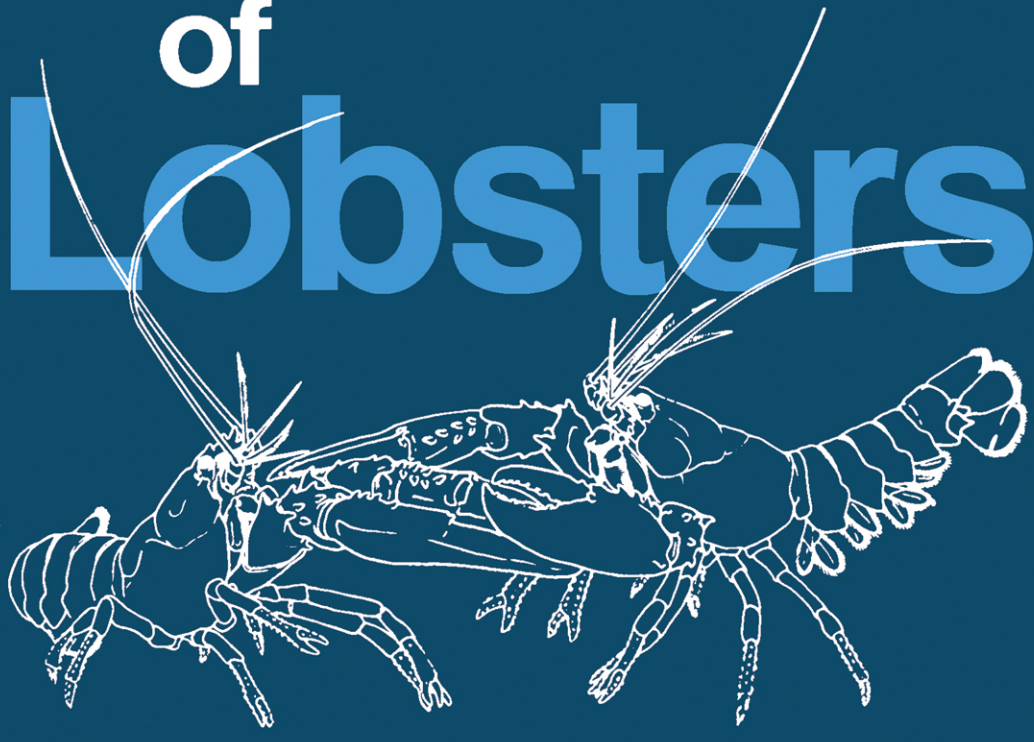
The Biology and Management of Lobsters



VOLUME I: Physiology and Behavior

Edited by J. STANLEY COBB and BRUCE F. PHILLIPS

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THE BIOLOGY AND MANAGEMENT OF LOBSTERS

Volume I

Homarus americanus, the American Lobster. Photo by Thecla Dake.

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Volume I

Physiology and Behavior

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Preface

For over 100 years, lobsters have been the subject of extensive research and intense fishing pressure. Interest in the fundamental and the applied biology of lobsters has been growing steadily over a long time, not only because of the commercial importance of the group, but also because they are an excellent and fertile substrate for physiological, biochemical, and neurobiological research. These two volumes are intended to provide a review and synthesis of the great quantity of research that has been done on the biology of lobsters and to integrate this with management strategies and problems.

The decision to produce this book was made at a workshop on Lobster ecology and physiology held in Perth, Western Australia, in 1977. The participants drew attention to the fact that, although some treatments of lobster biology have been provided for general audiences, there was a need to assemble a volume that reviewed and synthesized previous research, in addition to presenting current information on significant areas of ongoing research. The proceedings of the workshop were published shortly thereafter by CSIRO. This book represents a revision and expansion of these proceedings. To provide a wider coverage of the field, we invited several additional investigators to contribute to this effort.

The animals colloquially called lobsters, rock lobsters, or marine crayfish fall into several taxonomically distinct groups: the clawed lobsters (Nephropidae), the spiny lobsters (Palinuridae), the slipper lobsters (Scyllaridae), and the coral lobsters (Synaxidae). Despite the taxonomic differences, it seems appropriate to treat them together. As W. Herrnkind pointed out at the workshop, the lobster is a very significant biological entity. It is widely distributed, large in size, long lived, abundant, and ecologically consequential.

Although lobsters are a morphologically diverse group composed of many species, the ecological differences between them are not great, and they appear to be physiologically quite similar. A greater understanding of how lobsters achieve their biological success will be an important scientific contribution. Their commercial importance as a fishery heightens interest and broadens the areas of participation, as well as providing a certain direction and support for some of the research.

In these volumes, we are addressing a diverse audience—lobster biologists certainly—but more generally, researchers in the fields of crustacean physiology, behavior, and ecology, who will, it is hoped, find this information useful. The reviews of population dynamics and fishery management strategies contain many lessons for fisheries biologists and managers. The synthesis of the existing knowledge of basic lobster biology is necessary to the advancement of crustacean aquaculture.

The topics selected for review here represent areas of current active research where there is sufficient knowledge unique to lobsters to make a coherent contribution. We have intentionally limited the scope of the work, excluding detailed treatment of cell biology and genetics. Despite this, it has been necessary to produce two volumes, the first devoted to physiology and behavior, the second to ecology and management.

A summary of the biology of lobsters constitutes the subject matter of the first chapter of Volume I in order to provide a general background for readers of both volumes. It broadly outlines the life history, physiology, ecology, and fishery of the whole group of animals known as lobsters. The remaining chapters in this volume cover aspects of growth, neurobiology, reproduction, nutrition, pathology, movement patterns, and social behavior. In the second volume, ecology and population dynamics are treated along with descriptions of fisheries management and aquaculture. All represent areas of active research that have not recently been synthesized into a useful form. We especially asked all the authors to write chapters that would reflect their own research interests in the broad context of a review of the current status of the field.

To the many friends and colleagues who have helped in the preparation of this volume, we extend heartfelt thanks. Fortunately for us they have been many, but their large numbers make individual acknowledgment almost impossible. We wish to thank in particular the following for their encouragement, advice, and critical comments: P. F. Berry, Oceanographic Research Institute, Durban; L. B. Holthius, Rijksmuseum van Natuurlijke Historie, Leiden; M. S. Laverack, Gatty Marine Laboratory, St. Andrews, Scotland; and W. Wales, Scottish Marine Biological Association.

The authors of Chapter 3 thank F. Lang and M. Mote for their comments on the manuscript, and the author of Chapter 7 thanks G. Davis, R. Nishimoto, A. F. Walton, W. Lindberg, D. Wynne, and R. Lipcius. Herrnkind's research has been supported by the National Science Foundation, the National Geographic Society, the Florida Department of Natural Resources, and Florida State University. As noted above, the book was conceived during a workshop on lobster biology supported by the National Science Foundation (U.S.A.) and the Department of Science (Australia). We began it while J. S. Cobb was on his sabbatical leave from the University of Rhode Island as the Visiting Scientist at CSIRO Division of Fisheries and Oceanography, Perth, Australia. Much of his research

has been supported by the U.S. Sea Grant program. P. Barbour, S. Dennerlein, J. Downey, S. Koerner, G. McBride, R. Saunders, and C. Squires cheerfully provided excellent help in preparing the text. Finally, we owe a great debt of gratitude to our wives, Laurie and Dale, and our children, who have put up with too many late nights and too many long trips while we worked on this book.

J. S. Cobb
B. F. Phillips

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Ecology and Management

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Chapter 1

General Biology

B. F. PHILLIPS, J. S. COBB, AND R. W. GEORGE

THE BIOLOGY AND MANAGEMENT OF LOBSTERS, VOL. I

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I. INTRODUCTION

There are four major families of decapod crustacea commonly referred to as "lobsters" (Fig. 1). The clawed lobsters (family Nephropidae) include the well known European *Homarus gammarus,* the American *Homarus americanus* and the Norway lobster *Nephrops norvegicus,* as well as a number of lesser known species. The other three families do not carry claws. The Palinuridae, or spiny lobsters, so called because of the many spines on the carapace and basal segments of the long second antennae, are also often referred to as rock lobsters.

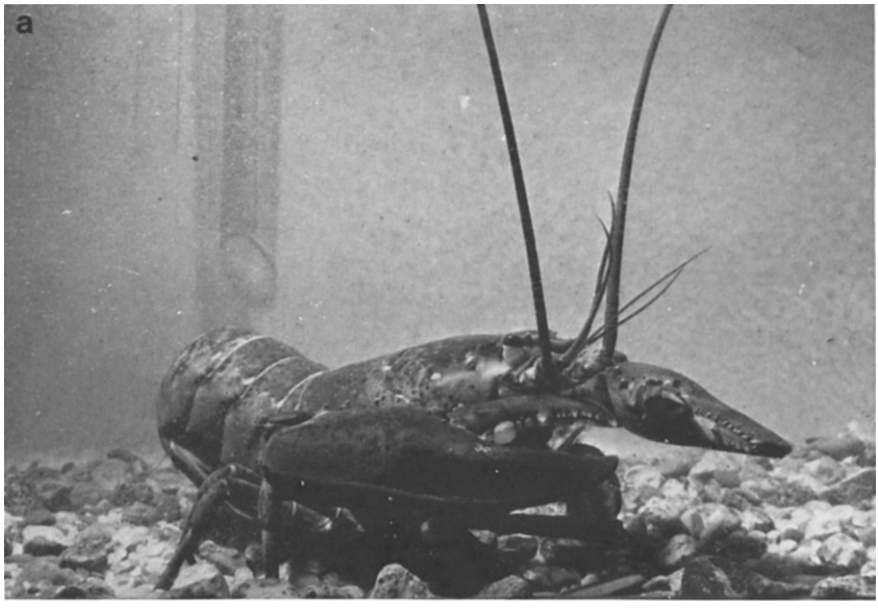
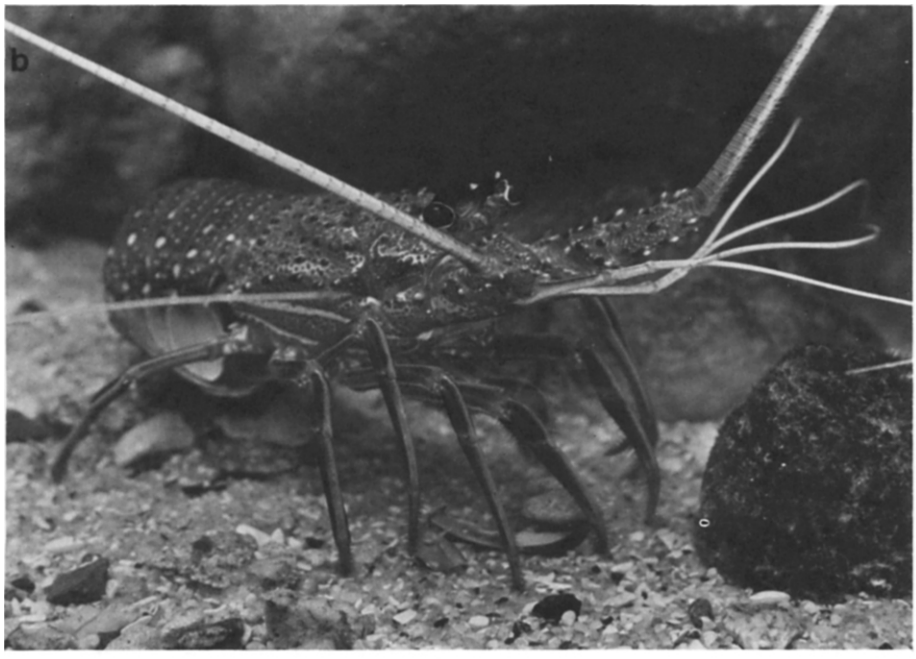


Fig. 1. General representatives of each family of lobsters. (a) The American lobster *Homarus americanus* (photo by Eric Scott). (b) The spiny lobster *Panulirus cygnus* (photo by W. Van Aiken). (c) The slipper lobster *Scyllarides squammosus* (photo by W. Van Aiken). (d) The coral lobster *Palinurellus gundlachi gundlachi* (photo by W. Van Aiken).



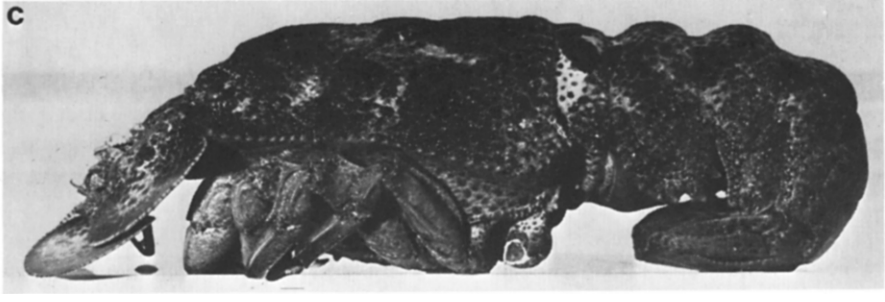


Fig. 1. *(continued)*

They, like the clawed lobsters, have a subcylindrical carapace but carry horns over the eyes rather than having a rostrum between the eyes. The coral lobsters of the family Synaxidae have a subcylindrical carapace, moderate length second antennae, and a rostrum between the eyes. The slipper lobsters, family Scyllaridae, are also known as Spanish lobsters, and shovel-nosed lobsters. They

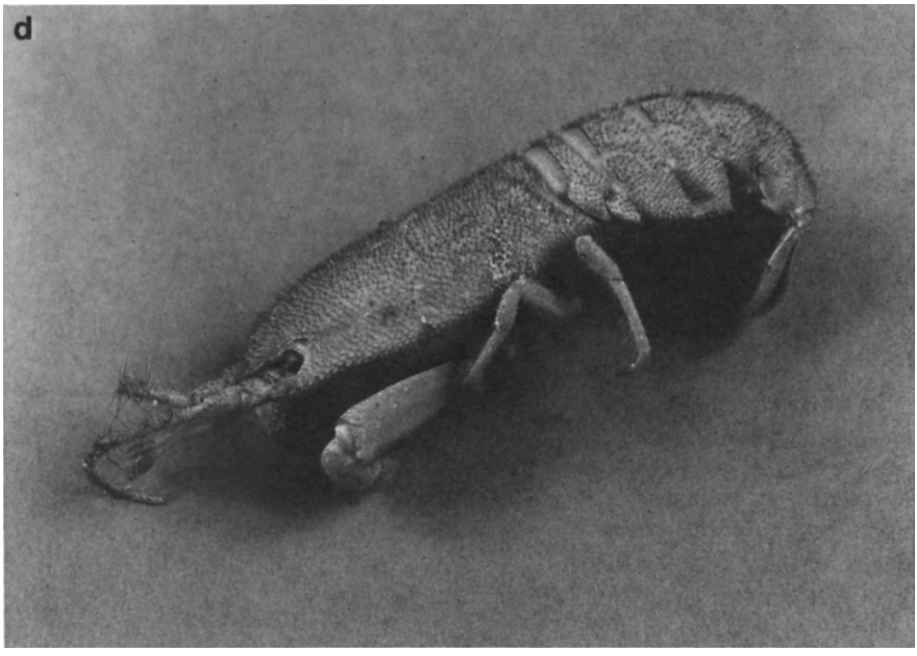


Fig. 1. (*continued*)

have a flattened carapace that bears no rostrum or horns anteriorally, and have short, broad second antennae. The lobsters are known by a wide variety of vernacular names (e.g., Farmer, 1975, lists 53 names for *Nephrops norvegicus* alone). The vernacular names used in this volume will be those first mentioned above, or will be identified at the time they are used.

The adults of the clawed and spiny lobsters might well be considered as ecological equivalents because of their large size and generally similar habits and habitats. Many of the species that are important commercially live in relatively shallow water, where food is available and where rocks, reefs, or marine growths are present for shelter. Many of the *Nephrops* species and most of the slipper lobsters occur on relatively soft, sandy, or muddy substrates. Most lobsters are nocturnally active and all have similar prey and predators.

In many respects, the life cycle and behavior, particularly of the larval and juvenile stages, are markedly different between families. The clawed lobsters that have been studied carry eggs for a relatively long period, have a short and simple free-swimming larval period, and as adults, live singly in burrows excavated in mud under rocks. In contrast, the known species of spiny and slipper

lobsters carry the eggs for a relatively short period, have a long larval life, and the adult spiny lobsters usually live gregariously in shelters in rocky or coral reef systems. The coral lobsters are known from only a few adult specimens found among coral boulders and a few larval specimens caught in plankton nets.

This chapter gives a general overview of the biology of the diverse group of decapods known as lobsters. Our intent is twofold: to introduce the following chapters and give a common background, and to supply information that is not covered elsewhere in the book. The chapters that follow are up-to-date comprehensive reviews of the "state of the art" for many aspects of lobster biology, but in a number of other areas, information is lacking. It is hoped that this chapter will be read for general background and the rest of the book consulted for specific details. Authors of chapters have been encouraged to provide comprehensive references to material within their subjects, but the final reference list should not be taken as a complete bibliography on lobsters. Those seeking such a listing should consult works such as Nowak (1972) for *Homarus americanus*, Kanciruk and Herrnkind (1976) for spiny lobsters, and Farmer (1975) for *Nephrops norvegicus*.

II. DISTRIBUTION AND GENERAL ECOLOGY

A. Larvae

The distribution and dispersal of lobsters is effected by the planktonic larval phase in their life history. The larval life of the clawed lobster is very different from that of the spiny, slipper, or coral lobsters. The clawed lobsters have a short and simple larval period (3 weeks, 4 stages), whereas the spiny, slipper, and coral lobsters have a long (3–22 months) and complex larval period, i.e., the larvae possess a phyllosoma (leaflike) form and pass through many stages.

Homarus americanus larvae molt four times. First, second, and third-stage larvae look differently and behave differently from the adult. They are free-swimming for the first three stages, which last 10–20 days, depending on water temperature (Hughes and Matthiessen, 1962). After molting into the fourth stage, the larva resembles the adult, yet continues to swim for several days before seeking the bottom. Fifth-stage lobsters are probably completely bottom-seeking, although swimming has been observed. The larvae of *H. gammarus* are very similar to those of *H. americanus* but are generally larger at all stages, the differences being particularly marked in the stage I larvae (Gruffydd *et al.*, 1975).

In *N. norvegicus* there are four pelagic stages similar to *Homarus* (Santucci, 1926). Both *Nephrops* and *Homarus* larvae are figured in Chapter 1, Vol. II. Almost nothing is known of the ecology of the larvae of other clawed lobster genera. Berry (1969) concluded that a deep water species, *Metanephrops an-*

damanicus, has a single zoea larva that probably settles almost immediately after release from the egg.

The larval stages of spiny lobsters, slipper lobsters, and coral lobsters are so dissimilar from the adults and from the larvae of other crustacea that they were originally thought to be adult forms. Not until the early 1900s was it discovered that they were larval forms of lobsters. The larvae molt many times and remain in the phyllosoma state for up to 13 months. The first phyllosoma stage is very small, less than 2 mm in length. Because this stage is almost transparent, it is only just visible to the human eye. At the last phyllosoma stage (Fig. 2) the larvae measure about 35 mm long (Johnson, 1956). This stage subsequently

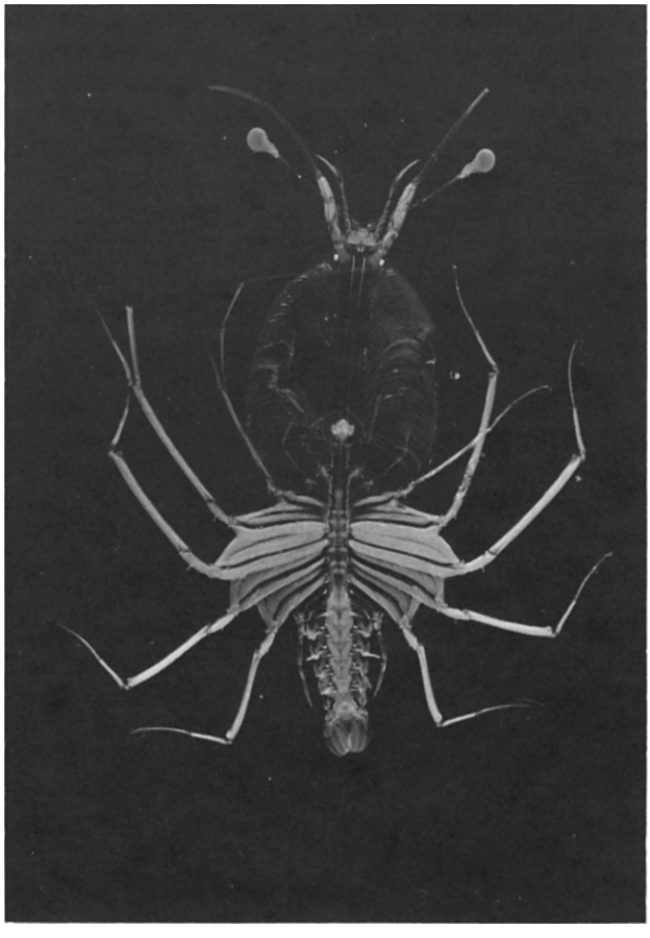


Fig. 2. Stage IX phyllosoma larvae of the spiny lobster *Panulirus cygnus.*

molts into another almost transparent stage, the puerulus. The puerulus is a transitional form which begins as an active swimmer and later settles in shallow (1–20 m) inshore reef and lagoon areas (Phillips *et al.*, 1978). After settling the puerulus molts into a small, pigmented lobster, not identical with, but very similar to, the adult.

B. Juveniles and Adults

In almost every marine habitat one is likely to find a lobster of one sort or another. Some have been trawled at great ocean depths of 3000 m or more. Others live in holes on shallow tidal reefs and can be taken by hand at low tide. However, certain zoogeographic regions or depth zones are usually dominated by separate groups of lobsters (Fig. 3). In the cold temperate continental shelf region of the North Atlantic, two genera of clawed lobsters dominate, *Homarus* and *Nephrops*. *Homarus americanus* is found on the continental shelf area of the western North Atlantic, and *H. gammarus* and *N. norvegicus* are distributed in the eastern North Altantic. Additionally, *H. gammarus* is found in the more rocky, shallow areas, in contrast to the deeper waters and muddy bottoms inhab-

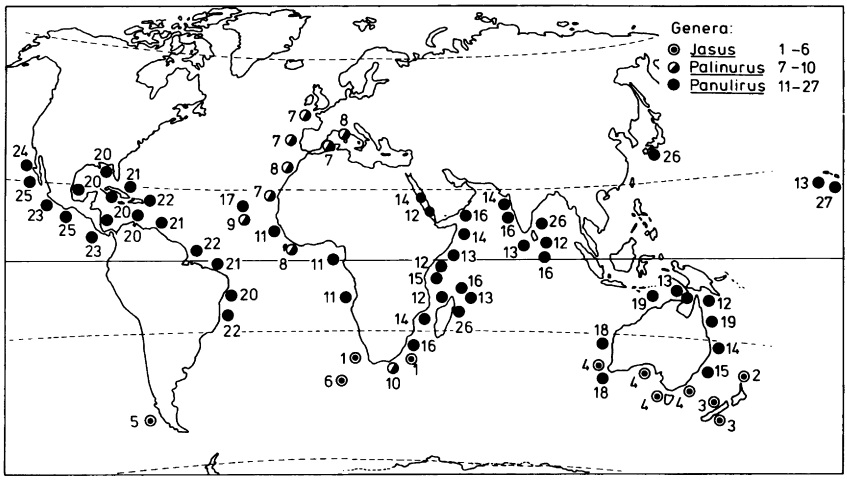


Fig. 3. Distribution of the main commercial species of the genera *Jasus, Palinurus,* and *Panulirus* in the world's oceans.

Genus *Jasus:* (1) *J. lalandii* (2) *J. verreauxi* (3) J. edwardsii (4) *J. novocholandiae* (5) *J. frontalis* (6) *J. tristani.*

Genus *Palinurus:* (7) *P. elephus* (8) *P. mauritanicus* (9) *P. charlestoni* (10) *P. gilchristi.*

Genus *Panulirus:* (11) *P. regius* (12) *P. ornatus* (13) *P. penicillatus* (14) *P. versicolor* (15) *P. longipes* (16) *P. homarus homarus* (17) *P. echinatus* (18) *P. cygnus* (19) *P. polyphagus* (20) *P. argus* (21) *P. laevicanda* (22) *P. guttatus* (23) *P. gracilis* (24) *P. interruptus* (25) *P. inflatus* (26) *P. japonicus* (27) *P. marginatus.*