holotype] (Cameron) [Oriental]
53. *Sychnostigma* sp. [Ethiopian]
54. *Epirhyssa peruana* Enderlein [Neotropical]
55. *Epirhyssa oranensis* Porter [Neotropical]
56. *Epirhyssa tylota* Porter [Neotropical]
57. *Epirhyssa cochabambae* Porter [Neotropical]
58. *Sychnostigma* sp. [South African]
59. *Sychnostigma maculiceps* (Cameron) [Oriental]
60. *Triancyra scabra* Baltazar [Oriental]
61. *Sychnostigma* "cruciatum" sensu Kamath & Gupta [Oriental]
62. *Sychnostigma simile* Baltazar [Oriental]
63. *Sychnostigma assamense* Kamath & Gupta [Oriental]
64. *Sychnostigma cinctum* Baltazar [Oriental]
65. *Sychnostigma atrum* Kamath & Gupta [Oriental]
66. *Sychnostigma flavobalteatum* (Cameron) [Oriental]
67. *Sychnostigma* sp. [South African]
68. *Triancyra diversa* (Cushman) [Oriental]
69. *Triancyra maculicornis* (Cameron) [Oriental]
70. *Myllenyxis* sp. [Oriental]
71. *Megarhyssa bicolor* Baltazar [Oriental]
72. *Myllenyxis cava* Kamath & Gupta [Oriental]
73. *Myllenyxis oceanica* (Mocsáry) [Oriental]
74. *Sychnostigma japonica* (Cameron) [Palearctic]
75. *Sychnostigma persicum* Kamath & Gupta [Oriental]
77. *Sychnostigma asperum* Kamath & Gupta [Oriental]
78. *Epirhyssa pyrrha* Porter [Neotropical]
79. *Myllenyxis papuana* Kamath & Gupta [Oriental]
80. *Myllenyxis* sp. [Oriental]

# APPENDIX 3

## Pimpline data set

(0 = plesiomorphy; 1 = apomorphy; - = state unknown)

| Taxon<br>Nos. | Character Nos. |     |     |   |     |     |    |    |      |      |    |      |    |      |      |      |      |    |   |   |   |   |   |   |  |
|---------------|----------------|-----|-----|---|-----|-----|----|----|------|------|----|------|----|------|------|------|------|----|---|---|---|---|---|---|--|
|               | 1              | 2.2 | 3.2 | 5 | 7   | 8.2 | 10 | 12 | 14.1 | 15.1 | 16 | 18.1 | 19 | 21.1 | 21.3 | 23.1 | 24.1 | 25 |   |   |   |   |   |   |  |
|               | 2.1            | 3.1 | 4   | 6 | 8.1 | 9   | 11 | 13 | 14.2 | 15.2 | 17 | 18.2 | 20 | 21.2 | 22   | 23.2 | 24.2 |    |   |   |   |   |   |   |  |
| 1             | 0              | 1   | 0   | 0 | 0   | 0   | 1  | 0  | 0    | 1    | 0  | 0    | 0  | 0    | 0    | 0    | 0    | 1  | 1 | 1 | 0 | 0 | 0 | 0 |  |
| 2             | 0              | 1   | 0   | 0 | 0   | 0   | 1  | 0  | 0    | 1    | 0  | 0    | 0  | 0    | 0    | 0    | 1    | 0  | 1 | 0 | 0 | 0 | 1 | 0 |  |
| 3             | 0              | 1   | 0   | 0 | 0   | 0   | 1  | 0  | 0    | 1    | 1  | 0    | 0  | 0    | 0    | 0    | 1    | 1  | 1 | 0 | 0 | 1 | 0 | 0 |  |
| 4             | 0              | 1   | 0   | 1 | 0   | 0   | 1  | 0  | 0    | 1    | 1  | 0    | 0  | 0    | 0    | 0    | 1    | 0  | 1 | 0 | 0 | 0 | 0 | 1 |  |
| 5             | 0              | 1   | 0   | 0 | 0   | 0   | 1  | 0  | 0    | 0    | 0  | 0    | 0  | 0    | 0    | 0    | 1    | 0  | 1 | 1 | 0 | 0 | 1 | 0 |  |
| 6             | 0              | 1   | 0   | 0 | 0   | 0   | 1  | 0  | 0    | 1    | 0  | 0    | 0  | 0    | 0    | 0    | 1    | 0  | 1 | 1 | 0 | 0 | 1 | 0 |  |
| 7             | 0              | 1   | 0   | 0 | 0   | 0   | 1  | 0  | 0    | 1    | 0  | 0    | 0  | 0    | 0    | 0    | 1    | 0  | 0 | 0 | 0 | 0 | 0 | 0 |  |
| 8             | 0              | 1   | 0   | 0 | 0   | 0   | 1  | 0  | 0    | 0    | 0  | 0    | 0  | 0    | 0    | 0    | 1    | 0  | 0 | 0 | 0 | 0 | 0 | 1 |  |
| 9             | 0              | 1   | 0   | 0 | 0   | 0   | 1  | 0  | 0    | 1    | 1  | 0    | 0  | 0    | 0    | 0    | 1    | 1  | 1 | 0 | 0 | 1 | 0 | 0 |  |
| 10            | 0              | 1   | 0   | 0 | 0   | 0   | 1  | 0  | 0    | 1    | 1  | 0    | 0  | 0    | 0    | 0    | 1    | 0  | 1 | 0 | 0 | 0 | 0 | 0 |  |
| 11            | 0              | 1   | 0   | 0 | 0   | 0   | 1  | 0  | 0    | 1    | 1  | 0    | 0  | 0    | 0    | 0    | 1    | 0  | 0 | 0 | 0 | 0 | 0 | 1 |  |
| 12            | 0              | 0   | 0   | 0 | 0   | 0   | 0  | 0  | 1    | 1    | 0  | 0    | 0  | 0    | 0    | 0    | 1    | 1  | 1 | 0 | 0 | 1 | 0 | 0 |  |
| 13            | 0              | 1   | 0   | 0 | 0   | 0   | 0  | 0  | 1    | 1    | 0  | 0    | 0  | 0    | 0    | 0    | 1    | 1  | 1 | 0 | 0 | 1 | 0 | 0 |  |
| 14            | 0              | 0   | 0   | 0 | 0   | 0   | 0  | 0  | 0    | 0    | 0  | 0    | 0  | 0    | 0    | 0    | 1    | 1  | 1 | 0 | 0 | 1 | 0 | 0 |  |
| 15            | 0              | 1   | 0   | 0 | 0   | 0   | 1  | 0  | 1    | 1    | 0  | 0    | 0  | 0    | 0    | 0    | 1    | 0  | 1 | 1 | 0 | 0 | 0 | 1 |  |
| 16            | 0              | 0   | 0   | 0 | 0   | 0   | 0  | 0  | 0    | 0    | 0  | 0    | 0  | 0    | 0    | 0    | 1    | 1  | 0 | 0 | 0 | 1 | 0 | 0 |  |
| 17            | 0              | 0   | 0   | 1 | 0   | 0   | 0  | 0  | 0    | 0    | 0  | 0    | 0  | 0    | 0    | 0    | 1    | 1  | 0 | 0 | 1 | 1 | 0 | 0 |  |
| 18            | 1              | 0   | 0   | 0 | 0   | 0   | 0  | 0  | 0    | 1    | 0  | 0    | 0  | 0    | 0    | 0    | 1    | 1  | 1 | 0 | 0 | 1 | 0 | 0 |  |
| 19            | 0              | 0   | 0   | 0 | 0   | 0   | 0  | 0  | 1    | 0    | 0  | 0    | 0  | 0    | 0    | 0    | 1    | 0  | 1 | 1 | 0 | 1 | 0 | 1 |  |
| 20            | 0              | 0   | 0   | 0 | 0   | 0   | 0  | 0  | 1    | 1    | 0  | 0    | 0  | 0    | 0    | 0    | 1    | 1  | 1 | 0 | 0 | 1 | 1 | 0 |  |
| 21            | 0              | 0   | 0   | 0 | 0   | 0   | 0  | 0  | 1    | 0    | 0  | 0    | 0  | 0    | 0    | 0    | 1    | 0  | 0 | 0 | 0 | 0 | 0 | 0 |  |
| 22            | 0              | 0   | 0   | 0 | 0   | 0   | 0  | 0  | 1    | 0    | 0  | 0    | 0  | 0    | 0    | 0    | 1    | 0  | 0 | 0 | 0 | 0 | 0 | 0 |  |
| 23            | 0              | 0   | 0   | 0 | 0   | 0   | 0  | 0  | 0    | 0    | 0  | 0    | 0  | 0    | 0    | 0    | 1    | 0  | 0 | 1 | 1 | 0 | 0 | 1 |  |
| 24            | 0              | 0   | 0   | 0 | 0   | 0   | 0  | 0  | 0    | 0    | 0  | 0    | 0  | 0    | 0    | 0    | 1    | 0  | 0 | 0 | 1 | 1 | 0 | 0 |  |
| 25            | 1              | 0   | 0   | 0 | 0   | 0   | 0  | 0  | 1    | 1    | 0  | 0    | 0  | 1    | 0    | 1    | 1    | 1  | 0 | 0 | 0 | 0 | 0 | 1 |  |
| 26            | 1              | 0   | 0   | 0 | 0   | 0   | 0  | 0  | 1    | 1    | 0  | 0    | 0  | 1    | 0    | 1    | 1    | 0  | 0 | 0 | 0 | 0 | 0 | 0 |  |
| 27            | 0              | 0   | 0   | 0 | 0   | 0   | 0  | 0  | 1    | 1    | 0  | 0    | 0  | 1    | 0    | 1    | 1    | 0  | 0 | 0 | 0 | 0 | 0 | 1 |  |
| 28            | 0              | 0   | 0   | 0 | 0   | 0   | 0  | 0  | 1    | 1    | 0  | 0    | 0  | 1    | 0    | 0    | 1    | 1  | 0 | 0 | 0 | 0 | 0 | 1 |  |
| 29            | 1              | 0   | 0   | 0 | 1   | 0   | 0  | 0  | 1    | 0    | 1  | 0    | 0  | 1    | 0    | 0    | 0    | 1  | 0 | 0 | 0 | 0 | 1 | 0 |  |
| 30            | 1              | 0   | 0   | 0 | 0   | 0   | 0  | 0  | 1    | 0    | 0  | 0    | 0  | 0    | 0    | 0    | 1    | 0  | 0 | 0 | 0 | 0 | 1 | 0 |  |
| 31            | 0              | 1   | 0   | 0 | 0   | 0   | 0  | 0  | 1    | 0    | 0  | 0    | 0  | 0    | 0    | 0    | 0    | 0  | 0 | 0 | 0 | 0 | 1 | 0 |  |
| 32            | 0              | 1   | 0   | 0 | 0   | 0   | 0  | 0  | 1    | 0    | 0  | 0    | 0  | 0    | 0    | 0    | 1    | 1  | 0 | 0 | 0 | 0 | 1 | 0 |  |
| 33            | 0              | 0   | 1   | 0 | 0   | 0   | 0  | 0  | 1    | 0    | 0  | 0    | 0  | 0    | 0    | 0    | 0    | 0  | 0 | 0 | 0 | 0 | 0 | 1 |  |
| 34            | 0              | 0   | 0   | 0 | 0   | 0   | 0  | 0  | 1    | 0    | 0  | 0    | 0  | 0    | 0    | 0    | 1    | 1  | 0 | 1 | 0 | 0 | 1 | 1 |  |
| 35            | 0              | 0   | 0   | 1 | 0   | 0   | 0  | 0  | 0    | 0    | 0  | 0    | 0  | 0    | 0    | 0    | 1    | 0  | 0 | 0 | 1 | 1 | 0 | 1 |  |
| 36            | 0              | 0   | 0   | 1 | 1   | 0   | 0  | 0  | 1    | 0    | 0  | 0    | 0  | 1    | 0    | 1    | 1    | 0  | 0 | 0 | 1 | 1 | 0 | 1 |  |
| 37            | 0              | 0   | 0   | 1 | 1   | 0   | 0  | 0  | 1    | 0    | 0  | 0    | 0  | 1    | 0    | 1    | 1    | 0  | 0 | 0 | 1 | 1 | 1 | 1 |  |
| 38            | 0              | 0   | 0   | 1 | 1   | 0   | 0  | 0  | 1    | 0    | 0  | 0    | 0  | 0    | 0    | 0    | 1    | 0  | 0 | 0 | 1 | 1 | 1 | 1 |  |
| 39            | 0              | 0   | 1   | 0 | 0   | 1   | 0  | 0  | 0    | 1    | 0  | 0    | 0  | 0    | 0    | 0    | 0    | 0  | 0 | 0 | 0 | 1 | 1 | 1 |  |
| 40            | 0              | 0   | 1   | 0 | 0   | 1   | 0  | 0  | 0    | 1    | 0  | 0    | 0  | 0    | 0    | 0    | 0    | 0  | 0 | 0 | 0 | 1 | 1 | 1 |  |
| 41            | 0              | 0   | 1   | 0 | 0   | 1   | 0  | 0  | 1    | 0    | 1  | 0    | 0  | 0    | 0    | 0    | 0    | 0  | 0 | 0 | 0 | 1 | 1 | 1 |  |
| 42            | 0              | 0   | 1   | 0 | 0   | 1   | 0  | 0  | 1    | 0    | 1  | 0    | 0  | 0    | 0    | 0    | 1    | 0  | 0 | 0 | 1 | 1 | 1 | 1 |  |

|    | 26   | 27.2 | 29 | 31 | 33.1 | 34 | 36 | 38 | 40 | 42 | 44.1 | 45 | 47 | 49 | 51 | 53 |
|----|------|------|----|----|------|----|----|----|----|----|------|----|----|----|----|----|
|    | 27.1 | 28   | 30 | 32 | 33.2 | 35 | 37 | 39 | 41 | 43 | 44.2 | 46 | 48 | 50 | 52 | 54 |
| 1  | 1    | 0    | 0  | 0  | 0    | 0  | 0  | 0  | 1  | 0  | 0    | 0  | 1  | 0  | 0  | 0  |
| 2  | 1    | 0    | 0  | 0  | 0    | 1  | 0  | 0  | 0  | 1  | 0    | 0  | 0  | 1  | 1  | 0  |
| 3  | 1    | 1    | 0  | 0  | 0    | 0  | 0  | 0  | 1  | 0  | 0    | 0  | 1  | 1  | 0  | 0  |
| 4  | 1    | 0    | 0  | 0  | 0    | 0  | 0  | 0  | 1  | 0  | 0    | 0  | 0  | 1  | 1  | 0  |
| 5  | 1    | 1    | 0  | 0  | 0    | 0  | 0  | 0  | 1  | 0  | 0    | 0  | 0  | 1  | 1  | 0  |
| 6  | 1    | 1    | 1  | 0  | 0    | 0  | 0  | 0  | 1  | 0  | 0    | 0  | 1  | 1  | 0  | 0  |
| 7  | 1    | 1    | 0  | 0  | 0    | 0  | 0  | 0  | 1  | 0  | 0    | 0  | 1  | 0  | 0  | 0  |
| 8  | 1    | 1    | 0  | 0  | 0    | 0  | 0  | 0  | 1  | 0  | 0    | 0  | 0  | 1  | 1  | 0  |
| 9  | 1    | 0    | 0  | 0  | 0    | 1  | 0  | 0  | 0  | 1  | 0    | 0  | 0  | 1  | 1  | 0  |
| 10 | 1    | 0    | 0  | 0  | 0    | 1  | 0  | 0  | 0  | 1  | 0    | 0  | 0  | 1  | 1  | 0  |
| 11 | 1    | 0    | 0  | 0  | 0    | 1  | 0  | 0  | 0  | 1  | 0    | 0  | 0  | 1  | 1  | 0  |
| 12 | 1    | 1    | 0  | 0  | 0    | 1  | 0  | 0  | 1  | 0  | 0    | 0  | 0  | 1  | 1  | 0  |
| 13 | 1    | 1    | 0  | 0  | 0    | 1  | 0  | 0  | 1  | 0  | 0    | 0  | 0  | 1  | 1  | 0  |
| 14 | 1    | 1    | 0  | 0  | 0    | 1  | 0  | 0  | 1  | 0  | 0    | 0  | 0  | 1  | 1  | 0  |
| 15 | 1    | 0    | 0  | 1  | 0    | 1  | 0  | 0  | 0  | 1  | 0    | 0  | 0  | 1  | 1  | 0  |
| 16 | 1    | 0    | 0  | 0  | 0    | 1  | 1  | 0  | 1  | 1  | 0    | 0  | 0  | 1  | 0  | 0  |
| 17 | 1    | 0    | 0  | 0  | 0    | 1  | 1  | 0  | 1  | 1  | 0    | 0  | 0  | 1  | 1  | 0  |
| 18 | 1    | 1    | 0  | 0  | 0    | 1  | 1  | -  | -  | 0  | 0    | 0  | 0  | 1  | 1  | 0  |
| 19 | 1    | 0    | 0  | 0  | 0    | 1  | 1  | 0  | 1  | 1  | 0    | 1  | 0  | 1  | 1  | 0  |
| 20 | 1    | 1    | 0  | 0  | 0    | 1  | 1  | 0  | 1  | 1  | 0    | 0  | 0  | 1  | 1  | 0  |
| 21 | 1    | 0    | 0  | 0  | 0    | 1  | 1  | -  | -  | 1  | 0    | 0  | 0  | 1  | 1  | 0  |
| 22 | 1    | 0    | 0  | 0  | 0    | 1  | 1  | 0  | 1  | 1  | 0    | 0  | 0  | 1  | 1  | 0  |
| 23 | 1    | 0    | 0  | 0  | 0    | 1  | 1  | -  | -  | 1  | 0    | 0  | 0  | 1  | 1  | 0  |
| 24 | 1    | 1    | 0  | 0  | 0    | 1  | 1  | 0  | 1  | 1  | 0    | 0  | 0  | 1  | 1  | 0  |
| 25 | 1    | 0    | 0  | 0  | 0    | 1  | 0  | 1  | 0  | 0  | 1    | 0  | 0  | 1  | 1  | 1  |
| 26 | 1    | 0    | 0  | 0  | 0    | 1  | 0  | 1  | 0  | 0  | 0    | 0  | 0  | 1  | 1  | 1  |
| 27 | 1    | 0    | 0  | 0  | 0    | 1  | 0  | 1  | 0  | 0  | 0    | 0  | 0  | 1  | 1  | 1  |
| 28 | 1    | 0    | 0  | 0  | 0    | 1  | 0  | -  | 0  | 0  | 0    | 0  | 0  | 1  | 1  | 1  |
| 29 | 1    | 0    | 0  | 0  | 0    | 1  | 0  | 1  | 0  | 0  | 0    | 0  | 0  | 1  | 1  | 1  |
| 30 | 1    | 0    | 0  | 0  | 0    | 1  | 0  | -  | -  | 1  | 0    | 0  | 0  | 1  | 1  | 1  |
| 31 | 1    | 0    | 0  | 0  | 0    | 0  | 0  | 0  | 0  | 1  | 0    | 0  | 0  | 1  | 1  | 0  |
| 32 | 1    | 0    | 0  | 0  | 0    | 1  | 0  | 0  | 0  | 1  | 0    | 0  | 0  | 1  | 1  | 0  |
| 33 | 0    | 0    | 0  | 1  | 0    | 0  | 0  | 1  | 0  | 0  | 1    | 0  | 0  | 1  | 0  | 0  |
| 34 | 0    | 1    | 0  | 0  | 0    | 1  | 0  | -  | -  | 0  | 0    | 0  | 0  | 1  | 1  | 0  |
| 35 | 0    | 1    | 1  | 0  | 0    | 0  | 0  | -  | -  | 0  | 1    | 0  | 1  | 1  | 0  | 0  |
| 36 | 0    | 0    | 0  | 1  | 0    | 1  | 0  | -  | -  | 0  | 1    | 0  | 1  | 1  | 1  | 0  |
| 37 | 0    | 0    | 0  | 1  | 0    | 0  | 0  | -  | -  | 0  | 1    | 0  | 1  | 1  | 1  | 0  |
| 38 | 0    | 0    | 0  | 1  | 0    | 1  | 0  | 0  | 0  | 0  | 1    | 0  | 0  | 0  | 1  | 1  |
| 39 | 0    | 0    | 0  | 0  | 1    | 0  | 0  | 0  | 0  | 0  | 1    | 0  | 0  | 0  | 1  | 0  |
| 40 | 0    | 0    | 0  | 0  | 1    | 0  | 0  | 0  | 0  | 0  | 1    | 1  | 0  | 1  | 1  | 0  |
| 41 | 0    | 1    | 0  | 0  | 1    | 0  | 0  | -  | -  | 0  | 0    | 0  | 0  | 1  | 1  | 0  |
| 42 | 0    | 1    | 0  | 0  | 1    | 0  | 0  | -  | -  | 0  | 0    | 0  | 0  | 1  | 1  | 0  |

### Rhyssine data set (for both analyses)

Taxon  
Nos.

1 2 3 4 5 6 7 8 9 10 11.1 12 13.2 14 15 16 17 18.2 19

[illegible]





## APPENDIX 5

### Initial LEQUB output for the data sets

#### 1. Initial LEQU output for the Townes data set.

Incompatibilities: observed expected ratio - polar

|      |   |    |       |      |   |   |      |   |    |       |      |   |   |
|------|---|----|-------|------|---|---|------|---|----|-------|------|---|---|
| 1    | : | 22 | 28.01 | 0.79 | - | 0 | 2.1  | : | 23 | 38.41 | 0.6  | - | 0 |
| 2.2  | : | 16 | 27    | 0.59 | - | 0 | 3.1  | : | 26 | 29.56 | 0.88 | - | 0 |
| 3.2  | : | 21 | 24.08 | 0.87 | - | 0 | 4    | : | 9  | 24.55 | 0.37 | - | 0 |
| 5    | : | 16 | 37.14 | 0.43 | - | 0 | 6    | : | 19 | 25.06 | 0.76 | - | 0 |
| 7    | : | 6  | 19.5  | 0.31 | - | 0 | 8.1  | : | 37 | 38.07 | 0.97 | - | 0 |
| 8.2  | : | 27 | 37.41 | 0.72 | - | 0 | 9    | : | 18 | 13.05 | 1.38 | - | 0 |
| 10   | : | 16 | 27.9  | 0.57 | - | 0 | 11   | : | 10 | 23.55 | 0.42 | - | 0 |
| 12   | : | 26 | 32.2  | 0.81 | - | 0 | 13   | : | 23 | 13.05 | 1.76 | - | 0 |
| 14.1 | : | 29 | 29.66 | 0.98 | - | 1 | 14.2 | : | 34 | 36.91 | 0.92 | - | 0 |
| 15.1 | : | 28 | 32.9  | 0.85 | - | 0 | 15.2 | : | 34 | 39.19 | 0.87 | - | 0 |
| 16   | : | 8  | 13.05 | 0.61 | - | 0 | 17   | : | 17 | 34.93 | 0.49 | - | 0 |
| 18.1 | : | 31 | 37.68 | 0.82 | - | 0 | 18.2 | : | 31 | 38.14 | 0.81 | - | 0 |
| 19   | : | 8  | 13.33 | 0.6  | - | 0 | 20   | : | 36 | 38.97 | 0.92 | - | 0 |
| 21.1 | : | 27 | 38.12 | 0.71 | - | 0 | 21.2 | : | 27 | 35.32 | 0.76 | - | 0 |
| 21.3 | : | 7  | 19.17 | 0.37 | - | 0 | 22   | : | 24 | 32.53 | 0.74 | - | 0 |
| 23.1 | : | 34 | 39.14 | 0.87 | - | 0 | 23.2 | : | 32 | 33.86 | 0.95 | - | 0 |
| 24.1 | : | 33 | 35.15 | 0.94 | - | 0 | 24.2 | : | 27 | 36.95 | 0.73 | - | 0 |
| 25   | : | 40 | 39.24 | 1.02 | - | 0 | 26   | : | 24 | 35.39 | 0.68 | - | 1 |
| 27.1 | : | 39 | 38.67 | 1.01 | - | 0 | 27.2 | : | 13 | 12.58 | 1.03 | - | 0 |
| 28   | : | 24 | 34.73 | 0.69 | - | 0 | 29   | : | 9  | 24.55 | 0.37 | - | 0 |
| 30   | : | 29 | 39.2  | 0.74 | - | 0 | 31   | : | 17 | 34.93 | 0.49 | - | 0 |
| 32   | : | 19 | 24.87 | 0.76 | - | 0 | 33.1 | : | 15 | 29.51 | 0.51 | - | 0 |
| 33.2 | : | 13 | 25.83 | 0.5  | - | 0 |      |   |    |       |      |   |   |

Grand total - 512 681.51 0.75

| Ranking |      |      |     |      |    |      |      | ratios |      |
|---------|------|------|-----|------|----|------|------|--------|------|
| 7       | 21.3 | 4    | 29  | 11   | 5  | 31   | 17   | 33.2   | 33.1 |
| 10      | 2.2  | 2.1  | 19  | 16   | 26 | 28   | 21.1 | 8.2    | 24.2 |
| 22      | 30   | 6    | 32  | 21.2 | 1  | 12   | 18.2 | 18.1   | 15.1 |
| 15.2    | 23.1 | 3.2  | 3.1 | 14.2 | 20 | 24.1 | 23.2 | 8.1    | 14.1 |
| 27.1    | 25   | 27.2 | 9   | 13   |    |      |      |        |      |

## 2. Initial LEQU output for the final pimpline data set.

Incompatibilities: observed expected ratio - polar

|      |   |    |       |      |   |   |      |   |    |       |      |   |    |
|------|---|----|-------|------|---|---|------|---|----|-------|------|---|----|
| 1    | : | 29 | 37.87 | 0.77 | - | 0 | 2.1  | : | 26 | 56.63 | 0.46 | - | 0  |
| 2.2  | : | 25 | 36.86 | 0.68 | - | 1 | 3.1  | : | 33 | 40.76 | 0.81 | - | 0  |
| 3.2  | : | 32 | 32.43 | 0.99 | - | 0 | 4    | : | 13 | 32.91 | 0.4  | - | 0  |
| 5    | : | 18 | 53.17 | 0.34 | - | 0 | 6    | : | 28 | 33.41 | 0.84 | - | 0  |
| 7    | : | 8  | 26.11 | 0.31 | - | 0 | 8.1  | : | 50 | 56.29 | 0.89 | - | 0  |
| 8.2  | : | 38 | 55.63 | 0.68 | - | 0 | 9    | : | 22 | 17.46 | 1.26 | - | 0  |
| 10   | : | 13 | 32.91 | 0.4  | - | 0 | 11   | : | 12 | 31.9  | 0.38 | - | 0  |
| 12   | : | 36 | 44.54 | 0.81 | - | 0 | 13   | : | 26 | 17.46 | 1.49 | - | 0  |
| 14.1 | : | 36 | 40.79 | 0.88 | - | 3 | 14.2 | : | 53 | 53.61 | 0.99 | - | 0  |
| 15.1 | : | 39 | 46.36 | 0.84 | - | 1 | 15.2 | : | 45 | 58.44 | 0.77 | - | 1  |
| 16   | : | 11 | 17.46 | 0.63 | - | 0 | 17   | : | 21 | 49.31 | 0.43 | - | 0  |
| 18.1 | : | 31 | 58.06 | 0.53 | - | 0 | 18.2 | : | 4  | 16.97 | 0.24 | - | 0  |
| 19   | : | 11 | 17.74 | 0.62 | - | 0 | 20   | : | 48 | 57.19 | 0.84 | - | 0  |
| 21.1 | : | 30 | 56.98 | 0.53 | - | 0 | 21.2 | : | 30 | 51.33 | 0.58 | - | 0  |
| 21.3 | : | 9  | 25.78 | 0.35 | - | 0 | 22   | : | 33 | 45.99 | 0.72 | - | 0  |
| 23.1 | : | 44 | 58.38 | 0.75 | - | 1 | 23.2 | : | 45 | 48.19 | 0.93 | - | 1  |
| 24.1 | : | 44 | 50.43 | 0.87 | - | 1 | 24.2 | : | 42 | 52.89 | 0.79 | - | 0  |
| 25   | : | 59 | 57.44 | 1.03 | - | 0 | 26   | : | 28 | 50.66 | 0.55 | - | 1  |
| 27.1 | : | 54 | 56.89 | 0.95 | - | 0 | 27.2 | : | 21 | 16.99 | 1.24 | - | 0  |
| 28   | : | 31 | 37.76 | 0.82 | - | 0 | 29   | : | 13 | 32.91 | 0.4  | - | 0  |
| 30   | : | 41 | 57.42 | 0.71 | - | 0 | 31   | : | 21 | 49.31 | 0.43 | - | 0  |
| 32   | : | 28 | 31.45 | 0.89 | - | 0 | 33.1 | : | 18 | 38.63 | 0.47 | - | 0  |
| 33.2 | : | 16 | 32.99 | 0.49 | - | 0 | 34   | : | 46 | 59    | 0.78 | - | 0  |
| 35   | : | 12 | 31.9  | 0.38 | - | 0 | 36   | : | 12 | 33.16 | 0.36 | - | 0  |
| 37   | : | 12 | 26.11 | 0.46 | - | 0 | 38   | : | 58 | 55.78 | 1.04 | - | 1  |
| 39   | : | 33 | 52.57 | 0.63 | - | 2 | 40   | : | 16 | 33.51 | 0.48 | - | 0  |
| 41   | : | 8  | 26.11 | 0.31 | - | 0 | 42   | : | 13 | 32.91 | 0.4  | - | 10 |
| 43   | : | 19 | 41.76 | 0.45 | - | 0 | 44.1 | : | 13 | 32.64 | 0.4  | - | 0  |
| 44.2 | : | 8  | 25.85 | 0.31 | - | 0 | 45   | : | 24 | 37.26 | 0.64 | - | 0  |
| 46   | : | 38 | 38.1  | 1    | - | 2 | 47   | : | 41 | 37.76 | 1.09 | - | 2  |
| 48   | : | 19 | 41.76 | 0.45 | - | 0 | 49   | : | 27 | 26.11 | 1.03 | - | 0  |
| 50   | : | 32 | 41.33 | 0.77 | - | 1 | 51   | : | 12 | 31.9  | 0.38 | - | 0  |
| 52   | : | 24 | 37.26 | 0.64 | - | 0 | 53   | : | 13 | 32.91 | 0.4  | - | 0  |
| 54   | : | 17 | 33.8  | 0.5  | - | 0 |      |   |    |       |      |   |    |

Grand total - 906 1342.09 0.68

| Ranking |      |      |      |      |      |      |      |      |      | ratios |  |
|---------|------|------|------|------|------|------|------|------|------|--------|--|
| 18.2    | 41   | 7    | 44.2 | 5    | 21.3 | 36   | 11   | 35   | 51   |        |  |
| 10      | 4    | 29   | 53   | 42   | 44.1 | 17   | 31   | 43   | 48   |        |  |
| 2.1     | 37   | 33.1 | 40   | 33.2 | 54   | 21.1 | 18.1 | 26   | 21.2 |        |  |
| 19      | 39   | 16   | 52   | 45   | 2.2  | 8.2  | 30   | 22   | 23.1 |        |  |
| 1       | 15.2 | 50   | 34   | 24.2 | 12   | 3.1  | 28   | 6    | 20   |        |  |
| 15.1    | 24.1 | 14.1 | 8.1  | 32   | 23.2 | 27.1 | 3.2  | 14.2 | 46   |        |  |
| 25      | 49   | 38   | 47   | 27.2 | 9    | 13   |      |      |      |        |  |

3. Initial LEQU output for the rhyssine data set without male gaster characters.

Incompatibilities: observed expected ratio - polar

|      |   |    |       |      |   |   |      |   |    |       |      |   |   |
|------|---|----|-------|------|---|---|------|---|----|-------|------|---|---|
| 1    | : | 33 | 46.01 | 0.72 | - | 9 | 2    | : | 24 | 37.46 | 0.64 | - | 0 |
| 3    | : | 18 | 28.5  | 0.63 | - | 0 | 4    | : | 14 | 15.64 | 0.9  | - | 0 |
| 5    | : | 0  | -     | -    | - | 0 | 6    | : | 45 | 53.4  | 0.84 | - | 5 |
| 7    | : | 48 | 55.14 | 0.87 | - | 0 | 8    | : | 48 | 55.09 | 0.87 | - | 0 |
| 9    | : | 58 | 55.02 | 1.05 | - | 0 | 10   | : | 32 | 44.98 | 0.71 | - | 0 |
| 11.1 | : | 17 | 38.99 | 0.44 | - | 0 | 11.2 | : | 21 | 31.79 | 0.66 | - | 0 |
| 12   | : | 6  | 15.64 | 0.38 | - | 0 | 13.1 | : | 52 | 50.09 | 1.04 | - | 0 |
| 13.2 | : | 31 | 40.15 | 0.77 | - | 0 | 14   | : | 3  | 28.5  | 0.11 | - | 4 |
| 15   | : | 40 | 53.1  | 0.75 | - | 0 | 16   | : | 25 | 51.03 | 0.49 | - | 1 |
| 17   | : | 40 | 50.49 | 0.79 | - | 0 | 18.1 | : | 3  | 27.12 | 0.11 | - | 4 |
| 18.2 | : | 15 | 43.49 | 0.34 | - | 1 | 18.3 | : | 45 | 53.26 | 0.84 | - | 0 |
| 19   | : | 13 | 28.5  | 0.46 | - | 0 | 20   | : | 34 | 37.46 | 0.91 | - | 0 |
| 21   | : | 45 | 54.36 | 0.83 | - | 0 | 23   | : | 12 | 15.64 | 0.77 | - | 0 |
| 24.1 | : | 43 | 53.31 | 0.81 | - | 4 | 24.2 | : | 16 | 27.48 | 0.58 | - | 0 |
| 24.3 | : | 13 | 22.53 | 0.58 | - | 0 | 25.1 | : | 18 | 23.27 | 0.77 | - | 0 |
| 25.2 | : | 19 | 28.35 | 0.67 | - | 0 | 26   | : | 0  | -     | -    | - | 0 |
| 27.1 | : | 33 | 52.68 | 0.63 | - | 1 | 27.2 | : | 39 | 48.26 | 0.81 | - | 0 |
| 28   | : | 44 | 50.49 | 0.87 | - | 0 | 29.1 | : | 28 | 31.31 | 0.89 | - | 0 |
| 29.2 | : | 46 | 53.26 | 0.86 | - | 0 | 30   | : | 8  | 15.64 | 0.51 | - | 0 |
| 31.1 | : | 3  | 27.73 | 0.11 | - | 4 | 31.2 | : | 44 | 51.98 | 0.85 | - | 0 |
| 32.1 | : | 44 | 52.42 | 0.84 | - | 0 | 32.2 | : | 26 | 40.12 | 0.65 | - | 4 |
| 33   | : | 3  | 28.5  | 0.11 | - | 4 | 34   | : | 15 | 46.01 | 0.33 | - | 1 |
| 35   | : | 39 | 46.01 | 0.85 | - | 0 | 36.1 | : | 38 | 52.69 | 0.72 | - | 0 |
| 36.2 | : | 32 | 41.56 | 0.77 | - | 0 | 38   | : | 49 | 55.17 | 0.89 | - | 0 |
| 39   | : | 22 | 43.84 | 0.5  | - | 0 | 40.1 | : | 37 | 49.1  | 0.75 | - | 0 |
| 40.2 | : | 24 | 34.3  | 0.7  | - | 0 | 41   | : | 37 | 50.49 | 0.73 | - | 0 |
| 42.1 | : | 3  | 28    | 0.11 | - | 0 | 42.2 | : | 26 | 44.49 | 0.58 | - | 2 |
| 43.1 | : | 36 | 36.79 | 0.98 | - | 0 | 43.2 | : | 32 | 43.17 | 0.74 | - | 0 |
| 47.1 | : | 43 | 48.56 | 0.89 | - | 0 | 48.1 | : | 44 | 51.06 | 0.86 | - | 0 |
| 48.2 | : | 33 | 36.55 | 0.9  | - | 0 | 49   | : | 17 | 39.42 | 0.43 | - | 0 |
| 50.1 | : | 12 | 37.14 | 0.32 | - | 0 | 50.2 | : | 24 | 28.18 | 0.85 | - | 0 |

Grand total - 856 1215.36 0.7

| Ranking |      |      |      |      |      |      |      |      | ratios |  |
|---------|------|------|------|------|------|------|------|------|--------|--|
| 5       | 26   | 33   | 14   | 42.1 | 31.1 | 18.1 | 50.1 | 34   | 18.2   |  |
| 12      | 49   | 11.1 | 19   | 16   | 39   | 30   | 24.3 | 24.2 | 42.2   |  |
| 27.1    | 3    | 2    | 32.2 | 11.2 | 25.2 | 40.2 | 10   | 1    | 36.1   |  |
| 41      | 43.2 | 15   | 40.1 | 23   | 36.2 | 13.2 | 25.1 | 17   | 24.1   |  |
| 27.2    | 21   | 32.1 | 6    | 18.3 | 31.2 | 35   | 50.2 | 48.1 | 29.2   |  |
| 7       | 8    | 28   | 47.1 | 38   | 29.1 | 4    | 48.2 | 20   | 43.1   |  |
| 13.1    | 9    |      |      |      |      |      |      |      |        |  |

#### 4. Initial LEQU output for the rhyssine data set with male gaster characters.

Incompatibilities: observed expected ratio - polar

|      |   |    |       |      |   |   |      |   |    |       |      |   |   |
|------|---|----|-------|------|---|---|------|---|----|-------|------|---|---|
| 1    | : | 33 | 47.79 | 0.69 | - | 9 | 2    | : | 24 | 38.83 | 0.62 | - | 0 |
| 3    | : | 18 | 29.45 | 0.61 | - | 0 | 4    | : | 14 | 16.15 | 0.87 | - | 0 |
| 5    | : | 0  | -     | -    | - | 0 | 6    | : | 47 | 55.39 | 0.85 | - | 5 |
| 7    | : | 50 | 57.14 | 0.88 | - | 0 | 8    | : | 50 | 57.09 | 0.88 | - | 0 |
| 9    | : | 60 | 57.02 | 1.05 | - | 0 | 10   | : | 32 | 46.72 | 0.68 | - | 0 |
| 11.1 | : | 17 | 40.46 | 0.42 | - | 0 | 11.2 | : | 21 | 32.9  | 0.64 | - | 0 |
| 12   | : | 6  | 16.15 | 0.37 | - | 0 | 13.1 | : | 54 | 52.03 | 1.04 | - | 0 |
| 13.2 | : | 31 | 41.71 | 0.74 | - | 0 | 14   | : | 3  | 29.45 | 0.1  | - | 4 |
| 15   | : | 40 | 55.08 | 0.73 | - | 0 | 16   | : | 25 | 52.98 | 0.47 | - | 1 |
| 17   | : | 40 | 52.43 | 0.76 | - | 0 | 18.1 | : | 3  | 28.07 | 0.11 | - | 4 |
| 18.2 | : | 17 | 45.23 | 0.38 | - | 1 | 18.3 | : | 45 | 55.26 | 0.81 | - | 0 |
| 19   | : | 13 | 29.45 | 0.44 | - | 0 | 20   | : | 36 | 38.83 | 0.93 | - | 0 |
| 21   | : | 45 | 56.36 | 0.8  | - | 0 | 23   | : | 12 | 16.15 | 0.74 | - | 0 |
| 24.1 | : | 45 | 55.31 | 0.81 | - | 4 | 24.2 | : | 16 | 28.43 | 0.56 | - | 0 |
| 24.3 | : | 13 | 23.29 | 0.56 | - | 0 | 25.1 | : | 18 | 24.04 | 0.75 | - | 0 |
| 25.2 | : | 19 | 29.3  | 0.65 | - | 0 | 26   | : | 0  | -     | -    | - | 0 |
| 27.1 | : | 33 | 54.67 | 0.6  | - | 1 | 27.2 | : | 39 | 50.16 | 0.78 | - | 0 |
| 28   | : | 46 | 52.43 | 0.88 | - | 0 | 29.1 | : | 28 | 32.42 | 0.86 | - | 0 |
| 29.2 | : | 48 | 55.25 | 0.87 | - | 0 | 30   | : | 8  | 16.15 | 0.5  | - | 0 |
| 31.1 | : | 3  | 28.68 | 0.1  | - | 4 | 31.2 | : | 44 | 53.96 | 0.82 | - | 0 |
| 32.1 | : | 45 | 54.41 | 0.83 | - | 0 | 32.2 | : | 27 | 41.67 | 0.65 | - | 4 |
| 33   | : | 3  | 29.45 | 0.1  | - | 4 | 34   | : | 17 | 47.79 | 0.36 | - | 1 |
| 35   | : | 39 | 47.79 | 0.82 | - | 0 | 36.1 | : | 38 | 54.68 | 0.69 | - | 0 |
| 36.2 | : | 32 | 43.19 | 0.74 | - | 0 | 38   | : | 51 | 57.17 | 0.89 | - | 0 |
| 39   | : | 22 | 45.52 | 0.48 | - | 0 | 40.1 | : | 37 | 51.02 | 0.73 | - | 0 |
| 40.2 | : | 24 | 35.56 | 0.68 | - | 0 | 41   | : | 37 | 52.43 | 0.71 | - | 0 |
| 42.1 | : | 3  | 28.96 | 0.1  | - | 0 | 42.2 | : | 26 | 46.23 | 0.56 | - | 2 |
| 43.1 | : | 38 | 38.16 | 1    | - | 0 | 43.2 | : | 32 | 44.85 | 0.71 | - | 0 |
| 47.1 | : | 45 | 50.44 | 0.89 | - | 0 | 48.1 | : | 44 | 53.02 | 0.83 | - | 0 |
| 48.2 | : | 33 | 37.92 | 0.87 | - | 0 | 49   | : | 17 | 40.89 | 0.42 | - | 0 |
| 50.1 | : | 12 | 38.51 | 0.31 | - | 0 | 50.2 | : | 24 | 29.13 | 0.82 | - | 0 |
| 51   | : | 16 | 47.79 | 0.33 | - | 0 | 52   | : | 14 | 44.18 | 0.32 | - | 0 |

Grand total - 886 1306.48 0.68

| Ranking |      |      |      |      |      |      |      |      | ratios |  |
|---------|------|------|------|------|------|------|------|------|--------|--|
| 5       | 26   | 33   | 14   | 42.1 | 31.1 | 18.1 | 50.1 | 52   | 51     |  |
| 34      | 12   | 18.2 | 49   | 11.1 | 19   | 16   | 39   | 30   | 24.3   |  |
| 42.2    | 24.2 | 27.1 | 3    | 2    | 11.2 | 32.2 | 25.2 | 40.2 | 10     |  |
| 1       | 36.1 | 41   | 43.2 | 40.1 | 15   | 36.2 | 23   | 13.2 | 25.1   |  |
| 17      | 27.2 | 21   | 24.1 | 18.3 | 31.2 | 35   | 50.2 | 32.1 | 48.1   |  |
| 6       | 29.1 | 4    | 29.2 | 48.2 | 7    | 8    | 28   | 38   | 47.1   |  |
| 20      | 43.1 | 13.1 | 9    |      |      |      |      |      |        |  |

# APPENDIX 6

## Emergence records from Thompson (numbers of each sex and totals per year)

(Totals shown week by week. Week 1 = 22-29th April)

| Week | 1955 |      |        | 1956 |      |        | 1957 |      |        |
|------|------|------|--------|------|------|--------|------|------|--------|
|      | tot  | male | female | tot  | male | female | tot  | male | female |
| 1    | 0    | 0    | 0      | 0    | 0    | 0      | 17   | 15   | 2      |
| 2    | 0    | 0    | 0      | 0    | 0    | 0      | 12   | 11   | 1      |
| 3    | 44   | 39   | 5      | 2    | 43   | 9      | 22   | 14   | 8      |
| 4    | 30   | 20   | 10     | 1    | 49   | 12     | 41   | 32   | 19     |
| 5    | 98   | 57   | 41     | 7    | 33   | 24     | 37   | 19   | 18     |
| 6    | 72   | 27   | 45     | 5    | 17   | 8      | 34   | 12   | 22     |
| 7    | 45   | 12   | 33     | 6    | 5    | 1      | 15   | 2    | 13     |
| 8    | 20   | 5    | 15     | 3    | 1    | 2      | 10   | 3    | 7      |
| 9    | 7    | 4    | 3      | 1    | 0    | 0      | 10   | 9    | 1      |
| 10   | 0    | 0    | 0      | 2    | 1    | 0      | 11   | 10   | 1      |
| 11   | 5    | 4    | 1      | 3    | 2    | 0      | 5    | 3    | 2      |
| 12   | 6    | 6    | 0      | 1    | 3    | 0      | 4    | 2    | 2      |
| 13   | 5    | 5    | 0      | 0    | 1    | 0      | 1    | 0    | 1      |
| 14   | 0    | 0    | 0      | 0    | 0    | 0      | 2    | 0    | 2      |
| 15   | 0    | 0    | 0      | 0    | 0    | 0      | 1    | 1    | 0      |
| 16   | 0    | 0    | 0      | 0    | 0    | 0      | 0    | 0    | 0      |
| 17   | 0    | 0    | 0      | 0    | 0    | 0      | 0    | 0    | 0      |
| 18   | 0    | 0    | 0      | 0    | 0    | 0      | 1    | 1    | 0      |

| Week | 1958 |      |        | 1959 |      |        | 1960 |      |        |
|------|------|------|--------|------|------|--------|------|------|--------|
|      | tot  | male | female | tot  | male | female | tot  | male | female |
| 1    | 0    | 0    | 0      | 79   | 74   | 5      | 0    | 0    | 0      |
| 2    | 0    | 0    | 0      | 143  | 131  | 12     | 3    | 3    | 0      |
| 3    | 1    | 1    | 0      | 249  | 182  | 67     | 151  | 120  | 31     |
| 4    | 6    | 4    | 2      | 76   | 42   | 34     | 138  | 93   | 45     |
| 5    | 18   | 13   | 5      | 106  | 65   | 41     | 129  | 79   | 50     |
| 6    | 7    | 6    | 1      | 32   | 15   | 17     | 50   | 25   | 25     |
| 7    | 12   | 7    | 5      | 8    | 4    | 4      | 4    | 2    | 2      |
| 8    | 7    | 2    | 5      | 19   | 14   | 5      | 7    | 4    | 3      |
| 9    | 1    | 0    | 1      | 32   | 30   | 2      | 13   | 12   | 1      |
| 10   | 0    | 0    | 0      | 47   | 45   | 2      | 16   | 15   | 1      |
| 11   | 0    | 0    | 0      | 63   | 59   | 4      | 21   | 19   | 2      |
| 12   | 2    | 2    | 0      | 9    | 8    | 1      | 12   | 11   | 1      |
| 13   | 0    | 0    | 0      | 3    | 3    | 0      | 12   | 11   | 1      |
| 14   | 2    | 2    | 0      | 1    | 0    | 1      | 2    | 1    | 1      |
| 15   | 0    | 0    | 0      | 1    | 1    | 0      | 2    | 1    | 1      |
| 16   | 0    | 0    | 0      | 3    | 3    | 0      | 2    | 1    | 1      |
| 17   | 0    | 0    | 0      | 2    | 2    | 0      | 2    | 1    | 1      |
| 18   | 0    | 0    | 0      | 0    | 0    | 0      | 2    | 1    | 1      |

Forewing and male gaster data.

*Megarhyssa greenei*

*Rhyssa persuasoria*

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| 16.4 | 7.4 | 3.2 |
| 15.2 | 7.0 | 3.1 |
| 14.0 | 5.4 | 2.7 |

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| 17.6 | 4.1 | 4.8 |
| 14.2 | 3.2 | 4.0 |
| 12.1 | 3.2 | 3.4 |
| 11.2 | 3.9 | 4.7 |
| 12.0 | 3.4 | 2.6 |

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