PAL
5816

Palæontographica Americana

NUMBER 55 **MARCH 18, 1986**

MCZ
LIBRARY

MAY 2 1986

HARVARD
UNIVERSITY

A Restudy of the Fossil Scorpionida of the World

by

Erik N. Kjellesvig-Waering

Organized for Publication
by
Anneliese S. Caster and Kenneth E. Caster

Paleontological Research Institution
1259 Trumansburg Road
Ithaca, New York, 14850 U.S.A.

PALEONTOLOGICAL RESEARCH INSTITUTION

Officers

PRESIDENT ..... WILLIAM A. OLIVER, JR.
VICE-PRESIDENT ..... WILLIAM P. S. VENTRESS
SECRETARY ..... HENRY W. THEISEN
TREASURER ..... ROBERT E. TERWILLEGAR
ASSISTANT TREASURER ..... JOHN L. CISNE
DIRECTOR ..... PETER R. HOOVER
LEGAL COUNSEL ..... HENRY W. THEISEN

Trustees

BRUCE M. BELL (to 6/30/87)
E. ANN BUTLER (to 6/30/88)
RICHARD E. BYRD (to 6/30/86)
JOHN L. CISNE (to 6/30/88)
J. THOMAS DUTRO, JR. (to 6/30/87)
LEE B. GIBSON (to 6/30/86)
HARRY LEFFINGWELL (to 6/30/87)
AMY MCCUNE (to 6/30/86)
CATHRYN NEWTON (to 6/30/88)
WILLIAM A. OLIVER, JR. (to 6/30/86)
JAMES E. SORAUF (to 6/30/88)
ROBERT E. TERWILLEGAR (to 6/30/87)
HENRY W. THEISEN (to 6/30/86)
RAYMOND VAN HOUTTE (to 6/30/88)
WILLIAM P. S. VENTRESS (to 6/30/87)

BULLETINS OF AMERICAN PALEONTOLOGY
and
PALAEONTOGRAPHICA AMERICANA

PETER R. HOOVER ..... EDITOR

REVIEWERS FOR THIS ISSUE

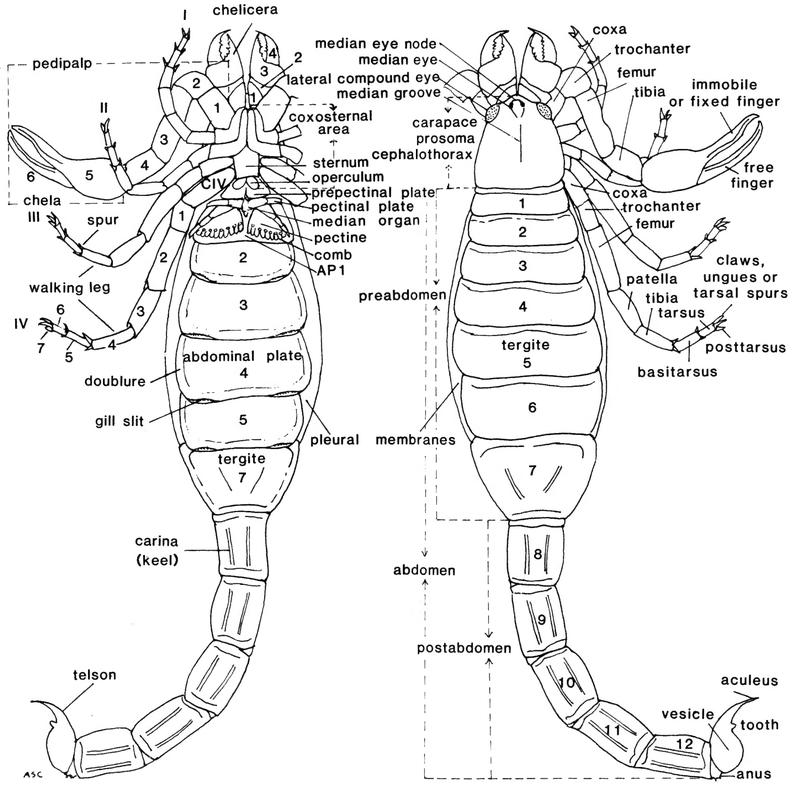
OSCAR F. FRANCKE W. D. IAN ROLFE

A list of titles in both series, and available numbers and volumes may be had on request. Volumes 1–23 of *Bulletins of American Paleontology* have been reprinted by Kraus Reprint Corporation, Route 100, Millwood, New York 10546 USA. Volume 1 of *Palaeontographica Americana* has been reprinted by Johnson Reprint Corporation, 111 Fifth Ave., New York, NY 10003 USA.

Subscriptions to *Bulletins of American Paleontology* may be started at any time, by volume or year. Current price is U.S. $25.00 per volume. Numbers of *Palaeontographica Americana* are priced individually, and are invoiced separately on request. Purchases for professional use by U.S. citizens are tax-duductible.

for additional information, write or call:

Paleontological Research Institution
1259 Trumansburg Road
Ithaca, NY 14850 U.S.A.



Text-figure 3.—External morphology of scorpions; based on a composite branchioscorpionid scorpion.

ABBREVIATIONS OF REPOSITORIES

AMNH	American Museum of Natural History, New York, NY, U.S.A.
BM(NH)	British Museum (Natural History), London, England, U.K.
BMS	Buffalo Museum of Science, Buffalo, NY, U.S.A.
BU	Birmingham University, Birmingham, England, U.K.
CIURCA	Personal collection of Samuel J. Ciurca, Rochester, NY, U.S.A.
CUGM	Cornell University Geological Museum, Ithaca, NY, U.S.A.
DLD	Personal collection of David L. Douglass, Western Springs, IL, U.S.A.
FMNH	Field Museum of Natural History, Chicago, IL, U.S.A.
FSU	Florida State University, Tallahassee, FL, U.S.A.
FWU	Institüt für Paläontologie, Friedrich-Wilhelm Universität, Bonn, WEST GERMANY
GSC	Geological Survey of Canada, Ottawa, Ontario, CANADA
GSE	Institute of Geological Sciences, Edinburgh, Scotland, U.K.
GSM	Geological Survey Museum, London, England, U.K.
GUM	Göttingen University Museum, Göttingen, WEST GERMANY
ISM	Illinois State Museum, Springfield, IL, U.S.A.
KM	Kilmarnock Museum, Ayrshire, Scotland, U.K.
KU	University of Kansas Museum of Natural History, Lawrence, KS, U.S.A.
LAS	Paleontological Institute, Academy of Sciences, Leningrad, U.S.S.R.
NMP	National Museum, Prague, CZECHOSLOVAKIA
NYSM	New York State Museum, Albany, NY, U.S.A.
PU	Princeton University Museum, Princeton, NJ, U.S.A.
RC	Personal collection of Richard Cramer, Forest Park, IL, U.S.A.
RSM	Royal Scottish Museum, Edinburgh, Scotland, U.K.
SM	Sedgwick Museum, University of Cambridge, Cambridge, England, U.K.
SMF	Natur-Museum und Forschungs-Institüt Senckenberg, Frankfurt-am-Main, WEST GERMANY
SMN	Staatliches Museum für Naturkunde, Stuttgart, WEST GERMANY
SRM	Svensk Riksmuséet, Stockholm, SWEDEN
UI	University of Illinois Geological Museum, Urbana, IL, U.S.A.
UL	Université de Laval, Cité Québec, Québec, CANADA
UMM	University of Manchester Museum, Manchester, England, U.K.
UMMP	University of Michigan Museum of Paleontology, Ann Arbor, MI, U.S.A.
USNM	U.S. National Museum of Natural History, Smithsonian Institution, Washington, DC, U.S.A.
YPM	Peabody Museum, Yale University, New Haven, CT, U.S.A.

MORPHOLOGICAL ABBREVIATIONS USED IN TEXT-FIGURES

a	areole
Abo	anterior border
Ac	aculeus
ant	anterior
ant L	anterior lamella (of pectines)
AP	abdominal plate (numbered **AP1**, **AP2**, **AP3**, etc.)
art	articulation
c	coxa (numbered **CI**, **CII**, **CIII**, **CIV**, or **IC**, **IIC**, **IIIC**, **IVC**, etc.)
cc	cephalic cheeks
Ch	chelicera (joints numbered **Ch1**, **Ch2**, **Ch3**, **Ch4**)
Ch3	hand of chelicera; immovable finger of chelicera
Ch4	free finger of chelicera
Chfls	chelical flange suture
CM	maxillary lobe of coxa (numbered **CMI**, **CMII**, or **CM1**, **CM2**, or **ICM**, **IICM**, etc.)
cmr	cephalic marginal rim
cn	condyle
CP, Cp	carapace
cr	crests (of cauda)
cs	cephalic shield
d, dbl, doub	doublure ($\mathbf{d_2}$ = doublure of chelicera joint 2)
D, dor	dorsal
dt	denticles
fl	fulcra
g	gill, or gill tract
gp	gill pouch or branchial chamber
gs	gill slits (only on abdominal plates)
I, II, III,	leg number (joints in arabic numerals (*q.v.*), ascending from proximal to distal [may be further qualified as "D" (dorsal) or "V" (ventral). P.R.H.])
inf cr	inferior crest (of cauda)
int Ch se	intercheliceral setae
int oc	interocular ridge
intt	intersegmental tissue
La	labium or labia
lat cr	lateral crest (of cauda)
LCE	lateral compound eye (facetted), whether schizochroal or holochroal
LE	lateral eye (if facetted, see **LCE**)
Lmr	lateral marginal rim (of carapace)
mcr	median crest (of carapace)
Me, me	median eyes
Mea	median appendage (of pectinal lobe)
mL	middle lamella (of pectines)
MO	median organ of prepectinal plate
mr	marginal rim of facetted eyes
ms	median sulcus
Oc, oc	ocelli (median eyes)
OP, Op	operculum
P	pedipalp (joints numbered **P1**, **P2**, etc.)
P5	hand of pedipalp; immovable finger of pedipalp
P6	free finger of pedipalp
PC, Pc	pectines
PL	pectinal lobe (basal pectinal lobe of intermediate lamella)
pmr	posterior marginal rim (of carapace)
pp	pectinal plate
ppp	prepectinal plate
Pt	pectinal teeth
S, s	spurs (follow leg joint number, as **II5s**)
Sk, soc	socket
ST, St	sternite (numbered **St1**, **St2**, **St3**, etc.)
stig	stigma, stigmata
Str	sternum
sul	sulcus
sup cr	superior crest (of cauda)
sup sp	superior spur
T	tergite (numbered **T1**, **T2**, **T3**, etc.)
tbr	trichobothria
Tel	telson
th	tooth or teeth
trr	transverse ridge
V, ven	ventral
1	trochanter (with leg number in roman numerals: **I1**, **II1**, **III1**, **IV1**, etc.)
2	femur (with leg number in roman numerals, as **II2**)
3	patella (with leg number in roman numerals, as **III3**)
4	tibia (with leg number in roman numerals, as **II4**)
5	basitarsus (with leg number in roman numerals, as **IV5**)
6	tarsus (with leg number in roman numerals, as **I6**)
7	posttarsus (with leg number in roman numerals, as **III7**)

The Paleontological Research Institution
acknowledges with special thanks
the contributions of the following individuals and institutions

PATRONS

($1000 or more at the discretion of the contributor)

James E. Allen (1967)
American Oil Company (1976)
Atlantic Richfield Company (1978)
Christina L. Balk (1970, 1982, 1983)
Hans M. Bolli (1984)
Mr. & Mrs. Kenneth E. Caster (1967)
Chevron Oil Company (1978, 1982)
Exxon Company (1977 to date)
Lois S. Fogelsanger (1966)
Gulf Oil Corporation (1978)
Merrill W. Haas (1975)
Robert C. Hoerle (1974–77)
Richard I. Johnson (1967)
J. M. McDonald Foundation (1972, 1978)
Mobil Oil Corporation (1977 to date)
Samuel T. Pees (1981)
Richard E. Petit (1983)
Robert A. Pohowsky (1982)
Texaco, Inc. (1978, 1982)
Union Oil of California (1982 to date)
United States Steel Foundation (1976)
Charles G. Ventress (1983 to date)
Christine C. Wakeley (1976–1984)
Norman E. Weisbord (1983)

INDUSTRIAL SUBSCRIBERS

(1986)

($250 per annum)

Exxon Production Research Company
Mobil Exploration and Producing Services
Shell Development Company

(continued overleaf)

LIFE MEMBERS

($200)

R. Tucker Abbott
James E. Allen
Christina L. Balk
Robert A. Black
Bruce M. Bell
Hans Bolli
Ruth G. Browne
John L. Carter
Anneliese S. Caster
Kenneth E. Caster
John E. DuPont
Arthur N. Dusenbury, Jr.
R. H. Flower
Lois S. Fogelsanger
A. Eugene Fritsche
Ernest H. Gilmour
Merrill W. Haas
Anita G. Harris
Steven M. Herrick
Robert C. Hoerle
F. D. Holland, Jr.
Richard I. Johnson
David B. Jones
Peter Jung
David Garrett Kerr
Cecil H. Kindle
Mary E. Kindle
William F. Klose, II
Jíří Kříž
Thorwald Kruckow
Hans G. Kugler
Egbert G. Leigh, Jr.
Gerard A. Lenhard
Donald R. Moore
Sakae O'Hara
Samuel T. Pees
Richard E. Petit
Robert A. Pohowsky
John Pojeta, Jr.
Donald E. Ransom, Jr.
Anthony Reso
Arthur W. Rocker
John B. Saunders
Judith Schiebout
Miriam W. Schriner
David H. Stansbery
Charles G. Ventress
Emily H. Vokes
Harold E. Vokes
Christine C. Wakeley
Norman E. Weisbord
Ralph H. Willoughby
Armour C. Winslow
Victor A. Zullo

Membership dues, subscriptions, and contributions are all important sources of funding, and allow the Paleontological Research Institution to continue its existing programs and services. The P.R.I. publishes two series of respected paleontological monographs, *Bulletins of American Paleontology* and *Palaeontographica Americana,* that give authors a relatively inexpensive outlet for the publication of significant longer manuscripts. In addition, it reprints rare but important older works from the paleontological literature. The P.R.I. headquarters in Ithaca, New York, houses a collection of invertebrate type and figured specimens, among the five largest in North America; an extensive collection of well-documented and curated fossil specimens that can form the basis for significant future paleontologic research; and a comprehensive paleontological research library. The P.R.I. wants to grow, so that it can make additional services available to professional paleontologists, and maintain its position as a leader in providing Resources for Paleontologic Research.

The Paleontological Research Institution is a non-profit, non-private corporation, and all contributions are U.S. income tax deductible. For more information on P.R.I. programs, memberships, or subscriptions to P.R.I. publications, call or write:

Peter R. Hoover
Director
Paleontological Research Institution
1259 Trumansburg Road
Ithaca, New York 14850, U.S.A.
607-273-6623

Palæontographica Americana

NUMBER 55 MARCH 18, 1986

A Restudy of the Fossil Scorpionida of the World

by

Erik N. Kjellesvig-Waering

Organized for Publication
by
Anneliese S. Caster and Kenneth E. Caster

Paleontological Research Institution
1259 Trumansburg Road
Ithaca, New York, 14850 U.S.A.

Library of Congress Card Number: 86-60462

AUTHOR'S DEDICATION

for my wife

Virginia

Printed in the United States of America
Allen Press, Inc.
Lawrence, KS 66044, U.S.A.

Erik Norman Kjellesvig-Waering, 1912–1979

VITA

Erik Norman Kjellesvig-Waering was born in Habana, Cuba on February 9, 1912; his mother being Cuban and father Norwegian made him a Norwegian citizen by law, a "Cubegian" by nature and at age 21 when he became an American citizen—a 1000% extremely patriotic American. His father was a civil engineer who paved the streets of Habana with cobble stones from Norway.

He was one of six children, all educated in the United States at their mother's insistence. Commuting from Cuba, he received his elementary education in New Jersey from the age of eight; attended High School in a military academy in North Carolina and received his Bachelor of Science Degree in Geology from the University of North Carolina.

His father sat him on a stump in a little woods in New Jersey at the age of 5, and told him to be a geologist. He said he would either be the best or the worst, no matter what he chose, as Erik was never mediocre or neutral or middle of the road, even at that tender age.

While working on his degree at the University, he supplemented his income with employment at the University library. During private research in connection with his geology courses, he became fascinated with paleontology, in fact so infatuated that during the remainder of his life, he devoted all his free time including vacations, to the study of paleontology, specifically eurypterids and living and fossil scorpions.

He was a man of many talents; strong, of sharp mind, quick decisions, and deep determination in all things he deemed to be right, a lover and student of history, biology, and ecology, and a champion of the underdog, with a flamboyant and energetic personality, punctuated always with a wonderful wit and sense of humor.

Over the period of his career he maintained an executive position in Exploration with various oil companies including DeGolyer MacNaughton, Inc. for whom he worked three years in Mexico; Helmerich & Payne, Inc. and Shell Oil Company in Oklahoma and Texas. He spent 23 years living and working in Cuba, Jamaica, Guatemala, Antigua, Venezuela, Argentina, Trinidad, Norway and Mozambique for Amoco International Oil Company. During this time he collected various turtles, snakes, shellfish, coral and other specimens for the American Museum of Natural History in New York and the Field Museum of Natural History in Chicago, being a member of both.

He owned one of the largest and most varied private collections of Scorpionida in the world, which now rests with his extensive collection of Coleoptera and eurypterids in the Florida State Collection of Arthropods.

He spent 20 years writing this monograph while figuring prominently in the field of geology with the oil industry and writing many other papers pertaining to eurypterids and fossil and living scorpions, gathering a great deal of pertinent material in person in museums and universities behind the Iron Curtain, Europe, the Caribbean, Central, South and North America, Southeast Asia and Africa. All descriptions and figures were obtained from the actual specimens either loaned to him by universities, museums and individuals, or collected by him in his extensive travels.

During his fatal illness, he tried to finish this work and had just completed the figures and manuscript, but did not have time to organize the latter for publication. It was his request that his dear friend Dr. Kenneth E. Caster be the one to categorize and join together his last great work.

At the time of his death, July 16, 1979, he was living in Marco Island, Florida where he had retired from the oil business. He left his wife Virginia, two sons, Richard and Ronald and two grandchildren, Kristen and Keith.

CONTENTS

Page

Abstract 9
Compiler's Introduction 9
Compilers' Acknowledgments 10
Editor's Preface 11
Characteristics and Nature of Fossil Scorpions
A General Statement 11
Carapace 12
Eyes 12
Coxosternal Region 15
Prosomal Appendages 16
Operculum 19
Pectines 19
Preabdomen 20
Cauda 21
Ornamentation 21
The Ventral Side of the Bilobosternina, Lobosternina, Holosternina, and Meristosternina 21
Prepectinal Plate 22
Sternites and Abdominal Plates 23
Direction of Evolution 24
Breathing Mechanisms 25
Comparison of Scorpions and Eurypterids 26
Evolutionary Changes in Scorpions 27
The Triassic Scorpions 28
Classification
Introduction 34
Abbreviations of Repositories ..... foldout inside front cover
Morphological Abbreviations used in Text-figures ..... foldout inside front cover
Suborders 35
Infraorder Lobosternina 36
Infraorder Holosternina 36
Infraorder Meristosternina 36
Infraorder Bilobosternina 36
Infraorder Orthosternina 36
Taxobases 37
Systematic Paleontology
Order Scorpionida Latreille
Suborder Branchioscorpionina, new suborder 38
Infraorder Holosternina, new infraorder 38
Superfamily Proscorpioidea Scudder 39
Family Proscorpiidae Scudder 39
Genus *Proscorpius* Whitfield 39
Proscorpius osborni (Whitfield) 39
Genus *Archaeophonus* Kjellesvig-Waering 48
Archaeophonus eurypteroides Kjellesvig-Waering 50
Family Waeringoscorpionidae Størmer 52
Genus *Waeringoscorpio* Størmer 52
Waeringoscorpio hefteri Størmer 52
Family Labriscorpionidae, new family 52
Genus *Labriscorpio* Leary 52
Labriscorpio alliedensis Leary 53
Superfamily Stoermeroscorpionoidea, new superfamily 53
Family Stoermeroscorpionidae, new family 53
Genus *Stoermeroscorpio,* new genus 53
Stoermeroscorpio delicatus, new species 53
Superfamily Allopalaeophonoidea, new superfamily 56
Family Allopalaeophonidae, new family 56
Genus *Allopalaeophonus,* new genus 56
Allopalaeophonus caledonicus (Hunter) 57
Superfamily Palaeoscorpioidea Lehmann 61
Family Palaeoscorpiidae Lehmann 61
Genus *Palaeoscorpius* Lehmann 61
Palaeoscorpius devonicus Lehmann 61
Family Hydroscorpiidae, new family 63
Genus *Hydroscorpius,* new genus 63
Hydroscorpius denisoni, new species 63
Superfamily Archaeoctonoidea Petrunkevitch 66
Family Archaeoctonidae Petrunkevitch 66
Genus *Archaeoctonus* Pocock 66
Archaeoctonus glaber (Peach) 66
Genus *Pseudoarchaeoctonus,* new genus 68
Pseudoarchaeoctonus denticulatus, new species 68
Superfamily Acanthoscorpionoidea, new superfamily 70
Family Acanthoscorpionidae, new family 70
Genus *Acanthoscorpio,* new genus 70
Acanthoscorpio mucronatus, new species 70
Family Stenoscorpionidae, new family 73
Genus *Stenoscorpio,* new genus 73
Stenoscorpio gracilis (Wills) 74
Stenoscorpio pseudogracilis (Wills) 74
Superfamily Gigantoscorpionoidea, new superfamily 75
Family Gigantoscorpionidae, new family 76
Genus *Gigantoscorpio* Størmer 76
Gigantoscorpio willsi Størmer 76
Superfamily Mesophonoidea Wills 79
Family Mesophonidae Wills 79
Genus *Mesophonus* Wills 79
Mesophonus perornatus Wills 80
Mesophonus (?) *pulcherrimus* Wills 80
Mesophonus (?) *pulcherrimus* var. *immaculatus* Wills 80
Mesophonus (?) *maculatus* (Brauer, Redtenbacher, and Ganglbauer) 81
Family Mazoniidae Petrunkevitch 81
Genus *Mazonia* Meek and Worthen 81
Mazonia woodiana Meek and Worthen 81
Mazonia wardingleyi (Woodward) 84
Family Centromachidae Petrunkevitch 84
Genus *Centromachus* Thorell and Lindström 86
Centromachus euglyptus (Peach) 86
Family Heloscorpionidae, new family 86
Genus *Heloscorpio,* new genus 86
Heloscorpio sutcliffei (Woodward) 88
Family Liassoscorpionidae, new family 90
Genus *Liassoscorpionides* Bode 90
Liassoscorpionides schmidti Bode 90
Family Phoxiscorpionidae, new family 93
Genus *Phoxiscorpio,* new genus 93
Phoxiscorpio peachi, new species 93
Family Willsiscorpionidae, new family 94
Genus *Willsiscorpio,* new genus 94
Willsiscorpio bromsgroviensis (Wills) 94
Superfamily Eoctonoidea, new superfamily 94
Family Eoctonidae, new family 96
Genus *Eoctonus* Petrunkevitch 96

Eoctonus miniatus Petrunkevitch 96
Family Buthiscorpiidae, new family 101
Genus *Buthiscorpius* Petrunkevitch 102
Buthiscorpius buthiformis (Pocock) 102
Buthiscorpius lemayi, new species 103
Family Allobuthiscorpiidae, new family 105
Genus *Allobuthiscorpius,* new genus 105
Allobuthiscorpius major (Wills) 105
Genus *Aspiscorpio,* new genus 106
Aspiscorpio eagari, new species 106
Family Anthracoscorpionidae, new family 107
Genus *Anthracoscorpio* Kušta 107
Anthracoscorpio juvenis Kušta 107
Anthracoscorpio dunlopi Pocock 109
Anthracoscorpio (?) species 109
Genus *Lichnoscorpius* Petrunkevitch 110
Lichnoscorpius minutus Petrunkevitch 110
Genus *Allobuthus,* new genus 112
Allobuthus macrostethus, new species 112
Genus *Coseleyscorpio,* new genus 113
Coseleyscorpio lanceolatus, new species 113
Family Garnettiidae Dubinin 113
Genus *Garnettius* Petrunkevitch 113
Garnettius hungerfordi (Elias) 114
Garnettius (?) species 120
Superfamily Spongiophonoidea, new superfamily 120
Family Spongiophonidae, new family 121
Genus *Spongiophonus* Wills 121
Spongiophonus pustulosus Wills 121
Family Praearcturidae, new family 121
Genus *Praearcturus* Woodward 121
Praearcturus gigas Woodward 121
Genus *Brontoscorpio* Kjellesvig-Waering
Brontoscorpio anglicus Kjellesvig-Waering 126
Infraorder Meristosternina, new infraorder 126
Superfamily Tiphoscorpionoidea, new superfamily 126
Family Tiphoscorpionidae, new family 126
Genus *Tiphoscorpio,* new genus 126
Tiphoscorpio hueberi, new species 126
Superfamily Cyclophthalmoidea Thorell and Lindström 129
Family Cyclophthalmidae Thorell and Lindström 129
Genus *Cyclophthalmus* Corda 129
Cyclophthalmus senior Corda 129
Clyclophthalmus robustus, new species 132
Cyclophthalmus (?) *sibiricus* Novojilov and Størmer 133
Family Microlabiidae, new family 133
Genus *Microlabis* Corda 133
Microlabis sternbergii Corda 134
Superfamily Palaeobuthoidea, new superfamily 135
Family Palaeobuthidae, new family 135
Genus *Palaeobuthus* Petrunkevitch 135
Palaeobuthus distinctus Petrunkevitch 135
Infraorder Lobosternina Pocock (restricted) 141
Superfamily Palaeophonoidea Thorell and Lindström 142
Family Palaeophonidae Thorell and Lindström 142
Genus *Palaeophonus* Thorell and Lindström 142
Palaeophonus nuncius Thorell and Lindström 142
Palaeophonus (?) *lightbodyi* Kjellesvig-Waering 149
Superfamily Anthracochaeriloidea, new superfamily 149
Family Anthracochaerilidae, new family 149
Genus *Anthracochaerilus,* new genus 149
Anthracochaerilus palustris, new species 150
Superfamily Isobuthoidea Petrunkevitch 151
Family Isobuthidae Petrunkevitch 152
Genus *Isobuthus* Frič 153
Isobuthus kralupensis (Thorell and Lindström) 153
Genus *Boreoscorpio,* new genus 154
Boreoscorpio copelandi, new species 154
Genus *Feistmantelia* Frič 156
Feistmantelia ornata Frič 156
Genus *Bromsgroviscorpio,* new genus 157
Bromsgroviscorpio willsi, new species 157
Family Eobuthidae, new family 158
Genus *Eobuthus* Frič 158
Eobuthus rakovnicensis Frič 158
Eobuthus cordai, new species 160
Eobuthus holti Pocock 162
Eobuthus (?) species of Wills 162
Family Eoscorpiidae Scudder 162
Genus *Eoscorpius* Meek and Worthen 162
Eoscorpius carbonarius Meek and Worthen 163
Eoscorpius pulcher (Petrunkevitch) 177
Eoscorpius mucronatus, new species 181
Eoscorpius distinctus (Petrunkevitch) 181
Eoscorpius sparthensis Baldwin and Sutcliffe 184
Eoscorpius species 186
Eoscorpius casei, new species 186
Genus *Trachyscorpio,* new genus 188
Trachyscorpio squarrosus, new species 188
Trachyscorpio (?) species 190
Genus *Eskiscorpio,* new genus 190
Eskiscorpio parvus, new species 191
Family Pareobuthidae, new family 192
Genus *Pareobuthus* Wills 192
Pareobuthus salopiensis Wills 193
Family Kronoscorpionidae, new family 193
Genus *Kronoscorpio,* new genus 193
Kronoscorpio danielsi (Petrunkevitch) 193
Superfamily Paraisobuthoidea, new superfamily 198
Family Paraisobuthidae, new family 198
Genus *Paraisobuthus,* new genus 198
Paraisobuthus prantli, new species 198
Paraisobuthus frici, new species 203
Paraisobuthus duobicarinatus, new species 204
Paraisobuthus virginiae, new species 207
Genus *Leioscorpio,* new genus 209
Leioscorpio pseudobuthiformis, new species 209
Family Telmatoscorpionidae, new family 210
Genus *Telmatoscorpio,* new genus 210
Telmatoscorpio brevipectus, new species 210
Family Scoloposcorpionidae, new family 212
Genus *Scoloposcorpio,* new genus 212
Scoloposcorpio cramondensis, new species 213
Genus *Benniescorpio* Wills 214
Benniescorpio tuberculatus (Peach) 214
Family Opsieobuthidae, new family 214
Genus *Opsieobuthus,* new genus 214
Opsieobuthus pottsvillensis (Moore) 214
Superfamily Loboarchaeoctonoidea, new superfamily 216
Family Loboarchaeoctonidae, new family 216
Genus *Loboarchaeoctonus,* new genus 216
Loboarchaeoctonus squamosus, new species 216

Superfamily Pseudobuthiscorpioidea, new superfamily 218
Family Pseudobuthiscorpiidae, new family 218
Genus *Pseudobuthiscorpius,* new genus 219
Pseudobuthiscorpius labiosus, new species ... 219
Family Petaloscorpionidae, new family 220
Genus *Petaloscorpio,* new genus 220
Petaloscorpio bureaui, new species 220
Family Waterstoniidae, new family 222
Genus *Waterstonia,* new genus 222
Waterstonia airdriensis, new species 222
Waterstonia (?) *brachistodactyla,* new species 224
Infraorder Bilobosternina, new infraorder 225
Superfamily Branchioscorpionoidea, new superfamily 225
Family Branchioscorpionidae, new family 225
Genus *Branchioscorpio,* new genus 225
Branchioscorpio richardsoni, new species ... 226
Family Dolichophonidae Petrunkevitch 229
Genus *Dolichophonus* Petrunkevitch 230
Dolichophonus loudonensis (Laurie) 230
Suborder Neoscorpionina Thorell and Lindström 231
Infraorder Orthosternina Pocock 231
Superfamily Scorpionoidea Leach 232
Family Palaeopisthacanthidae, new family 232
Genus *Palaeopisthacanthus* Petrunkevitch 232
Palaeopisthacanthus schucherti Petrunkevitch 232
Genus *Compsoscorpius* Petrunkevitch 236
Compsoscorpius elegans Petrunkevitch 236
Family Scorpionidae Leach 239
Genus *Mioscorpio,* new genus 239
Mioscorpio zeuneri (Hadži) 239
Genera *Incertae Sedis*
Genus *Titanoscorpio,* new genus 240
Titanoscorpio douglassi, new species 240
Genus *Wattisonia* Wills 242
Wattisonia coseleyensis Wills 242
Genus *Palaeomachus* Pocock 242
Palaeomachus anglicus (Woodward) 242
Scorpionida genus and species indeterminate of Størmer 242
Appendix 1. The Stratigraphic Distribution of the Fossil Scorpionida 249
Appendix 2. Index of Synonyms 253
Appendix 3. Index of Specimens by Repository 254
References Cited 256
Plates 259
Index 278

LIST OF ILLUSTRATIONS

Text-figure Page
1. Phylogenetic lines of development in the Scorpionida 25
2. A comparison of the ventral morphology of the Eurypterida and three infraorders of the Scorpionida 27
3. External morphology of scorpions ..... foldout inside front cover
4. Ventral plating in scorpionids, illustrating the basic differences between infraorders 37
5. Key to the classification of the Scorpionida, showing the relationship of the higher taxa .... foldout inside back cover
6. *Proscorpius osborni* (Whitfield). Specimen I, BMS E25162 40
7. *Proscorpius osborni* (Whitfield). Specimen II, CIURCA 041771-1 42
8. *Proscorpius osborni* (Whitfield). Specimen III, CIURCA 040564 44
9. *Proscorpius osborni* (Whitfield). Specimen III, CIURCA 040564 45
10. *Proscorpius osborni* (Whitfield). Specimen IV, CIURCA 072869-9B 46
11. *Proscorpius osborni* (Whitfield). Specimens V and VI, CIURCA 042570-1A and 040668-1 47
12. *Proscorpius osborni* (Whitfield). Specimens VI and I, CIURCA 040668 and BMS E25162 48
13. *Proscorpius osborni* (Whitfield). Reconstructions based on specimens from the Ciurca collection 50
14. *Archaeophonus eurypteroides* Kjellesvig-Waering. CIURCA 062065-1 51
15. *Stoermeroscorpio delicatus,* n. gen., n. sp. CIURCA 041771-1,2 54
16. *Stoermeroscorpio delicatus,* n. gen., n. sp. Reconstructions based on the holotype, CIURCA 041771-1,2 ... 55
17. *Allopalaeophonus caledonicus* (Hunter). Holotype 59
18. *Allopalaeophonus caledonicus* (Hunter). Reconstructions based on the holotype, KM unnumbered specimen 59
19. *Palaeoscorpius devonicus* Lehmann. Holotype, FWU Egr 263 62
20. *Hydroscorpius denisoni,* n. gen., n. sp. Holotype, FMNH (PE) 6176 64
21. *Archaeoctonus glaber* (Peach). Holotype, GSE 5858, 5859, and juvenile form, GSE 2039 66
22. *Pseudoarchaeoctonus denticulatus,* n. gen., n. sp. Holotype, GSE 2038 69
23. *Acanthoscorpio mucronatus,* n. gen., n. sp. Holotype, FMNH (PE) 6177b 70
24. *Acanthoscorpio mucronatus,* n. gen., n. sp. Holotype, FMNH (PE) 6177a 72
25. *Stenoscorpio gracilis* (Wills). Specimen, SM 164 74
26. *Gigantoscorpio willsi* Størmer. Specimen, GSE 2137 ... 75
27. *Gigantoscorpio willsi* Størmer. Holotype, BM(NH) In.42706a,b, and specimen, GSE 2134 77
28. *Mesophonus perornatus* Wills. Coxosternal area 80
29. *Mazonia woodiana* Meek and Worthen. Taelle specimen, FMNH (PE) 39253 82
30. *Mazonia wardingleyi* (Woodward). Holotype, BM(NH) In.18561 84
31. Details of the organization of the coxosternal and pectinal regions of *Opsieobuthus pottsvillensis* (Moore), *Centromachus euglyptus* (Peach), and *Tityus trinitatis* Pocock (male and female) 86
32. *Heloscorpio sutcliffei* (Woodward). Holotype, BM(NH) In.18564 88
33. *Liassoscorpionides schmidti* Bode. Holotype, GUM 525-1 90
34. *Phoxiscorpio peachi,* n. gen., n. sp. Holotype, GSE 2140 93
35. *Eoctonus miniatus* Petrunkevitch. Holotype, YPM 131 95
36. *Tarsopterella scotica* (Woodward). Reconstruction of the of the gill chamber by Charles E. Waterston 97
37. *Eoctonus miniatus* Petrunkevitch. FMNH (PE) 16498 98
38. *Eoctonus miniatus* Petrunkevitch. Reconstruction 100
39. *Eoctonus miniatus* Petrunkevitch. FMNH (PE) 32202 101

40. *Buthiscorpius buthiformis* (Pocock). Holotype, BM(NH) In.18596 102
41. *Buthiscorpius lemayi,* n. sp. Holotype, FMNH (PE) 21600 104
42. *Aspiscorpio eagari,* n. gen., n. sp. Holotype, UMM L 8182 106
43. Species of *Anthracoscorpio* Kušta, 1885 108
44. *Anthracoscorpio* ? sp. YPM 126 109
45. *Lichnoscorpius minutus* Petrunkevitch. Holotype, BM(NH) In.31266 111
46. *Garnettius hungerfordi* (Elias). Holotype, USNM 125453a,b 114
47. Species of *Garnettius* Petrunkevitch, 1953 116
48. *Garnettius hungerfordi* (Elias). Restoration based on holotype, USNM 125453a,b 119
49. *Praearcturus gigas* Woodward 122
50. *Tiphoscorpio hueberi,* n. gen., n. sp. Holotype, USNM 252629 126
51. *Cyclophthalmus senior* Corda. Holotype, NMP Inv. 801 (dorsal side) 130
52. *Cyclophthalmus senior* Corda. Holotype, NMP Inv. 801 (ventral side) 131
53. *Cyclophthalmus robustus,* n. sp. BM(NH) In.13976 ... 133
54. *Microlabis sternbergii* Corda. Holotype, NMP Inv. 802 134
55. *Palaeobuthus distinctus* Petrunkevitch. Specimen I, holotype, YPM 133 136
56. *Palaeobuthus distinctus* Petrunkevitch. Specimen II, YPM 127 138
57. *Paleobuthus distinctus* Petrunkevitch. Specimen III, YPM 130 140
58. *Palaeobuthus distinctus* Petrunkevitch. Reconstruction 141
59. *Palaeophonus nuncius* Thorell and Lindström. Holotype, SRM Ar. 32235 143
60. *Palaeophonus nuncius* Thorell and Lindström. SRM Ar. 32235, 32242, 32243 144
61. *Palaeophonus nuncius* Thorell and Lindström. SRM Ar. 32235, 31591, 31818 146
62. *Palaeophonus nuncius* Thorell and Lindström. Reconstruction 148
63. *Anthracochaerilus palustris,* n. gen., n. sp. Holotype, BM(NH) In.39764 150
64. *Isobuthus kralupensis* (Thorell and Lindström). Holotype, NMP Inv. 837 153
65. *Boreoscorpio copelandi,* n. gen., n. sp. Holotype, GSC 12778 155
66. *Feistmantelia ornata* Frič. Holotype, NMP Inv. 828 ... 157
67. *Eobuthus rakovnicensis* Frič. Holotype, NMP Inv. 822 159
68. *Eobuthus cordai,* n. sp. Holotype, NMP Inv. 838; paratype, NMP Inv. 834 161
69. *Eoscorpius carbonarius* Meek and Worthen. Specimen I, holotype, FMNH (UC) 8949 164
70. *Eoscorpius carbonarius* Meek and Worthen. Specimen I, holotype, FMNH (UC) 8949 164
71. *Eoscorpius carbonarius* Meek and Worthen. Specimen II, YPM 128 and Specimen III, USNM 37977 169
72. *Eoscorpius carbonarius* Meek and Worthen. Specimen IV, USNM 37986 171
73. *Eoscorpius carbonarius* Meek and Worthen. Specimens IV and V, USNM 37986, 37987 171
74. *Eoscorpius carbonarius* Meek and Worthen. Specimen VI, YPM 139 173
75. *Eoscorpius carbonarius* Meek and Worthen. Specimen VII, FMNH (PE) 32084 174
76. *Eoscorpius pulcher* (Petrunkevitch). Holotype, BM(NH) In.39772 177
77. *Eoscorpius pulcher* (Petrunkevitch). BM(NH) In.39766 179
78. *Eoscorpius mucronatus,* n. sp. Holotype, GSM PF 1392–1393 181
79. *Eoscorpius distinctus* (Petrunkevitch). Specimen I, holotype, BM(NH) In.13909 182
80. *Eoscorpius distinctus* (Petrunkevitch). Specimen II, BM(NH) I.3172 183
81. *Eoscorpius sparthensis* Baldwin and Sutcliffe. Holotype, UMM L 6271A,B 184
82. *Eoscorpius casei,* n. sp. Holotype, PU 87266 186
83. *Trachyscorpio squarrosus,* n. gen., n. sp. Holotype, BM(NH) In.25985, paratypes, BM(NH) In.25986 and In.25984; and *Trachyscorpio* (?) sp., BM(NH) In.39765 188
84. *Eskiscorpio parvus,* n. gen., n. sp. Holotype, GSE 2139 191
85. *Kronoscorpio danielsi* (Petrunkevitch). FMNH (PE) 32085 195
86. *Paraisobuthus prantli,* n. gen., n. sp. Holotype, BM(NH) I.2950 199
87. *Paraisobuthus prantli,* n. gen., n. sp. Holotype, BM(NH) I.2950 200
88. *Paraisobuthus prantli,* n. gen., n. sp. Holotype, BM(NH) I.2950 200
89. *Paraisobuthus frici,* n. sp. Holotype, NMP Inv. 827; paratype, NMP Inv. 826; NMP GH L973 (73) 203
90. *Paraisobuthus duobicarinatus,* n. sp. Holotype, GSM 30245 and 30246 204
91. *Paraisobuthus virginiae,* n. sp. Holotype, YPM 132 ... 207
92. *Leioscorpio pseudobuthiformis,* n. gen., n. sp. Holotype, BM(NH) In.22832 209
93. *Telmatoscorpio brevipectus,* n. gen., n. sp. Holotype, YPM 129 211
94. *Scoloposcorpio cramondensis,* n. gen., n. sp. Holotype, GSE 2173; paratype, GSE 5862 213
95. *Opsieobuthus pottsvillensis* (Moore). Holotype, FMNH (UC) 37984 215
96. *Loboarchaeoctonus squamosus,* n. gen., n. sp. Holotype, BM(NH) I.988; paratype, BM(NH) In.12848 217
97. *Pseudobuthiscorpius labiosus,* n. gen., n. sp. Holotype, BM(NH) I.1555 219
98. *Petaloscorpio bureaui,* n. gen., n. sp. Holotype, UL 1092 220
99. *Waterstonia airdriensis,* n. gen., n. sp. Holotype, RSM 1957.1.4996 223
100. *Waterstonia* (?) *brachistodactyla,* n. sp. Holotype, RSM 1978.5.1 225
101. *Branchioscorpio richardsoni,* n. gen., n. sp. Holotype, FMNH (PE) 6175a,b 226
102. *Dolichophonus loudonensis* (Laurie). Holotype, RSM 1897.32.196 230
103. *Palaeopisthacanthus schucherti* Petrunkevitch. Holotype, YPM 140 233
104. *Palaeopisthacanthus schucherti* Petrunkevitch. Holotype, YPM 140 234
105. *Compsoscorpius elegans* Petrunkevitch. Holotype, BM(NH) I.7883 236
106. *Compsoscorpius elegans* Petrunkevitch. Paratype, BM(NH) In.15862 238
107. *Compsoscorpius elegans* Petrunkevitch. Paratype, BM(NH) In.31261 239
108. *Titanoscorpio douglassi,* n. gen., n. sp. Holotype 240
109. *Palaeomachus anglicus* (Woodward). Holotype, BM(NH) I.944a,b 242
110. Coxosternal areas of the Holosternina 243
111. Coxosternal areas of the five infraorders 243
112. Coxosternal areas of the Lobosternina 243
113. Morphological stages, but not necessarily phylogenetic development, of the floor of the oral tube 243
114. Coxosternal region and oral tube condition of some Recent scorpions, introduced for comparison 243

A RESTUDY OF THE FOSSIL SCORPIONIDA OF THE WORLD

By

ERIK N. KJELLESVIG-WAERING

Organized for Publication
by
Anneliese S. Caster and Kenneth E. Caster

ABSTRACT

This study, based on personal examination of all available specimens in the world, many of them new, ranging in age from the Silurian through the Jurassic, plus a lone specimen from the Miocene, comprises a reclassification of the Scorpionida into two suborders: The Branchioscorpionina, mainly aquatic and possessing gills; and the Neoscorpionina, terrestrial and pulmonate. The five infraorders are based on the nature of the abdominal plates or sternites. These are the Lobosternina, restricted, the Orthosternina, restricted, the Bilobosternina, new, the Holosternina, new, and the Meristosternina, new. The 21 superfamilies, 13 of which are new, are based on the general coxosternal pattern. The 48 families, 34 of which are new, are based on the maxillary lobes, shape of sternum, presence or absence of lateral compound eyes, and the termination of the legs.

The following new taxa are described: Labriscorpionidae, n. fam.; Stoermeroscorpionoidea, n. superfam., Stoermeroscorpionidae, n. fam., *Stoermeroscorpio delicatus,* n. gen., n. sp.; Allopalaeophonoidea, n. superfam., Allopalaeophonidae, n. fam., *Allopalaeophonus,* n. gen.; Hydroscorpiidae, n. fam., *Hydroscorpius denisoni,* n. gen., n. sp.; *Pseudoarchaeoctonus denticulatus,* n. gen., n. sp.; Acanthoscorpionoidea, n. superfam., Acanthoscorpionidae, n. fam., *Acanthoscorpio mucronatus,* n. gen., n. sp.; Stenoscorpionidae, n. fam., *Stenoscorpio,* n. gen.; Gigantoscorpionoidea, n. superfam., Gigantoscorpionidae, n. fam.; Heloscorpionidae, n. fam., *Heloscorpio,* n. gen.; Liassoscorpionidae, n. fam.; Phoxiscorpionidae, n. fam., *Phoxiscorpio peachi,* n. gen., n. sp.; Willsiscorpionidae, n. fam., *Willsiscorpio,* n. gen.; Eoctonoidea, n. superfam., Eoctonidae, n. fam; Buthiscorpiidae, n. fam., *Buthiscorpius lemayi,* n. sp.; Allobuthiscorpiidae, n. fam., *Allobuthiscorpius,* n. gen.; *Aspiscorpio eagari,* n. gen., n. sp.; Anthracoscorpionidae, n. fam., *Anthracoscorpio* ? sp.; *Allobuthus macrostethus,* n. gen., n. sp.; *Coseleyscorpio lanceolatus,* n. gen., n. sp.; *Garnettius* ? sp.; Spongiophonoidea, n. superfam., Spongiophonidae, n. fam.; Praearcturidae, n. fam.; Tiphoscorpionoidea, n. superfam., Tiphoscorpionidae, n. fam., *Tiphoscorpio hueberi,* n. gen., n. sp.; *Cyclophthalmus robustus,* n. sp.; Microlabiidae, n. fam.; Palaeobuthoidea, n. superfam., Palaeobuthidae, n. fam.; Anthracochaeriloidea, n. superfam., Anthracochaerilidae, n. fam., *Anthracochaerilus palustris,* n. gen., n. sp.; *Boreoscorpio copelandi,* n. gen., n. sp.; *Bromsgroviscorpio willsi,* n. gen., n. sp.; Eobuthidae, n. fam., *Eobuthus cordai,* n. sp.; *Eoscorpius mucronatus,* n. sp., *E. casei,* n. sp.; *Trachyscorpio squarrosus,* n. gen., n. sp., *Trachyscorpio* (?) sp.; *Eskiscorpio parvus,* n. gen., n. sp.; Pareobuthidae, n. fam.; Kronoscorpionidae, n. fam., *Kronoscorpio,* n. gen.; Paraisobuthoidea, n. superfam., Paraisobuthidae, n. fam., *Paraisobuthus prantli,* n. gen., n. sp., *P. frici,* n. sp., *P. duobicarinatus,* n. sp., *P. virginiae* n. sp.; *Leioscorpio pseudobuthiformis,* n. gen., n. sp.; Telmatoscorpionidae, n. fam., *Telmatoscorpio brevipectus,* n. gen., n. sp.; Scoloposcorpionidae, n. fam., *Scoloposcorpio cramondensis,* n. gen., n. sp.; Opsieobuthidae, n. fam., *Opsieobuthus,* n. gen.; Loboarchaeoctonoidea, n. superfam., Loboarchaeoctonidae, n. fam., *Loboarchaeoctonus squamosus,* n. gen., n. sp.; Pseudobuthiscorpioidea, n. superfam., Pseudobuthiscorpiidae, n. fam., *Pseudobuthiscorpius labiosus,* n. gen., n. sp.; Petaloscorpionidae, n. fam., *Petaloscorpio bureaui,* n. gen., n. sp.; Waterstoniidae, n. fam., *Waterstonia airdriensis,* n. gen., n. sp., *W.* (?) *brachistodactyla,* n. sp.; Branchioscorpionoidea, n. superfam., Branchioscorpionidae, n. fam., *Branchioscorpio richardsoni,* n. gen., n. sp.; Palaeopisthacanthidae, n. fam.; *Mioscorpio,* n. gen.; *Titanoscorpio douglassi,* n. gen., n. sp.

COMPILER'S INTRODUCTION

This restudy of the fossil scorpions of the world was undertaken by the late Erik N. Kjellesvig-Waering about twenty years ago as a by-product of his many years of devoted study of the Eurypterida, to which the scorpions are closely related, and his passion for collecting living scorpions, dating from his boyhood in Cuba. It was begun largely because of his dissatisfaction with the analyses of fossil scorpions in the many works of the late Alexander Petrunkevitch of Yale University. This was capped by Petrunkevitch's treatment of the group in the *Treatise on Invertebrate Paleontology* (1955).

When Waering died in 1979, the research for the scorpion manuscript was largely completed, but left in a chaotic state. He undertook the work genus by genus and specimen by specimen, as he could obtain the type materials from various collections in Europe and America, with no small supplement of new materials that came to hand over the years from the same sources and from amateur collectors. His *modus operandi* was to describe and illustrate the material seriatim, expecting to integrate the manuscript in a final reworking, which alas, he never lived to accomplish, although he left a large volume of substantive notes, and many memoranda to himself ("don't forget to . . ."), as well as marginal annotations in the published source ma-

terials. All of this material has been available to us as we have endeavored to fulfill his desires as best we could judge them. Unfortunately, over the long period in which he worked on fossil scorpions, he underwent several changes of mind on morphological and taxonomic matters, without enough time spared him to reconcile his various opinions. Throughout the manuscript, we have followed the general policy of employing what seemed to be his last views on all these matters. This has entailed much textual reorganization and reconciliation, together with some relabelling of drawings and general coordination of the material at hand. The resultant manuscript gives Waering's considered opinion about fossil scorpions, and any emendations or clarifications made by the organizers are clearly indicated.

Waering had several times discussed the scorpion manuscript with us during visits in both Cincinnati and Marco Island, Florida. He and I had been longtime collaborators on eurypterid studies and I had agreed to look over the final scorpion manuscript before submitting it for publication. His final instructions to his wife were to submit the manuscript to me to render into publishable form. As a result, in the summer of 1980, Mrs. Caster and I spent a month with Mrs. Waering, collecting his papers, returning borrowed specimens, and finally removing all of his fossil scorpion papers and library, rubber molds and microfilms, to the Geology Department of the University of Cincinnati, where they are deposited.

Immediately upon returning to Cincinnati after the intensive weeks in Florida, I suffered a temporary disability and found myself unable to continue with the task in hand. Fortunately for me, as well as for the project, my wife, Anneliese S. Caster, like myself, a former student in paleontology under Gilbert D. Harris of Cornell University, and who had been involved in the endeavor from the start, took over, and is largely responsible for the completed task. This has been almost full-time occupation for more than three years, and has entailed reconciliation of various sections of the manuscript, elimination of duplication, considerable literature research, drafting of supplementary charts and figures and, in brief, coming up with a manuscript of which Erik Waering would have been proud. This monograph is the culminating and major work of a very fine paleontologist, but it was quite unacceptable for publication before the devoted efforts of Anneliese S. Caster. We are both grateful to our late professor, G. D. Harris, and for the years spent in his laboratory, where, despite the absence of scorpions on the agenda in that mollusk-oriented environment, all students were treated as "zealous companions in research." I myself am particularly grateful for my wife's assistance, but so must all scorpion specialists be, for without her labors Erik Waering's final work would never have been published. As she now says, this task has caused her to know far more about scorpions than she ever thought she wanted to know!

Kenneth E. Caster
Emeritus Professor of Geology
University of Cincinnati
Cincinnati, OH 45221, U.S.A.

COMPILERS' ACKNOWLEDGMENTS

Waering left a partial list of those to whom he was grateful for assistance and loans of specimens over the many years of the project: we have gleaned from his text the names of others to whom he was so indebted. Any not formally acknowledged below will understand that their omission was unintentional.

First, Erik would have been, and we deeply are, indebted to Mr. John Swearingen, Chairman of the Board of Amoco Production Company, and the Amoco Foundation, Inc. of Standard Oil Company (of Indiana) for a generous grant to the University of Cincinnati Foundation, which makes the costly publication of the manuscript by the Paleontological Research Institution possible. Erik served as a Vice-President of Amoco for several years, and this grant is a tribute to him, both as a scientist and as a valued employee. It is enlightened recognition of his long years of "extracurricular" activity in pure scientific research from Trinidad to Norway, the while fulfilling his contractual responsibilities with distinction.

Special thanks are due the late Dr. Leif Størmer of Oslo, Norway, who was a constant source of advice and information, and who supplied the X-ray photographs of *Palaeoscorpius devonicus* made by Lehmann; and also to the late Dr. R. C. Moore of Lawrence, Kansas, for considerable advice on taxonomic matters.

Many European colleagues have gone out of their way to arrange study facilities and loans of types, also making casts of specimens, further preparing specimens on request, and furnishing locality information. Special mention must be made of the assistance of Dr. H. W. Ball and Dr. A. E. Rixon of the British Museum (Natural History); Dr. Peter Brand, Dr. Adrian Rushton and Dr. R. B. Wilson of the Institute of Geological Sciences, London; Dr. Michael Eagar of the University of Manchester Museum; Dr. Harry B. Whittington and Dr. D. Price of the Sedgwick Museum, Cambridge; Dr. W. D. Ian Rolfe of the Hunterian Museum, Glasgow; Dr. Charles D. Waterston of the Royal Scottish Museum, Edinburgh; Dr. F. W. Shotten at Birmingham University; and the Trustees of the Kilmarnock Mu-

seum. On the Continent, Dr. Radvan Horný, Dr. Ivo Chlupáč and Dr. J. Šetlik of the National Museum, Prague, have shown every courtesy, as have Dr. H. K. Erben of Bonn, Dr. H. Jahnke of Göttingen, Dr. Jovan Hadži, and Dr. M. Warth of the Staatliches Museum für Naturkunde, Stuttgart; likewise Mr. R. Skoglund of the Riksmuséet, Stockholm.

Closer to home, special appreciation goes to Drs. G. Arthur Cooper, Richard Boardman, Frederick J. Collier, Francis M. Hueber, and Porter M. Kier of the United States National Museum and the Smithsonian Institution, for many courtesies shown. Through Drs. Eugene S. Richardson, Jr., Robert H. Denison, Matthew H. Nitecki, and Robert Hansman of the Field Museum of Natural History, Chicago, the Cottonwood Canyon material became available; they were also an invaluable source of information on the scorpions of the Mazon Creek area. Ms. Clarita M. Nuñez of the Field Museum and Dr. Derek Briggs, visiting scientist from the University of London, and Mr. Bret S. Beall at the University of Michigan Museum of Paleontology, located some missing types and supplied their accession numbers. Further thanks are due Dr. Karl Waage, Mrs. Virginia Starquist and Mrs. J. Lawson of Yale Peabody Museum; Dr. John W. Wells of Cornell University; Dr. Donald Baird and Gerard R. Case of Princeton University; Dr. Daniel Blake and Dr. Harold W. Scott of the University of Illinois Museum; Dr. Richard L. Leary of the Illinois State Museum, Springfield; Dr. Murray Copeland, University of Toronto, and Dr. René Bureau, Laval University, Québec.

Almost no paleontological research is complete without the cooperation of the private collector, and this monograph is no exception. The following have been most generous in lending their specimens for study and description, and subsequently depositing them in museums; Mr. Samuel Ciurca, Mr. Ray Bandringa, Mr. Richard X. Cramer, Mr. David Lyon Douglass, Mr. Chris Durden, Ms. Bea Vogel, Mr. Jerry Herdina, Mr. Wm. Stephen LeMay, and Mrs. K. Taelle.

For much assistance toward a better understanding of Recent scorpions, Drs. Fred Bennett, Oscar F. Francke, R. F. Lawrence, P. R. San Martin, Max Vachon, and David Sissom were particularly helpful.

Mr. Jorge E. Lopez Ricalo, draftsman with Amoco, who lettered many of the drawings for this paper, must not be forgotten.

Most sincere thanks of all go to Waering's wife, Virginia, who kept a sick man happily engaged in his work, and to whom fell the drudgery of typing the various stages of this monograph. It was Waering's wish that this work be dedicated to her in appreciation.

Very special acknowledgment goes to Dr. Peter R. Hoover, Director of the Paleontological Research Institution for seeing the manuscript into print, and to Dr. Oscar F. Francke and Dr. W. D. Ian Rolfe for their careful review of the manuscript prior to publication. Because of the circumstance of publication of a posthumous paper, any suggested substantive alterations in the text were impossible, and subsequent reviews of the printed monograph must deal with these. Obviously, Waering's treatment and assignments of some groups are open to debate, as is any work so revisionary and wide-ranging as this one. Alas, that Dr. Petrunkevitch is no longer with us!

Anneliese S. Caster
425 Riddle Road
Cincinnati, OH 45220, U.S.A.

EDITOR'S PREFACE

The compilation and editing of the notes and portions of manuscript left to the Casters by the late Erik N. Kjellesvig-Waering has been a long, often frustrating, but in the end immensely rewarding, process.

We have tried, by initialling the footnotes interspersed through the text, to assign responsibility for this or that statement. Annie Caster (written commun., 1985) states, "Footnotes are a problem. Where Waering left no direct text for a species, I tried to follow the format that Petrunkevitch used in the *Treatise,* giving no more than synonymy, general statement, . . . occurrence, and specimen no., and I don't feel that that needs a footnote."

In many ways, the preparation of a manuscript for posthumous publication is similar to the adventure games now so popular for small computers. The author has left much solid information, many clues, and not a few dead ends, and one must go back, and back again, with periods of reflection between, to sort it all out. The difference between the manuscript and the computer game is that there is a clear end to the game: in the manuscript, we must arbitrarily choose some suitable point on the refinement rarefaction curve and let the reader take it from there. It's in your court now.

Peter R. Hoover
Ithaca, NY

CHARACTERISTICS AND NATURE OF FOSSIL SCORPIONS

A General Statement

In the fossil record, what is essentially meant by fossil scorpions are the gill-bearing forms known in the Paleozoic and the Triassic. Except for two in the Jurassic, the rest of the Mesozoic has not definitely furnished any scorpions as yet, whereas the Tertiary has furnished only three species in Europe and two in North America. All Tertiary forms were pulmonate and lived

on land. The Carboniferous *Palaeopisthacanthus* of the Mazon Creek area in Illinois and *Compsoscorpius* of the Coseley area of Britain are the only known pulmonate scorpions that lived in the Paleozoic. Both are monotypic, the former known only from a single specimen, the latter from three. All known British Triassic scorpions are gill-bearing.

The gill-bearing scorpions did not survive into modern time, but, fortunately, the relatively great number of specimens preserved was a direct result of their basic ecological setting in a water medium, where preservational factors were at an optimum. I suspect that even the Paleozoic pulmonates may have lived in water or in the vegetation above the water, as in a swamp forest, where again chances of preservation were high. The scarcity of Tertiary forms is probably a consequence of the fact that all were land-living and likely had developed the established characteristics of the modern scorpion, such as being cryptozoic and mainly solitary animals. The chances of this type of animal being preserved are, of course, much less, which is reflected by their rarity in the fossil record. The Tertiary scorpions are not found in normal sediments of aquatic origin, as were all Paleozoic forms, but in deposits on dry land. For example, one, *Scorpio schweiggeri* Holl, 1829, Oligocene, is known from volcanic ash falls. Another, *Mioscorpio zeuneri* (Hadži, 1931), Miocene (covered in this monograph), was preserved in calcareous deposits (travertine) accumulated from springs (one in a lake, the other on land). The other three (*Tityus eogenus* Menge, 1869, Baltic amber, Oligocene (?); *Centruroides beynai* Schawaller, 1979, Dominican amber, Tertiary; *Tityus ambarensis* Schawaller, 1982, Dominican amber, Tertiary) were preserved in gum from conifers (amber). All but one are known from a single specimen.

Morphological differences are considerable between the lobosternous, holosternous, meristosternous and bilobosternous scorpions on one side and the orthosternous (which include all living forms), on the other. However, as early as the Middle Pennsylvanian, orthosternous scorpions were present, and these have all the characteristics of the living families. In fact, in the case of *Palaeopisthacanthus,* it is close to the Chaerilidae.

The differences between fossil and living scorpions are as listed:

CARAPACE

The differences between the carapaces of most fossil scorpions and those of the living ones are immediately evident in the shape of the anterior margin and the position of the median eyes, as well as the presence of compound eyes in some. In fossil forms, the anterior margin is almost always produced into a shovellike protrusion very similar to that found in eurypterids, which were undoubtedly water-dwellers. The purpose of this plowlike device is considered to be the same in both groups, a very handy digging device for concealment in the mud (see *Hughmilleria banksii* Salter, Text-fig. 79C). Some living scorpions such as the troglobite *Typhlochactas,* a chactid, and *Brachistosternus,* a bothriurid, have a slightly protruding anterior, but this protrusion seems to serve to drape the carapace over the chelicerae, a secondary separation of the chelicerae, and should not be mistaken for the large glossate process of fossil scorpions and eurypterids. Other shapes of carapaces are known in water-dwelling scorpions, as, for example, *Hydroscorpius denisoni.* Here the carapace is rounded and rather hemicircular in shape. With this peculiar shape, there is no comparison with living scorpions, as all living scorpions are roughly quadrate or rectangular. However, one of the eurypterids, *Parahughmilleria,* has a similar rounded carapace, and of course, is an undoubted water animal. Nowhere in the fossil record are emarginate anterior margins, such as occur in *Centruroides* and *Tityus* (Buthidae), to be found, or deeply-lobed anterior margins like those of nearly all burrowing scorpions, such as *Broteochactas* (Chactidae) or the genera *Scorpio, Opisthacanthus* and *Opisthophthalmus* (Scorpionidae). The only living scorpions that resemble the majority of the fossil forms in having a pointed anterior margin are the uniquely interesting *Typhlochactas,* a troglobite scorpion from the El Abra caves of Mexico (Mitchell, 1968) and *Brachistosternus* (Bothriuridae) from the Andean region of South America. With regard to the burrowing scorpions, it is interesting to note that the only obviously burrowing type found in the fossil state is *Garnettius hungerfordi* (Elias) from the Upper Pennsylvanian of Kansas. This genus was armed with large serrated anterior legs remarkably like those of living burrowing beetles such as *Copris, Phanaeus* and *Pinotus.* However, it was also furnished with a projecting anterior margin. Inasmuch as it definitely is holosternous, the scorpion seems to be adapted for digging in muds in an aquatic environment, perhaps like so many of the living crabs.

EYES

The median eyes of fossil scorpions are generally located on a prominent eye node, which protrudes above the level of the carapace and usually is located forward. In some Triassic scorpions, these median eyes are located further forward than in known Paleozoic forms (see *Mesophonus* in Wills, 1947, pl. 1, figs. 1, 2). Here the eyes and eye node actually become part of the anterior protrusion, and extend anterior to the

rest ("shoulders") of the anterior margin. In others (*Mazonia woodiana* Meek and Worthen; see Kjellesvig-Waering, 1969) the median eyes are very large, rounded, and located on the anterior part, but behind the level of the anterior margin. Large eyes, anteriorly located, but possibly elliptical in shape, are present in some (see *Waterstonia airdriensis,* Text-fig. 99A).

Before proceeding further on a discussion of morphology of the lateral eyes in fossil scorpions, it is necessary to define the two main types, as confusion exists on this subject. In this connection, I am following the terminology and descriptions used by Harrington (1959, pp. O88–O91) with regard to the Trilobita (both definitions by Harrington, Moore, and Stubblefield, 1959, pp. O121 and O126).

Schizochroal eyes

Eye with visual surface consisting of a number of biconvex lenses, rounded or polygonal in outline, each lens covered by individual cornea, and separated from others by sclerotic walls (syn. aggregate eye).

Holochroal eyes

Compound eye consisting of numerous adjoining planoconvex or biconvex lenses, covered by a continuous cornea (syn. compound eye).

More significantly, with regard to the schizochroal or aggregate eyes, the eye groups consist of ocelli that do not differ in structure from simple eyes, and function in the same way (Lawrence, 1953, p. 143); with regard to the holochroal or compound eyes, the cornea is formed by an aggregation of separate visual elements known as ommatidia, each ommatidium corresponding to a single facet of the cornea (Lawrence, 1953, p. 144).

The lateral eyes in fossil scorpions comprise large, subelliptical, bulbous structures, generally placed at the anterolateral margins of the carapace. These have been considered by authors who have recognized them (Wills, 1947, p. 20; Kjellesvig-Waering, 1966, p. 365) as compound lateral eyes. Petrunkevitch (1953, p. 35) did not agree with Wills' (1947, p. 20) determination of "compound facetted lateral eyes", in the Triassic *Mesophonus.* However, it is obvious that Petrunkevitch did not distinguish between compound and aggregate eyes as he follows with the statement, "I compared them with the compound eyes of fossil Trilobita, Xyphosura and Eurypterida and cannot find much similarity with these". (Only the eyes of pterygotid eurypterids were then known in detail.) Petrunkevitch (1953, p. 35) denied that the lateral "compound" eyes of *Mesophonus* were eyes and considered them organs of "unknown function, possibly chemoreceptors". Although Petrunkevitch had numerous specimens available to him that had these prominent, bulbous lateral eyes, he consistently either overlooked or denied their existence ("*Typhloscorpius*" *distinctus,* "*Eoscorpius*" *danielsi, Eoscorpius carbonarius,* "*Lichnophthalmus*" *pulcher, Eoctonus miniatus, Buthiscorpius buthiformis,* etc.).

The eyes of Trilobita are both compound (holochroal) and aggregate (schizochroal). The Xiphosura, at least the living forms, have compound eyes, although of a very simple nature.

The Eurypterida are divided into two suborders, and in the Eurypterina, as exemplified by the Upper Silurian *Baltoeurypterus tetragonophthalmus* (Fischer), the eye is composed of several thousand rounded ocelli, each being clear or transparent, whereas the surrounding tissue is brown and opaque. On the inner dorsal edges of the lateral eye, each ocellus is surrounded by sclerotic walls as thick as the diameter of each. These ocelli become more crowded toward the median part of the eye, where for the most part they are obliterated. The ocelli definitely protrude over the rest of the surface of the eye, giving a "pebbly" appearance to the cornea. This is based on several specimens from the Gerard Holm Collection at the Riksmuséet (Stockholm) and represent chitinous skins that had been etched out of the limestone matrix by the use of acids. Wills (1965, p. 102) gives a good description of the lateral eye in the same species. The only point where I disagree is in the number of facets in the "compound" eye. Wills states that they comprise "several hundred minute facets", whereas I would estimate the number close to 5000. The eye in some Eurypterina is therefore compound, although in parts, for example as indicated by the thick sclerotic walls, it appears to be somewhat schizochroal, at least on the basis of definitions given above. We have no knowledge of the eye in other Eurypterina such as the superfamilies Mixopteroidea and Stylonuroidea.

With regard to the Pterygotina, the eyes have been determined by Clarke and Ruedemann (1912, pp. 36–42) as holochroal or compound and similar to the eyes of *Limulus.* The lateral eye of *Baltoeurypterus* is very different from that of *Limulus,* where the ommatidia are closely packed into hexagonal walls, all adjoining one another and covered by a thick, smooth cornea. In contrast, the lateral eye of the Eurypterina has the same covering skin with rounded, thickened, clear areas that correspond to the lenses and give the cornea a slightly pebbly appearance under high magnification and, in part at least, each visual unit is surrounded by thick sclerotic walls (see Wills, 1965, pp. 101–102, pl. 2, figs. 6–8), and has setae scattered throughout the eye itself. One may deduce that the setae on the cornea of

the Eurypterina may indicate a simpler type of "compound" eye than that present in *Limulus.* The point is that this type of eye is neither holochroal or schizochroal, but is important to the present study because this is the type of "compound" eye present in some of the fossil scorpions. The number of individual eye units is greatly reduced in fossil scorpions, but not exclusively so, for in the Proscorpiidae, the lateral eye is composed of very minute ocelli, probably reaching as many as one thousand. This approaches the number of visual units in the genus *Erieopterus,* where two species are known with approximately 1000 facets, for example, *E. hypsophthalmus* (Kjellesvig-Waering, 1958b, pp. 1112–1114) and *E. turgidus* (Stumm and Kjellesvig-Waering, 1962, pp. 196–198).

The lateral eyes of some fossil scorpions are developed as bulbous, elliptical structures located at the anterolateral margins, with a distinct rim surrounding each, as in *Eoscorpius distinctus* (Petrunkevitch), which enclosed a cluster of approximately one hundred, rounded, dorsally-convex (possibly plano-convex or biconvex) lenses, separated from one another by sclerotic walls, or enclosed a lesser number of facets, as in "*Lichnophthalmus*" *pulcher* (Petrunkevitch) and *Eoscorpius carbonarius* (Meek and Worthen), which contained less than 30 visual units. Another type known in fossil scorpions is that present in the genera *Eoctonus* and *Buthiscorpius,* which have small elliptical eyes that are distinctly intramarginal and retain only eight rounded eye lenses, but are contained within a restricted, well-defined, elliptical area. The lateral eyes characterizing *Eoscorpius,* "*Lichnophthalmus*", *Eoctonus* and *Buthiscorpius* differ from compound eyes in the Eurypterina only by the lesser number of visual units or so-called facets. Are these eyes holochroal or schizochroal? My interpretation is that they are intermediate between the two. In the Silurian genera *Palaeophonus, Proscorpius, Stoermeroscorpio,* and *Archaeophonus,* the individual units or facets are much smaller in size than those noted for the above genera. They are located on large bulbous elliptical, marginal, entirely smooth eyes and undoubtedly number more than 1000 facets. Although one might assign the eyes of the Carboniferous genera mentioned above (*Eoscorpius,* "*Lichnophthalmus*", *Eoctonus* and *Buthiscorpius*) to the schizochroal category, it would be difficult to include *Proscorpius* and other Silurian genera in a category other than that suggested by the lateral eye of the Eurypterina—namely, compound or holochroal. Throughout the present text and explanation of figures, the lateral eyes of fossil scorpions are referred to as compound or holochroal, but what is meant is that the eyes are of the type present in the Eurypterina, which here are shown to have elements of both holochroal and schizochroal eyes.

Obviously the whole question of compound versus aggregate eyes in fossil forms of Arthropoda needs detailed revision, as, equally obviously, the simplistic definitions given in the *Treatise of Invertebrate Paleontology* break down in practice.

As stated by Lawrence (1953, p. 145), there can be no sharp division between compound and aggregate eyes based upon outward appearance in living forms. For example, the rounded, separated eyes of *Isotoma,* a collembolan, are considered holochroal or compound. Nevertheless, they probably would not be identified as such if found in the fossil state; indeed, they would surely be identified as schizochroal. The same is true of the compound eyes in *Lepisma,* a thysanuran and *Gerufa,* an Isopoda, where the eyes are separated from one another, at least in part of the eye surface (see Lawrence, 1953, text-figs. 48A, C, D). Identification of the eye types by outward appearance would be much more difficult in some fossil forms.

The fact that the living scorpions have simple lateral eyes, truly schizochroal, does not by any means preclude the presence of compound eyes in some of the fossil scorpion groups that were destined for extinction, as very likely was the case for the Lobosternina and Holosternina.

The presence of both types of eyes is known in other arthropods such as the Trilobita, and it would be surprising if this were not the case in the Scorpionida. One might infer that primitive compound eyes developed into aggregate eyes, a line of development that is suggested in the phylogeny of the Trilobita, for example, the Phacopina from Cambrian forms with primitive holochroal eyes. The development of the compound eye reached its highest degree of complexity in the pterygote insects, whereas the Eurypterina-type of primitive schizochroal-holochroal eye was destined for extinction along with the rest of the infraorders Holosternina and Lobosternina, not to mention the Eurypterina itself. It is necessary to emphasize that the living scorpions comprise eight families representing only one superfamily, and thus only a minute part of the entire Scorpionida, which is essentially a fossil group.

Regardless of whether or not it is possible to separate lateral eyes in fossil arthropods into holochroal, schizochroal and intermediate types, all were undoubtedly homologous, and evidence points to the development of the schizochroal from the holochroal. Certainly, the possibility of the "compound" eyes of fossil scorpions developing into the one to five simple eyes of modern scorpions is clearly indicated and probable.

There is a good relationship between the size of the median eyes and the presence or lack of lateral com-

pound eyes. If no lateral compound eyes occur, the median eyes are very large (for example, *Mazonia* and *Waterstonia*). If the lateral compound eyes are present, the median eyes are reduced in size. If the compound eyes are of medium size, the median eyes are similarly reduced (see *Eoscorpius carbonarius* Meek and Worthen) and if the lateral eyes are large, the median eyes are small (see *Kronoscorpio danielsi* (Petrunkevitch), Pl. 14; *Garnettius hungerfordi* (Elias), Text-fig. 46A; and *Eoscorpius distinctus* (Petrunkevitch), Pl. 13, figs. 1–4).

Even in the Upper Paleozoic pulmonate scorpions, *Palaeopisthacanthus* and *Compsoscorpius,* the median eyes occur in the middle part of the anterior half of the carapace. Nothing has been found in the fossil record to indicate eyes in the posterior half, as are present in the African genera *Opisthophthalmus* and *Opisthacanthus* (Scorpionidae), which are active burrowers, although there have been erroneous reports of these posterior eyes in the literature, as in the descriptions of *Palaeoscorpius* Lehmann, 1944, *Proscorpius* Whitfield by Clarke and Ruedemann, 1912, and others.

There is no known occurrence of eyeless scorpions in the fossil record, although Petrunkevitch (1949, 1953 and 1955) reported some cases. This is incorrect and is due to preservational factors or improper cleaning of the fossil. In the case of "*Typhloscorpius*" *distinctus* Petrunkevitch, 1949, a supposedly eyeless scorpion from the Carboniferous of England, a review of the holotype revealed improper or insufficient cleaning in the preparation of the fossil, as well as carelessness in observation of obvious morphological structures (see photographs and drawings of the holotype of *Eoscorpius distinctus* (Petrunkevitch)) (Pl. 13, figs. 1–4; Text-figs. 79A, B). The same can be said of "*Typhlopisthacanthus*" *mazonensis* (Petrunkevitch, 1955, p. 71, fig. 43(5)), *Dolichophonus* (Petrunkevitch, 1955, p. 70, fig. 38(4)) and others.

COXOSTERNAL REGION

It is in this area that one realizes that all modern scorpions represent but an infinitesimal remnant of an ancient, highly diversified, and successful large group of animals. It might well be argued, and with reasonable supporting data, that, instead of the eight families that are to be recognized in the present taxonomy of living scorpions, there should be only three: Buthidae, Scorpionidae and Bothriuridae. The Chaerilidae, Diplocentridae, Chactidae, Vaejovidae and Iuridae should be included in the Scorpionidae, where they were before families were based on the inconclusive and inconsequential presence, or absence, of trivial spurs on the ends of some (not all) tarsi and basitarsi. If both living and fossil scorpions are to be placed in the same taxonomic scheme, then I strongly recommend the usage of the three families for living scorpions, relegating the other families mentioned above to subfamily status. The present investigation is no place for a revision of modern scorpions, but there is no doubt that the above grouping would be highly beneficial to modern scorpionological taxonomy.[1]

The sternum in modern scorpions is essentially pentagonal in shape, although in the Buthidae it is triangulo-pentagonal, and in the Bothriuridae it has been greatly narrowed to become almost invisible from the exterior, as it has been folded inwardly between the genital plates and the base of the second pair of coxae. As Petrunkevitch has shown, boiling in KOH will unfold the true shape of the sternum, and it is very broadly pentagonal. The Scorpionidae have a very large pentagonal sternum with straight linear margins, and it is this type of sternum that is found in many families of fossil scorpions, at least as far back as the Lower Carboniferous, and in all three major divisions, Lobosternina, Meristosternina and Holosternina. The Chaerilidae have a large pentagonal sternum with the base bowed inwardly. This is duplicated in some Carboniferous genera such as *Eoctonus* of the Eoctonidae, and *Anthracochaerilus* of the Anthracochaerilidae.

It is interesting to note that, regardless of family, all neonates of living scorpions retain a large pentagonal sternum. In contrast to the pentagonal sternum of Recent scorpions, the earliest known scorpions from the Silurian and Lower Devonian reveal broadly ovoid, pointed ovoid, or lacrimiform sterni, such as *Waeringoscorpio* Størmer, *Archaeophonus* Kjellesvig-Waering and *Branchioscorpio,* n. gen.; pointed, elongate lacrimiform sterni as in *Kronoscorpio,* n. gen.; to hexagonal-ovoid in the Carboniferous genera *Cyclophthalmus* Corda and *Eobuthus* Frič; or rectangulo-pentagonal as in the Lower Carboniferous *Archaeoctonus* Pocock, nearly rounded pentagonal in *Gigantoscorpio* Størmer of the Upper Carboniferous, to an equilateral triangle as in *Spongiophonus* Wills of the Triassic.

Petrunkevitch (1913), following Kraepelin, Pocock, Karsch and other early scorpion taxonomists, recognized that the sternum had great taxonomic value. Unfortunately, he abandoned this important taxobasis because he thought that in practice the system broke down with regard to fossils (1953). This is incorrect.

---

[1] We are grateful to Dr. O. F. Francke for calling attention to papers dealing with the familial classification of Recent scorpions since Waering's death: Francke (1979, J. Arachnol. 7:19–32); Lamoral (1980, Proc. 8th Intern. Cong. Arachnol., Vienna, pp. 439–444); Francke and Soleglad (1982, J. Arachnol. 9:233–258); and Francke (1982, Synopsis and Classification of Living Organisms, McGraw-Hill Book Co., pp. 73–75). A.S.C. & K.E.C.

What obviously was doomed to failure was his idea that a meaningful taxonomy must be based on convenience of preservational features. Actually, there will be many specimens that are not sufficiently well preserved to be determinable, but this is an unfortunate truth which all paleontologists have necessarily accepted. Under no circumstances, however, should a morphological character be considered improper because it is preserved with difficulty. The sternum is very often well preserved and, with careful work and experimentation with various lights and angles of lighting, as well as liquids or various methods of study in the dry state, it is quite possible to work out the structure of the sternum practically as well as any other structure in fossil scorpions. Petrunkevitch, in order to show that the sternum was an unreliable taxobasis, stated that neonates of the Buthidae and Bothriuridae had a broadly pentagonal sternum which in adult stadia became subtriangular or inwardly folded respectively. Therefore, he came to the surprising conclusion that this indicated unreliability, a conclusion that does not merit comment.

As with the pentagonal shape of the sternum in living scorpions, the arrangement of the coxae is entirely the same in all families: the last two pairs abut the sternum, whereas the maxillary lobes of the second pair meet at midsection, anterior to the sternum, thus squeezing the first pair of coxae away from the midsection, causing the first pair to lie behind and to the sides of the maxillary lobes of the second pair. The oral opening, therefore, is composed of a tunnel with the maxillary lobes of the second pair of coxae forming most of the base, the maxillary lobes of the first pair making up the rest of the base, while the large inner sides of the trochanters of the pedipalps form most of the sides, and the roof is formed by the bases of the chelicerae.

In the case of fossil scorpions, this basic arrangement, as well as the position of the coxae vis-à-vis the sternum, is common in some families such as the Eoctonidae, Anthracochaerilidae, Eobuthidae and others in the Carboniferous. Thus, this specialized coxosternal arrangement that characterizes the Orthosternina was present in all three other major divisions: Lobosternina, Meristosternina and Holosternina, as well as the Bilobosternina. However, it is greatly changed in many other families, and these changes are considered of greater than familial importance. In some genera, such as the Carboniferous *Eoscorpius* of the Eoscorpiidae, the first two pairs meet at the midsection, above a small pentagonal sternum in the usual manner present in Recent scorpions, but only the third pair of coxae abuts the sternum, whereas the fourth pair abuts the genital opercular plates.

With regard to the scorpions with pointed, oval or lacrimiform sterni, one must note that, in the Upper Silurian, the genus *Proscorpius* did not develop maxillary lobes in the first two pairs of coxae. Here the bottom of the entrance to the mouth was composed of the first two pairs of coxae, and the sides probably were the inner part of the trochanters of the pedipalps, with the bases of the chelicerae forming the roof. The succeeding three pairs of legs abut against the lacrimiform sternum. In *Proscorpius* the first pair of coxae had distinct masticatory edges, armed with small teeth, or a true gnathobase such as characterizes the eurypterids. Mastication, therefore, was not delegated entirely to the chelicerae as in living scorpions, but at least in part to the gnathobase as in eurypterids. In the Lower Devonian *Branchioscorpio,* maxillary lobes are well developed in the first two pairs of coxae, indicating that this development, present in living scorpions, will occur in much older scorpions than those found in the Lower Devonian. The last two pairs of coxae abut against the lacrimiform sternum.

PROSOMAL APPENDAGES

Apart from the coxae, which as shown above have undergone great rearrangement in position, the prosomal appendages are for the most part not greatly unlike those of living scorpions except in certain important areas. The chelicerae of living scorpions are composed of three segments and are not capable of appreciable side or ventral movement. All Paleozoic scorpions that I have studied show consistently that the chelicerae are composed of four distinct joints. The basal one (**Ch1**) is cup-shaped, followed by another cup-shaped band (**Ch2**), the manus with its fixed ramus (**Ch3**) and the free dactyl or ramus (**Ch4**). The dactyls carry well-developed teeth and in the genera *Proscorpius* and *Allopalaeophonus* from the Silurian, the free ramus is decidedly falcate. Enormous chelicerae, apparently rather flattened, are present in some Upper Carboniferous genera such as *Garnettius* and some species, like *Mazonia wardingleyi.* Many show thick long setae, some in brushlike masses located on the inner sides of the chelicerae. These appear to have had some function other than to form a cushion between the chelicerae and it is here suggested that these setae were movable and may have been used in passing food particles to the oral opening. However, the four-jointed chelicerae, particularly in some Lower Devonian forms, were long enough to be capable of moving food to the mouth by bending downward and backward to reach the mouth. In the shorter four-jointed chelicerae, bending backward to the oral opening could not have been done so well, and then only partly.

The denticles on each side of the dactyls are generally preserved in fossils, although nearly always both sides

of the dactyls (superior and inferior) are flattened together, so that interpretation of the position of the rows of denticles, and their sizes or shapes, is difficult. It is only rarely that the chelicerae are found in an inflated or natural state. The differences in dentition, however, do not seem to be outstandingly diagnostic, and certainly not a taxobasis above family level, if that high. Vachon (1963) has shown that the living scorpions do have differences on the family level. This interesting factor could be explored further in fossil scorpions, but not enough data are available to me at present to comment further.

The pedipalps are remarkable in fossil scorpions merely for the fact that they have not changed appreciably since the Middle Silurian. They are composed of the same number of joints and are identical in nearly all aspects. Some are narrow and long, as in the Lower Devonian *Branchioscorpio* and the Upper Carboniferous *Cyclophthalmus,* and others, denoting the more fossorial types, are short and stout, such as the Lower Devonian *Palaeoscorpius* and the Upper Carboniferous *Garnettius.* Nowhere in the fossil record, except in the Miocene (*Mioscorpio*), are scorpions found with the greatly inflated manus of living scorpions such as *Scorpio* and *Heterometrus.*

Slight or no difference in size of the fossil setae has been noted, and none has been found to be the long type that characterizes the trichobothria of today. However, this does not mean that they could not have been present in the Paleozoic forms, particularly the terrestrial ones. Surely it is reasonable to assume that the pulmonate orthosternous *Palaeopisthacanthus* and *Compsoscorpius* had trichobothria developed. But the only reason this is assumed is because the setal bases are arranged in linear rows and clusters much like in the living scorpions. This is an acceptable argument, as most may agree. On the other hand, true aquatic scorpions have identical setal openings, but here the same facts are not acceptable!

Trichobothria, as we know them, seem to be specialized for cryptoenvironments and not aqueous ones, which were the main habitat of most of the Paleozoic scorpions so far recovered. In this respect, it is interesting to note that one of the troglobite scorpions has unusually long trichobothria developed for a cavern environment, which is merely a "macrocryptoenvironment". Whether or not trichobothria were developed in aquatic scorpions remains a possibility, but I consider it a likely one. At any rate, on the species level, the arrangement of the trichobothria is a taxobasis of importance, and has been used by the writer in preliminary separation or identification of fossil scorpions. This taxobasis will become more important when more fossil scorpions have been found.

Some fossil scorpions developed sensory setae on the pedipalps which, in basic structure, are very similar to the trichobothria of Recent scorpions: see the Carboniferous *Mazonia* (Kjellesvig-Waering, 1969, p. 171) and *Gigantoscorpio* (Størmer, 1963, p. 122). These setae are arranged in definite rows, groups, or small clusters, resembling the trichobothria of living scorpions. On the other hand, it is difficult to think that the setae could be as long as those developed on present day trichobothria, although the shorter setae developed for aquatic life could have the same sensory function as the long ones do today. Of course it is not known if the fossil aquatic scorpions had developed trichogen cells, or whether such cells were developed for atmospheric environments. It seems possible that they did develop them, but for a water existence, as shown by the many specimens with definitely placed rows and arrangement of setal openings on the pedipalps, as in Recent scorpions.

The Upper Carboniferous *Paraisobuthus prantli,* n. gen., n. sp. developed a long manus with long dactyls—the dorsal side was smooth, but the entire ventral side was a dense mat of setae (see Text-figs. 87B, D, E), which are not considered to be trichobothria.

The "cutting" edges of the dactyls of fossil scorpions were developed as are those today, and the type of teeth, setae, etc., along the inner edge is as important a taxobasis as it is in living scorpions, particularly on the generic scale, according to our understanding today. In the Silurian, the genera *Palaeophonus* and *Proscorpius* have dactyls with cultrate edges. Others have a single file of small denticles as in the Lower Devonian *Branchioscorpio,* the Upper Carboniferous *Titanoscorpio* and many others. Some, like the Upper Carboniferous *Paraisobuthus,* have a row of setae along the edge and, possibly, the immovable finger ends in a double or split end where the single ramus would be accommodated. *Brontoscorpio,* the gigantic Upper Silurian scorpion, has four to five or more rows of thick denticles along the edges. The genus *Palaeomachus* of the Upper Carboniferous has a large swelling on the inner edge near the base of the free ramus, much as is present in the males of some species of the living genus *Tityus* (Buthidae). There is, however, a great difference and that is that the swelling, instead of fitting into a corresponding indentation on the opposite finger, fits into a boss on the side of the fixed finger. The two dactyls, therefore, must have had a slight scissorlike action in *Palaeomachus* (see Text-fig. 109C).

The legs are remarkable in fossil scorpions. They are of two general types in the Lower Paleozoic, one, the very short, stout legs of *Palaeophonus* and *Allopalaeophonus,* which terminate in a long, but robust, single spine (the posttarsus). This is generally mistaken

for a claw. Actually, the claws of present-day scorpions are the tarsal spurs, and the termination is the greatly reduced posttarsus. The thick legs of these scorpions are considered eurypteroid in aspect, and suggest that these scorpions were adapted for digging under water. This habitat explains the long sinuous shape, much like other burrowers, such as the living *Broteochactas* (Chactidae), and may be responsible for the short "eurypterid" legs. *Broteochactas,* as well as other good burrowers, also had short legs, but not to the extent present in these early scorpions. At the same time, scorpions with legs much like those living today lived concurrently with the "primitive" Palaeophonidae. These include *Dolichophonus, Proscorpius, Waeringoscorpio, Archaeophonus* and *Branchioscorpio* from the Silurian and the Lower Devonian. In *Proscorpius* the legs are relatively short, tubular, but slender and not of the above-mentioned "eurypteroid" type. In all scorpions, both living and fossil, the leg count, past the coxa, is consistently seven joints, counting the posttarsus.

Only in the Silurian genus *Archaeophonus* Kjellesvig-Waering was there a possibility of a double trochanter, which would have raised the leg count to eight joints past the coxa. It is now believed that the supposed double trochanter is in reality a single one and that a crack obliterated the joint or misled me to that interpretation (Kjellesvig-Waering, 1966). It can safely be said that all scorpions so far known have seven joints past the coxa on each leg.

The legs of these Silurian scorpions, *Proscorpius* and *Archaeophonus* are as remarkable as those of the Palaeophonidae in that they have an extremely long tarsus, with very short, poorly developed tibial and basitarsal spurs, one on each side. The long tarsus ends in short double claws, which are covered with at least a row of minute spines on the bottom of each claw. The posttarsus is greatly reduced. One might speculate here as to how this scorpion walked, and the fact that it lived on very soft muddy magnesium carbonate bottom may indicate that the entire tarsus was placed flat on the substratum. The small spines underneath the claws may also indicate that traction was needed against slippery surfaces such as algae.

The long tarsus continues into late Paleozoic time (see *Kronoscorpio*), although in many, such as *Eoscorpius,* the tarsus was becoming reduced. In *Gigantoscorpio* the tarsus had become even more reduced.

In some Carboniferous scorpions an enormous tibial spine was developed on the fourth leg. In "*Europhthalmus longimanus*" (see Text-fig. 77C), *Boreoscorpio copelandi,* n. gen., n. sp. and others, the tibial spine is developed to an extraordinary length. Again it might be well to speculate. All scorpions with such a spikelike tibial spine have the spine on the outside of the last pair of legs and all occur in the Upper Carboniferous where "coal swamp" conditions prevailed. It appears that this spine could be used to anchor a scorpion when it is walking vertically up a tree root or trunk, underwater or above water, as the abdominal plates or "sternites" each had a pouch for the gills and enough space to carry water to moisten them, as in many living gill-bearing amphibious animals such as crabs, etc. An anchor was also needed to hold firm when the stinger was thrown overhead and thrust forward—the two spines, anchored in plant material so common on the floor of the swamp forest, would give the backward support needed. Tibial and basitarsal spines were also very thick, serrated, rounded, and occurred in many different sizes and shapes. In the modern scorpions, all are merely small, spinelike vestiges. I suspect, judging from the eurypterid leg, that it would not be surprising to find paired spines higher on the joints, such as femoral spines, in fossil scorpions.

Perhaps the most remarkable thing about the legs of some of the more primitive scorpions, such as those constituting the superfamilies Palaeophonoidea (Lobosternina), and Allopalaeophonoidea and Archaeoctonoidea (Holosternina), is that they are distinctly terete and not flattened as in most scorpions in the Upper Carboniferous to the Recent.

As in modern scorpions, the last joint of the leg is the transtarsus or posttarsus. Anterior to this joint are the claws, which are homologous to the tarsal spurs. In some scorpions, such as the Silurian Palaeophonidae, the foot of the scorpion ended in a sharp, pointed transtarsus without development of curved claws, which resembled the terminal joint of the walking legs of eurypterids. However, there are two tarsal spurs, one on each side. These legs are adapted for a water habitat, but like the crabs, could as easily be adapted for land. The fact that the Palaeophonidae were lobosterns shows that the adaptation of the pointed terminal joint was for grasping rock surfaces or perhaps reefal environments, probably under water, as the scorpion was gill-bearing.

By the early Devonian at the latest, the three-"toed" combination was developed. *Palaeoscorpius* retained the short, pointed posttarsus, but had developed two spurs on each side which are equivalent to basitarsal spurs, so these legs seem to be adapted for the same environment as the palaeophonids. As early as the Middle Silurian the scorpions had developed the foot that is present today. The Silurian scorpions such as *Dolichophonus* (leg terminations unknown, but the type of body indicates that the double claws were developed), *Archaeophonus,* and *Proscorpius* had developed

a posttarsus that had assumed a posterior position on the leg joint (tarsus) and two claws that were anterior to the posttarsus. These scorpions were true water dwellers and the leg terminations were presumably developed for walking on underwater shore plants as well as roots, trunks and harder bottoms.

In Carboniferous time the development of the terminal joints reached its greatest diversity. Some scorpions, such as *Eoscorpius, Eobuthus, Isobuthus,* etc., developed large curved claws that were armed with small spines on the ventral side. This development, however, occurred as early as Middle Silurian, as it is present in the Wenlockian *Allopalaeophonus* (see Textfig. 17C). These claws could only be adapted for holding onto some object, such as underwater roots, leaves, stems, etc., present in swamp forests. All of these scorpions were either holosternous or lobosternous, thus were water-dwellers breathing through gills. We could assume that some of these scorpions lived among the underwater roots and trunks of trees and other plants, but were capable of excursions above water on these plants, thus occupying the same position as many crabs living today.

Some Carboniferous scorpions such as "*Lichnophthalmus*" *pulcher* (see Wills, 1959, figs. 5, 6) had the posttarsus developed into an incredibly long "dagger". The double claws showed the ventral spines so suitable for arboreal existence. It seems almost certain that the long dagger was also developed for arboreal life.

Kronoscorpio, a lobostern, developed the claws into very long straight spines, and the posttarsus was developed into an equally long spine. Thus, this would result in a very widespread, trifurcate, terminal arrangement and give a "snow shoe" action for walking on soft muddy bottoms. The two long "claws" would be on the anterior, and the posttarsus on the posterior.

OPERCULUM

The opercular plates are of different sizes and shapes, and double as in Recent scorpions. Although not much attention has been given to the opercular plates as a taxobasis, they may be rather diagnostic. Thus they vary from large subquadrate plates, as in the Lower Devonian *Branchioscorpio,* to small subquadrate plates, as in the Lower Carboniferous *Gigantoscorpio willsi* Størmer (see description of part of the holotype. pp. 76–77, below). Others are elongated, with the long axis parallel to the length of the scorpion, and fitting together against the lower part of the sternum, as in the Upper Carboniferous *Kronoscorpio* or the Lower Carboniferous *Centromachus*; or elliptical, as in the Upper Carboniferous *Eoscorpius* and *Eobuthus*; or may be very small rounded-elliptical ones as in the Upper Carboniferous *Anthracoscorpio*; or rounded as in the Upper Carboniferous *Waterstonia.* Another type is pyriform, but with the blunt ends adjoining, as in the Upper Carboniferous pulmonate *Palaeopisthacanthus,* or nearly rectangular, as in *Anthracochaerilus,* also from the Carboniferous. With some exceptions, it might be said that all structures of the opercular plates are not greatly different from those present in living scorpions. Possibly the most interesting genital operculum is present in the Upper Carboniferous *Paraisobuthus,* in which the opercular plates are identical to the lobostern plates of the body except that they are greatly reduced, to become miniatures of these plates. In this case it seems that the two plates never separated, but remained as a single bilobed plate.

PECTINES

Much has been written about the function of the pectines. Today they are regarded by some as chemoreceptors, and by others as mechanoreceptors (Kaestner, 1940, 1968; Levi and Levi, 1968).[2] This may be the case, but none of these authors has bothered to mention that the pectines were fully developed, and for aquatic life, in the lower Paleozoic!

The possibility of the pectines being used as swimming organs, advanced by Dr. Størmer (1963) in his original description of *Gigantoscorpio willsi,* is plausible, although it seems to me that the pectines had a more important function. The entire pectine is very broad and long, making an excellent tool for swimming, or indeed for digging. The third joint is long and ends in a point. Perhaps these old scorpions did not reproduce like those living today, and possibly followed the copulatory practice of the Xiphosura and eurypterids. That is, they laid eggs in a shallow "nest" which had been scooped out in the soft mud or sand by the pectines, and subsequently fertilized by the male. The proximity of the pectines to the reproductory operculum may be significant in this case. This would explain this association in the living scorpions. As a chemoreceptor there would be little point in being so intimately associated with the sex opening, both male and female. The functions of the pectines in living scorpions are dubiously connected with reproduction, although the pectines are very close to the reproductory organs. However, Kaestner (1968, p. 103) shows that they are important in the selection and preparation of a site for spermatophore deposition. If this were so, one would expect the females to have pectines less well-developed than the males. Furthermore, the Brazilian *Tityus serrulatus* is parthenogenic and, although only

[2] The fine structure of the sensory pegs on scorpion pectines was described by J. D. Carthy (1968, Symp. Zool. Soc. London, 23:251–261). Neurophysiological studies have been reported by C. Hoffmann (1964, Naturwiss. 51:172) (Francke, written commun., 1983).

females are known, the pectines are as well-developed as in other species of *Tityus.* It is suggested that the position of the pectines in relation to the opercula is a consequence of their previous development as aids in scooping out a nest for the accommodation of eggs, and directly connected to arranging the eggs and mixing the spermatozoa with the eggs in order to assure fertility. Certainly the function of the pectines as a chemoreceptor does not seem to be warranted in an aquatic animal. The teeth do indicate a perfect "brushlike" function and it is here suggested that the teeth were used in mixing the eggs with the spermatozoa. It should be noted that the pectines of living (pulmonate) scorpions are all much narrower than the majority of the fossil aquatic scorpions.

Holosternous and lobosternous scorpions, which were aquatic and breathed through gills, developed pectines that were much more variable in structure than those of living scorpions. In the Upper Silurian *Proscorpius osborni* (Whitfield) they are composed of a finlike unjointed anterior plate, without differentiation into a jointed rachis and a middle lamella—the plate is also without rounded sclerites or areoles. Fulcra are well-developed and teeth are elongated but relatively stout. The Lower Devonian *Branchioscorpio richardonsoni,* n. gen., n. sp. also has the large unjointed and undifferentiated plate, no fulcra, and very round large flat teeth. In the Upper Paleozoic, *Gigantoscorpio* (see Størmer, 1963, pp. 54–57), *Eoscorpius, Telmatoscorpio, Kronoscorpio* (see this paper) and many others had a well-developed, jointed rachis, as in modern scorpions, and a greatly-expanded middle lamella with areoles of irregular size and shape. In others the areoles are all consistently small and rounded throughout the middle lamella. Fulcra were well-developed and the teeth were numerous, well in excess of 50 on each comb. In many of these the entire pectine was so long (anteriorly to posteriorly) that it was as long or longer than the width (as measured along the row of denticles). In the genus *Anthracochaerilus* the combs were very narrow and long, without the development of fulcra, and with very thin, nearly needlelike, teeth of which as many as 150 were present on each comb.

The larger, or in particular, the wider the pectine, the more it is broken into areoles both on the middle lamella and the rachis. In living scorpions, those with very wide pectines also develop areoles (*Brachistosternus, Bothriurus,* etc.). Those that have short pectines do not develop the areoles, but in some cases the middle lamella and rachis are indistinguishable, as the entire pectine comprises a single plate.

Although there is considerable variation in the pectines of living scorpions, this variation is minor compared to that of fossil scorpions. This is to be expected, as present day scorpions belong to a very small remnant group representing only one superfamily, whereas fossil ones belong to many superfamilies involving several infraorders. However, the fundamental structure is the same in all, both fossil aquatic and the living, even to the presence of peg organs in the teeth. In some scorpions, such as *Paraisobuthus,* a dilated inner areole probably denotes the female, as it does in many living scorpions such as the genus *Tityus* in the Buthidae. There is no question, therefore, that in aquatic, gill-bearing scorpions the pectines were composed of the same external structures, namely rachis, middle lamella, fulcra (or no fulcra as in some living scorpions, for example, *Ananteris*), teeth and peg organs. Whatever function is given to the pectines of living pulmonate scorpions, it is going to be very difficult not to apply the same function to the fossil gill-bearing ones. As stated above, that function may well be connected with reproduction.

We may now speculate with a reasonable degree of accuracy on the origin of the pectinal, prepectinal and opercular plates. The question is, are the pectinal, prepectinal and opercular plates in Orthosternina modified abdominal plates or sternites? There are several specimens, both in fossil and living scorpions, that give us a rather good idea of the origin.

The evidence is that in both fossil and living scorpions, regardless of whether the scorpion may have abdominal plates or sternites, or a combination of both, as in *Branchioscorpio,* these plates are modified abdominal plates. There are several pertinent specimens that are important in this respect, and information from the eurypterids is of particular importance.

In the rather closely related eurypterids, it has been shown that many, for example, *Eurypterus, Baltoeurypterus,* and others, demonstrate a forward gradation of the type of plates on the ventral side of the preabdomen. Thus in *Eurypterus* the posterior plates are found to be of the holosternous type, grading into meristosternous-holosternous, to entirely meristosternous plates. In *Mixopterus kiaeri* Størmer (Størmer, 1955, p. 35) the development is from holosternous on the fifth plate to protolobosternous on the fourth to lobosternous on the third and other plates. In *Carcinosoma* (see Kjellesvig-Waering, 1958a, p. 299) it was noted that the fifth abdominal plate was holosternous, the others meristosternous. The development is anteriorly. (See: Clarke and Ruedemann, 1912; Holm, 1896, 1897, 1898, 1899, for numerous examples.) Similarly, the median organ shows the same progressive development anteriorly.

PREABDOMEN

The dorsal side of the preabdomen in fossil scorpions

is very similar to that present in Recent scorpions. All scorpions, regardless of age, have seven tergites in the preabdomen and not eight as advanced by Petrunkevitch (1913, 1949, 1953, 1955), mainly based on a misconception of the preabdomen of *Mazonia woodiana* (see Kjellesvig-Waering, 1969, p. 171). Dubinin (1962, fig. 1225), not satisified with eight tergites in the preabdomen, gave *Mazonia woodiana* nine! A complete *Mazonia woodiana* is described here and shown in Text-figure 29B, which should remove all doubts concerning the validity of this theory. All tergites of fossil scorpions, as of many living ones, have well-developed transverse ridges on the anterior. The tergites are shaped exactly like those of living forms with the exception of one genus, the Upper Silurian *Proscorpius,* which has well-developed alae at each anterolateral angle. These alae are common among the Eurypterida.

The underside of the preabdomen is the area where, in my opinion, the most important macro-evolutionary changes have taken place. These changes are described below and will not be repeated here. In contrast to the bandlike sternites of living scorpions (*orthosternous*) with round to elliptical to slitlike stigmata perforating the center of each half of the sternite, fossil scorpions are: *bilobosternous,* being composed of two separate free rounded plates without any stigmata; *lobosternous,* consisting of two rounded or lobed plates joined at midsection and without stigmata and with a thick doublure; *meristosternous,* where two apparently holosternous plates are joined by a suture at midsection, but without stigmata; and *holosternous,* where the plates are bandlike, without any suture or stigmata. All four types overlap the succeeding abdominal plate as in eurypterids, and in contrast to the Orthosternina, which have sternites embedded in the tissue and not overlapping. It is known that the meristosterns and the holosterns, which are considered to be gill-bearing, had the opening from the gills through a large narrow slit in the doublure of the abdominal plate, at each posterior lateral angle. The bilobosterns and the lobosterns apparently had the gills directly below the plates, but probably were open throughout the entire posterior parts.

CAUDA

The cauda of fossil scorpions does not differ from that of Recent ones. It is composed of five segments and the telson. As in Recent forms, fossil ones have narrow to wide caudae. The females, both living and fossil, have a distinctly shorter and thicker cauda than do the males, and in the latter the twelfth tergite is longer and more slender than in the females. Some fossil forms, like the Upper Carboniferous *Eoscorpius pulcher* and *Palaeobuthus distinctus,* have an enormously developed, scimitarlike aculeus with only a small vesicle (see Text-figs. 56B, 77A). No Paleozoic or Mesozoic scorpion has been found with a subaculear tooth, as this apparently was a Tertiary development.

ORNAMENTATION

The ornamentation of fossil scorpions is much like that of Recent forms, except that some scorpions have a dermal covering that is highly and coarsely pustulose. The Lower Carboniferous *Archaeoctonus glaber* (Peach) has raised, long scalelike ornamentation that is an exact duplicate of that which characterizes the superfamily Mixopteroidea of the Eurypterida. These include the distinctly scorpionid eurypterids that not only had the scorpionid shape, but also had telsons that likely had a pair of poison glands, as the entire cauda was capable of being curved overhead, as in the scorpion, for upward or forward thrusting. Compare the ornamentation of *A. glaber* in Text-figures 21A, D with that of *Paracarcinosoma* sp. (Kjellesvig-Waering, 1951, text-figs. 2j–l).

THE VENTRAL SIDE OF THE BILOBOSTERNINA, LOBOSTERNINA, HOLOSTERNINA AND MERISTOSTERNINA

The ventral side in the above infraorders, which include nearly all the Paleozoic scorpions, is quite different from that of the Orthosternina, or living scorpions. These differences are apart from the well-known characteristic of having abdominal plates overlapping one another as in the eurypterids. The number of gill-bearing abdominal plates in these orders is five—again, precisely the same number found in eurypterids. This important fact has not been recognized until now. Living scorpions have only four lung-bearing sternites.

The Paleozoic Bilobosternina, Lobosternina, Holosternina and Meristosternina were thought to have four, rather than five "sternites" because only a few specimens were found in which the underside had not been telescoped into the anterior part of the preabdomen, as would occur due to molting. Unfortunately, it was also due to the prejudiced assumption that five gill-bearing "sternites" were not possible and therefore not expected. Heretofore all modern authors, myself included, accepted the assumption that fossil scorpions had to have four "sternites", as is the case with living forms.

It is unfortunately the area immediately behind the carapace where obstruction occurs, and it is caused by the lateral widening of the preabdomen. Therefore, when the animal crawled out of its empty skin, telescoping occurred, resulting in covering of the important ventral structures by the large pectines. It is thought

that nearly all fossil scorpions found are exuviae, as the associated eurypterids were. Thus only a few specimens escaped telescoping and those had pectines so large that the overlying structures were completely masked. A particularly good specimen showing the true relationship of the underside to the dorsal is the holotype of *Microlabis sternbergii* Frič, which has very small pectines, unusual for Paleozoic forms, not large enough to obliterate the structures dorsal to it. The specimen reveals five distinct meristosternous abdominal plates. Although this specimen has been known since 1904, no importance whatsoever had been given to the presence of the five "sternites". Petrunkevitch (1953, p. 23) reported five plates in the holotype, but failed to attach the slightest importance to their presence.

In this context, it is well to recall that Thorell (1886, p. 270), in his intense controversy with Whitfield, had questioned the five "sternites", which Whitfield stated were present in the Silurian *Proscorpius osborni.* All who worked on this group agreed with Thorell, including myself (1966, p. 365). I now have several more specimens showing that there is no doubt whatsoever that five gill-bearing abdominal plates occur (see Text-figs. 6C, 7A, 11A). The holostern *Palaeoscorpius devonicus* Lehmann also clearly shows five abdominal plates (see P1. 3, fig. 1).

In the Lobosternina it is difficult to find a specimen where the large pectines normally present in this infraorder have not completely covered the structures dorsal to the pectines, or that telescoping in the region of the pectines has not masked the structures. Nevertheless, the holotype of *Paraisobuthus prantli,* although not well-preserved in the area of the abdomen, does show the five abdominal plates.

Thus we have five abdominal plates present in the Lobosternina, Holosternina and Meristosternina, and it can safely be assumed that the Bilobosternina also had five abdominal plates.

Also of considerable taxonomic interest, and located in the same area where telescoping of the anterior of the preabdomen is most prevalent, is the pectinal plate (anchor plate or basal pectinal plate), which is well known in living as well as fossil scorpions. In fossil scorpions, however, the plate retains a well-developed median organ in some forms; in others this median organ is completely absent. This may be due to sexual differentiation, but there are not sufficient fossil specimens at present to fully determine that.

PREPECTINAL PLATE

There is some confusion in the literature concerning a small plate that occurs anterior to the pectinal plate and which is named the prepectinal plate (**ppp**). Petrunkevitch (1913, 1949, 1953 and 1955) did not recognize the prepectinal plate. Størmer, in his excellent description of *Gigantoscorpio willsi* (1963, pp. 53–59), was the first to figure a greatly diminished plate with a median organ; unfortunately, this plate was not in place and was therefore identified as part of the pectinal plates ("basal plate of pectines"). This organ can now be identified as the prepectinal plate (**ppp**) and properly occurs anterior to the pectinal plate (**pp**) and posterior to the operculum. A revised reconstruction of this area of *G. willsi* is given in Text-figure 76C. The plate here retains the median organ, which is not always present in some other genera. For comparison of the prepectinal plate, see *Opsieobuthus pottsvillensis* (Text-fig. 31A), *Centromachus euglyptus* (Text-fig. 31B) and *Eoscorpius pulcher* (Text-fig. 27B).

Curiously enough, the prepectinal plate has not been recognized in living scorpions, but it is present in at least some of the New World buthids, but only in the males (no New World buthid males are known without it, but all have not been investigated). The plate is very small and of the same color as the rest of the scorpion integument. For example, in the dark brown *Tityus trinitatis* Pocock, the sclerite is a wing-shaped narrow plate lying next to the operculum (see Text-fig. 31C). It may serve a function connected with the operculum, but this is a secondary adaptation, and it certainly is the prepectinal plate. The female *T. trinitatis* does not have this plate (see Text-fig. 31D).

Although I have made only a cursory search for the presence of the prepectinal plate in living scorpions, it is present in males of the following (all of which are New World Buthidae):

Centruroides gracilis (Latreille)
Centruroides keysi Muma (=*C. guanensis* Franganillo)
Centruroides margaritatus (Gervais)
Microtityus rickyi Kjellesvig-Waering
Tityus pictus Pocock
Tityus trinitatis Pocock

The prepectinal plate is not present in males of the following (Chactidae, Diplocentridae, Buthidae, Scorpionidae, Bothriuridae, Vaejovidae):

Bothriurus bonariensis (Koch)
Broteas granimanus Pocock
Hadogenes troglodytes (Peters)
Ischnurus ochropus Koch
Mesobuthus gibbosus (Brulle)
Nebo heirichonticus Simon
Opisthacanthus laevipes Pocock
Pandinus viatoris (Pocock)
Uroplectes triangulifer marchalli (Pocock)
Paruroctonus mesaensis Stahnke

The prepectinal plate is not present in females of the following (Buthidae, Chaerilidae, Vaejovidae, Bothriuridae):

Bothriurus bonariensis (Koch)
Buthus trilineatus Peters
Centromachetes obscurus Mello-Leitão
Centruroides keysi Muma (=*C. guanensis* Franganillo)
Centruroides margaritatus (Gervais)
Centruroides gracilis (Latreille)
Chaerilus celebensis Pocock
Chaerilus truncatus Karsh
Mesobuthus gibbosus (Brulle)
Microtityus rickyi Kjellesvig-Waering
Parabuthus villosus Peters
Tityus rufofuscus Pocock
Tityus smithi Pocock
Tityus trinitatis Pocock
Uroplectes triangulifer marchalli (Pocock)
Paruroctonus mesaensis Stahnke

In scorpions, the prepectinal plate would be opposite or is the counter somite of the pregenital tergite, whereas the pectinal plate and appendage (pectines) would be the counter somite of the first (adult) tergite. The rest of the tergites and "sternites" are each equivalent. This means that the fundamental preabdomen of scorpions consisted of eight somites, although in the adult fossil scorpion, the dorsal side consisted of seven dorsal segments, whereas the ventral comprised eight somites, and seven in other fossil scorpions, depending on the presence of the prepectinal plate. Apparently the preabdomen of living scorpions is composed of seven somites in New World Buthidae males, and six in New World Buthidae females and all other families, including Euro-Asian and African Buthidae, depending on the presence of the prepectinal plate.

The prepectinal plate assumes importance in any attempt to homologize the segmentation of the Scorpionida with any other groups, as it appears to be the opposing or ventral part of the somite of which the pregenital tergite is the dorsal part.

There should not be any confusion with regard to the above and to Petrunkevitch's ill-fated hypothesis of the eight tergites in the dorsal preabdomen of the *adult* fossil scorpions (*Mazonia, Proscorpius,* etc.). This has been completely disproved (Kjellesvig-Waering, 1969, pp. 171–190).

STERNITES AND ABDOMINAL PLATES

The sternites of living scorpions and the abdominal plates of lobosternous, holosternous and other fossil scorpions are neither the same nor even homologous. The current view, as stated by Størmer (1976, p. 149) is that the two are the same structure: ". . . *Mesophonus* probably forms a transition between the early Palaeozoic scorpions, in which the abdominal plates probably were attached in front only, and the Recent forms in which the ventral plates are attached all around as ordinary sternites." There is a different conclusion, which I believe is worth considering: the sternites of the living scorpions are part of the ventral body wall, whereas the abdominal plates are appendages of the somite and lie below (outside) the ventral body wall. Most forms that had abdominal plates (the lobosterns, meristosterns and holosterns among the scorpions and the entire order Eurypterida) never developed sclerotized sternites as that protection was not needed, because the ventral body wall was covered by the abdominal plates. In the bilobosterns the ventral body wall was partially uncovered and sternites developed. The Phalangiotarbida had both abdominal plates and sternites: six abdominal plates covering the six pairs of gill chambers, and three sclerotized sternites as the last three segments of the opisthosoma.

In my opinion, there was no migration of the so-called stigmata from the doublures of the lobosternous, holosternous and meristosternous scorpions as has been advanced (Størmer, 1976, pp. 149–150). For example, the "stigmata" that characterized the British Triassic scorpions are considered to be intermediate between the early Paleozoic scorpions and Recent forms, as advanced by Wills (1947, p. 33) and Størmer (1963, p. 110; 1976, p. 149). But this is not possible, for the so-called stigma of the Triassic mesophonids was merely an opening into the gill chamber (not an opening into the body (lungs)). Although both authors consider the known British Triassic scorpions to have lungs, this is impossible, since it can be shown that the so-called lungs were not attached to the "stigmata" as are the true lungs in living scorpions, but were attached instead to the body wall, with the posterior spinous (rounded) and considerably anterior to the wide "stigmata" (see Wills, 1947, text-figs. 7, 18, 51). In order for these structures to be lungs, they would have to be turned around 180°, and attached to the wide "stigmata". Apart from this, if the sternites of living scorpions were homologous to the abdominal plate, the so-called lungs would have to migrate from the body wall, forward and downward along the dorsal side of the abdominal plate, and then back again anteriorly to end at the present position of stigmata of the sternites that characterize the Orthosternina.

Ontogenetically the lungs are clearly invaginations of the body wall or sternite (not abdominal plate). The lungs are aborted during ecdysis, attached to the sternite, showing that they are part of the ectoderm or body wall. In the ontogeny of scorpions the stigmata and lungs move *slightly* forward, as reported by Kaestner (1940, p. 113), but this slight migration of the stigmata should not be confused with the gills of holosternous, lobosternous and meristosternous scorpions. This occurs on the sternite and has nothing whatever to do with migration of the gill slits on the doublures of the ancient scorpions. There never was

an invagination of the gills for the gills would then form sacs and we do know that all gills so far found in fossil scorpions are simple lamina, not sacs of any form.

It should be noted that doublures were never formed on the true sternites, as they were not needed, because the sternite never formed a gill chamber. Doublures of the abdominal plates are simply part of the gill chamber as Waterston (1975, p. 249, text-fig. 3) showed in great detail in his excellent paper on the eurypterid gills, and confirmed here in the scorpions. He was able to reveal the delicate structures in the large eurypterid *Tarsopterella scotica* (Woodward). This type of breathing mechanism is precisely what I feel must be present in the Lobosternina, which was also suggested by Waterston. In the description of the scorpion *Paraisobuthus duobicarinatus,* gill tracts are described identical to those present in the eurypterids.

It is well known that the quantities of oxygen available in water are very small compared to the quantity present in air. Thus it is essential, during the absorption of oxygen from water, that a sufficient amount of water be circulated over the gills so that the required amount of oxygen may be obtained. This implies that the opening (in and out) through which the oxygen is introduced to the breathing mechanism from a water source must necessarily be large enough to accommodate the large volumes of water required. Conversely, the amount of air needed to supply the required oxygen is much smaller. This is clearly revealed by the stigmata of living or pulmonate scorpions, which are very small, each being approximately one-eighth to one-twelfth the width of the sternite. On gilled scorpions, the gill opening on the abdominal plate doublure is several times wider. For example, in the Triassic scorpions the gill openings are each one-fourth the width of the abdominal plate, and in the Lobosternina the gill slit is nearly as wide as the entire abdominal plate (see Text-fig. 83E). In the Amblypygida the stigma is much larger than in most Arachnida, nevertheless, it is only about one-sixth the width of the sternite. This order, however, has only one pair of lungs as against the four pairs of lungs in pulmonate scorpions and the five pairs of gills in gilled scorpions. These wide gill chamber openings were certainly not needed if oxygen from an atmospheric source were involved.

Similarly, there is no homology between the book-gills of the Xiphosura and the book-lungs of scorpions. In the Xiphosura the book-gills are appendages that hang from the body wall into the water, whereas the lungs of scorpions are invaginations of the ectoderm. The homology claimed for both structures by Lankester (1881), Waterston (1975, p. 251) and others is difficult to justify. The difficulty seems to be the lack of recognition of the fact that the ventral plate in living scorpions is a true sternite, whereas the Xiphosura have abdominal plates *outside* the sternite, which remain unsclerotized. In fossil Xiphosura, where the opisthosoma is segmented, the sternites would be developed in much the same manner as in the Eurypterida.

If it is not true that the abdominal plates of gilled scorpions are *not* homologous to the sternites of pulmonate scorpions, then we must accept the fact that the two are homologous and, indeed, the same. This means that living scorpions do not have true sternites. It may be well to speculate on that possibility.

In the first place, scorpions such as the lobosterns, meristosterns and holosterns, comprising nearly our entire knowledge of fossil scorpions, were terminal groups that did not continue into any lines that led to the present-day scorpions. The possibility of Triassic scorpions having large stigmata and lungs, which later migrated anteriorly, is totally unacceptable. The fact that the so-called lungs are shown to be attached to the body wall with the posterior end facing the "stigmata" and without any connection to the "stigmata", plus the well-developed gill chamber, proves that the "lungs" are gills. These gills could not possibly develop into lungs, as they would first require invagination in order to be lungs, and second, as stated above, an unlikely migration down into the abdominal plate where, in some unknown fashion, the gill chamber was obliterated. The abdominal plate became fused with the body wall, obliterating the ventral layer, and the doublures were also obliterated. This is, of course, highly unlikely if not impossible.

DIRECTION OF EVOLUTION

The scorpion *Branchioscorpio richardsoni* seems to reveal the direction of evolution of these early scorpions (see Text-figs. 2 and 101A–G). This scorpion has a well-developed coxosternal area with the tubular area anterior to the mouth. The tubular oral chamber anterior to the mouth is considered by Størmer (1976, p. 154) to be a specialization for land living, and the writer agrees. The development of rounded, oval abdominal plates at first was mistaken by the writer to be a very primitive development of the abdominal plates, but after being faced with the fact that the coxosternal region was greatly advanced and specialized, I have arrived at the conclusion that these oval plates, joined only at the inner anterior part, without doublures, actually are equally as advanced as the coxosternal arrangement. What we have then, is that this scorpion is intermediate between the lobosterns and the living scorpions, and the oval plates are in the process of being reduced completely. If this hypothesis

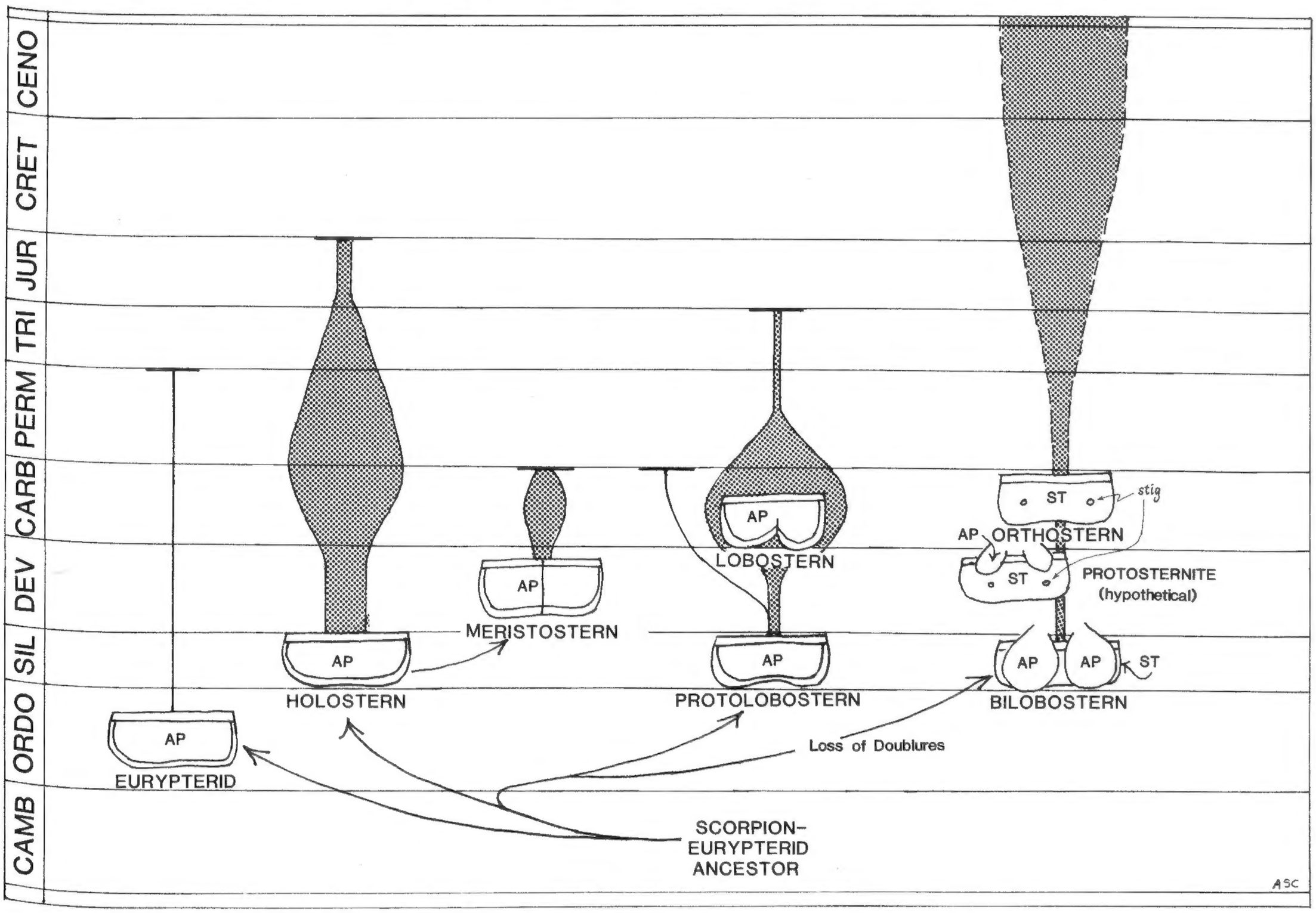
is correct, then someday we should find a scorpion that has carried this reduction further until the underlying sternites have become sclerotized, when the group left the water completely. Once the abdominal plates are reduced—along with the gills, gill chamber and doublures—the sternites with their invaginated lungs will be developed. Sclerotization of the sternites, as well as slight sclerotization of the lung books, had to take place as the body wall was exposed.

It seems safe to assume that *Branchioscorpio richardsoni* had gills and, even equipped with an oral tube, could only leave the water for short periods, as the rounded opercula of the abdominal plates exposed the gills to the drying action of air. It appears as if this species of scorpion were an amphibious one, living much like some of the amphibious crabs.

This hypothesis would explain the invagination of the lungs in the embryo of living scorpions and will clarify the discrepancies in the abdominal plate–sternite relationship. So far we have not found the intermediate stage of development, but we do have one specimen that points to that conclusion, *Branchioscorpio richardsoni*. A phylogenetic tree showing these lines of development is shown in Text-figure 1.

BREATHING MECHANISMS

Our knowledge of the breathing mechanisms of scorpions, except for the living pulmonates, is meager, but considerable knowledge of the mechanisms of fossil scorpions has been gained since the works of Petrunkevitch (1955), who considered all to be pulmonates, and Wills (1947) who erroneously considered the British Triassic scorpions to be pulmonates. In his work on the Carboniferous scorpions, Wills did consider the lobosterns to be aquatic, but still thought the holosterns were terrestrial forms (1960, p. 330).



Text-figure 1.—Phylogenetic lines of development in the Scorpionida. After a sketch by Kjellesvig-Waering.

The bilobosternous condition is known only from the Silurian and the Early Devonian. In structural transition from the archaic condition of exclusively possessing abdominal plates (**AP**) and gills for branchial aquatic respiration, to the sternite (**ST**) condition with lungs and stigmata (**stig**), for aerial respiration, they are analogues of that other great Devonian pioneer group, the Amphibia, which were achieving comparable structural and functional transition.

Between the bilobosternous condition and the orthosternous, two, probably correlated, changes occurred: the first sternite, present beneath the abdominal plates of the bilobosterns, is lost, as are the paired abdominal plates of all segments.

I follow the definitions of lungs and gills given by Krogh (1941 (1968), p. 27), namely: lungs are all *cavities* serving respiratory purposes, lungs being the typical organs for air breathing, whereas gills are *appendages* used for respiratory purposes and being the typical organs for respiration of *dissolved* oxygen. There are, of course, water lungs (holothurians, etc.), tracheal respiration and other forms not pertinent to the present discussion. We may dispense with the water lungs, but tracheal respiration is possibly important to this study. Tracheal respiration represents "air filled tubes originating from special openings in the integument, the "spiracles", and repeated branching reaching out to all parts of the body, thus obviating the convection by a circulating fluid" (Krogh, 1941 (1968), p. 114). Tracheae are primarily developed for air breathing and only secondarily adapted for an aquatic existence (Krogh, 1941 (1968), p. 115). Levi (1976) lists two types of tracheae, namely sieve and tubular tracheae, and summarizes the breathing mechanisms of living Arachnida, where each order is shown to have either book-lungs or tracheae, and of the Palpigradi, which lack respiratory and circulating systems. Our concern here is with the various types present in the Scorpionida. Although we have but meager knowledge of scorpion gill systems, the breathing mechanisms may be summarized as follows:

1. Lungs: Pulmonate scorpions are known from the Middle Pennsylvanian to the present. The stigmata are round, slitlike or oval in shape, and occur in the posterior half of the sternite. There are four pairs of book-lungs, which are attached to the sternite. All pulmonates belong to the Orthosternina.

2. Gills such as characterize *Tiphoscorpio hueberi:* These are single lamellae composed of white, sponge-like tissue and consist of rounded, concentrically-ribbed layers of three distinct sizes, and with large spines on the lateral margins. *Tiphoscorpio* is a Meristosternina. The gills occur in a well-developed gill chamber. Water likely enters at the anterolateral angle and is expelled at the posterior gill slit located between the doublure and the abdominal plate. The gills are attached to the anterior of the gill chamber, which is on the exterior of the body wall.

3. Gill tracts of the type present in *Paraisobuthus duobicarinatus:* These are also typical of the eurypterids, namely, an oval area on the body wall (not the abdominal plate) composed of white spongy tissue with numerous cone-spines on the ventral surface of the gill tracts. The gill tracts occur in a gill chamber, and water enters at the anterolateral angle and is expelled at the rear of the abdominal plate. *Paraisobuthus* is a Lobosternina.

4. Gills that characterize most of the British Triassic scorpions: Wills (1947), for example, reported *Willsiscorpio bromsgroviensis* (Wills), in which the gills are composed of a single (?) lamella of spongy tissue, with a fringe of spinelets on the posterior border. The anterior is not known, but the gill should be attached to the anterior of the gill chamber—certainly not to the abdominal plate. Water presumably enters at the anterolateral angles and is expelled by the posteriorly-located gill slits. *Mesophonus perornatus* Wills has similar gills, but without the fringe of spinelets. Both *Willsiscorpio* and *Mesophonus* are Holosternina.

5. Tracheae: The possibility of tracheae in fossil scorpions must be admitted, although I consider the type should be described as gills. Størmer (1970) described some peculiar ribbon-shaped gills for the Devonian scorpion *Waeringoscorpio hefteri* Størmer. These are irregular oval bodies with what appear as ribbons or possibly crushed tubes. These are found outside the body, but it must be stated that this scorpion has undergone ecdysis, and in life these gill-like or tracheal structures may have been inside the gill chamber, although this is not a necessary consideration, since they could have been the type that could be extended into the water outside of the abdominal plates and back into the gill chamber. It is possible, but not probable, that these are branchial leaves, each of which is composed of masses of trachioles (see Krogh, 1941, p. 141, fig. 83). More likely, however, the structures are true gills, consisting of a single lamella, oval in shape and reinforced by linear ribbing.

COMPARISON OF SCORPIONS AND EURYPTERIDS

Throughout the known geological history of the scorpion, stretching from the Middle Silurian to the present, approximately 450 million years, only three major characters were developed that were *universally unique* to the scorpions in comparison to the eurypterids. These are:

1. The development of chelae on the pedipalps.
2. The development of combs.
3. The development of paired poison glands and an aculeus with semiterminal openings for the delivery of the poison.

All other characters may be found in either the eurypterids, or gilled or pulmonate scorpions, but the three mentioned above seem to be major departures from the Eurypterida. For example, swimming paddles are not known in scorpions, but there are eurypterids also without them. Lungs are not known in eurypterids, but there are scorpions without lungs. Scorpions developed claws, but many did not have claws.

It emerges now that the most striking difference between the Eurypterida and the Scorpionida is the de-

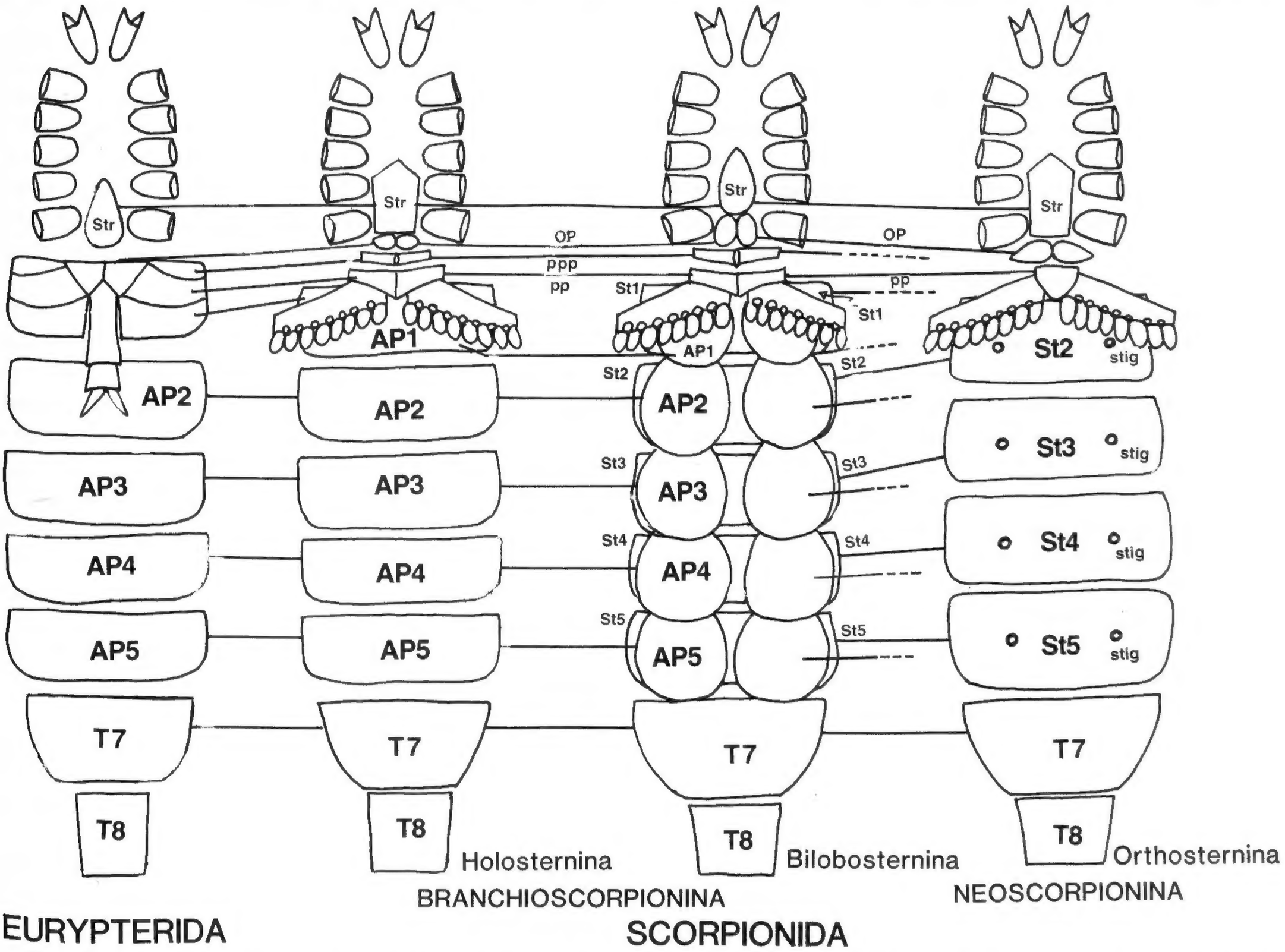
velopment of pectines in the latter during Silurian time. The homology of these structures with anything in the eurypterids is problematical, but when the median organ of eurypterids is further studied, these homologies may appear.

A word should be said regarding the poison-bearing telson of the scorpions, as some eurypterids, as well as some of the carcinosomatids, megalograptids and mixopterids have a rather bulbous telson with a downwardly curved spike that *superficially* resembles the stinger of the scorpion. Some authors have advanced the possibility that this telson may have harbored a pair of poison glands as in the scorpions. I do not consider this to be the case as the two telsons are greatly different and should not be confused. The scorpion aculeus is like a hypodermic needle—very slender, sharp and with the poison duct openings on each side of the point. The eurypterid telson does not show any openings whatsoever and, furthermore, is a very blunt spine incapable of penetration except into the softest tissue. It is a powerful weapon and would serve greatly to fend off any attacks from above. The poison glands, if they were present in the eurypterid telson, would be located too far back and the poison would have to travel so far that it would be totally ineffective. In order to be effective, the poison has to be injected instantaneously into the victim. The eurypterid telson of the above families is not a short, slender, sharp, falconate structure as in the scorpion stinger.

The overall conclusion of these comparisons is that eurypterids and scorpions are closely related and deserve a high classification that bespeaks this.

EVOLUTIONARY CHANGES IN SCORPIONS

Beginning as early as the Lower Devonian, several important changes took place in the known fossil scorpions, some involving lines of phylogenetic significance. These changes were not necessarily concurrent with one another and seem to be associated with the emergence from water to land, and are listed in what



Text-figure 2.—A comparison of the ventral morphology of the Eurypterida and three infraorders of the Scorpionida. For simplicity, the meristosterns, protolobosterns and lobosterns of the Branchioscorpionina, to which the holosterns and bilobosterns belong, are not shown. Their homologies are directly and indisputably with the holosterns. See foldout inside front cover for explanation of abbreviations.

seems to be the approximate order of importance or significance.

1. The loss of abdominal plates and gills, and the development and sclerotization of the sternites and the appearance of lungs. These have been shown in Text-figure 2.

2. The forward development of the mesosomatic underside, resulting in the nearly total loss of the prepectinal plate and the first abdominal plate. The modern scorpions, therefore, have only the second to the fifth sternites (inclusive) developed.

3. The development of the maxillary lobes of the first two coxae into the oral tube and the concurrent reduction in size of the chelicerae (see also 9 below).

4. The movement of the coxosternal area forward: that is, the development of the forward displacement of the fourth pair of coxae from the genital opercula to the sternum.

5. The dispersal of the lateral facetted eyes into lateral individual eyes, numbering five or less on each side.

6. The backward displacement of the median eyes from the anterior margin to the middle of the carapace or further, posteriorly.

7. A great reduction in the length of the tarsus on each leg.

8. The disappearance of the spines underneath the ungues, as well as shortening of the unguis and posttarsus.

9. Reduction of the chelicera from four to three joints by disappearance of the second joint (see also 3 above).

10. Almost total disappearance of the anterior glossate process of the carapace, present only in a greatly reduced state in very few living scorpions—the South American *Brachistosternus* and the Mexican *Typhlochactas.*

11. The early scorpions (*Proscorpius, Stoermeroscorpio, Archaeophonus, Palaeophonus,* etc.) have short, terete legs, round in cross-section. These become greatly flattened and semi-elliptical or flatter in cross-section and become lengthened.

12. The lengthening of the third and fourth coxae.

13. The gradual reduction in tibial and basitarsal spurs, both in size and occurrence on each leg. This change is considered to be by far the least important of the changes listed above.

THE TRIASSIC SCORPIONS

Our knowledge of Triassic scorpions is due entirely to Wills, who in 1910, and particularly in 1947, minutely described the surprisingly well-preserved scorpion fauna encountered in the Lower Keuper rocks of Worcestershire, England. The scorpions, mostly disjointed, were freed from the soft shale so that their preservation is almost as if the fragments belonged to living specimens. Unfortunately, they are disjointed, and being abundant fragments, their respective morphological identification is essential and paramount to reconstruction of the animal and determination of the various taxa present. The scorpion skins are so well preserved, that the original cuticle and color are present, including many details such as sensory hairs and other parts not commonly fossilized. It is because of Wills' excellent detailed descriptions that it is possible to propose several important taxonomic changes in that fauna, which will have important significance to the overall taxonomy of the Scorpionida.

The aspect of the Triassic scorpion fauna is surprisingly primitive and resembles closely some of the more primitive groups in the Carboniferous. Indeed, the coxosternal arrangement of *Spongiophonus,* with the lack of development of maxillary lobes on the second pair of coxae, and the junction of the first pair at midsection with only the anterior half of the second pair of coxae meeting at the midline (see Text-fig. 110L), shows unusually and unexpectedly primitive characters that were relicts from the more primitive Paleozoic groups, such as the Archaeoctonidae. There is nothing in the Triassic fauna to indicate any relationship with living forms whatsoever, but there is much that is analogous to those of the Paleozoic. For instance, these Triassic scorpions, with the exception of one lobostern, are holosternous and unlike modern scorpions, all of which are orthosternous.

I venture to speculate, not timidly, that the known Triassic scorpions continued with gills and remained in an aquatic environment into extinction sometime in the Mesozoic. We know that England, as well as America, had developed land scorpions, with as well-developed stigmata and lungs as those living today, as early as the Upper Carboniferous. Nevertheless, not one single fragment of a pulmonate scorpion occurs in the remarkable and incredibly rich Triassic material studied by Wills.

These scorpions, belonging to the infraorder Holosternina and one specimen to the Lobosternina, are aquatic or amphibious scorpions for the following reasons:

1. The Triassic scorpions are morphologically much closer to Paleozoic scorpions than to Recent ones. The holosternous Silurian scorpion, *Proscorpius osborni* Whitfield, or the Carboniferous *Mazonia woodiana* Meek and Worthen had large openings in the posterior edge of the "sternites" or doublures, much like those present in the Triassic genera.

2. If the Triassic scorpions were pulmonate forms, some, at least, would have been breathing air through stigmata that perforated the face of the sternites. Stigmata of this type had been developed by Middle Penn-

sylvanian time at the latest in North America (Vogel and Durden (1966) and discussions of *Palaeopisthacanthus schucherti* Petrunkevitch, below), and in the Upper Carboniferous in England (see *Compsoscorpius* here), and were round and indistinguishable from those present in certain living scorpions. Stigmata in living scorpions are small, round or oval perforations or slits through the middle of each half of the sternite. It must be stressed that stigmata, *if present, would be readily preserved in fossils.* Incidentally, the small round ones that characterize some of the Chactidae and Chaerilidae, the smallest and most inconspicuous type, have already been found. Preservation would be much easier for some other types of stigmata, *e.g.,* the slits that occur in families such as the Buthidae and Scorpionidae, which are surrounded by a lip or limbated, than for the small round holes already found in the Pennsylvanian Mazon Creek *Palaeopisthacanthus.* Throughout the scorpionid literature neontologists, in interpreting fossils, repeatedly suggest that the stigmata might have occurred, but "being small they probably were not preserved". In fact, in the case of *Palaeophonus nuncius,* several well-known workers insisted that an inconclusive "crack" on one side of the "sternite" had to represent the stigma, although it was clear that the animal was bilaterally symmetrical and that the fortuitous "crack" was not present on the other side of the "sternites". Any scorpion with stigmata perforating the cuticle of the sternite will show these stigmata in the same way that setae, setal sites and other much smaller structures are shown in complete clarity and preservation. I have examined the specimen in question (holotype of *Palaeophonus nuncius* Thorell and Lindström) and the supposed "stigma" is not even a crack or perforated slit, but an indentation which does not perforate the skin. I have also examined other specimens of "sternites" (see Text-fig. 60I) so perfectly preserved that they retain the original cuticle and even color, and can state without question that no perforations that could be considered stigmata occur.

It must be emphasized that of the many "sternites" recovered by Wills, none showed true stigmata; all were holosternous (except for one lobostern) with large slits either on the doublures opening internally, or marginally located at the posterior lateral sides. These plates are not sternites, but are abdominal plates, each of which has gill chambers.

3. The large slitlike openings on the doublures are indicative of water-dwellers rather than terrestrial forms. These long slits, bordered by large serrations, were located on the doublures, which were probably flexible and movable so that the serrations could keep extraneous material from the gills. Whereas aerial respiration requires only very small stigmata in order to furnish adequate oxygen to the book-lungs, aquatic respiration requires larger apertures in order to pass the necessary large volume of oxygenated water over the gills. As Wills points out (1947, pp. 100–101), the position of the large slitlike opening of the Triassic holosterns is the same as found in the abdominal plates covering the gills of eurypterids, the Carboniferous scorpion *Isobuthus* and the Silurian scorpion *Allopalaeophonus caledonicus* (Hunter). Curiously, however, he considers the Triassic forms to be lung-bearing and terrestrial rather than aquatic, breathing through gills!

4. The habitat of the known Triassic scorpions is the same as that of most other scorpions in the Upper Paleozoic. They commonly occur with *Estheria,* and a clam of doubtful generic designation has also been reported. *Estheria* indicates lagoons, probably of brackish water origin, perhaps stagnant. However, these lagoons had to be very widespread as the scorpions have been found in various locations, for example, Bromsgrove, Northfield, and even in a boring (or borings?) at Charford Mills, Birmingham, England. In each case they occur in a greenish, very carbonaceous and micaceous shale. These scorpions are so abundant and persistent that Wills suggests that the shale (1947, p. ii) might serve as a much-needed marker horizon! One collects these scorpions by selecting the type of shale, not by actually finding the scorpion parts in the rock. They are so numerous that they can be removed from the soft shale by the use of warm water.

5. It seems safe to assume that the great majority of fossil scorpions are ecdysial exuviae. If a concentration is found, as occurs in the related eurypterids, it is likely because they congregated in that particular area during ecdysis in order to escape the destructive action of waves, currents or predators, or it represents subsequent selective deposition. The fine textures and fine, evenly-layered sediments bespeak undoubted quiet conditions, which were best suited for ecdysis.

Probably another safe assumption is that the pulmonate scorpions were solitary cryptozoic forms in the past, just as they are today, therefore, if the Triassic scorpions were terrestrial forms, ecdysis always should have occurred under protection, such as underneath rocks, logs, bark and various types of debris. Hygrophilic forms, living in tropical rain forests or jungles, always perform ecdysis under rocks, logs or bark. The same is true of semi-xerophilic forms. In regard to truly desert forms (Wills postulates that the Triassic scorpions were desert dwellers), ecdysis also always occurs under protection, for example, under rocks or in burrows. These conditions are hardly conducive to the mass accumulation of exuviae into a common aquatic burial.

It may be possible to have a concentration of the solitary scorpions due to a natural phenomenon such as a flood. However, in this case, other animals, cer-

tainly the countless other small terrestrial arthropods known to be living in Triassic time, would have been swept into the same burial site. However, in the stratum in question, the lithological characteristics are against the possibility of flood conditions. If the Triassic scorpions were terrestrial forms, it would be extremely unlikely that their exuviae would be repeatedly swept or blown into pools, covered by sediments, all of the same type and age and occurring at several localities, each time being associated with the same common, water-dwelling companion (*Estheria*) and still be so abundant as to have the burial sites or horizon serve as a stratigraphical marker bed.

These scorpions occur in "very carbonaceous" shales, an environment suggesting, as Wills points out, stagnant conditions. It follows that there was little or no current to transport extraneous material. Then, how is it possible to have the great numbers of scorpion parts in the widespread "marker" bed unless the scorpions were living in that environment? Winds could carry extraneous material into stagnant pools (assuming that these are pools and not widespread, contiguous bodies of water). Regardless of the type of transportation, it would be incredible that of all the many land arthropods living during Triassic time in England, only the scorpions were selected and swept into the pools inhabited by *Estheria.* One would have to come to the unmistakable conclusion that England at the time was literally covered and crawling with land scorpions, as they were the only traces, other than plants, that found their way into these stagnant pools. England likely did have terrestrial pulmonate scorpions during Paleozoic and later time, such as occurred in America, and this is indicated by the three specimens that are the holotypes and *only known specimens* of *Compsoscorpius elegans* Petrunkevitch, *C. elongatus* Petrunkevitch and *Typhlopisthacanthus anglicus* Petrunkevitch (all represent the same species). The only doubt present is the fact that the underside of these three specimens is unknown, therefore we cannot be positive that they had stigmata. I believe that the presence of three lateral eyes on the carapace and the nearly central median eyes, as in *Palaeopisthacanthus* and in many living scorpions, indicate terrestrial scorpions.

A truly terrestrial, cryptozoic arthropod is necessarily among the rarest of all fossils. This certainly seems to be the case with all Paleozoic Scorpionida, where only one certain and three possibly pulmonate and presumably terrestrial specimens have been found. The only other terrestrial scorpions known in the fossil record are extremely rare, as for example, in the Cenozoic, and are known from sinter beds or amber (Baltic and Dominican) where they were obviously trapped.

6. As evidence of land or desert existence, Wills (1947, p. 93) compares the tarsalia of one of the Triassic scorpions, which is very hairy, with the living *Liobuthus,* which presumably uses the hairy tarsalia for digging in the sand or for walking on soft sand. These structures may be used as well in a watery environment, as can be noted in countless examples among living aquatic animals (insects, crustacea, etc.) living on sandy or muddy bottoms. In Lower Triassic beds other than those of Britain, Gall (1971, pp. 33–34, unpubl. thesis) reports at least one scorpion[3] that is truly a pulmonate with typical sternites in the Upper Bunt sandstone of France. But this scorpion is very different from the known British Triassic forms. Another specimen represents a mesophonid.

7. Identification of the "lung lamellae" is crucial in determination of the mode of respiration, but not concerning the question of environment, for the Triassic scorpions may still be aquatic, but breathe air. In either case, with regard to environment, the above arguments apply. As to the identification of the lungs, it should be stressed that only single rounded laminae, some with spinules at the edge, have been found. No actual *book-lungs* have been recovered. Both the rounded laminae and the bordering protecting spinules may as easily be interpreted to be parts of gills rather than book-lungs.

There are no external structural differences between book-gills and book-lungs. The large oval impressions noted on many Carboniferous scorpion "sternites" (see descriptions of *Eoscorpius, Telmatoscorpio, Buthiscorpius, Eoctonus,* etc.) are much like those present in the eurypterids, which are considered as undoubted gills. They are much too large in comparison with living scorpion book-lungs and their orientation is not as in the modern book-lungs. For example, in living scorpions the laminae of the book-lungs are perpendicular against the stigmata. They are therefore also perpendicular to the sternite. The single leaf shown by Wills as a purported lung could not have been perpendicular to the sternal plate as occurs in modern scorpion book-lungs. The great width of these fossil tissues would seriously crowd the internal organs if the laminae were perpendicular and not horizontal to the stigmatal opening or parallel to the sternite. Although it may be argued that only one plate of the book-lung is preserved, this argument does not seem reasonable, as certainly the edges of more of the laminae should have been preserved in the several specimens known.

It is noteworthy that the specimen of *Palaeopisthacanthus schucherti* Petrunkevitch, an undoubted pul-

[3] There are about 15 beautifully preserved specimens, some of them complete, apparently belonging to more than one taxon, that merit further study. A.S.C.

monate scorpion in which the stigmata are clearly preserved, does not show the presence of round depressions as described here (for *Telmatoscorpio, Eoctonus, Eoscorpius,* etc.). These depressions are the gill pouches or chambers for the accommodation of large flat gills.

Slowly, information about the types of gills present in fossil scorpions is being accumulated. Størmer shows single, rounded-out, filamentous structures in the German Lower Devonian holosternous scorpion *Waeringoscorpio hefteri* Størmer (1970, pp. 342–343). The gills of a British Carboniferous lobosternous scorpion, *Paraisobuthus duobicarinatus,* which are almost identical to those in Eurypterida, are described below. Peculiar rounded, concentric gills occur in the New York Upper Devonian meristosternous scorpion *Tiphoscorpio hueberi,* n. gen., n. sp. The gills preserved in the Triassic scorpions are much too fragmentary to offer much evidence as to the type present. Nevertheless, one thing is certain, they are not book-lungs as has previously been postulated by others, nor could they be oriented as in living scorpions, for even the fragments would be too large to be erected vertically to the posterior gill openings. To be vertical to the sternite would require a scorpion to be much thicker than wide.

The Triassic scorpion gills are attached to the anterior of the body wall and are hanging free within a gill chamber composed of the abdominal plate as in other Paleozoic Holosternina and Lobosternina.

8. All Triassic scorpions reported by Wills have abdominal plates rather than sternites. The abdominal plates have well developed doublures, a structure not found in true sternites. This means that the Triassic scorpion had gills which occurred *outside* the body wall, whereas living scorpions have book-lungs and these are *inside* the body wall. The so-called stigmata on the doublures are nothing but large gill slits, and should not be confused with the small stigmata of the sternites (see discussion of abdominal plates vs. sternites, p. 23).

9. The Triassic and Paleozoic genera, even as far back as the Silurian, were commonly equipped with a downwardly bent, shovel- or plowlike triangular anterior process, which is identical to the process in the aquatic eurypterids. It seems logical to assume that identical structures had similar functions. The plowlike process served as an excellent tool for digging into the soft mud bottoms, and for covering most of the dorsal surface of the eurypterid or scorpion with sediments. In the case of the scorpion, the anteriorly-located median eyes, placed on a high ocellar node, would project above the mud, whereas most of the body remained covered. It is significant that any scorpion that was equipped with the anterior glossate process also had median eyes at the anterior of the carapace. Those without the anterior glossate process had median eyes that had receded toward the central part of the carapace. To go further, burrowing terrestrial (living) scorpions such as *Opisthacanthus, Scorpio, Heterometrus, Scorpiops* and many others, have a cordate or nearly bilobed anterior margin, thus the opposite of the glossate anterior, and the median eyes are located in the middle, or even further back, of the carapace in all.

Arguments may be advanced that in terrestrial burrowing arthropods, such as beetles, etc., an anterior digging process is present, but the eyes are always protected, not as in the water-dwelling and mud-digging scorpions, which had no protection over their eyes. In the beetles the anterior process is only used in soft material and all digging is done by fossorial legs.

In the eurypterids, unquestionably established as being aquatic, those with an anterior, downwardly bent, linguiform process (*Mixopterus, Eocarcinosoma, Hughmilleria, Megalograptus*) have the lateral eyes located in the anterior part of the carapace. Curiously enough, except for the genus *Hughmilleria,* the other three are eurypterids with many scorpionid characteristics, including the presence of a curved, stingerlike telson, although I do not consider that it contained paired poison glands. The large *Gigantoscorpio willsi* Størmer, which rivals some of the medium-sized eurypterids in size, also has the anterior glossate process. I doubt if anyone would seriously question the aquatic nature of such a large arthropod. (The Silurian *Brontoscorpio anglicus* Kjellesvig-Waering is even larger.) The logical conclusion seems to be that the median process was needed by certain scorpions for digging in soft bottoms in an aquatic medium.

10. Thus it appears that for scorpions a correlation can be made between forwardly-located median eyes and life in a water medium. What is meant here by "anteriorly located eyes" should not be mistaken, for certain genera of the living families Chaerilidae and Chactidae are considered to have anteriorly-located eyes. In these genera, as in the terrestrial fossil genus *Palaeopisthacanthus,* the eyes are well back of the anterior margin and actually lie in the center of the anterior half of the carapace. In many of the Carboniferous scorpions, all of them with the anterior glossate process, the eyes are located on the anterior node, well elevated from the rest of the carapace. In the Triassic scorpions discovered by Wills, all carapaces of the various genera (see discussion of Triassic genera in taxonomic part) had well-developed anterior nodes with median eyes, as well as the anterior glossate process. One genus, *Willsiscorpio,* has eyes so far forward that they lie on a linguiform process partly anterior to the anterior margin of the carapace.

11. The presence of large slitlike openings on the

doublures (therefore covered) of the abdominal plates, which do not have direct access to the external surface, is sufficient to invite skepticism of considering the scorpion to be a pulmonate or terrestrial arthropod. It is reasonable to assume that the doublures were flexible and perhaps opened and closed by muscle action. The presence of these internal openings in terrestrial arthropods is incongruous, as it means that when the animal is at rest, the weight of the body would be sufficient to close the slitlike openings, thus depriving the lungs of air, or seriously obstructing the flow. The only way in which such an arthropod could breathe is by constant muscular action to keep the "sternites" open at all times, even when at rest. This is certainly a highly improbable breathing procedure. On the other hand, if the animal lived in an aqueous environment, these slits would not close, as the buoyancy of the water alone would be enough to counteract the weight of the body. I know of no land arthropod that has stigmata which do not lead directly to the exterior, whether the openings are ventral, dorsal or lateral, as the only purpose of the stigmata is access to air. Even in the case of the peculiar breathing apparatus of the scutigeromorph centipedes, which have a type of tracheal lung differing from other arthropods in being situated on the dorsal surface, the stigmatal slit opens through the tergite (Lawrence, pers. commun., 1966).

Other Triassic scorpions had large slits at the posterior lateral part of the abdominal plate. Again the same objections listed above would apply. The objection concerning the closing of the slits when the animal is at rest is of particular importance in this matter.

The known British Triassic scorpions had chelicerae composed of four joints, as commonly found in Paleozoic scorpions. Living scorpions have three joints. The four joints were not previously recognized in Triassic scorpions, but they can be plainly seen in Wills' (1947) figure 38BV (see description of specimen No. 178 on page 33 herein). This too reveals that these scorpions have closer affinity to the Paleozoic scorpions than to modern pulmonate ones.

For the reasons given above, the British Triassic scorpions are considered to be gill-bearing and not lung-bearing, as Wills believed (1910, 1947). Within this context, it may be well to summarize the chronology of the taxonomy of the Triassic scorpions, as some of it is highly confusing and erroneous, and is necessary because of the changes proposed.

In 1910 (p. 307), Wills "provisionally" established the suborder Mesophonidea with the family Mesophonidae, although I have not been able to find the diagnosis or description of either. The genus *Mesophonus* was established and described with the species *M. perornatus, M. bromsgroviensis, M. gracilis,* and *M. pulcherrimus.* In 1947 Wills retained the suborder Mesophonidea, and the family Mesophonidae, although again no diagnosis or description of either was given. The family Mesophonidae, which contained only the genus *Mesophonus,* was enlarged to include the genus *Spongiophonus* with only one species, *S. pustulosus.* The genus *Mesophonus* comprised the same species given above, but further species were described. These were *M. opisthophthalmus, M. pseudogracilis,* "*M. infans* forms A, B, C, D and E", and *M. pulcherrimus* var. *immaculatus.*

Petrunkevitch (1953) did not accept the suborder Mesophonidea Wills, 1910, but did accept the family Mesophonidae Wills, 1910. Petrunkevitch, following Wills (1947), referred the genus *Spongiophonus,* along with the type genus *Mesophonus,* to this family. In the *Treatise* (1955), Petrunkevitch essentially followed this treatment. The superfamily Mesophonoidea Wills (*nom. transl.* Petrunkevitch) was then established, though not using the characters derived from the coxosternal arrangement of the type genus *Mesophonus,* but of an altogether different scorpion, *Spongiophonus* (erroneously referred to as "*Spongiotarsus*" in the *Treatise*). The construction of the coxosternal region of *Spongiophonus* is erroneously labeled by Petrunkevitch as *Mesophonus* (1955, fig. 40(6)). Therefore, it was not surprising that *Mesophonus* and *Spongiophonus* were put in the same family. No two scorpions could possibly be more different.

Dubinin (1962) essentially followed Wills and Petrunkevitch, recognizing the family Mesophonidae Wills, 1910, with two genera, *Mesophonus* Wills, 1910, and *Spongiophonus* Wills, 1947. The family, however, was referred to the superfamily Scorpionoidea, which was enlarged to include all living scorpions as well as most of the Carboniferous families. The superfamily Scorpionoidea as such had little or no meaning.

The family Mesophonidae Wills is therefore "accepted" today as having two genera, *Mesophonus* and *Spongiophonus,* regardless of what the higher taxonomic divisions may be. To place *Mesophonus* and *Spongiophonus* in the same family is difficult to understand as they obviously have totally different coxosternal patterns. The coxosternal arrangement of *Mesophonus* is not well known, but enough is preserved to determine without question that it has no affinity, at least on superfamily level, to *Spongiophonus.*

Before proceeding further with my diagnosis of the Triassic scorpions, certain morphological interpretations and determinations, which differ from Wills (1910, 1947), must be clarified, since part of the taxonomy proposed here is based on a new study and reinterpretation of some of Wills' original material. I have studied a number of Wills' pertinent specimens

that have a direct bearing on this problem. These specimens were kindly lent me by Dr. Harry Whittington, and are deposited in the Sedgwick Museum at Cambridge, England; other specimens were studied at Birmingham University through the kindness of Dr. F. W. Shotten. It was gratifying to note that the drawings made by Wills are highly accurate and could not be improved upon. I do differ from Wills in the determination of some of the morphological parts (references are to Wills, 1947); these differences are as follows:

1. Text-figure 13 (pl. V, fig. 3) labelled *M. pseudogracilis*? Wills (specimen No. 094): Admittedly, the specimen is folded and broken and thus permits various interpretations. I differ from Wills who showed the first "sternite" (abdominal plate) to be bilobed, whereas the rest are obviously not. The supposed bilobation, in my interpretation, is not present, and the first abdominal plate is seen to be of the same type as the succeeding, with a wide posterior prolongation of the central part. I am also unable to see a distinct central triangular disc or area, except possibly as an elevated area (ventrally), but not as a triangular plate with suture-like definition as figured. This group of "sternites" is referred to *M. perornatus.*

2. Text-figure 14 labelled *M. bromsgroviensis* ? Wills (specimen No. 0163): This "sternite" has been assigned to the first "sternite" (Wills IX), although, as Wills shows, it is a distinct bilobed abdominal plate having the gill openings between the base of the plate and the doublure, and located considerably away from the lateral margins. He states (1947, p. 34) that the living *Rhopalurus borelli* has a trilobed sternite, as shown in Pocock's (1904) figure reproduced in Werner (1934, p. 52, fig. 33). The first sternite of *R. borelli* is hardly trilobed—it merely has two stridulation areas, separated by a smooth central section, but these are not, in any sense, lobes. Furthermore, one is a sternite and the other an abdominal plate.

Wills stated, and further inferred, that since the first "sternite" of some living scorpions differed from the other "sternites", this was likely the case with No. 0163, and he assigned it to *Mesophonus* ("For this reason I assign these two anomalous sternites (Nos. 0163 and 094) to the same segment in *Mesophonus*"). The first sternite in living scorpions may be slightly different, but these are subtle differences like the addition of a stridulating area, slightly larger punctations, smooth central area, etc., but never of the magnitude shown in specimen No. 0163. No. 0163 is the abdominal plate of a distinct lobostern, deeply cleft at the middle, with the gill openings at the base of the plate, in a more central location and surrounded by much coarser denticles on the lips of the gill openings than in the other "sternites" known in this fauna. These are major morphological differences. This specimen, in my opinion, clearly indicates the presence of a Lobosternina in the Triassic of Britain. It is not *Mesophonus,* as that genus clearly is a Holosternina. The supposed lobation of No. 094 does not exist, in my opinion.

3. Wills'(1947) text-figure 38 BV (Wills, 1910, pl. 25, fig. 6; specimen No. 178): The four joints characteristic of the chelicerae on Triassic scorpions are clearly shown in both the specimen and Wills' excellent drawing. Referring to Wills (1947, text-fig. 38 BV), the points of difference are: I consider his "**c**" to be the basal joint; his "**?c**" is the second joint ("**cf**" in reconstruction); the rest is the hand and fixed ramus, which is the third joint. The fourth joint is the free ramus or dactyl. The four-jointed character of the chelicerae in the Triassic scorpions is another area where they are revealed as being closer to the Paleozoic scorpions, than to Recent ones, which have only three joints.

4. Text-figure 40A–C, labelled *Mesophonus* sp., (specimen No. 040): This important specimen reveals what have been determined as the third and fourth pairs of coxae, the latter abutting a narrow pentagonal sternum. This arrangement of the coxae would mean that the first three pairs of coxae meet at midline, above the sternum, which is abutted only by the fourth pair. This results in a very unusual and improbable, if not impossible, coxal arrangement. Furthermore, the pair of coxae that Wills identified as the fourth pair does not have the shape of the usual fourth pair of coxae and is too short and too wide to be the fourth pair. This pair of coxae, marked "**C4**" on text-figure 40B, is undoubtedly the third pair. The pair anterior to this, marked "**C3**", is the second pair.

Specimen No. 0110 in plate VIII, figure 3, completes the restoration of the *Mesophonus* coxosternal pattern. Wills claims that this is the fourth coxa, which he mounted on the plate with the posterior edge uppermost. This specimen is one of the most important reported in Wills' monograph. It is mounted correctly, otherwise the so-called base of the coxa would have articulations, which do not occur at the base of any coxa. The specimen is not the fourth coxa but the first coxa and of extreme importance to taxonomy because of the presence of a small piece of the uppermost part of the second maxillary lobe, which can clearly be seen on plate VIII, figure 3 (Wills, 1947) to the left of the uppermost part of the first maxillary lobe. There seems to be little doubt that these two coxae belong to the same species as that represented above (specimen No. 040). The entire coxosternal area of *Mesophonus* comprises the first two pairs of coxae with well-developed maxillary lobes, meeting at the midline, anterior to the

narrow sternum, which is abutted by a single pair. The fourth pair, although unknown, must abut the genital operculum. This new restoration (Text-fig. 28), which is made with considerable confidence, results in the taxonomic determination that the genus *Mesophonus* Wills, 1910, is to be assigned to an emended family Mesophonidae Wills, 1910, and is clearly referable to the emended superfamily Mesophonoidea Wills, 1910, which includes such well-known genera as *Centromachus* Thorell and Lindström, 1885, and *Mazonia* Meek and Worthen, 1868. The family Mesophonidae Wills, 1910, is here emended (restricted) and seems to have clear priority over the Mazoniidae Petrunkevitch, 1953. All three families, incidentally, are emended here and bear no resemblance to their original descriptions. On the basis of the type of ornamentation, specimen Nos. 040 and 0110, which together give a nearly complete picture of the parts of the coxosternal region that reveal major taxonomic values, are referred to the lectotype *Mesophonus perornatus* Wills, 1910. As will be shown below, *Mesophonus opisthophthalmus* Wills, 1947, is a junior synonym of the lectotype.

5. Text-figure 40D shows a poorly preserved specimen (No. 164) that retains the last three coxae of the left side as well as part of the sternum and part of a genital operculum: The skins are very thin, and interpretation, because of folding on the slide, is very difficult. Nevertheless, it appears that the sternum is definitely elongate-elliptical, and it is reasonable to suspect that the last three pairs of coxae abut it, although it is not impossible that only the second and third pairs abut the sternum, whereas the fourth pair abuts the genital opercula. On Text-figures 25A, B are two possible interpretations. Wills refers this specimen to *Mesophonus gracilis* Wills (1947, p. 116). I agree, although here the species is referred to the new genus *Stenoscorpio.*

Wills (1910, 1947) and Petrunkevitch (1953, 1955) recognized one superfamily, Mesophonoidea Wills, 1910, including two genera, *Mesophonus* Wills, 1910, and *Spongiophonus* Wills, 1947. The genus *Mesophonus* included the species *M. perornatus, M. opisthophthalmus, M. gracilis, M. pseudogracilis, M. bromsgroviensis, M. pulcherrimus* and *M. pulcherrimus* var. *immaculatus,* whereas the genus *Spongiophonus* included only one species, *S. pustulosus.*

My review of the British Triassic scorpions results in the presence of two infraorders, Holosternina and Lobosternina, three superfamilies in the Holosternina, namely Acanthoscorpionoidea, Mesophonoidea (emended) and Spongiophonoidea (new) and one undesignated superfamily in the Lobosternina. The families represented are Mesophonidae Wills (emended), Willsiscorpionidae (new), Stenoscorpionidae (new), Spongiophonidae (new), and an undesignated family represented by the lobosternous scorpion. Genera represented are *Mesophonus* (emended) with the species *M. perornatus* Wills, *M.* ? *pulcherrimus* Wills and *M.* ? *pulcherrimus* var. *immaculatus* Wills; *Willsiscorpio,* n. gen. with the species *W. bromsgroviensis* (Wills); *Stenoscorpio,* n. gen. with the species *S. gracilis* (Wills) and *S. pseudogracilis* (Wills); *Spongiophonus pustulosus* Wills and *Bromsgroviscorpio,* n. gen. with the species *B. willsi,* n. sp. The species *Mesophonus opisthophthalmus* Wills, 1947, was found to be a junior synonym of *M. perornatus* Wills, 1910.

CLASSIFICATION

INTRODUCTION

The order Scorpionida is essentially a fossil group and any classification, if at all meaningful, must necessarily be based on the fossil record. This basic fact has not been fully appreciated. Of the 56 families herein recognized, only eight are living, all of which belong (or should belong) to one superfamily out of 21 known superfamilies. Like the order Xiphosurida, the Scorpionida is an ancient and successful group that survived from at least the early Paleozoic to the present. Indeed, scorpions have changed less in general external form since Silurian time, than have the Xiphosurida.

In the classification of scorpions, as in all taxonomy, the problem is to find the proper taxobases. The classification proposed by Petrunkevitch (1955), which was largely followed by Dubinin (1962), is founded on trivial traits. Important characters, such as gills, type of abdominal plates, lateral facetted eyes, and many of the coxosternal patterns of Paleozoic scorpions, were unknown, but in many instances the existence of some of these taxobases was categorically denied. The proposed classification embraces each of these characters. The ill-conceived postulation of an eight-segmented preabdomen in the adult unfortunately formed the main basis of Petrunkevitch's most recent classification (see Kjellesvig-Waering, 1969). I believe there is little argument that the respiratory structures, whether gills or lungs, are a fundamental taxobasis, for this involved not only one of the most radical morphological changes, but a great change of primary environment from a water medium to terrestrial existence. This was the last macroevolutionary change of the scorpions and probably was the greatest stress that the entire Scorpionida ever experienced. It was a change that very likely was responsible for the survival of the remaining scorpions. The first definite air-breathing scorpion that we know of occurs in the Upper Carboniferous. All known Silurian and Lower Devonian scorpions were probably aquatic and had gills, although, judging from the de-

velopment of the oral chamber in Lower Devonian time, many could have been amphibious, much like many of the living crabs. It therefore may not be too speculative to suggest that the change from gills to lungs began at least by the late Devonian, concomitant with the transition from fish to amphibian. However, the amphibious development of the scorpion, that is, development of the oral tube for terrestrial living, but still having gills (see *Branchioscorpio*), began much earlier—I would venture that early Silurian or late Ordovician may not be far from the mark. A further speculative suggestion is that the enormous increase of eurypterids, and especially of fishes, was responsible for the near extinction of the Paleozoic aquatic scorpions. This extinction probably finally took place in post-Triassic time, but within the Mesozoic. Certainly, if fish were later to be their main competitors or enemies, the land could not have been as hostile during Silurian and Devonian time as were the marginal seas, or even limnic environments. As proven by their presence today, the scorpions were well equipped for a terrestrial existence and survival once they developed lungs. Land, during the Silurian and Devonian, with the burgeoning of land plants and presence of herbivorous arthropods, offered countless ecological niches and food, which possibly had not existed previously. The scorpion soon found some niches that suited its requirements as a cryptozoic, carnivorous, solitary animal, including environments that ranged from the extremes of xerophilic to hygrophilic, as far as the macroclimate was concerned, but always in a microclimate that offered sufficient humidity. They remain in the same microclimate today.

We now have definite evidence that pulmonary, possibly hygrophilic, scorpions were living during late Carboniferous time, for example, the Palaeopisthacanthidae in Illinois (see Vogel and Durden, 1966, pp. 655–658).

It should be noted that the scorpion, whether inhabiting desert, subterranean, rain forest or even arboreal environments, is a cryptozoic, photophobic animal that lives only under conditions of considerable humidity. It is not possible for a modern scorpion to live in air devoid of moisture. All living scorpions, whether inhabiting deserts or not, are nocturnal. This is especially important for desert forms, in order to preserve their body fluids. They would quickly desiccate if exposed to the higher aridity of daylight hours. Cloudsley-Thompson (1962a, p. 204) notes that the desert sands in the Sahara have a relative humidity of 50% at a depth of 50 cm even in the summertime. This is due to moisture from both Pleistocene connate and Recent extra-Saharan waters that underlie most of the sand areas. The microclimates under rocks in the Sahara therefore reveal a considerable degree of humidity. To speak of "desert scorpions" as inhabiting a very dry environment is as highly misleading as it would be to speak of *desert* amphibians—and there are several that inhabit moist microenvironments of deserts. Both the scorpions and the amphibians take advantage of moist microclimates in the desert, where the optimum body moisture can be maintained. Both are nocturnal for the same reason.

Therefore, the presence of gills or lungs is considered to be the paramount taxobasis in the new classification, hence, the basis of the suborders. Although the use of such a basis for fossil scorpions may entail some subjectivity in the determination of gills or lungs, it is a classification based on essential characters of survival, and not on preservation, or paleontological convenience. We now have considerable criteria for determining the presence of these organs and, although deductions may not have been correct in each instance, the present alignments would seem to be closer to "natural" than any hitherto. In time, those fossil scorpions known only from the dorsal side will become better known by further discoveries, be it new materials or new information from old, by improved techniques, such as those developed and used so successfully by Wills (1959–1960). The fossil record is by no means as inadequate as some writers have postulated. Undoubtedly, in any classification dealing with fossils, some genera may always remain "*Incertae sedis*". Assuredly, better rapport between paleontologists and neontologists would greatly reduce the uncertainties. The history of scorpion classification well illustrates the important contributions of paleobiologists, scientists who are well grounded in both disciplines.

SUBORDERS

Two suborders are here recognized. The Branchioscorpionina possessed gills and were mainly aquatic. This includes most of the known Paleozoic and Triassic scorpions. The Neoscorpionina includes all pulmonate or mainly terrestrial scorpions.

The basis for subdivision into infraorders is essentially that proposed by Pocock (1911) for suborders, although it is greatly modified and enlarged. Pocock recognized that the sternites (*but not the abdominal plates*) separated the scorpions into two groups: the Lobosterni with bilobed sternites and the Orthosterni with transversely rectilinear sternites, as in modern scorpions. The first group he considered to be aquatic, respiring by gills, and the second included the modern scorpions with lungs and stigmata perforating the face of the sternites. This was also followed by Wills (1959). However, the two divisions do not include all types of "sternites" present in the fossil record. Pocock (1911)

did not recognize one very important factor, namely, that the lobosterns did not have sternites but abdominal plates.

Although Pocock did not recognize the difference between sternite and abdominal plate in scorpions, the basic idea of the use of the sternite–abdominal plates as a major division is very sound. Pocock's diagnosis can be preserved with only a few redefinitions. There is no danger of confusion if these definitions are followed. In the literature, the term lobosternous or suborder Lobosterni has meant only one character—that of the bilobation of the underlying plate. These are not sternites, but abdominal plates; nevertheless, I do not see any confusion in extending the term lobostern to those scorpions with abdominal plates. The etymology of the word certainly does not prohibit that use. In this manner we may preserve, intact, previous descriptions using the term lobostern. There are other abdominal plates not recognized by Pocock, or later authors. Therefore, with the following definitions, there should be no confusion concerning the sternite–abdominal plate nomenclature. In this connection, it is important to keep in mind that the sternite is part of the body wall—the abdominal plate is an appendage of the sternite or somite.

Four infraorders are recognized under the Branchioscorpionina:

INFRAORDER LOBOSTERNINA

The term Lobosterni was proposed by Pocock (1911) for scorpions with "sternites" that were deeply bilobate. It also includes abdominal plates that are gently bilobate, with a well-developed gill chamber, well-developed doublures and with gill slits or openings between the doublure and the abdominal plate. Lobosternous plates are not divided (see Text-fig. 4E). There are five lobosternous plates.

INFRAORDER HOLOSTERNINA
(new taxon)

This is one of the most important groups and most confused. Pocock had included this group with the Orthosterni. Abdominal plates rectilinear, undivided and having well-developed gill chambers, with the gill slit or opening between the doublure and the plate, or on the doublure proper. This includes more fossil scorpions than any other type. The type of plate is known from the Silurian through the Jurassic and includes nearly all the known British Triassic forms. The name is derived from the Greek: *holo* (whole) + *sternus* (chest) (see Text-fig. 4A). Eurypterids have holosternous plates. There are five non-paired holosternous plates.

INFRAORDER MERISTOSTERNINA
(new taxon, previously unrecognized)

Abdominal plates divided by a median suture, as in many eurypterids, and retaining well-developed gill chambers and doublures. The gill slit or opening is between the doublure and the abdominal plate. The name is derived from the Greek: *meristos* (divided) + *sternus* (chest) (see Text-fig. 4D). There are five pairs of meristosternous plates.

INFRAORDER BILOBOSTERNINA
(new taxon)

The abdominal plates consist of two completely separated, rounded lobes, without doublures. The sternites may have developed above the plates and become slightly sclerotized. Considered still to retain gills, although primitive lungs may have developed. This is, of course, the most interesting condition of the abdominal plates (see Text-fig. 4C). There are five pairs of bilobosternous plates. The name is derived from: Latin: *bi* (double); and Greek: *lobo* (lobe) + *sternus* (chest).

There is a fifth type of abdominal plate, the *protolobosternous,* which may possibly merit infraorder standing, but which is considered a variety of Lobosternina for the time being. Undivided, slightly lobate at the posterior end and without development of doublures, or if present, poorly developed. This type of abdominal plate is considered to be intermediate between the more primitive holostern and the more advanced lobostern (see Text-fig. 4B). There are five pairs of protolobosternous plates.

One infraorder is recognized under the Neoscorpionina:

INFRAORDER ORTHOSTERNINA

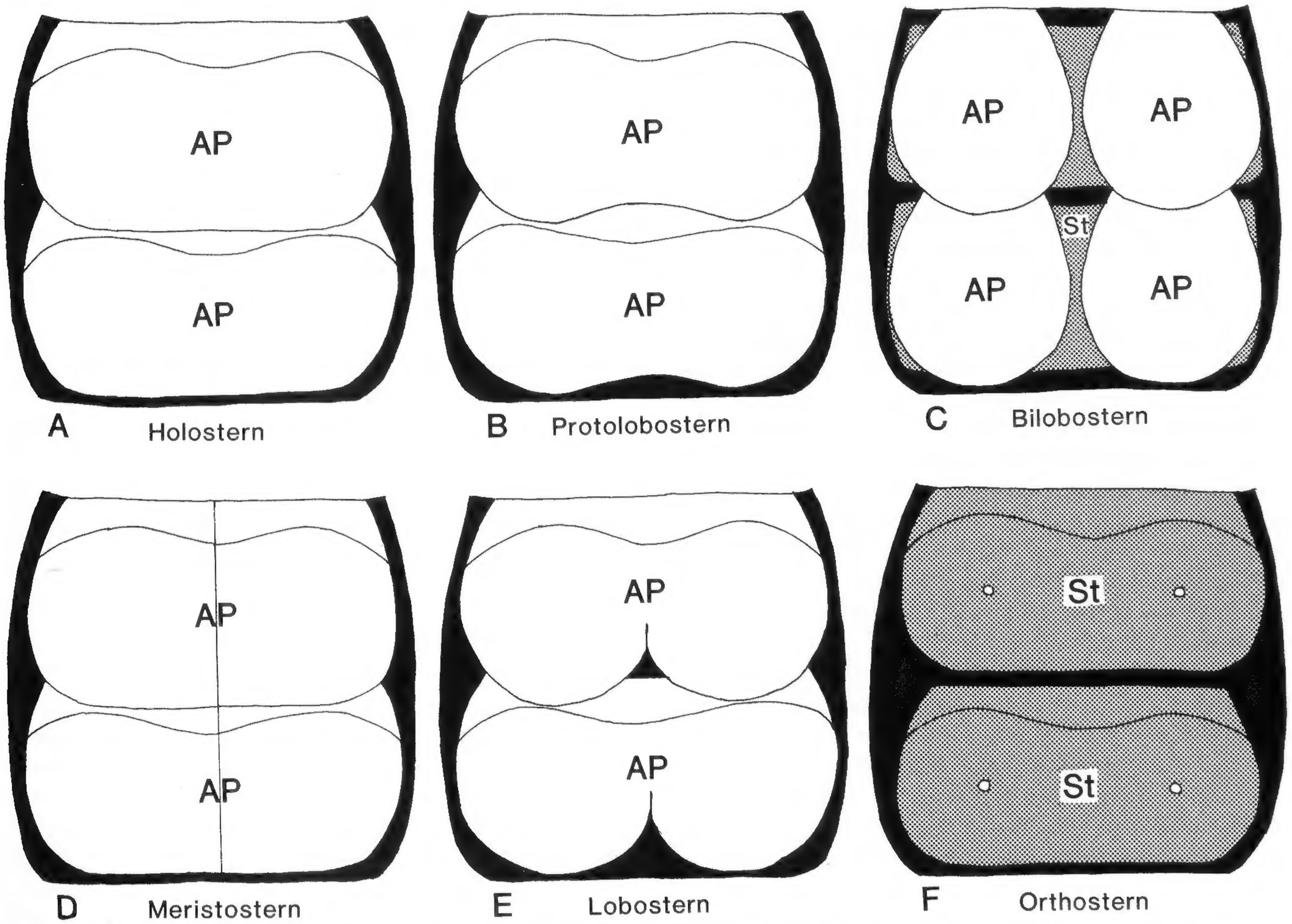
The term Orthosterni, as Pocock (1911) defined it, included the holosternous abdominal plates as well as the undivided, stigma-bearing, rectilinear, true sternites that characterize all living scorpions. The term is restricted to the latter, namely those with undivided sternites with stigmata perforating the sternite, and without doublures. There is little doubt that Pocock essentially meant this to be the case. Some New World Tityae have a deep median suturelike division of the sternites. This suturelike development seems to be secondary, as neonates and juveniles do not have this development; it is acquired only on more adult forms (see Text-fig. 4F). There are only four orthosternous plates.

Sternites are the only underplates with true stigmata and lungs. Abdominal plates, regardless of the type,

do not have stigmata, but have gill slits or gill chamber openings and gills. Somewhere in the fossil record we may expect to find the intermediate between the suborders (see Text-fig. 1), the "protosternites", which later developed the paired lung invaginations, and were originally non-sclerotized tissue lying dorsal of the sclerotized abdominal plates in all eurypterid and gill-respiring aquatic scorpions.

TAXOBASES

The arrangement of the coxae forms the basis for the separation of superfamilies. This is one of the taxobases employed by Petrunkevitch (1955), but not adhered to consistently. Families are based on the development of maxillary lobes, the shape of the sternum, as well as the nature of the termination of the legs and the presence or absence of lateral facetted eyes. The arrangement of the coxosternal area as an important taxobasis was first employed by Thorell and Lindström in 1885, and was later used more extensively by Petrunkevitch in his classifications of 1913, 1949, 1953 and 1955. Unfortunately, Petrunkevitch abandoned the use of the shape of the sternum in this connection (1953, p. 19): "in view of its relative unimportance and unreliability in the case of fossils . . .". This now seems to have been an unwise decision. Wills (1959, p. 266) also did not believe that the coxosternal arrangement and the shape of the sternum were essential for classification, but his objections were also based on practical reasons and not because of taxonomic value, as he states, "In the past, attempts have been made to use coxo-sternal features for purposes of classification, but the method breaks down in practice because these parts are so seldom seen and because, when visible, they can so rarely be related to dorsal features." While this is to a small degree true, taxonomy and phylogeny



Text-figure 4.—Ventral plating in scorpionids, illustrating the basic differences between infraorders. In A to E there are *five* paired, or single, gill-bearing abdominal plates (**AP**), as in the eurypterids. In the orthosterns alone (fig. F), which comprise the true and all living scorpions, there are only *four* ventral plates, the sternites (**St**), which bear stigmata.

The gill-bearing abdominal plates (**AP**) are not the same, nor homologous with, the stigma-bearing sternites (**St**). Although both kinds of plates serve the same, but analogous, function in ventral sheathing and external cover of the respiratory organs, they have quite different origins.

can hardly be soundly based on chance and expediency rather than on morphology. There is truly no one structure or combination which will be preserved every time—the coxosternal area is no exception. I disagree that a classification must necessarily be practical, although desirable where feasible; fundamental morphologic factors must take precedence. As for the dorsal surface, which is more commonly preserved, and which has also been largely employed as a taxobasis, Wills (1959, 1960, and in particular, 1964, p. 475) and others have shown conclusively in both fossil scorpions and eurypterids, that it is quite similar in many genera wherein the venters are quite dissimilar. It is improper, unrealistic, and therefore impracticable, to use different taxonomic characters for fossil and living organisms, or to base the fundamental taxonomy on most readily preserved or easily available morphology. A classification, if at all sound, should involve characters that indicate or involve major phyletic changes. As may be seen in the descriptions to follow, the underside is known in a surprising number of fossil scorpions. It is the view here, that the coxosternal area is among the most easily preserved structures, but one must study the specimen fully, and under various conditions, such as wet media, special lighting, etc.

It is my opinion that the hierarchy of taxobases according to degree of reliability is as follows:

For families, the presence and degree of development of maxillary lobes, shape of sternum, presence of lateral facetted eyes, as well as the termination of the legs. Spurs on the legs, which are considered important in present-day classification of scorpions, are given no importance whatsoever, for higher taxa, and only minor importance on the generic and species level.

For genera, the same criteria used in separating the genera of living scorpions: the shape of the carapace, position of median eyes, number of individual facets in the lateral eyes, type of combs, type and character and dentition of pedipalps and chelicerae, carinae on the mesosoma, etc.

The superfamilies of Birula (1917) do not appear to be necessary in dividing the present-day scorpions, as all eight families obviously belong to a single superfamily, if fossil forms are to be included and considered on a comparative basis. Inversely, if the superfamilies of Birula are accepted for the present-day scorpions, corresponding elevations in taxonomic levels must be made for the fossil groups. At the present state of knowledge, little or nothing would be gained by such proposals. It seems more reasonable to refer all living scorpions to the superfamily Scorpionoidea Leach, 1815. Moreover, arguments by some, myself included, might well be advanced that the number of living families is too large and that some could well be absorbed with possible better expression of generic relationships. It may reflect paleontologic bias, but in the broad survey of all known scorpions, the presence or absence of certain tibial or basitarsal spines on any particular leg, commonly employed by neontologists as a prime family taxobasis, seems trivial. However, there is little or no conflict between the classification proposed here and the present neontologic taxonomy. It is well to emphasize by repetition, the opening statement of this section, which is that the Scorpionida is essentially a fossil group.

Similarly, the use of the arrangement of dentition on the chelicerae for the determination of families, as proposed by Vachon (1963), is an excellent taxobasis for use with *Recent* scorpions. However, this taxobasis has importance only in dealing with living families, an infinitesimally small part of the Scorpionida. The method has no importance whatsoever as a taxobasis in dealing with the greater part of the Scorpionida, namely the entire Branchioscorpionina.

SYSTEMATIC PALEONTOLOGY

Order **SCORPIONIDA** Latreille, 1817

Suborder **BRANCHIOSCORPIONINA**, new suborder

Aquatic scorpions breathing through branchia or gills.

Type family.—Branchioscorpiidae, new family.

Remarks.—All but two of the families of fossil scorpions known and described from the Paleozoic and the Mesozoic belong to the Branchioscorpionina.

Infraorder **HOLOSTERNINA**, new infraorder

Branchioscorpionina with five rectangular undivided abdominal plates and well-developed gill chambers with gill slits opening between the doublure and the abdominal plate, or on the doublure proper.

Remarks.—The Holosternina were once included in Pocock's Orthosterni. The most successful group under the Branchioscorpionina, the Holosternina flourished from the Silurian through the Jurassic. From a half dozen species in the Silurian, it branched out into 41 species, classified herein under ten superfamilies, 25 families, and 32 genera. By the Jurassic the Holosternina had dwindled down to two species and became extinct.

Superfamily **PROSCORPIOIDEA**
Scudder, 1885
(*nom. transl.* Kjellesvig-Waering herein, *ex* subfamily Proscorpionini Scudder, 1885) emend.[4]

Holosternina with first pair of coxae meeting in front of, but all four pairs abutting large sternum; no maxillary lobes.

Type family.—Proscorpiidae Scudder, 1885.

Family **PROSCORPIIDAE** Scudder, 1885
(emend. Kjellesvig-Waering, 1966, *pro* Proscorpionidae Scudder, 1885)

Proscorpioidea bearing compound eyes at the anterolateral angles of the carapace and with anteriorly-located median eye node having small ocelli. Walking legs have two claws. Sternum ovoid, elongated.

Type genus.—*Proscorpius* Whitfield, 1885.

Genus **PROSCORPIUS** Whitfield, 1885
(emend.)

Proscorpiidae with subquadrate carapace with anteriorly-elevated cephalic area[5]; large bulbous compound eyes at the anterolateral corners; eye node scutelliform, highly elevated, located anteriorly, and having two small ocelli. Chelicerae large and strong, composed of four joints. Pedipalps have fingers meeting throughout their length, incurved toward the fixed finger; very small, bearing denticles; possibly linear. Sternum large, lacrimiform, with a narrow notch at the anterior for the small triangular plate of the labrum. The first pair of coxae meet in front, but all four pairs abut the sternum. Small round opercular plates occur posterior to the sternum. Short, tubular walking legs have bifid terminations and very small, double, basitarsal and tarsal spurs. Preabdomen elongated, consisting of seven tergites that are rounded at the corners. Pectines comprise large, paired, undivided lobelike (rachis) plates with about 20 teeth on a side. Five very wide and long abdominal plates of the holostern type are present, with indications of large slits at the epimeral angles. Cauda bearing double dorsal, lateral, and ventral crests. Terminalia consist of normal stinger.

Type species.—*Palaeophonus osborni* Whitfield, 1885.

Geological range.—Upper Silurian of New York.

Remarks.—Generic comparisons are discussed in Kjellesvig-Waering (1966, p. 362).

Proscorpius osborni (Whitfield, 1885)
Plate 1, Text-figures 6–13, 111A

1885a. *Palaeophonus osborni* Whitfield, p. 87, 1 fig.
1885b. *Proscorpius osborni* (Whitfield). Whitfield, pp. 181–187, pl. 20.
1885. *Proscorpius osborni* (Whitfield). Scudder, p. 739, fig. 915a.
1886. *Proscorpius osborni* (Whitfield). Whitfield, p. 216.
1886. *Proscorpius osborni* (Whitfield). Scudder, p. 28.
1886. *Proscorpius osborni* (Whitfield). Thorell, p. 269.
1899. *Proscorpius osborni* (Whitfield). Laurie, p. 577.
1901. *Proscorpius osborni* (Whitfield). Pocock, p. 309.
1904. *Proscorpius osborni* (Whitfield). Frič, p. 65, fig. 81.
1907. *Proscorpius osborni* (Whitfield). Frič, p. 6, pl. 3.
1912. *Proscorpius osborni* (Whitfield). Clarke and Ruedemann, pp. 387–400, figs. 81–83, pl. 88.
1913. *Proscorpius osborni* (Whitfield). Petrunkevitch, p. 32.
1944. *Proscorpius osborni* (Whitfield). Lehmann, p. 177.
1949. *Palaeophonus osborni* Whitfield. Petrunkevitch, pp. 129–131, fig. 189.
1953. *Proscorpius osborni* (Whitfield). Petrunkevitch, p. 12, fig. 118.
1954. *Proscorpius osborni* (Whitfield). Kjellesvig-Waering, p. 485.
1955. *Proscorpius osborni* (Whitfield). Petrunkevitch, p. P70, figs. 38(3), 39(A).
1962. *Proscorpius osborni* (Whitfield). Dubinin, p. 425, fig. 1220.
1966. *Proscorpius osborni* (Whitfield). Kjellesvig-Waering, pp. 361–373, pl. 42, figs. 2–3; pl. 43, figs. 2–4; pl. 44; text-figs. 1–4, 11–18.

Inasmuch as the earlier specimens were thoroughly covered in the 1966 paper, and all comparisons made therein, only the new Ciurca specimens[6] are covered below.

Type information.—All specimens come from the Fiddlers Green Dolomite Member of the Bertie Formation, commonly known as the "Bertie Waterlime", from the Upper Silurian, Ludlow age, of New York. The holotype, in the collections of the American Museum of Natural History, New York City, comes from Waterville, Oneida County. All other specimens were found in Herkimer County: AMNH 28383, CUGM 41973[7], and CIURCA 031966-1, 041771-1, 042570-1A, 040564 and 040668-1,2 in the upper part of the Fiddlers Green Dolomite at Passage Gulf; CIURCA 072869-9B from near Litchfield. The specimens col-

[4] The superfamily Proscorpioidea was mentioned by Kjellesvig-Waering (1966, p. 361) in his discussion of the Classification of the Silurian Scorpions of New York, but was not formally proposed. In the present manuscript the superfamily was scheduled for proposal, but the diagnosis not yet written at the time of his death. We have extracted this diagnosis from his data, in accordance with his ideas of superfamily criteria.

The six Ciurca specimens of *Proscorpius osborni* (Whitfield), which are analyzed below, furnish much new information for diagnostic revision at all systematic levels, including Kjellesvig-Waering's own previous (1966) emendation of previous systematic categories. A.S.C.

[5] Kjellesvig-Waering's diagnosis (1966, p. 362) adds: "and an elevated medianly divided band along the base", which may be present in the holotype, but which does not occur in any of the six Ciurca specimens. A.S.C.

[6] Kjellesvig-Waering, in the first phase of this manuscript, set up a new genus and species for the specimens from the Ciurca collection, with CIURCA 031966-1 as the holotype, but later reconsidered and placed them under *Proscorpius osborni* (Whitfield). A.S.C.

[7] Ed Landing (oral commun., May 7, 1985) reports that CUGM 41973 was transferred to the collections of the New York State Museum in Albany, NY in 1971, as NYSM 12948. P.R.H.

lected by Samuel J. Ciurca of Rochester, NY, are in his private collection, except for CIURCA 031966-1 which was deposited in the Buffalo Museum of Science as BMS E25162.

Specimen I.—BMS E25162 [=CIURCA 031966-1 (Text-figs. 6, 12A)], collected by Samuel J. Ciurca, 1966, from the upper part of the Fiddlers Green Dolomite at Passage Gulf, NY.

The specimen consists of a complete scorpion preserved from the inside of the dorsal side, in light gray, typical waterlime. The specimen has been compressed, with little relief present, although considerable details of the morphology can be ascertained by use of very oblique lighting. Features such as the coxosternal region can be made out faintly, particularly in the dry state. Otherwise, all details reported here have been determined by immersion in alcohol and use of different intensities and direction of lights.

The carapace is broad at the base, straight, with lateral margins that converge anteriorly. In life, the lateral margins were likely parallel. The anterior margin is produced into a wide snout that probably was originally slightly curved downward as in certain eurypterids. Two prominent bulbous compound eyes are located at the anterolateral margins. These are typical compound eyes and the facets, or ommatidia, are preserved in the right eye of the specimen. They are very small. The median ocellar node has two small median eyes on the lateral margins, and is located so that it lies on a plane slightly above or forward of the lateral compound eyes. The eye node is roughly elliptical and occupies the area of the snoutlike projection at the anterior of the carapace.

The prosomal appendages are only partly preserved. The chelicerae are particularly well preserved and show that they were formidable organs approximately three-quarters the length of the carapace. They, therefore, jutted forward into two large grasping organs located above the coxae of the pedipalps, as in modern scorpions. The chelicera is composed of four distinct joints; the last two are falcate and two large teeth were noted, at least on the free finger. It seems probable that more teeth occurred originally.

The distinct pedipalps are noteworthy for the great length of the first segment, which represents the coxa. This is tubular and reaches almost to the base of the fixed finger of the chelicera. The trochanter is round along the anterior margins and otherwise triangular in shape. The femur is very long and contrasts with the very short tibia. The palpus has a long hand followed by a recurving fixed finger. Along the edge of this finger is a well-developed longitudinal ridge. The free finger is long and blunt at the end, slightly curved forward and ornamented with a longitudinal narrow ridge. This longitudinal narrow ridge may serve to separate this as a species from other scorpions in the Fiddlers Green horizon.

The first walking leg consists of eight segments, all of which are very short and tubular, and terminates in two claws, the anterior claw being longer than the posterior. The other legs are also tubular, but are preserved only as fragments. On the first leg, and on what likely is the second leg, there are two spurs, which represent the tarsal spurs, on either side of the end of the penultimate joint.

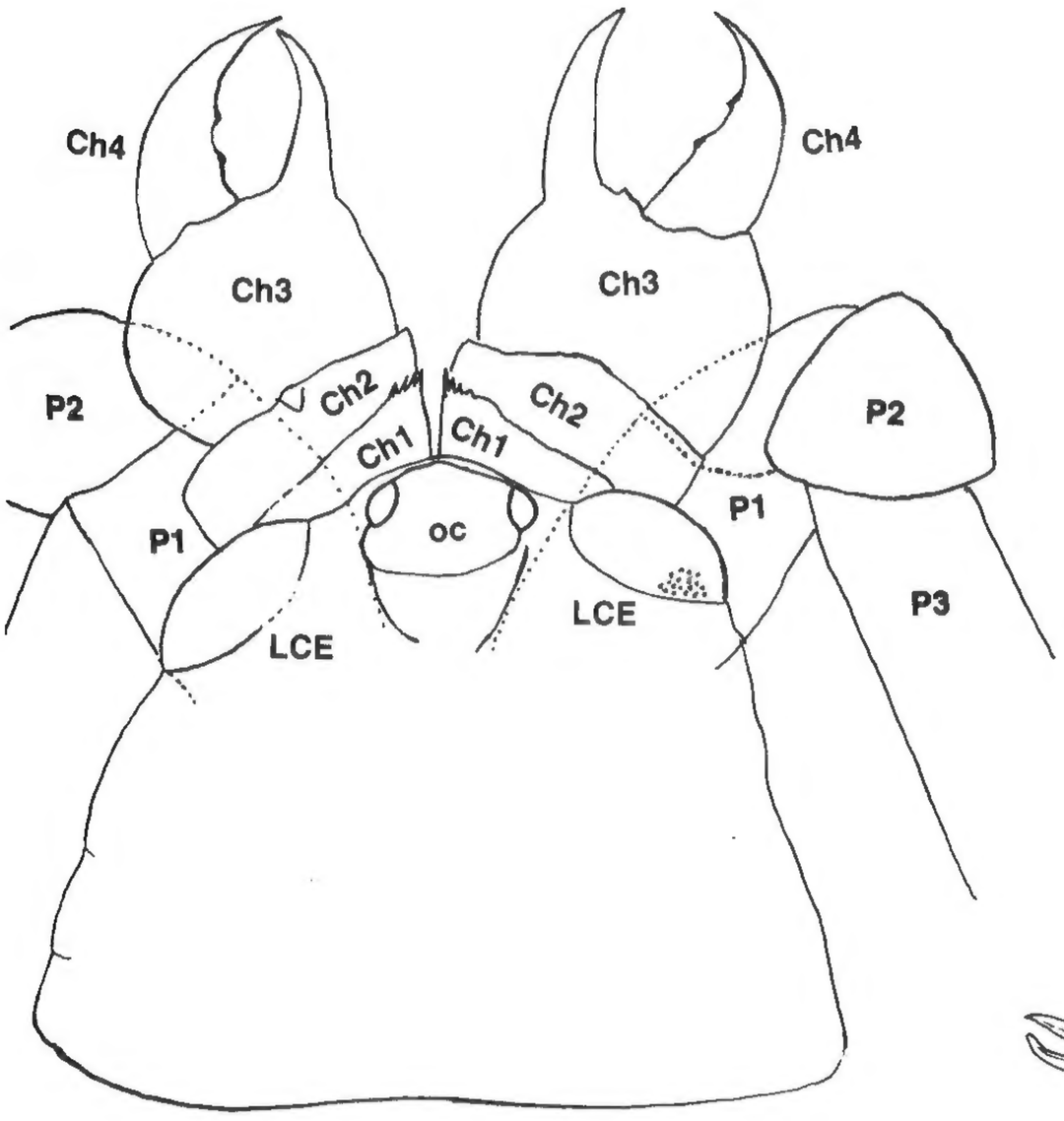
The coxosternal region is particularly interesting. The sternum is elongate-scutelliform, pointed anteriorly and truncated at the base. The lateral margins converge anteriorly. The last three pairs of coxae abut against the sternum, whereas the first pair of coxae meets directly in front of the sternum and abuts against the upper part of the sternum.

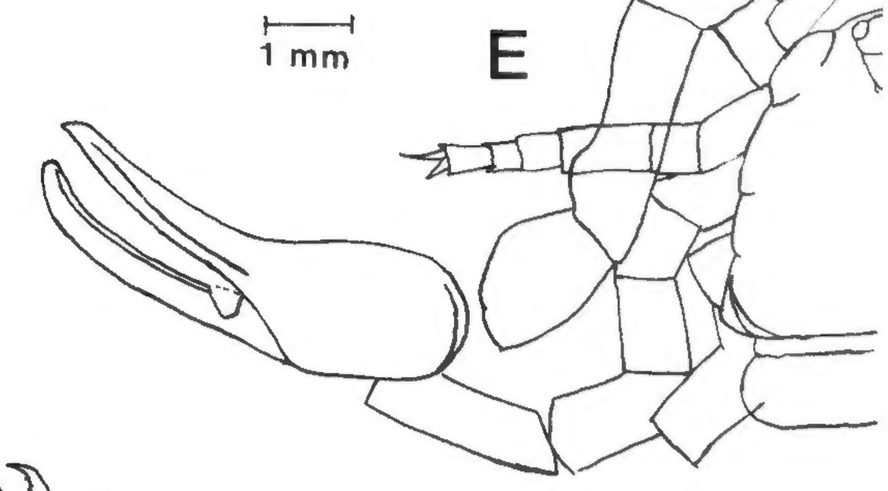
The preabdomen consists of the usual seven tergites. Greatest width is reached at the fifth tergite. Each tergite is bounded by an ear at the anterior lateral margins and by a prominent transverse ridge along the anterior edge. Both structures occur in living scorpions. All tergites are rounded at the epimeral corners. Each tergite increases progressively in length posteriorly. The last tergite has two prominent carinae located on the middle of each half. The caudal segments are all parallel, appear to be tubular, longer than wide, and each is surmounted on the dorsal side by two carinae. These carinae are in turn surmounted by granules. At least one ventral carina, composed of granules, occurs on the second to the fourth tergites and very likely on the first and fifth. The stinger is very well preserved. It reveals at least one dorsal carina on each side, although only one side has been noted. There is no sub-aculear node and the aculeus is highly curved and hooklike, which differs greatly from that present in the other scorpions of this horizon.

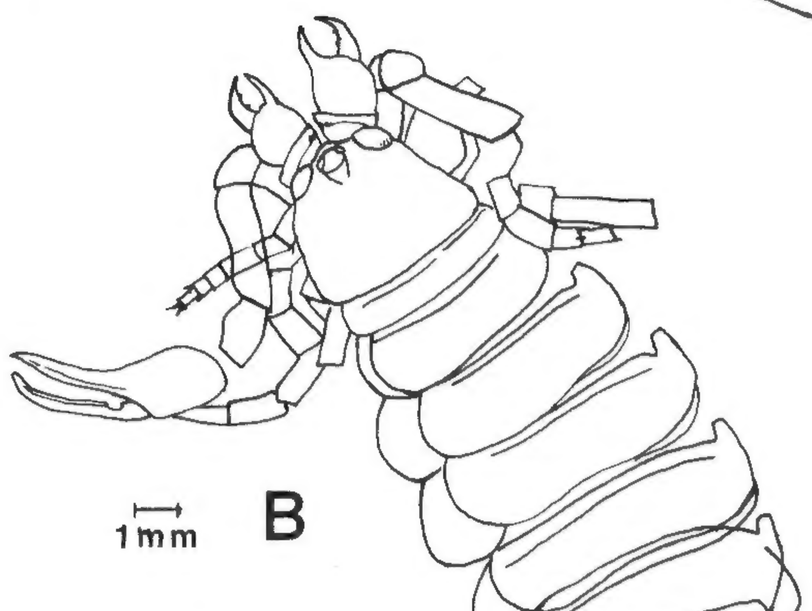
The abdominal plates are only preserved at the edges, but, very interestingly, these edges show that there were five, rather than four, plates present. These are rounded and apparently broadly emarginate along the central posterior part. There is no sign of any teeth in the first abdominal plate, and therefore the first plate could not

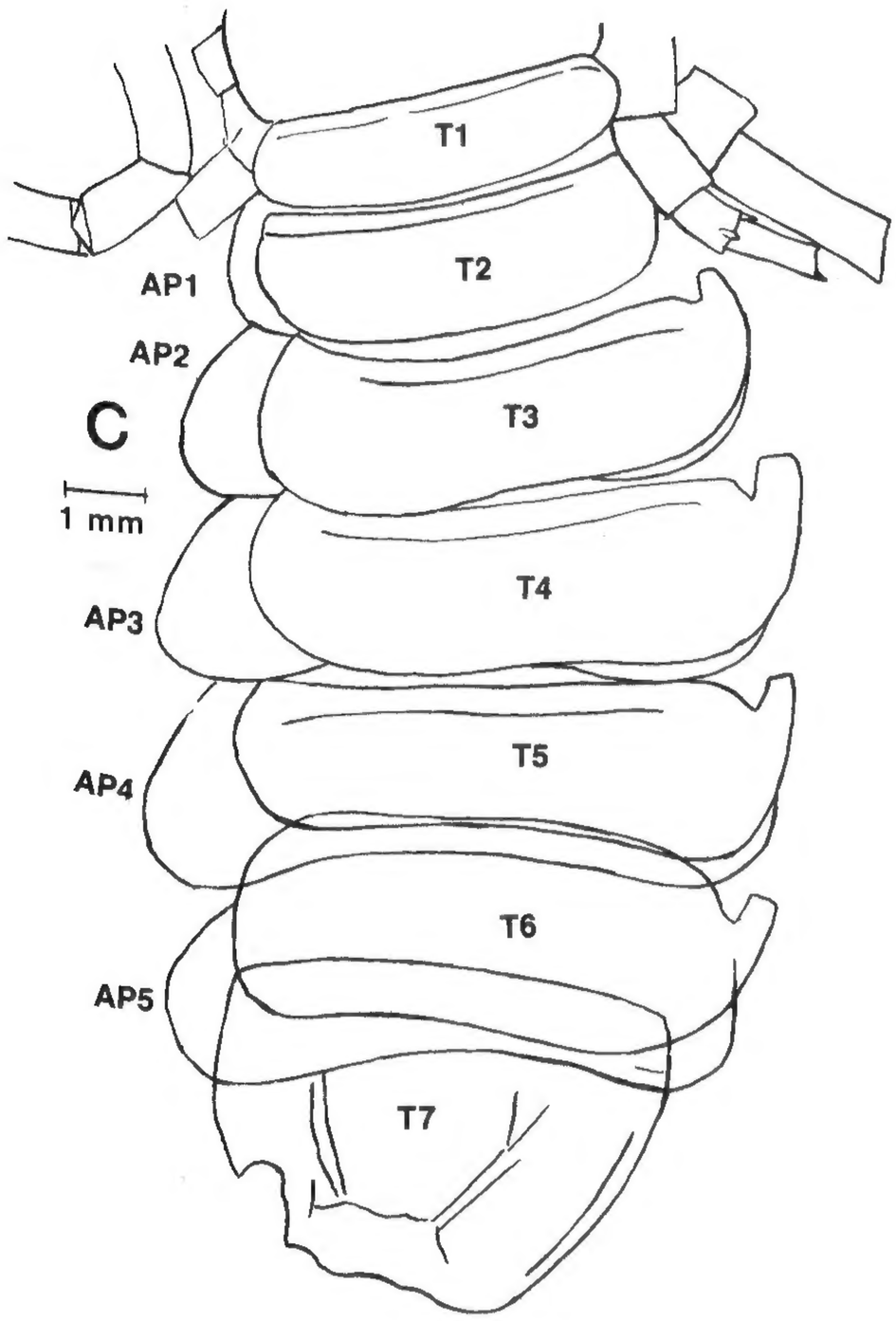
Text-figure 6.—*Proscorpius osborni* (Whitfield). From the Upper Silurian, Bertie Waterlime, Herkimer Co., NY. Specimen I, BMS E25162 (=CIURCA 031966-1). See also Text-figure 12A. See fold-out inside front cover for explanation of abbreviations.

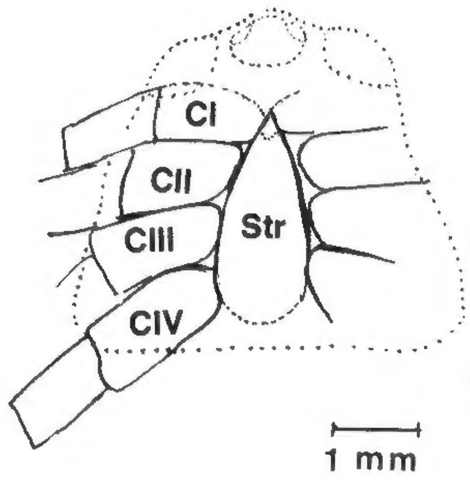
A. Anterior details of figure B, showing the carapace and first few appendages. Broken lines show underlying coxae of the pedipalps, which would be overlain, as in Recent scorpions, by parts of the chelicerae. **B.** Dorsal aspect of an unusually lovely specimen of fossil scorpionid. **C.** Mesosomal details. **D.** Coxosternal organization, taken from the counterpart. **E.** Left prosomal appendages. **F.** Distal postabdomen and telson.

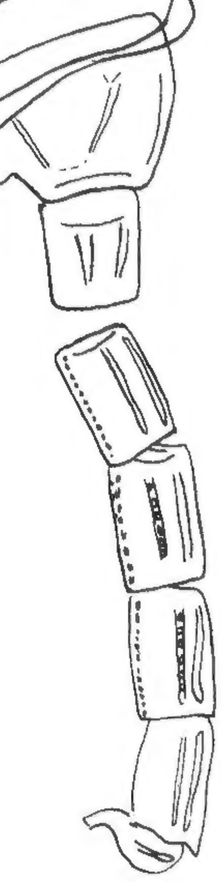

Ch4
Ch3
Ch2
Ch1
P2
P1
oc
LCE
P3
1 mm
A

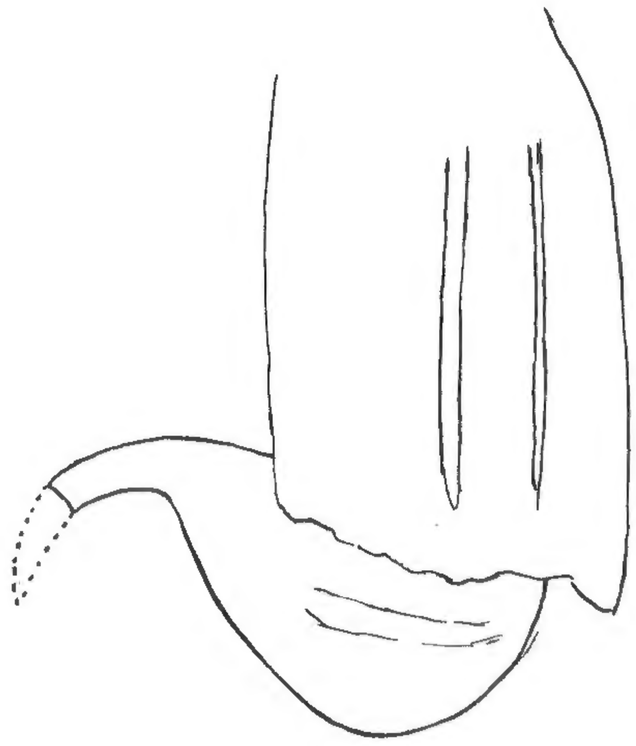

1 mm
E


1 mm
B


T1
T2
T3
T4
T5
T6
T7
AP1
AP2
AP3
AP4
AP5
C
1 mm


CI
CII
CIII
CIV
Str
1 mm
D




F
1 mm

be the anterior part of the combs. There is no sign of stigmata present on any abdominal plate. The species is definitely a holosternous scorpion.

Measurements (in mm) of Specimen I, BMS E25162 (=CIURCA 031966-1).—

Prosoma:			
Width at base:			4.8
Greatest width:			4.8
Length:			5.0
Location of median eyes:			
From anterior margin:			0.15
From posterior margin:			4.0
From lateral margin:			0.9
Diameter of median eyes:			0.1
Palpus:			
Chela length:			5.4
Hand width:			1.6
Hand length:			2.3
Free finger length:			3.2
Femur length (dorsolateral):			1.7
Tibia length (dorsolateral):			3.0
Mesosoma and metasoma:			
	length of tergite		middle width of tergite
No. 1	0.7		4.2
No. 2	1.6		5.0
No. 3	2.0		6.2
No. 4	2.1		6.6
No. 5	2.1		6.9
No. 6	2.3		6.4
No. 7	4.0	anterior	5.4
		posterior	3.2
No. 8	2.6		2.5
No. 9	3.0		2.2
No. 10	3.0		2.2
No. 11	3.2		2.1
No. 12	3.1		2.1
Vesicle:			
Length:	3.2±		
Width:	1.0		
Spine:	Not entire		

Remarks.—Occurs next to a fragment of the ventral shield of an eurypterid, probably *Eurypterus remipes remipes* De Kay. It was on a big slab on a bedding plane 115 mm from a horizon with large four-inch mud cracks; presumably below the mud cracks.

The genital plates and combs were not preserved.

Specimen II.—CIURCA 041771-1, part and counterpart of a complete specimen (Text-fig. 7) from the Upper Silurian, upper part of Fiddlers Green dolomite at Passage Gulf, Herkimer County, NY.

The specimen is preserved as a dorsal impression of the dorsal side, but with the edges of the abdominal plates, which are displaced laterally, seen from the dorsal side. Remarks here are restricted to parts not preserved in other specimens.

The preservation of the chelicerae is noteworthy (see Text-fig. 7B); the chela of the right chelicera is open, revealing the entire structure. The free ramus (**Ch4**) is decidedly hooked, slender, with numerous teeth, of which a central tooth is most prominent. The fixed ramus (**Ch3**) is very narrow, also with numerous teeth. The manus is not as long as wide by about one third. The chelicerae are preserved in their entirety, showing all four joints. The first joint is seen whole for the first time. This basal joint is triangular, cup-shaped, and very short. The second joint is a narrow, cup-shaped band, showing denticles at the inner edge. A faint joint line was noted on the central part, which was interpreted as the ventral side of the second joint (**Ch2**). This would give the joint vertical movement and considerable inside movement, as the joint line is on a diagonal, not as long as the dorsal side. The entire chelicera is covered with small punctae, which undoubtedly are the bases for the setae. These setae are more densely packed toward the median line where they would rub against the other chelicera, and were probably used to convey food to the oral opening.

The carapace is very poorly preserved; only the left posterolateral angle and the base are present. This part is typical of *Proscorpius osborni.*

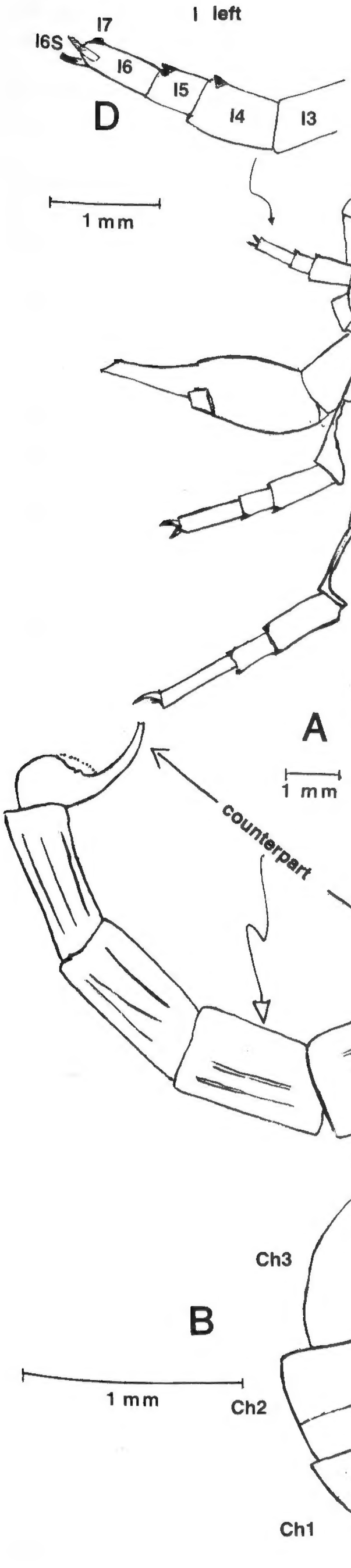
The legs are remarkable in their preservation. All are short, but not stout. The first two pairs are particularly stunted. All legs are armed with very small double basitarsal and tarsal spurs (see Text-figs. 7D–G). The termination is in a double claw, the anterior being larger than the posterior, and in the posttarsus, which is very small. The legs are also noteworthy for the long, narrow tarsus.

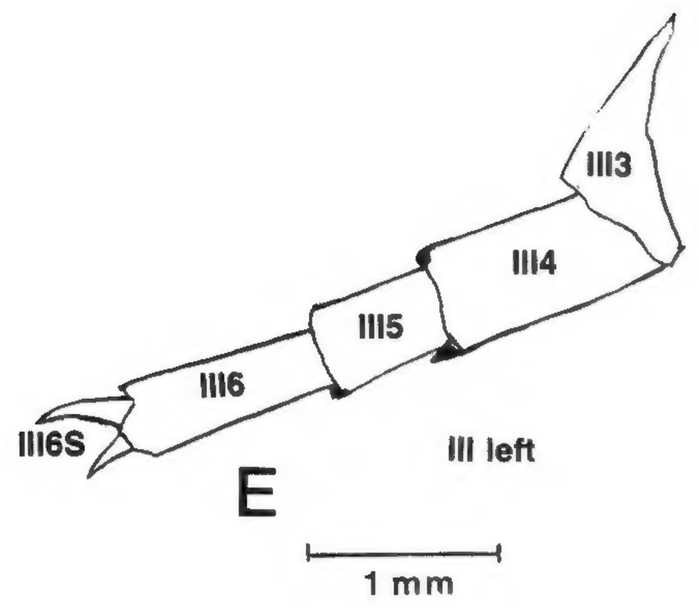
The tergites are typical for the species. The abdominal plates are rounded, and the third is of particular interest as it shows a wide slit at the junction of the doublure with the plate (see Text-fig. 7C). This doublure is like those described elsewhere (Wills, 1960, p. 299) and in this report where the gill-bearing holosternous forms are characterized. These tergites show the characteristic anterior prolongation at the anterolateral angle.

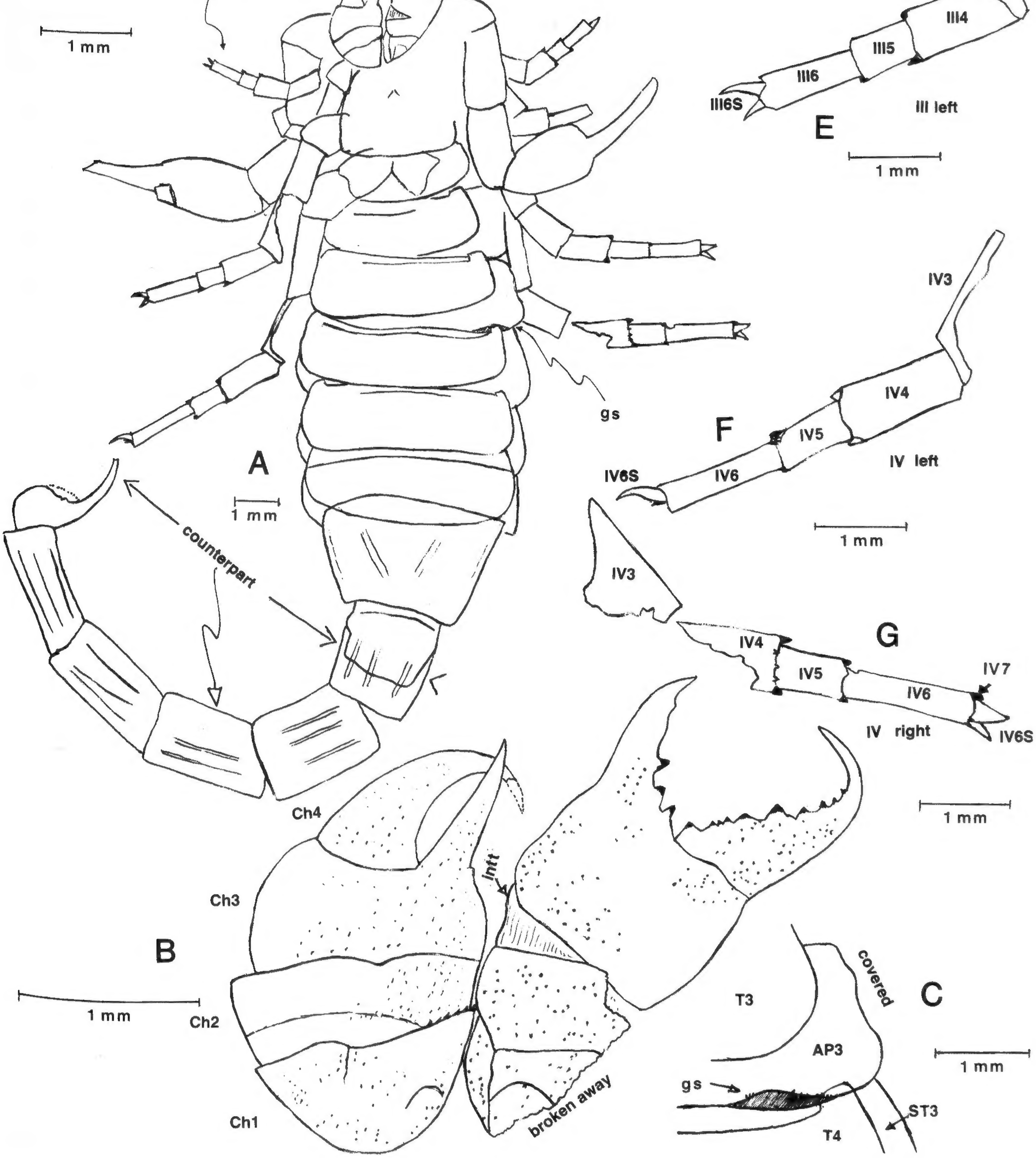
The cauda, preserved in its entirety, is rather stout, including a relatively large stinger, but the last tergite is very long, narrower than the preceding, and undoubtedly denotes a male. The telson, or stinger, comprises a large, bulbous, rounded vesicle followed by a curved narrow aculeus.

Text-figure 7.—*Proscorpius osborni* (Whitfield). From the Upper Silurian Bertie Waterlime, Herkimer Co., NY. Specimen II, CIURCA 041771-1. See foldout inside front cover for explanation of abbreviations.

A. General aspect of the specimen. **B.** Detail of the chelicerae, showing denticles. **C.** Showing gill slit of third abdominal plate (**AP3**). **D.** Terminal details of first left walking leg (**I**). **E.** Terminal details of the third left leg (**III**). **F.** Terminal details of the fourth left leg (**IV**). **G.** Terminal details of the fourth right leg (**IV**).


I left
I7
I6S
I6
I5
I4
I3
D
1 mm


III3
III4
III5
III6
III6S
III left
E
1 mm

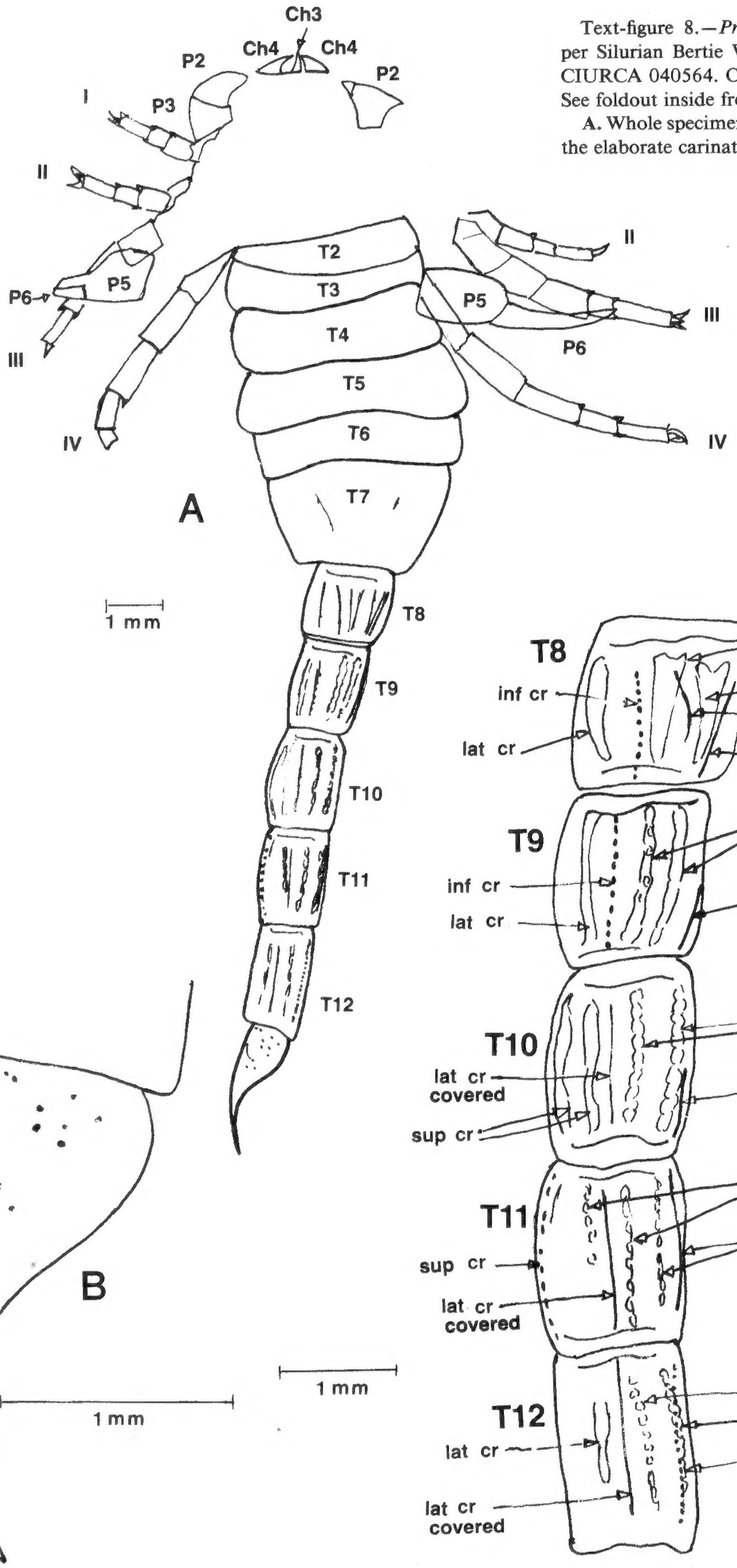

A
1 mm
counterpart
gs

IV3
IV4
IV5
IV6
IV6S
F
IV left
1 mm

IV3
IV4
IV5
IV6
IV7
IV6S
G
IV right
1 mm

Ch4
Ch3
Intt
B
1 mm
Ch2
Ch1
broken away

covered
T3
C
AP3
1 mm
gs
ST3
T4



Text-figure 8.—*Proscorpius osborni* (Whitfield). From the Upper Silurian Bertie Waterlime, Herkimer Co., NY. Specimen III, CIURCA 040564. Overall length from chelicera to tail is 19 mm. See foldout inside front cover for explanation of abbreviations.

A. Whole specimen. **B.** Detail of telson. **C.** Postabdomen showing the elaborate carination of tergites **T8–12.**

Remarks.—Sexual dimorphism in the form of the short (♀) and long (♂) twelfth tergite is particularly well illustrated in this species.

Specimen III.—CIURCA 040564 from the same Passage Gulf location and formation (Text-figs. 8, 9).

The rather small scorpion, preserved only on the dorsal side, consists of a single specimen without a counterpart. It is possibly the best preserved of the Passage Gulf specimens, although, unfortunately, the central part of the carapace has been lost. Considerable information, however, has been obtained from the parts preserved.

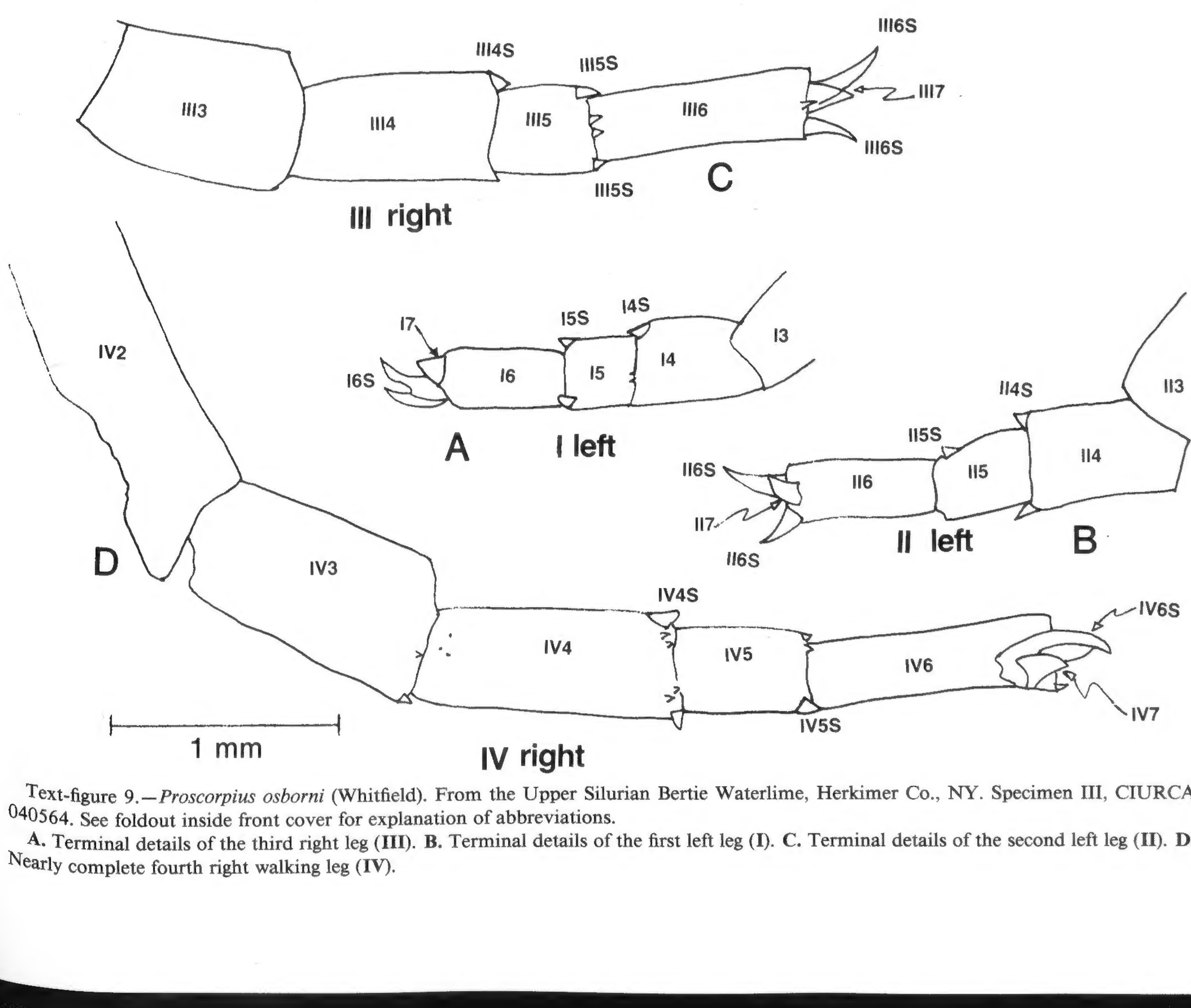
The prosomal legs are shown in great clarity (see Text-fig. 9) and it is clear that each leg contains two tibial and two basitarsal spurs. The tarsal spurs, of course, are the double ungues and are not greatly unlike those of living forms. The posttarsus is very short and also like that in living species. The short legs and the very long tarsus are clearly very different from those in living forms.

The cauda (see Text-figs. 8A, C) is so well preserved that details of the crests can be determined. It appears that all segments retain two superior, two lateral (on each side) and two ventral crests. The ventral crests are very narrow, marked by elongated, setaceous pustules. The superior and lateral crests are wider knobby carinae, partly setaceous.

The aculeus and vesicle are preserved in their entirety. The vesicle or stinger is slender, long, and curving (see Text-fig. 8B). No other specimen shows the aculeus as well.

Specimen IV.—CIURCA 072869-9B (Text-fig. 10) from the top of the Fiddlers Green Dolomite at confidential locality No. 1 of Mr. S. J. Ciurca.

The specimen, poorly preserved, consists of only one side of the abdomen, but reveals certain anatomical features of considerable importance. The specimen shows only the last five tergites of the preabdomen along with the imprint of the inside or ventral side of three abdominal plates. Part of the ventral side of the seventh preabdominal tergite is also shown. Of greatest importance is the fact that a large comb is preserved. This is triangular, very long, without any segmentation or any rounded sclerites, and appears to have been an



Text-figure 9.—*Proscorpius osborni* (Whitfield). From the Upper Silurian Bertie Waterlime, Herkimer Co., NY. Specimen III, CIURCA 040564. See foldout inside front cover for explanation of abbreviations.

A. Terminal details of the third right leg (**III**). **B.** Terminal details of the first left leg (**I**). **C.** Terminal details of the second left leg (**II**). **D.** Nearly complete fourth right walking leg (**IV**).

undivided rachis as in *Branchioscorpio richardsoni* of the Devonian. Although poorly preserved, several teeth can be faintly made out. These are relatively broad, but not of the broad type found in *Branchioscorpio richardsoni.* Large triangular fulcra separate the teeth. Although only a few of the teeth were preserved, it can be estimated that approximately 20 occupied the edge of each pectine. The discovery of the pectine in *Proscorpius* has verified the interpretation given to the extra anterior "sternite" which appears on the holotype (Kjellesvig-Waering, 1966, p. 365). It is thus confirmed that this extra "sternite" is the comb, the teeth of which had been covered by the first abdominal plate in the holotype. The pectines are very wide, and along with the narrowness of the abdominal plates, likely indicate that this specimen was a male. The two pectines would probably extend beyond the edges of the abdomen. The three well-preserved abdominal plates are very long with a narrow marginal rim, very likely raised in life, along the anterior edge, and all are rounded on the corners. Of particular interest is the fact that on the fifth abdominal plate can be seen what appears to be a large slit at the epimeral angles. This is much like the large slits present in the doublures of the Triassic scorpions (see Wills, 1947). The large slit also indicates a water-dweller, as it is much too large for anything that might have been useful for a pulmonate scorpion. Gills require a larger opening than lungs in order to receive enough oxygen and expel the volumes of water necessary.

The last preabdominal tergite is preserved so that the dorsal surface could be stripped away revealing the underside. There is no ornamentation on the dorsal surface, nor were any dorsal carinae noted. The ventral side, however, has a strong diagonal double carina. There was no ornamentation on any of the tergites or abdominal plates.

Another confirmatory feature presented by this scorpion has been that all the abdominal plates are completely holosternous.

Measurements (in mm) of Specimen IV (CIURCA 072869-9B).—

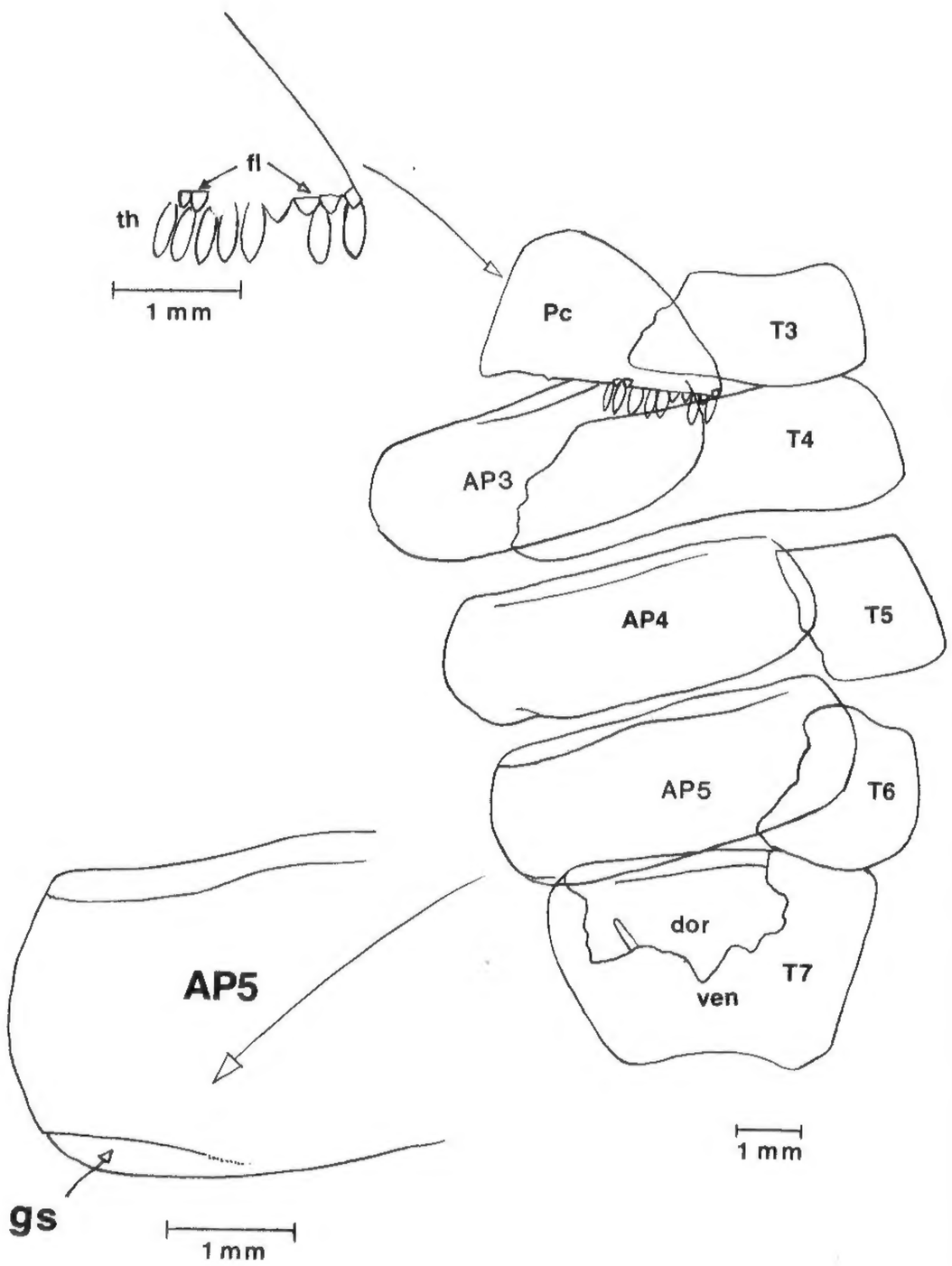
Pectines:	
Length of rachis (not including teeth)	2.0
Width of rachis (along line of fulcra)	3.1
Tooth length	.25
Tooth width	.09
Abdominal plate:	
Length (No. 3)	1.8
Width (No. 3)	5.2
Seventh tergite:	
Anterior width	4.6
Posterior width	2.7
Length	3.0

Specimen V.—CIURCA 042570-1A (Text-fig. 11A) from the Fiddlers Green Dolomite Member at Passage Gulf.

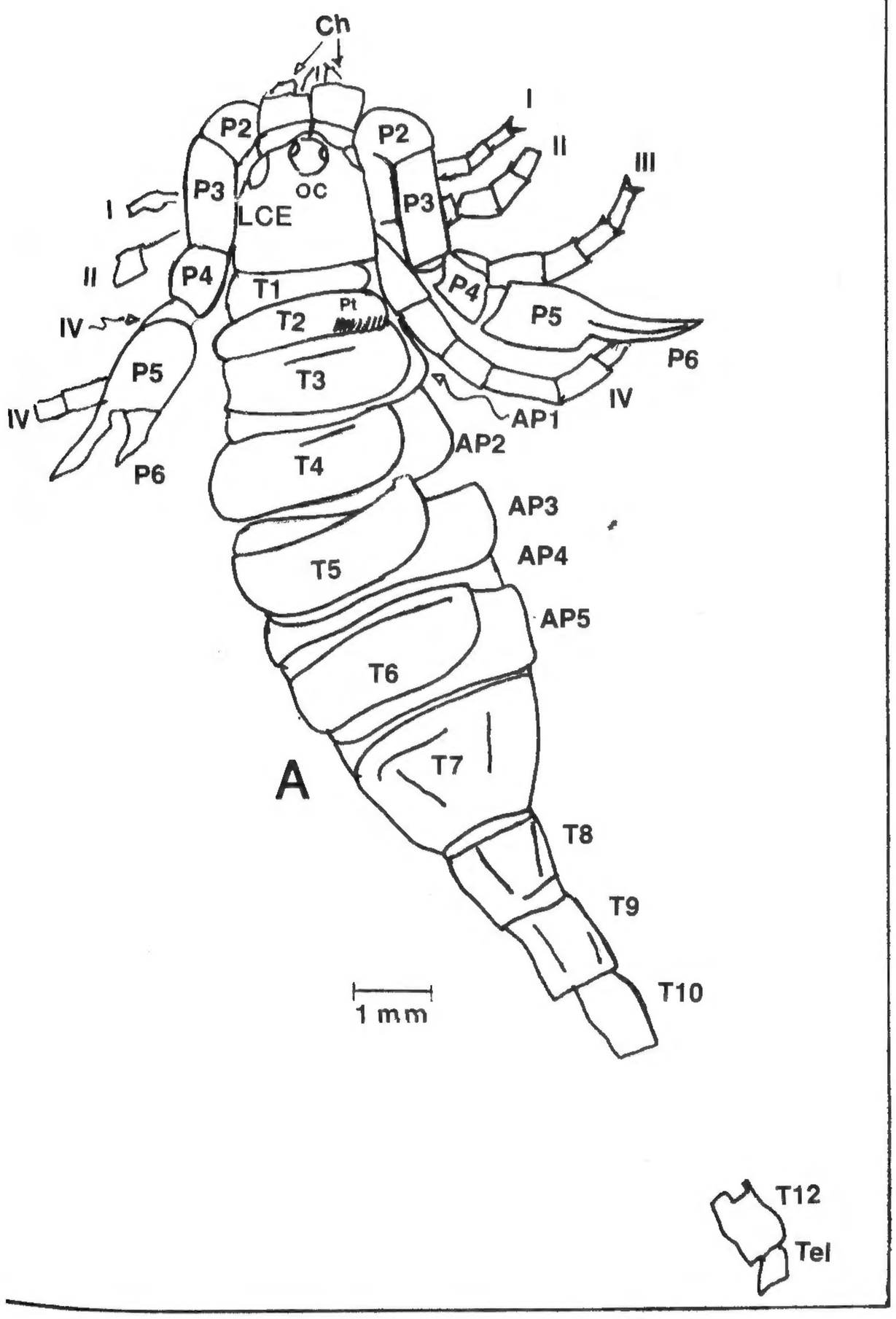
Consists of a single, nearly complete, specimen preserved as a dorsal impression. The entire specimen is estimated at an overall length of 17.5 mm from the anterior of the carapace to the estimated end of the cauda. It shows well-developed lateral compound eyes and the ocellar mound with well-preserved ocelli. The tergites are all much narrower than the underlying abdominal plates. The specimen merely verifies some of the details previously noted in other specimens.

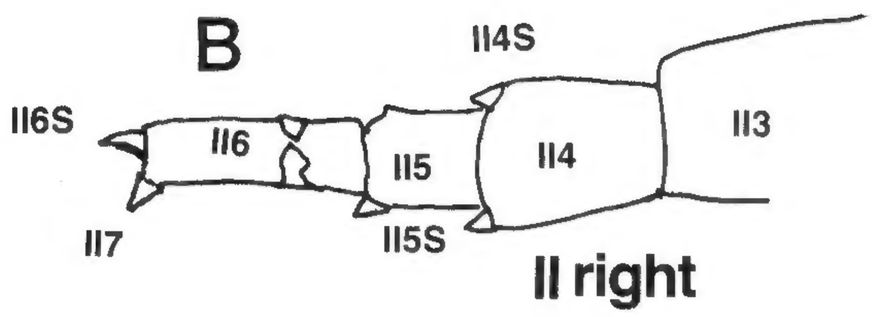
Specimen VI.—CIURCA 040668-1,2 (Text-figs. 11B–D, 12), from the Upper Silurian Bertie Waterlime, Herkimer Co., NY.

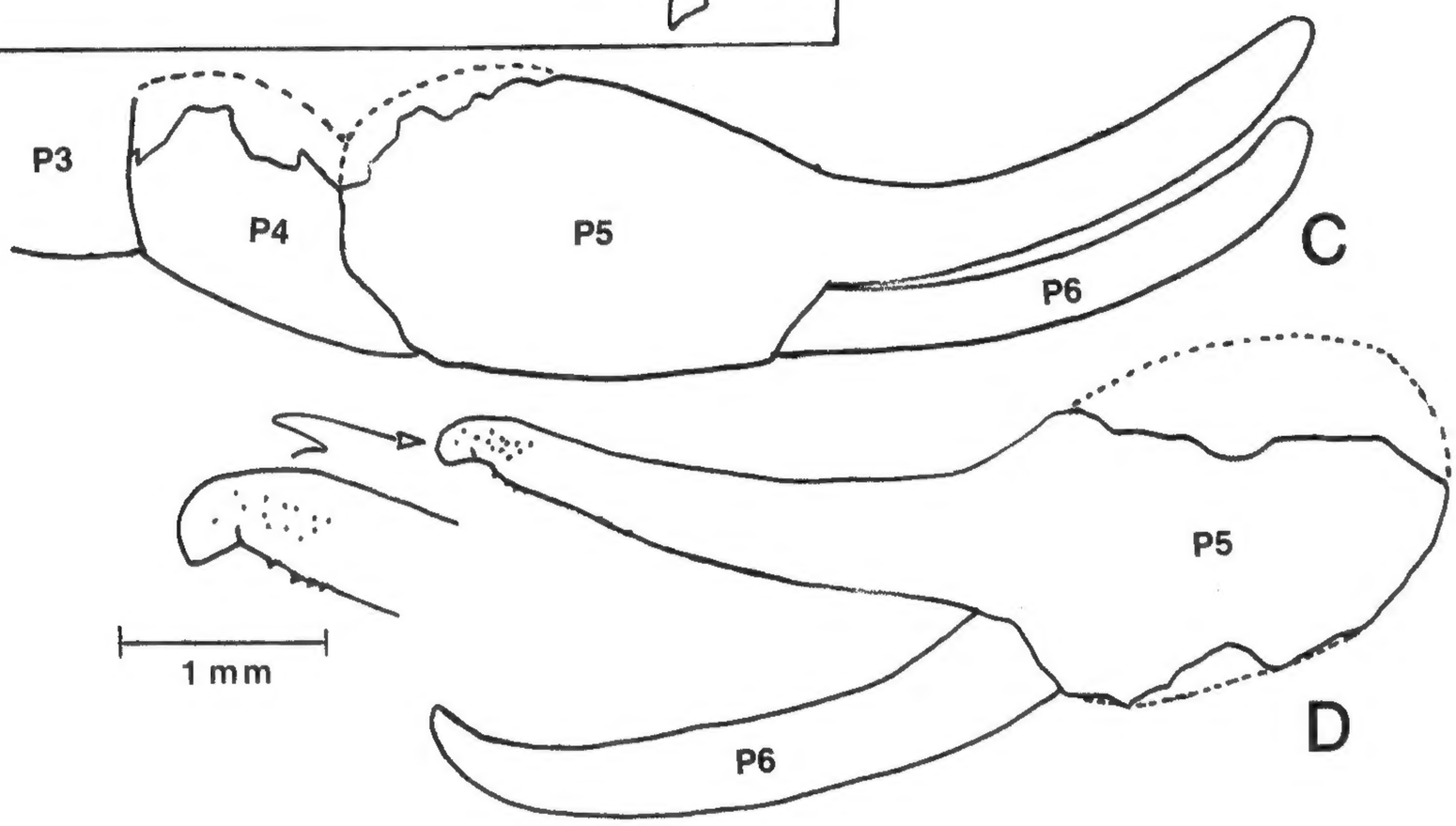
The underside of this specimen is well preserved and, under alcohol, many details hitherto unknown or not fully understood can be discerned. The coxosternal region is preserved in its entirety and reveals various structures not previously noted (see Text-fig. 12B). The sternum is lacrimiform with a narrow notch at the



Text-figure 10.—*Proscorpius osborni* (Whitfield). From the Upper Silurian Bertie Waterlime, Herkimer Co., NY. Specimen IV, CIURCA 072869-9B. Showing the abdominal plates and a gill slit on **AP5**; also the pectinal plate with a few teeth. See foldout inside front cover for explanation of abbreviations.







Text-figure 11.—*Proscorpius osborni* (Whitfield). From the Upper Silurian Bertie Waterlime, Herkimer Co., NY. Specimens V and VI, CIURCA 042570-1A and 040668-1. See also Text-figure 12. See foldout inside front cover for explanation of abbreviations.

A. Whole of Specimen V, CIURCA 042570-1A. **B.** Second right leg (**II**) on Specimen VI, CIURCA 040668-1, a counterpart. **C.** Right pedipalp, dorsal side, Specimen VI, CIURCA 040668-1. **D.** Left pedipalp, dorsal side, Specimen VI, CIURCA 040668-1.

anterior where the small, triangular plate of the labrum adjoins it. This triangular plate seems to fit where the sternum would be continued if it were pointed. The two structures are separated, however. The mouth therefore lies between the two plates. The triangular plate is bowed anteriorly, and in life would have had a scooplike appearance. The last three pairs of coxae, all short and truncated, abut the lacrimiform sternum. The first pair is remarkable in having a distinct gnathobase, a structure well known in the eurypterids, and, although expected in the early scorpions, that has not been found or noted until now. The posterior part of the first pair of coxae abuts the sternum and the labrum, but the greater part meets at midsection in front of the pointed labrum. The gnathobase is composed of small triangular denticles that occur in a single row, larger anteriorly and decreasing in size posteriorly almost exactly like the gnathobases adorning the coxae of the eurypterids. The mouth, therefore, was not at the end of a tube formed by the maxillary lobes, chelicerae and pedipalp bases, as in modern scorpions, although it occupied the same position relative to the carapace. Chewing occurred outside of the oral opening, as in the eurypterids, and very likely a pellet, made of the hard undigestible parts, was rejected. This seems to have been the method used by the eurypterids. The "coprolites" in the form of tubular bodies of apparently masticated chitinous skins associated with the eurypterid *Megalograptus ohioensis* (Caster and Kjellesvig-Waering, 1964, p. 337) apparently are not fecal in origin, but are rejected masticatory pellets.

The sternum is large, ovate, widest at the posterior end and, as mentioned before, has a deep triangular notch that accommodates the parrot-beaklike sclerite, which is the labrum. The chelicerae are composed of four joints, occur at a higher plane than the pedipalps, and the basal joints apparently have considerable lateral movement (see Text-fig. 7B of CIURCA 041771-1). The basal joint or coxa of the pedipalp is very long and is in the same position vis-à-vis the mouth as in living forms. It occurs, therefore, at a higher plane than the legs, but on the same plane as the coxae of the legs but below the chelicerae.

The legs are short, stout, with small triangular coxae that abut the sternum. The first pair abuts the upper part of the sternum and the labrum. Basitarsal and tibial spurs, apparently double, occur on each joint, but the first legs also show the presence of a femoral spur, possibly also doubled.

The opercular plates are small and round and occur directly posterior to the sternum. There are five abdominal plates.

Remarks.—The location of the mouth in *Proscorpius* shows that it was well forward of where the mouth is in present-day scorpions. This still is not so far forward as in Størmer's *Waeringoscorpio,* which is more primitive than *Proscorpius* although not so old in geologic age.

Størmer's excellent discussion of the probable evolution of the oral chamber (1970, pp. 345–348) can be largely substantiated and expanded. With the details furnished by the Ciurca specimens, in particular specimen VI (CIURCA 040668-1), and *Waeringoscorpio hefteri* Størmer, it is clear that the mouth migrated backward as in *Limulus* and possibly in the Eurypterida; the chelicerae occurred above the first or basal joint of the pedipalps, on the inner side of these joints. The base of this wide oral chamber, however, was open and here a labrum occurred, which functioned against the sternum. Furthermore, in such genera as *Eoscorpius, Kronoscorpio,* etc., the maxillary lobes of the first pair of coxae were extended and later the maxillary lobes of the second pair of coxae squeezed the first pair of maxillary lobes away from the midline, so that the two pairs of maxillary lobes formed the base of the oral chamber, whereas the sides were composed of the first joint of the pedipalps and the chelicerae formed the roof of the chamber. Each of these steps can be demonstrated by the fossil record.

Genus **ARCHAEOPHONUS**
Kjellesvig-Waering, 1966
(emend.)

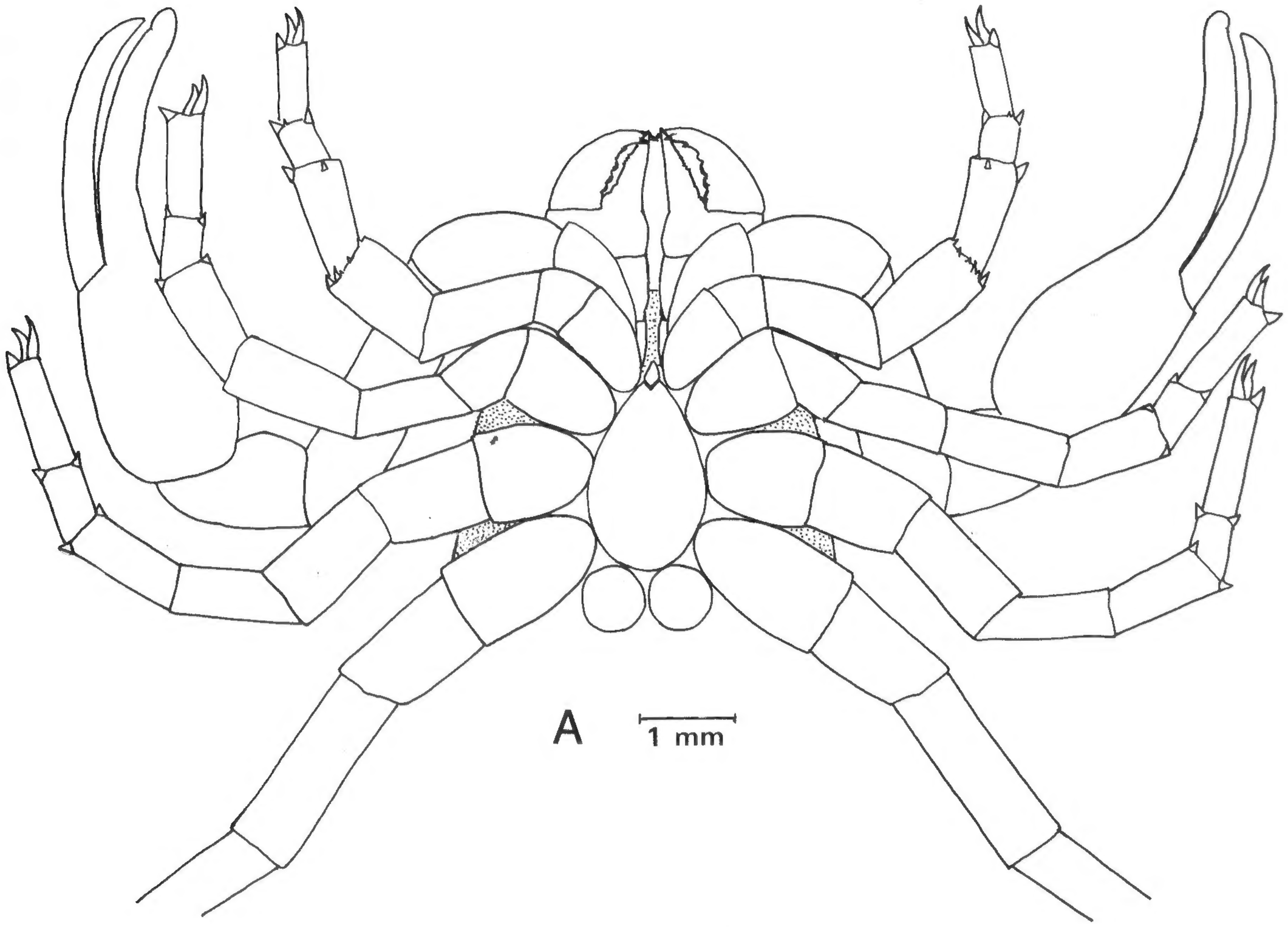
Proscorpiidae (?) with large, subquadrate carapace; large oval compound eyes located at anterolateral margins; central eye node anteriorly located with two very small ocelli; no raised cephalic area developed. Chelicerae of four joints, last leg with double trochanter. Preabdominal tergites with acute epimeral angles, not rounded.

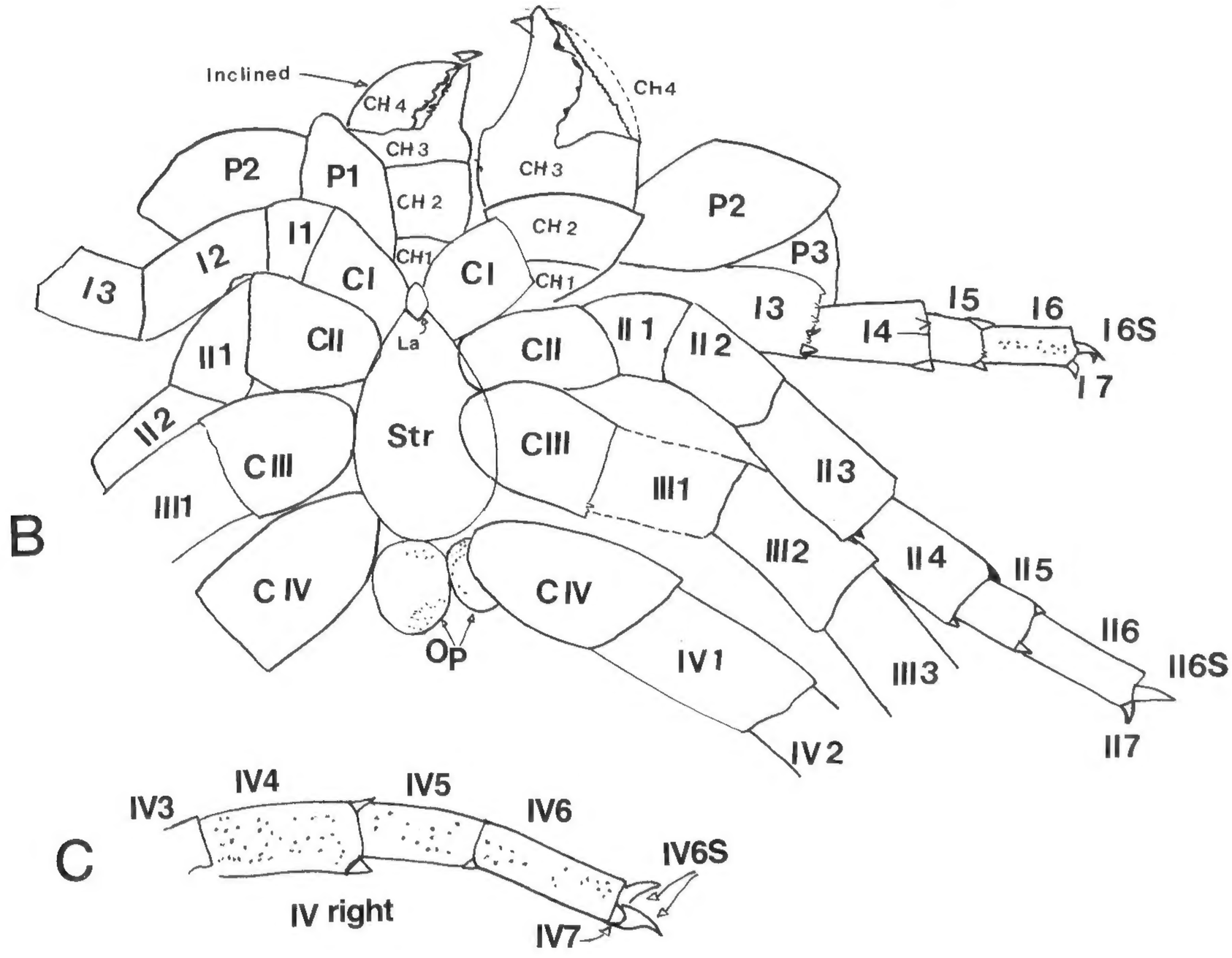
Type species.—*Archaeophonus eurypteroides* Kjellesvig-Waering, 1966.

Remarks.—The discovery of another specimen of this genus has necessitated revision of the original generic description. It should be noted that the differences in comparison with *Proscorpius* are significant, but, because the underside of *Archaeophonus* is not well known, it is provisionally retained in the Pro-

Text-figure 12.—*Proscorpius osborni* (Whitfield). From the Upper Silurian Bertie Waterlime, Herkimer Co., NY. Specimen VI, CIURCA 040668. See also Text-figure 11. See foldout inside front cover for explanation of abbreviations.

A. This reconstruction of the prosomal appendages was largely based on Specimen VI, CIURCA 040668, with the outline and size of the carapace in relation to the appendages from Specimen I, CIURCA 031966-1. **B.** Coxosternal area as shown by Specimen VI, CIURCA 040668-1. The left chelicera appears smaller because it is inclined. Claws on leg **II** taken from counterpart. **C.** Right fourth leg (**IV**), showing terminal detail, Specimen VI, CIURCA 040668-2.


A
1 mm


Inclined
CH 4
CH 3
CH 2
CH1
P2
P1
I1
I2
I3
CI
CII
CIII
C IV
La
Str
OP
II1
II2
III1
CH4
CH3
CH2
CH1
P2
P3
I3
I4
I5
I6
I6S
I7
II1
II2
II3
II4
II5
II6
II6S
II7
III1
III2
III3
IV1
IV2
B

IV3
IV4
IV5
IV6
IV6S
IV7
IV right
C

scorpiidae, until more specimens are forthcoming from the Passage Gulf locality.

Archaeophonus eurypteroides
Kjellesvig-Waering, 1966
Text-figure 14

1966. *Archaeophonus eurypteroides* Kjelleswig-Waering, pp. 373–375, pl. 42, fig. 1; pl. 43, figs. 1, 5; text-figs. 5–10.

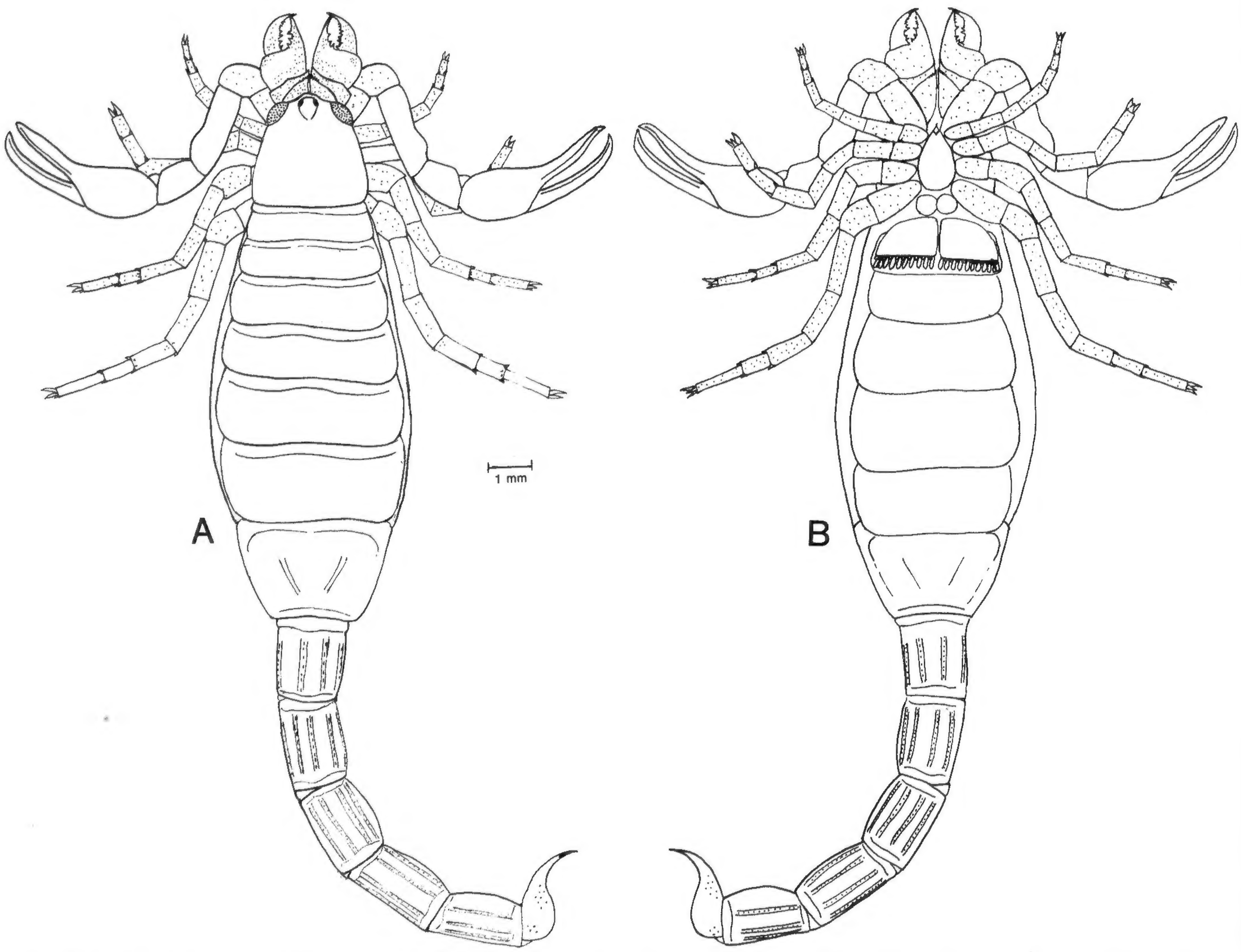
Type information.—Both the holotype, CUGM 41109[8], and CIURCA 062065-1 come from the Fiddlers Green Dolomite Member of the Bertie Formation, Upper Silurian, Ludlow age, upper part at Passage Gulf, Herkimer County, NY.

Specimen.—CIURCA 062065-1. Collected on May 20, 1965, by Samuel J. Ciurca.

The specimen is well preserved, nearly whole, and consists of only the dorsal side, but reveals several morphological structures not preserved on the holotype, which previously was the only known specimen. As in nearly all Bertie material, the specimen is preserved as a carbonized imprint, showing little relief but no distortion. Also, as in other Bertie material, the specimen is best studied under alcohol or when moistened with a mixture of glycerine and water. In the dry state, and using light at an angle, certain joints and structures can be well delineated. The following description is restricted to the parts not previously seen in the holotype or those which needed confirmation.

Principal among these new morphological structures are the large, bulbous, compound lateral eyes. An unusually large compound eye, the proportions of which suggest some of the eurypterids, is preserved on the

[8] Ed Landing (oral commun., May 7, 1985) reports that the holotype of *Archaeophonus eurypteroides* Kjellesvig-Waering, 1966 (CUGM 41109) was transferred to the collections of the New York State Museum in Albany, NY in 1971, as NYSM 12947. P.R.H.



Text-figure 13.—*Proscorpius osborni* (Whitfield). From the Upper Silurian Bertie Waterlime (Fiddler's Green Dolomite), Herkimer Co., NY. Reconstructions based on specimens in the collection of Samuel J. Ciurca, Rochester, NY.
A. Dorsal side. **B.** Ventral side.

anterolateral angles of the right side of the carapace. A median eye node is present midway on the anterior of the carapace, and the two small ocelli are barely perceptible. These ocelli are much like those present in eurypterids and not of the large size seen in Carboniferous or later scorpions.

The carapace is nearly square, very large, broadly rounded at the anteromarginal corners, and has a well-developed transverse ridge at the base.

The chelicerae (see Text-fig. 14B) are well preserved, particularly the left one, which is seen from the dorsal side. This structure is composed of four segments, not three as in living scorpions. The first two are short and bandlike, but allow these structures considerable lateral movement, again unlike those of living scorpions, which are quite rigid, pointing outward and hardly capable of side movement. The immovable finger is elongated and armed with small denticles, but it was not possible to determine their exact shape or arrangement. The free finger is very long, hooklike, and also armed with several denticles. It is certain that the action between these two teeth is scissorlike and that no double tooth termination is present on the free finger such as is present in the Buthidae.

The pedipalp is seen for the first time and this structure is stout, short, and although likely displaced forward, the trochanter is apparently much longer than in other scorpions. The femur and tibia are short and stout. The hand is very stout, with the immovable finger curved inward against the free finger which is correspondingly curved backward. This is the opposite of what occurs in all other scorpions which the writer has seen and is unlike those living.

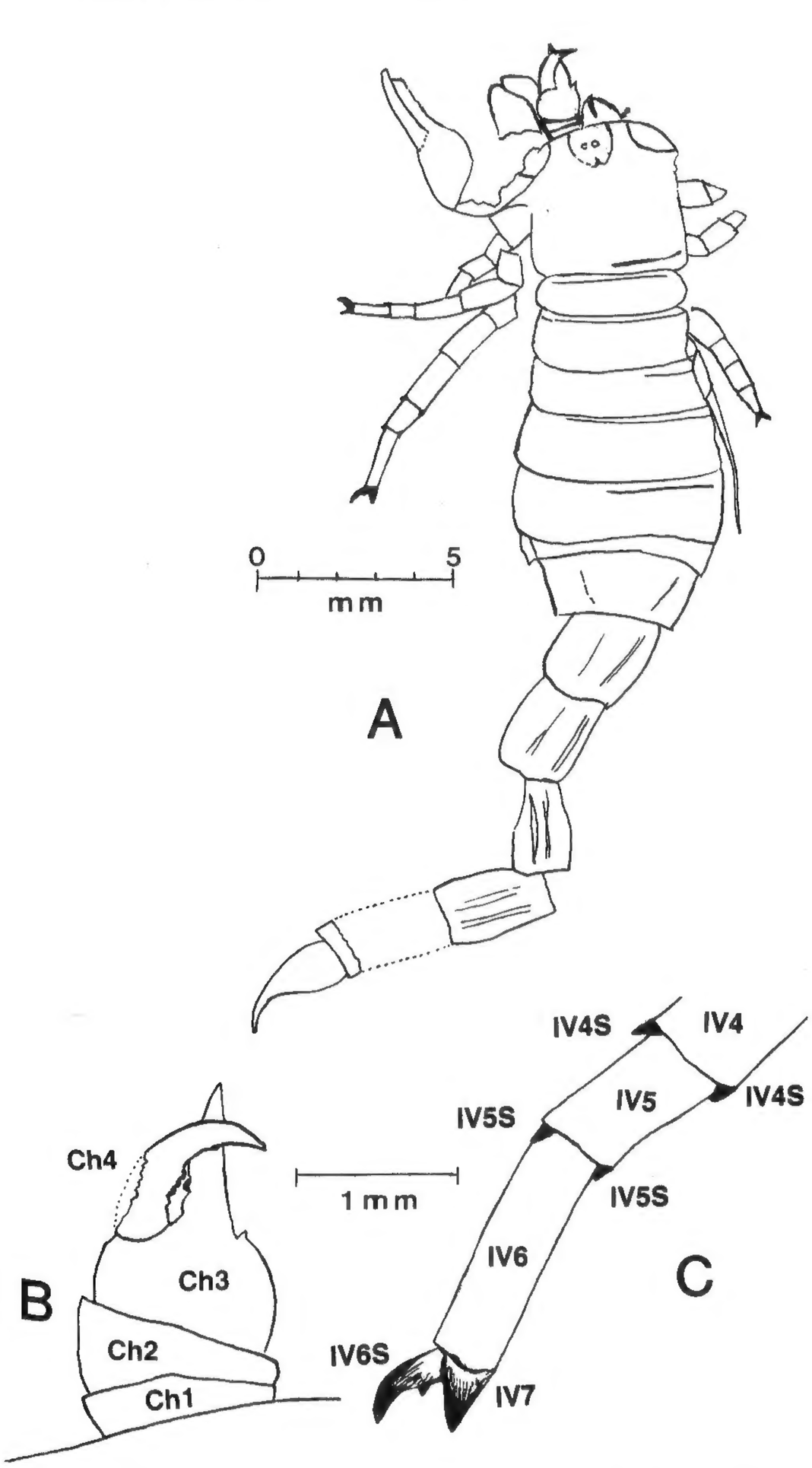
The walking legs are preserved in excellent condition. The last leg in particular confirms the presence of the unusually long tarsus, and the claws and post-tarsus are well preserved (see Text-fig. 14C). The post-tarsus forms a thick pointed heel, whereas the claws are curved and not greatly unlike those in living scorpions. Two small basitarsal and tibial spurs, one on each side, occur on the last leg and possibly on others, although not seen in the specimen. If present on the other legs, the spurs are very small. The fourth walking legs, as all the others, are very short and do not extend past the posterior end of the fifth tergite.

There are two dorsal median ridges on each tergite of the cauda. The telson, or stinger, is perfectly preserved, slender, and with the aculeus bent in a gentle hook.

No ornamentation was noted on the dorsal side of this scorpion.

Measurements (in mm) of CIURCA 062065-1.—

Carapace:	
Length	4.3
Width	4.3
Lateral eye:	
Length	1.5
Width	1.0
Pedipalp:	
Length of femur	2.0
Length of tibia	1.3
Width of hand	1.6
Length of palp	4.1 (incomplete)
Tergite length:	
1	0.8
2	1.3



Text-figure 14.—*Archaeophonus eurypteroides* Kjellesvig-Waering. From the Upper Silurian, Bertie Waterlime, Herkimer Co., NY. CIURCA 062065-1. See foldout inside front cover for explanation of abbreviations.

A. The whole specimen showing right lateral compound eye. **B.** Chelicera, showing "over-bite" of the free finger. **C.** Distal part of the left fourth walking leg.

Measurements of CIURCA 062065-1 (cont'd).—

Tergite length:		
3	1.4	
4	1.5	
5	1.7	
6	telescoped	
7	1.9	
8	2.4	
9	2.5	
10	2.5	
11	2.7	
12	2.8	(estimated)
Vesicle width:	1.0	
Length of stinger:	2.5	
Complete length estimated:	30.1	(not including chelicerae)
Preabdomen length:	10.4	
Postabdomen length:	15.4	

Remarks.—It seems that a correlation can now be made between the size of the median eyes and the size of the lateral compound eyes. In Silurian scorpions, such as *Proscorpius* and *Archaeophonus,* it appears that large lateral compound eyes are accompanied by small median eyes. In the Carboniferous and Triassic scorpions the lateral compound eyes are greatly diminished in size with a corresponding increase in the size of the median eyes. Some of the scorpions without lateral compound eyes, such as *Mazonia,* have very large median ocelli.

Family **WAERINGOSCORPIONIDAE** Størmer, 1870

Proscorpioidea[9] with all legs abutting and radiating from the sternum. Labium and labrum present.

Type genus.—*Waeringoscorpio* Størmer, 1970.

Remarks.—The family Waeringoscorpionidae Størmer, 1970, is unlike any other in the arrangement of the coxae vis-à-vis the large pyriform sternum. The archaeoctonoids differ in that the first pair of coxae has moved anteriorly and the coxae abut one another and not the sternum. Although the waeringoscorpionids now appear more closely related to the archaeoctonoids than to any other group in their development, only more information can resolve the degree of their actual relationships.

Genus **WAERINGOSCORPIO** Størmer, 1970

Waeringoscorpionidae with long slender postabdomen; dorsal side little known; powerful chelicerae; pedipalps with slender hand and fingers, inner edges cultrate; walking legs rather long; opercular plates ovoid; combs relatively small with 20–25 (?) teeth, median appendage present; ovate filamentous areas probably attached to ventral plates; postabdomen with long segments, each with close-set longitudinal ridges; telson triangular in outline.

Type species.—*Waeringoscorpio hefteri* Størmer, 1970.

Geological range.—Lower Devonian.

Remarks.—Størmer considered the abdominal plates to be moderately lobostern (?).

Waeringoscorpio hefteri Størmer, 1970
Text-figure 111B

1960. Scorpionlike eurypterid ? gen. et spec. indet. Størmer, pp. 87–91, text-fig. 1.
1970. *Waeringoscorpio hefteri* Størmer, pp. 336–343, pls. 1, 2, text-fig. 5.

Type information.—Holotype and only known specimen, SMF VIII 31. Type horizon: Lower Devonian, late Lower Emsian, Nellenköpfchen Schichten. Type locality: quarry in the Alkener Bach-Tal E. of Alken an der Mosel, MTB Münstermaifeld r 03800 : h 68670, W. Germany.

Family **LABRISCORPIONIDAE**, new family

Proscorpioidea (?) with large pentagonal sternum[10] and subcuneate coxae.

Type genus.—*Labriscorpio* Leary, 1980.

Remarks.—Regardless of whether the Labriscorpionidae have a pentagonal sternum as suggested here, or a rhombic sternum with a triangular labrum, as in the original description (Leary, 1980, p. 1255), the genus *Labriscorpio* must be placed in a new family assignable to the Proscorpioidea. It is unique and comparison with other families is superfluous.

The abdominal plates have not been found, therefore doubt exists on the position of the family with regard to higher taxonomic categories. *Labriscorpio* is close to either the Holosternina Proscorpioidea or the Lobosternina Loboarchaeoctonoidea. It is more primitive than *Loboarchaeoctonus* and approximately at the same level of development as *Proscorpius.* For the time being, until further confirmation is forthcoming from other specimens, the family Labriscorpionidae is retained in the superfamily Proscorpioidea.

Genus **LABRISCORPIO** Leary, 1980

Labriscorpionidae with first pair of coxae with an-

[9] Although Kjellesvig-Waering had preliminarily proposed a new superfamily for *Waeringoscorpio,* new material of *Proscorpius* (see Text-figs. 6D, 12A, B) that came to light during the course of his study showed the assignment to the Proscorpioidea to be the better solution. A.S.C.

[10] Leary (1980, p. 1255) says: "Labrum triangular. Sternum trapezoidal with posterior edge slightly more than twice as wide as anterior edge; sides slightly convex." Kjellesvig-Waering never saw the actual specimen and his knowledge of the scorpion was based on manuscript copy. A.S.C.

teriorly-directed spurs, legs very short; free finger of pedipalp cultrate and straight.

Type species.—*Labriscorpio alliedensis* Leary, 1980.

Geological range.—Late Mississippian or early Pennsylvanian.

Remarks.—The overall aspect of this scorpion is somewhat like *Archaeoctonus glaber* (Peach) and *Loboarchaeoctonus squamosus* from the Lower Carboniferous of Scotland.

Labriscorpio alliedensis Leary, 1980
Text-figures 111C, D

1980. *Labriscorpio alliedensis* Leary, pp. 1255–1257, 1 pl., 2 text-figs.

This unusual and taxonomically important scorpion has been adequately described, and my comments are restricted to another possible interpretation of the coxosternal area. The small piece in front of the sternum is regarded by Leary as a labrum, and indeed, this may be correct. However, this would mean that the mouth would occur between this triangular piece and a sub-rhombic sternum, and nothing is mentioned of the presence of an opening, which should have been preserved. My interpretation is that the sternum is pentagonal (see Text-figs. 111C, D) with all subcuneate coxae adjoining this pentagonal sternum, and it seems to me to be worth considering as an alternative to Leary's determination.

Type information.—Early Pennsylvanian or Late Mississippian channel fill, associated with numerous plants and a fish scale in the quarry of the Allied Stone Company, between Rock Island and Milan, Illinois (SE¼ sec. 14. T. 17 N., R. 2 W., Milan Quadrangle). The plant fossils indicate an upland flora, but the scorpion should not be considered as anything but a gill-bearing, water-dwelling scorpion, although it is probable that *Labriscorpio alliedensis* could take excursions out of the water, carrying water in its gill chambers.

The holotype is deposited in the collections of the Illinois State Museum, Springfield, IL and is accessioned as ISM 416899.

Superfamily **STOERMEROSCORPIONOIDEA**, new superfamily

Holosternina with first pair of coxae abutting anterior to the sternum and with poor development of maxillary lobes; second and third pairs of coxae abut against the sternum, and the fourth against the genital opercular plates.

Type family.—Stoermeroscorpionidae, new family.

Remarks.—Among the Holosternina, it differs from the Archaeoctonoidea in having the fourth pair of coxae abutting the genital opercula, and from the Mesophonoidea in having the second pair abutting against the sternum, and in the primitive development of maxillary lobes.

Family **STOERMEROSCORPIONIDAE**, new family

Stoermeroscorpionoidea with very large, elongate-pentagonal sternum with deep, triangular basal notch and large, elongate elliptical opercular plates, and lateral compound eyes.

Type genus.—*Stoermeroscorpio,* n. gen.

Remarks.—There is no family that warrants comparison as it is so different from all others.

Genus **STOERMEROSCORPIO**, new genus

Stoermeroscorpionidae with round ocellar node on an anteriorly-rounded, very elongate carapace, and lateral compound eyes.

Derivatio nominis.—Named for Dr. Leif Størmer.

Type species.—*Stoermeroscorpio delicatus,* n. sp.

Geological range.—Silurian.

Remarks.—This scorpion is so different from all others that there is no necessity for comparison. Having the characters mentioned above for the superfamily and family makes this a unique scorpion, likely representing a large group in the Silurian and older beds. It is a distinct pleasure to name this genus after my friend, Professor Leif Størmer of the Paleontological Institute of the University of Oslo.

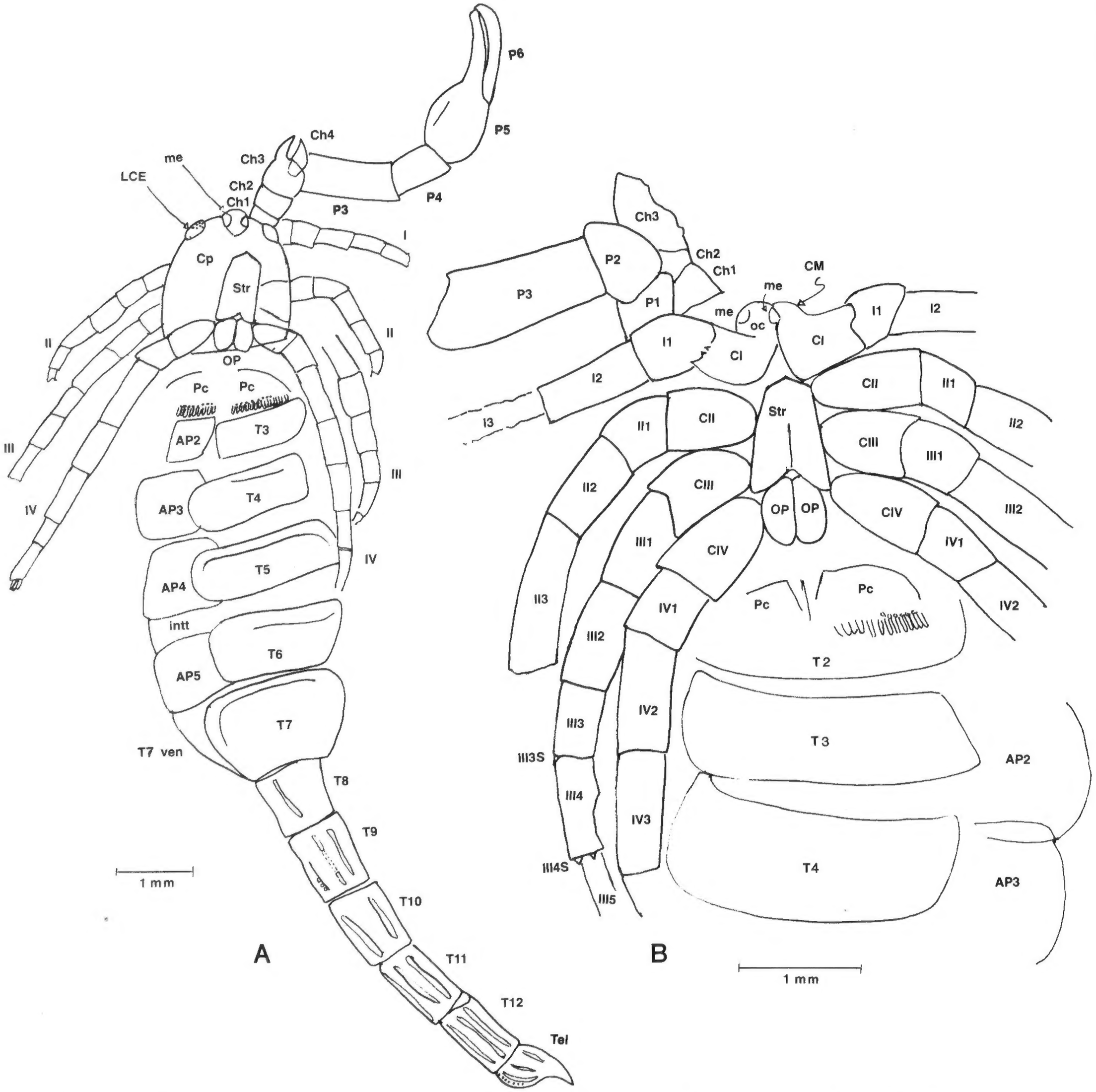
Stoermeroscorpio delicatus, new species
Text-figures 15, 16

Type information.—The holotype consists of part and counterpart of a nearly complete scorpion, showing most of the dorsal and ventral surfaces. It is registered as No. 041771-1,2, in the private collection of Samual J. Ciurca of Rochester, NY, and comes from the Silurian, upper Fiddlers Green Member of the Bertie Waterlime at Passage Gulf, Herkimer Co., NY. It occurs in the typical "waterlime", on the same layer as numerous eurypterids and several scorpions, as well as marine fossils. The ecological zone or biological community is what the writer refers to as the "Eurypteridae Zone" (see Kjellesvig-Waering, 1961, p. 794). The holotype is a small scorpion measuring 12 mm in total length from the anterior of the carapace to the base of the stinger. Overall it is a delicately constructed individual.

The carapace is rounded anteriorly and rather large, particularly in comparison with the common *Proscorpius osborni* that occurs in the same horizon. The lateral compound eyes are round, marginally located on the anterior of the carapace, and have relatively coarse ommatidia. The ocellar node is well developed, an-

teriorly and marginally placed, round, elevated, and has two small, rounded ocelli on the area slightly anterior to the middle of the ocellar node. The specimen is flat, but no ridges or ornamentation were discernible and it is assumed, probably correctly, that the surface of the carapace is smooth. There is no sign of a basal marginal rim, and the base is straight, with genal angles of 90°. The entire carapace is longer than wide by a ratio of 8 to 7.

The mesosoma does not differ from that of most other scorpions. It is slender; each tergite has a poorly-developed anterior transverse ridge, and the tergites increase in length progressively backward. The last preabdominal tergite is large, triangular and apparently



Text-figure 15.—*Stoermeroscorpio delicatus,* n. gen., n. sp. From the Upper Silurian Bertie Waterlime, Passage Gulf, Herkimer Co., NY. Holotype: CIURCA 041771-1,2. See foldout inside front cover for explanation of abbreviations.

A. Dorsal side, CIURCA 041771-2 (counterpart), 12 mm long from part of carapace to the stinger end. **B.** Ventral side, CIURCA 041771-1, showing coxosternal area and anterior preabdomen.

smooth: crests, if present, are weak.

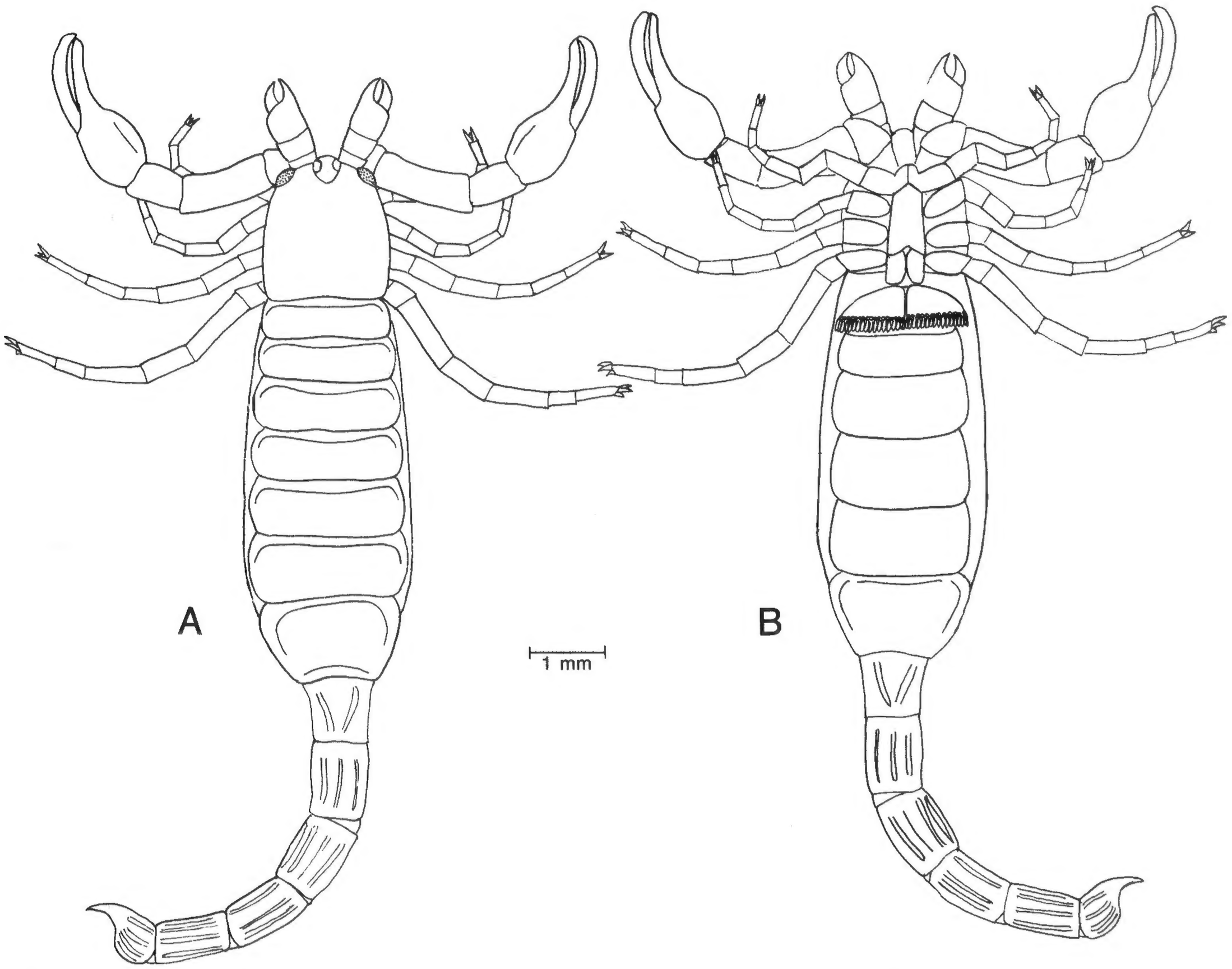
The postabdomen continues as a slender organ with lateral, superior and inferior crests, but in their flattened state they could not be precisely determined. Each tergite is "normal" and only on one tergite were small pustules, probably setaceous, developed on one of the inferior crests.

The telson, or stinger, is unusual in being very short and stout. The aculeus is particularly short. Three crests are developed on the vesicle and I interpret these as a superior, two laterals and an additional apparent line of scales which likely represents a single inferior "crest" that has become almost obsolete.

The coxosternal region, of course, is the area which is very surprising and exciting because of its phylogenetic implications. The sternum, in keeping with all Silurian and Devonian scorpions, is large—a large plate similar to that present (metastoma) in eurypterids. This large sternum is elongate-pentagonal with slightly tapering lateral margins, a rather obtuse anterior, and a deep, inverted triangular basal margin where the two, nearly elliptical, rather elongate, marginal plates are located.

The first pair of coxae is of particular interest. These abut against each other, anteriorly to the triangular part of the pentagonal sternum. The inner anterior parts of these coxae are produced forward into a pair of short, wide, maxillary lobes. The second and third pairs of coxae are short, rounded at the inner part, and truncated in contact with the trochanters. Both pairs abut the lateral margins of the sternum. The fourth pair, similar in shape to the second and third pairs, abuts against the genital opercula.

The chelicera is very slender, long, composed of four



Text-figure 16.—*Stoermeroscorpio delicatus,* n. gen., n. sp. Reconstruction based on the holotype, CIURCA 041771-1,2. From the Upper Silurian Bertie Waterlime (Fiddler's Green Dolomite), Herkimer Co., NY.

A. Dorsal side, based on CIURCA 041771-2. **B.** Ventral side, based on CIURCA 041771-1.

joints, with the chela small and curving. I was unable to note any teeth, which are undoubtedly present, but small. The hand is rounded on the margins but this may be due to flattening.

The pedipalp is known in its entirety. The trochanter is roughly triangular, but long. The first joint is seen to lie under the first leg, and far from the area of preoral chamber formed by the first two coxae. It is therefore to be noted that the pedipalp coxae had not joined in the formation of the preoral chamber as in later scorpions.

The femur is very long and slender, devoid of any noticeable ridges, which should be seen even in the flattened state, since folds (the crests of the cauda) were preserved. The brachium is very short. The chela is large, having a well-developed, stout hand with two curved dactyls. The fixed dactyl is incurved, whereas the free one is curved forward and overlaps the other at the end. Both are cultrate along the edge.

The four legs are present, but details of the ends and spurs will have to await better preserved specimens. It is certain, however, that the first pair is very short, that all the rest are slender, increasing in size backward, that the last pairs are longer than usual for the Bertie assemblage, and that the terminations are composed of a short posttarsus and two short ungues as in other Bertie scorpions. The legs are cylindrical.

The combs are barely discernible and this only in highly favorable light and wet with alcohol. Fulcra are definitely present and are very small, but, surprisingly, as many as 20 elongated teeth occur. I suspect that the rachis is not divided into anterior or median lamellae, although this is more of an impression I received from not being able to see any joint lines. It is not a point to be stoutly maintained.

The abdominal plates are the usual holosternous type.

Derivatio nominis.—*delicatus* (L.) = delicate.

Remarks.—The short maxillary lobes of the first pair of coxae are the oldest attempt at forming a preoral chamber and suggest that the labrum of forms such as *Proscorpius* and *Waeringoscorpio* is obsolete and has disappeared in this scorpion. Possibly this scorpion was becoming amphibious as early as the Upper Silurian, as the preoral chamber is considered an adaptation for land. The fact that *Stoermeroscorpio* was a Holosternina, having gills, meant that it could not live long out of water by carrying water in the pouches present in the inner part of the holostern plates. At any rate, this attempt at a preoral chamber was in its infancy, as the coxae or first joints of the pedipalps had not yet moved to the position that they hold today, namely on each side of the oral chamber, forming the lateral margins. For that matter, the chelicerae, although only one is present, show that they were far apart—as far apart as the pedipalp bases—and therefore could not take part in forming the roof of the oral chamber as they do today.

Another interesting feature of this scorpion is that it has the same type of short first legs found in *Proscorpius* and *Archaeophonus,* which lived in the same environment and walked over soft magnesium carbonate muds ("waterlimes" of eurypterid literature). There seems to be an adaptation for similar conditions. Of course, they could have lived on reefs or subaqueous rocks, but these are unknown in the Bertie mudflats. The type of rocks, as well as the nearly perfect complete preservation, precludes transportation of the fragile skins.

Superfamily **ALLOPALAEOPHONOIDEA,** new superfamily

Holosternina with first three pairs of coxae meeting in front of the sternum, without maxillary lobes; other pair of coxae abutting against the sternum; legs very thick, short, eurypteridlike, with posttarsus greatly developed as a single spine.

Type family.—Allopalaeophonidae, new family.

Family **ALLOPALAEOPHONIDAE,** new family

Allopalaeophonoidea with large pentagonal sternum. Small carapace without lateral compound eyes.

Type genus.—*Allopalaeophonus,* new genus.

Genus **ALLOPALAEOPHONUS**, new genus

Allopalaeophonidae with well developed, anteriorly located median eyes without apparent ocellar nodes. Anterior and lateral margins of carapace concave; walking legs without tibial spines.

Derivatio nominis.—*allo* (Gr.) = another, different + *Palaeophonus,* a scorpion genus.

Type species.—*Palaeophonus caledonicus* Hunter, 1886.

Geological range.—Silurian of Scotland.

Remarks.—Thorell and Lindström (1885, p. 24), in discussing *Palaeophonus caledonicus,* stated in a footnote to their classification: "If this species is provided with eyes, and if *P. nuncius* should prove destitute of eyes, a new genus must of course be formed for the reception of the former species." As it turned out, both species have median eyes, but *P. nuncius* has large lateral facetted eyes as well. The two species do have rather similar legs and share a general dorsal aspect of the body, but *P. nuncius* is a lobostern, and not closely related.

Allopalaeophonus caledonicus (Hunter)
Plate 2, figures 1–4; Text-figures 17, 18, 110O

1885. *Palaeophonus* sp. Peach, p. 297, fig. 1.
1886. *Palaeophonus caledonicus* Hunter, pp. 169–170.
1888. *Palaeophonus caledonicus* Hunter. Hunter, pp. 185–191.
1901. *Palaeophonus hunteri* Pocock, pp. 291–311, fig. 3, pl. 9.
1904. *Palaeophonus caledonicus* Hunter. Frič, pp. 63–64, text-fig. 79.
1911. *Palaeophonus caledonicus* Hunter. Bather, p. 676.
1912. *Palaeophonus hunteri* Pocock. Clarke and Ruedemann, p. 395, fig. 85.
1913. *Palaeophonus caledonicus* Hunter. Petrunkevitch, p. 32.
1923. *Palaeophonus hunteri* Pocock. Versluys and DeMoll, p. 109, figs. 15, 38A.
1934. *Palaeophonus caledonicus* Hunter. King, p. 563.
1944. *Palaeophonus hunteri* Pocock. Lehmann, p. 177.
1949. *Palaeophonus caledonicus* Hunter. Petrunkevitch, pp. 128–129, fig. 172.
1953. *Palaeophonus caledonicus* Hunter. Petrunkevitch, pp. 5, 8–10, figs. 6, 116.
1955. *Palaeophonus caledonicus* Hunter. Petrunkevitch, p. 69, figs. 38(2), 39B.
1962. *Palaeophonus caledonicus* Hunter. Dubinin, p. 425, fig. 1222.
1963. *Palaeophonus caledonicus* Hunter. Størmer, pp. 92, 94.
1966. *Palaeophonus caledonicus* Hunter. Kjellesvig-Waering, p. 359.

Specimen.—Holotype, KM unnumbered specimen. It is from the Silurian, Llandovery–Wenlock, at Dunside, Logan Water, Lesmahagow, Scotland.

The specimen was studied under alcohol, and as with the other chitinous forms preserved in the greenish black shales of Lesmahagow, details are beautifully revealed when immersed in a wet medium. Two silicone casts made by Dr. Ian Rolfe reveal much which can be discerned in much greater detail than on the original. The holotype specimen was kindly sent by the Kilmarnock Museum to Edinburgh, where I was able to study it.

Considerable confusion exists as to whether the dorsal or ventral side is preserved. Peach (1885) and Pocock (1901) believed that the ventral side was preserved with outlines of the eyes and carapace impressed through. Petrunkevitch (1953, p. 9) stated that the specimen was preserved as a dorsal impression with the ventral structures impressed through. There is no doubt that the specimen is preserved with the ventral side revealed and with the median eyes and outline of the carapace impressed through, as Peach and Pocock had stated. This can easily be proven because the eyes are preserved as molds of the internal part, imbedded in the shale as two small depressions.

The carapace is deeply emarginate along the anterior margin, with the base also emarginate. The sides apparently are straight or slightly incurving or concave. The median eyes appear elliptical, but actually are round, small, and placed anteriorly on the carapace, very close to the margin. Undoubtedly they are located on a small ocellar mound of slight elevation, as two small wrinkles occur on each side of the median eyes, which represent the compressed ocellar node. The node is clearly lacrimiform with the two round eyes placed on the anterior end. Small punctae are present on the anterior part of the node.

Petrunkevitch (1953, p. 9) shows two orbital ridges on each side of the anterior part of the carapace. These were not noted by Hunter (1886, 1888), Peach (1885) or Pocock (1901), and I have been unable to find them. This scorpion is a holostern and, therefore, if lateral eyes were present, they would be compound eyes, and orbital ridges are never developed with such eyes. Lateral orbital ridges are developed only in modern, land-living, scorpions to protect the few (one to five) lateral ocelli. If orbital ridges had been developed, it would mean that the eyes had been small ocelli as in present-day scorpions, and had disappeared, leaving the orbital ridge as a vestige. This is hardly possible and I consider the structure to be nothing more than fortuitous wrinkling of the carapace.

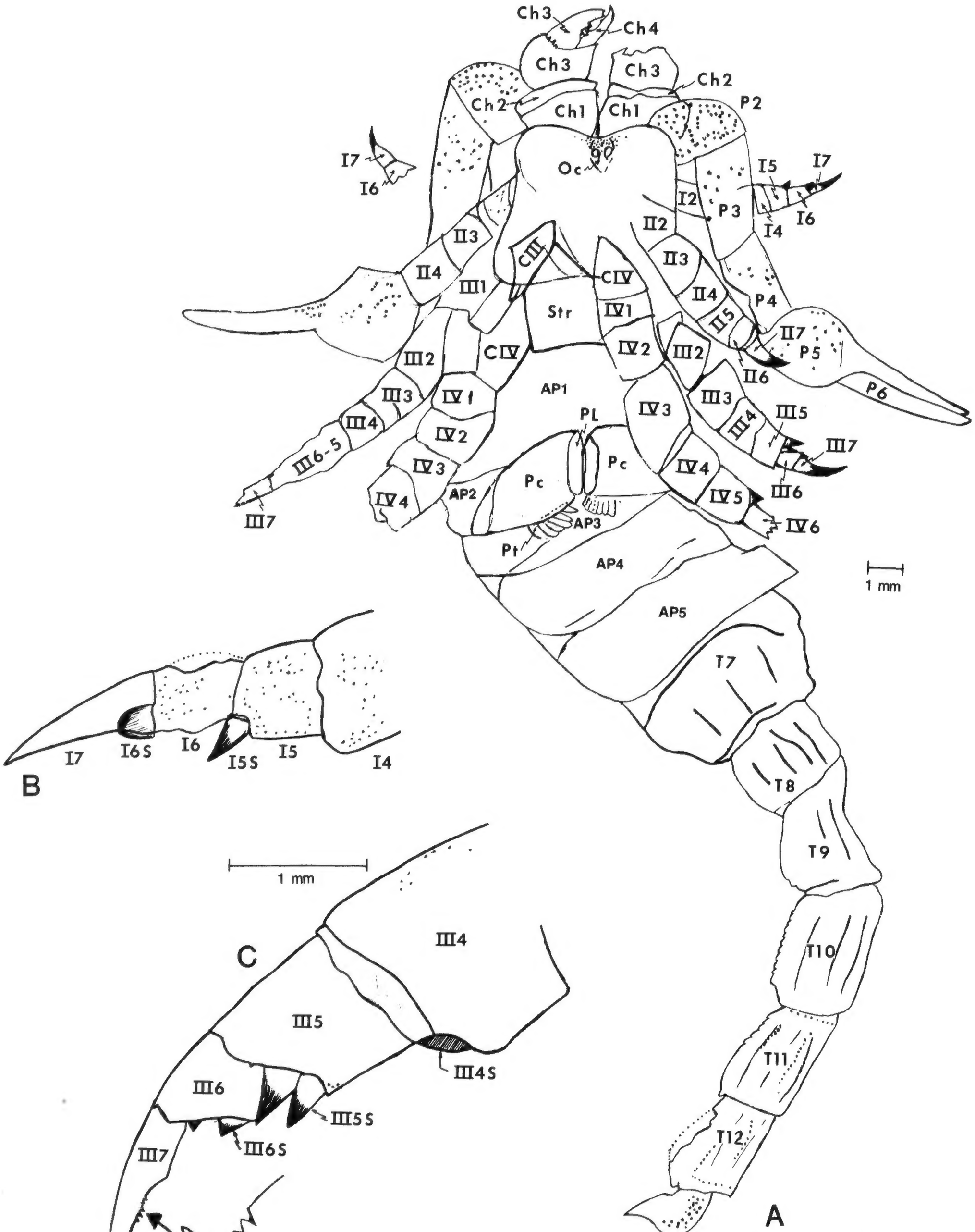
The most remarkable part of this scorpion is the small size of the carapace in relation to the great size of the chelicerae, pedipalps, legs and sinuous body. The appendages are well preserved and much new information of taxonomic value has been obtained by studying this specimen under alcohol.

The chelicerae are formidable structures, almost as long as the carapace, composed of four joints as in most other Paleozoic scorpions, with long fingers which are armed with teeth (see Text-fig. 17A). Inasmuch as the bases were covered, it would perhaps be safe to say that the chelicerae are actually as long as or longer than the carapace.

The pedipalps are stoutly constructed, with a remarkable development of coarse pustules, each with a sensory setal opening. The pustulation is particularly well developed on the trochanters. Here the setaceous pustules are crowded so that the entire surface is densely covered, anteriorly and posteriorly. Presumably the dorsal side would also be densely covered. The hand is short, mainly rounded and with curved fingers that are entirely cultrate on the inner edges.

The walking legs are spectacular in being very eurypteridlike; they were probably mainly cylindrical in life, massive structures that are progressively longer from anterior to posterior. The last pair of legs (**IV**) is very massive—at least half as thick again as the preceding. This estimate is made from the flattened legs, but in life would have been the same.

Each leg had two spurs on the ends of the tibia and of the basitarsus, as the spurs were found on the first (**I**) (see Text-fig. 17B) and the third (**III**) (see Text-fig. 17C), as well as on the intervening second (**II**) leg. It does not seem speculative to conclude that all legs had


Ch3
Ch4
Ch3
Ch3
Ch2
Ch2
Ch1
Ch1
P2
I7
I6
Oc
I5
I7
I2
P3
I4
I6
II2
II3
CIII
II4
III1
CIV
Str
IV1
II4
II5
P4
II7
P5
II6
P6
III2
CIV
AP1
IV2
III2
III3
IV1
IV3
III3
III4
III5
III4
III6-5
IV2
PL
III7
IV3
Pc
Pc
IV4
III6
IV4
IV5
AP2
AP3
IV6
Pt
AP4
1 mm
AP5
T7
T8
T9
T10
T11
T12
A
I7
I6S
I6
I5S
I5
I4
B
1 mm
III4
C
III5
III4S
III6
III5S
III7
III6S

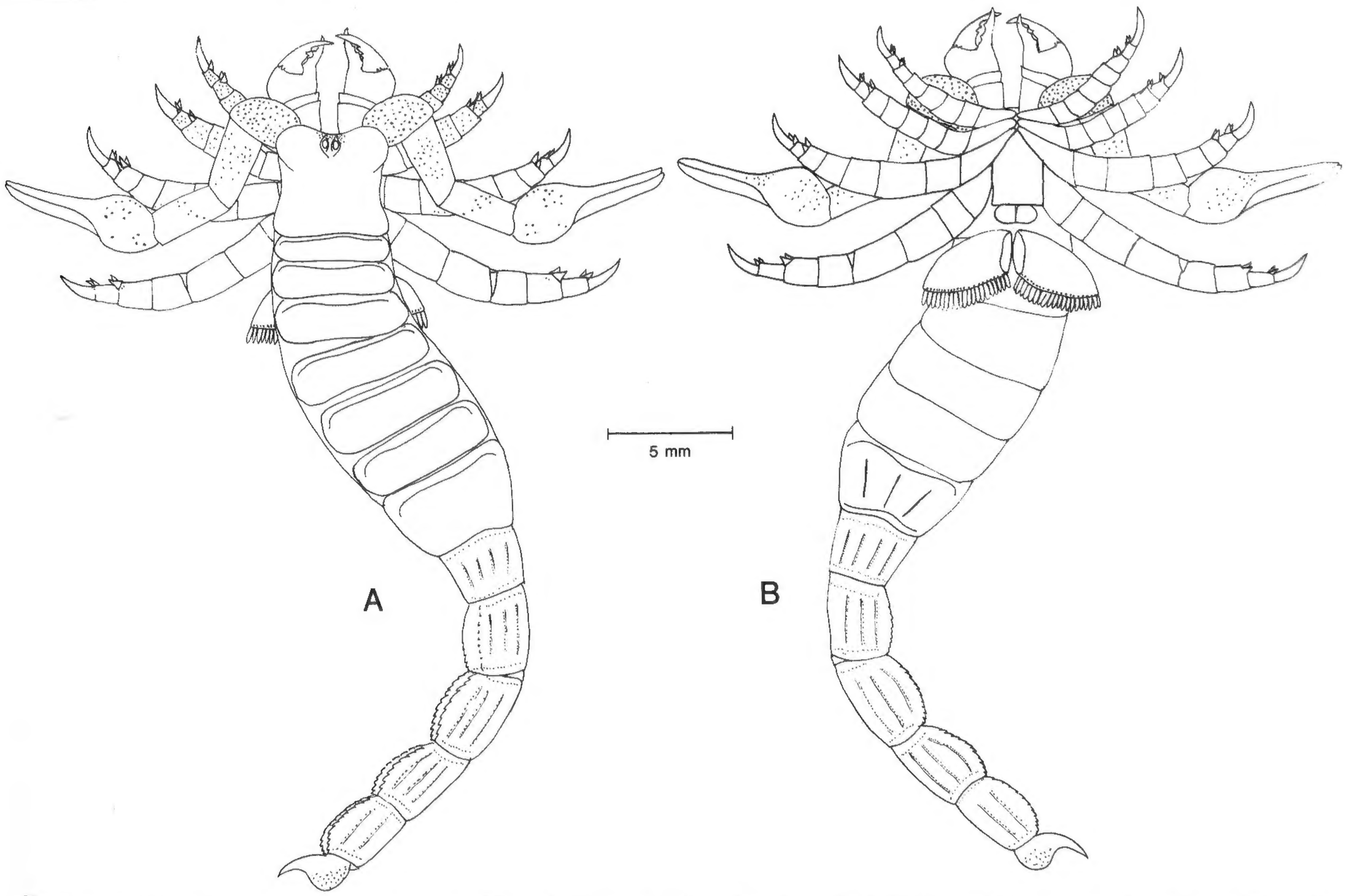
double tibial and basitarsal spurs. The terminal part of the leg consists of a very long, curved spine that is considered to be the posttarsus (7). This structure is similar to the terminal joint in eurypterids, except that the posttarsus of this scorpion has a row of ventral denticles—a development that is very common with scorpions found in the Carboniferous. It is thought that these spines furnished traction for the claws against soft surfaces such as are found on water plants. On one side of the posttarsus (and presumably on both sides) is a spur, which would be a tarsal spine (**6S**) (see Text-figs. 17B, C), homologous to the claw of present-day scorpions. (See *Remarks.*)

The coxosternal arrangement can be accurately reconstructed with ease. The coxae of the walking legs are short and triangular. The sternum is very large, and pentagonal in shape, as is prevalent in living scorpions, such as the families Scorpionidae, Vaejovidae, etc., a shape developed as early as Middle Silurian. Petrunkevitch (1953, p. 9) denies that the sternum is preserved, although both Peach (1885, p. 297) and Pocock (1901, p. 301) described it correctly. The short coxa of the third left leg clearly abuts the opposing coxa in front of the sternum, which would mean that the other coxae of the first three pairs of legs abut one another in front of the sternum. The coxa of the fourth leg on the left side is preserved in place, along the lateral margin of the sternum, thus a coxosternal arrangement such as is shown on Text-figure 110O seems indicated. This agrees with the interpretation given previously by Peach (1885) and Pocock (1901).

The opercular plates are not preserved. Peach (1885, p. 297) misinterpreted the two "bifid" plates described below to be the opercular plates. The pectines are well preserved, showing an unjointed rachis, and have two elongate plates (Peach's bifid plates) on their inner side.

Text-figure 17.—*Allopalaeophonus caledonicus* (Hunter). Holotype, KM unnumbered specimen. From the Silurian Llandovery–Wenlock, at Dunside, Logan Water, Lesmahagow, Lanarkshire, Scotland. See foldout inside front cover for explanation of abbreviations.

A. Entire holotype specimen, showing the ventral side revealed, but with the median eyes and outline of the carapace impressed through the flattened specimen, as Peach and Horne originally interpreted it. **B.** Terminus of the left first leg (**I**) showing the prominent spinelike terminal joint (**I7**). **C.** Terminus of the left third leg (**III**) and the curious serration (enlarged) on the last joint (**III7**).



Text-figure 18.—*Allopalaeophonus caledonicus* (Hunter). Reconstructions based on the holotype, KM unnumbered specimen. From the Silurian (Llandovery–Wenlock) of Scotland.

A. Dorsal surface. **B.** Ventral surface. The genital opercula are unknown and conjectural.

These are unknown in other scorpions. It is true, however, that some living scorpions have a dilated plate on the inner side of the pectines, such as some species of *Tityus,* where the female has a greatly enlarged rounded plate, or in the North African buthid *Leiurus quinquestriatus,* which has rather narrow plates on the inner side of the pectines, or in the Madagascan *Grosphus,* which is characterized by greatly elongated inner plates. The presence of these plates, therefore, could be merely a development of the inner plate of the pectine. There are no fulcra, although a linear series of small punctae was noted at the base of the rachis. The teeth are large, long, and about 15 to 20 would be present, if all had been preserved.

The abdominal plates are holosternous and, of course, without the slightest trace of stigmata. Peach (1885) considered this scorpion to be an "Ancient Air Breather", and indeed so named his paper, so that he encountered no difficulty in finding stigmata. Pocock (1901) and Petrunkevitch (1955) did not find any stigmata, and I thoroughly agree, although in Petrunkevitch's case, the stigmata would hardly be present as he thought that the dorsal side was present. Under alcohol, which would easily reveal stigmata, as well as on the silicone casts, nothing that remotely resembles a stigma is present. The holotype was viewed under excellent lighting at various angles. The specimen is clearly a holostern.

Each abdominal plate is bounded on the anterior by the usual transverse ridge. The ventral part of the last preabdominal tergite (No. 7) does not show the abrupt contraction that many scorpions do, but grades into the cauda, giving this scorpion a sinuous appearance such as occurs in many living scorpions, like *Broteochactas,* and other Chactidae. Three longitudinal ridges are shown, although undoubtedly there were four, as one of them was not preserved. Two carinae are present on the median part, and another on each side.

The cauda is preserved in its entirety, with superior, lateral and ventral carinae well developed. All carinae are surmounted with setaceous pustules. The superior carinae are roughly serrated. The telson is small, consisting of a small bulbous vesicle with a nearly straight aculeus. The vesicle is covered with setaceous pustules, particularly on the ventral part.

Remarks.—The sinuous shape, very small eyes, and great development of setae, presumably sensory, on the anterior region, such as the trochanters of the pedipalp, may indicate that this scorpion spent much of its time in burrows, a cryptozoic, but underwater, existence. The presence of small spines on the underside of the posttarsus indicates that, at least part of the time, it needed traction against some object, perhaps underwater plants.

Although Petrunkevitch believed that the dorsal, rather than the ventral side, was preserved, he stated (1953, p. 10), "I think it is safe to say that the coxae of the fourth pair of legs meet in the median line just on the edge of the carapace. The pentagonal area behind the fourth coxae may then be interpreted as the sternite of the first preabdominal segment later completely lost and now wanting in recent scorpions." It is difficult to understand this reasoning as a very torturous route has to be taken not to make the "pentagonal area" the sternum and not to have all the coxae meet as shown below. The coxosternal region is difficult to reconstruct. Although dislocated, nearly all parts are present. However, several factors are present that give a rather sound idea of the arrangement. The sternum is pentagonal, very large, and in making the reconstruction on Text-figure 110O it was apparent that in order to fit all the massive legs under the unusually small carapace, the only logical accommodation was in having the fourth pair of legs abut the sides of the pentagonal sternum with the third pair meeting in front of the sternum. The first two pairs, of course, abut one another at midsection. This reconstruction is by no means without some solid foundation, as the left side of the specimen shows exactly this type of arrangement, namely, the fourth coxa in position against the sternum with the third lying also, in position, in front of the triangular anterior part of the sternum. This coxosternal arrangement is a very primitive one, and in reconstruction is highly possible and not without factual basis.

There would have been no question about the pectinal teeth if the original specimen had been studied in alcohol.

As was stated in the description, the terminal spine of the leg is considered to be the posttarsus, whereas the two small spurs at the base of this spine, or end of the tarsus, are considered to be the tarsal spurs which later, by moving forward, became the claws known in many Paleozoic and Recent scorpions. This trend can be seen, further developed, in legs of *Palaeoscorpius devonicus* Lehmann from the Lower Devonian of Germany. The legs of the latter are short and stout, very much like those that characterize the Palaeophonidae and the Allopaleophonidae, except that the termination consists of three spines. The central one is considered to be the posttarsus, whereas the two adjoining are the tarsal spurs or claws. The posttarsus moved to a rear position, giving a trifid arrangement where each spine is equidistant from the others. When preserved in a flattened condition, this trifid arrangement appears as if all three spines were pointing in one direction. In *Kronoscorpio danielsi* (Petrunkevitch) the trifid arrangement is greatly developed, probably into a bird-

footlike impression, with the two long tarsal spines taking an anterior position and the posttarsus a posterior one. This would result in a cushioning effect, somewhat like snowshoes, which would enable the scorpion to walk on soft mud.

Superfamily **PALAEOSCORPIOIDEA** Lehmann, 1944 (emend.)

Holosternous scorpions with four pairs of coxae meeting in front of the sternum.

Type family.—Palaeoscorpiidae Lehmann, 1944 (emend.).

Remarks.—Petrunkevitch (1955, p. 70) defined this superfamily as follows: "Preabdomen with median longitudinal fold continuous with tail and resembling it." The X-ray photographs (see Pl. 3, fig. 1) show a distinct black part running through the central part of the preabdomen and continuing, not so clearly, through the caudal segments. In my opinion, this is merely the presence of the intestinal canal of this scorpion, and such interesting preservations are not unknown in the fossil record. For example, in the Silurian eurypterid *Carcinosoma newlini* (Claypole), Ruedemann (1919, fig. 33) showed a specimen in which the entire intestinal tract was preserved and this is very similar to that present in this Devonian scorpion. Heubusch (1962, p. 222) figures other eurypterids where the intestinal canal is preserved. If the intestinal tract is full, chances of preservation are, of course, considerably enhanced. Nevertheless, "a median longitudinal fold continuous with tail and resembling it" is hardly a character to be used for a genus, much less a superfamily, particularly when one is ignorant of the structure.

Family **PALAEOSCORPIIDAE** Lehmann, 1944 (emend.)

Sternum consisting of an equilateral pentagon. No maxillary lobes developed on the first two pairs of coxae. Legs with three short straight claws.

Type genus.—*Palaeoscorpius* Lehmann, 1944.

Genus **PALAEOSCORPIUS** Lehmann, 1944 (emend.)

Legs very short, with very wide joints, and probably armed with very short double tibial and tarsal spurs. Pedipalps massive.

Type species.—*Palaeoscorpius devonicus* Lehmann, 1944.

Geological range.—Lower Devonian.

Palaeoscorpius devonicus Lehmann, 1944
Plate 3, figure 1; Text-figures 19, 111E

1944. *Palaeoscorpius devonicus* Lehmann, pp. 177–185, figs. 1–4.
1953. *Palaeoscorpius devonicus* Lehmann. Petrunkevitch, pp. 5, 14.
1955. *Palaeoscorpius devonicus* Lehmann. Petrunkevitch, p. 73.
1962. *Palaeoscorpius devonicus* Lehmann. Dubinin, p. 428.

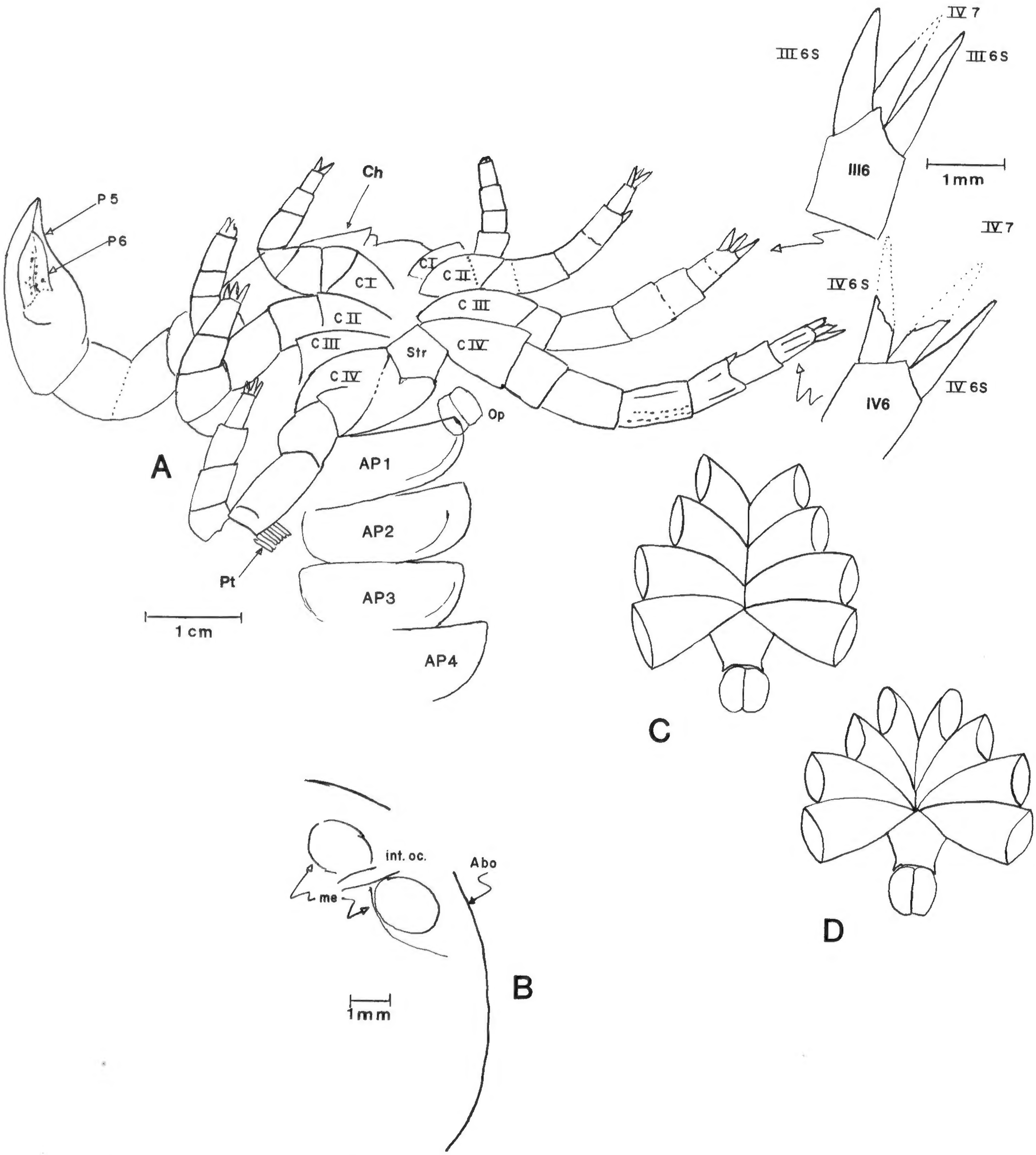
Material.—Two excellent plaster casts of the holotype, kindly made for the writer through the graciousness of Dr. H. K. Erben of the Institut für Paläontologie of the Rhine, Friedrich-Wilhelm Universität, Bonn, West Germany, where the holotype, FWU Egr 263 of the collection of W. M. Lehmann, is deposited. The casts are now deposited in the Field Museum of Natural History, Chicago, IL. Also used in this study is an X-ray photograph made by W. M. Lehmann, which Leif Størmer kindly sent to the writer.

It must be stated that the casts of this fossil are exceptionally fine, showing many details that even reveal certain minute, but important, structures. After the drawings were made, I was delighted to receive the X-ray photograph, which verified all the details that could be seen on the cast.

Type information.—Lower Devonian, Hunsrück Shale, Pit I, Eschenbach, near Bundenbach (Hunsrück), West Germany. This is a marine shale, and the specimen was found in the same pit as specimens of *Weinbergina opitzi,* a xiphosurid. Eurypterids also occur in the same strata. Inasmuch as the scorpion is a holostern, it is considered to be marine and to have been living in the habitat where found. It should be noted that the specimen is complete, suggesting little or no transportation, and that the type of shale hardly argues for the introduction of extraneous material by currents.

My description is supplementary to that of Lehmann, but in several important aspects differs from the original. This necessitates an emendation of the family and genus as defined by Lehmann. It also necessitates complete emendation of the superfamilial, familial and generic definitions given by Petrunkevitch (1955) in his classification, as the characters used are erroneous and trivial with respect to the taxonomic category. These changes and reasons have been discussed above.

In my study of the casts, drawings were made from each half by use of the Wild Drawing Tube (a type of camera lucida), then each drawing was superimposed on the other with the result that many structures that had not been previously noted could be easily identified. The drawing therefore is a composite, with the dorsal side eliminated. My main interest was in the determination of the important underside and the structure of the legs and abdominal plates. Many of the details are apparent when light is directed on the



Text-figure 19.—*Palaeoscorpius devonicus* Lehmann. Holotype, FWU Egr 263. From the Lower Devonian, Hunsrück Shale, Pit I, Eschenbach, near Bundenbach (Hunsrück), West Germany. See foldout inside front cover for explanation of abbreviations.

A. Underside of the holotype, taken from a cast, in two parts. Note large pedipalps. Distal details of legs **III** and **IV** shown. X-ray photos suggest that some refinement of the configuration of the abdominal plates may be in order. **B.** Obscure cephalic indications. **C.** Possible restoration of the coxosternal region, based on the holotype. **D.** Alternative restoration of the coxosternal region, made on the assumption of lateral dissociation of the leg bases during fossilization.

specimen at a very low angle. The degree of detail is remarkable in the casts, and even minute structures such as setal perforations are clearly apparent. The entire coxosternal region was completely revealed, as were all the joints of the legs. The left pedipalp was left out of the drawing as it caused confusion.

The important arrangement of the coxosternal region can now be described. The sternum consists of an equilateral pentagon. The coxae of all legs are short, mainly triangular, and appear most likely to lie immediately in front of the sternum, in a condition somewhat like that present in the Carboniferous Cyclophthalmidae. No maxillary lobes are present. The genital plates are nearly elliptical, narrow, and would lie directly posterior to the base of the sternum. Two reconstructions or interpretations of the coxosternal area are possible and are given in Text-figures 19C and 19D. I prefer the interpretation given in Text-figure 19D.

Another point of disagreement with the original description is the presence of three, distinct, straight claws on the legs. The middle claw would correspond, of course, to the posttarsus. All legs are stout and all comprise eight podomeres as in living scorpions (coxa to posttarsus). Spurs, also short and stout, were noted on the posterior of the left second leg, which would correspond to a basitarsal spur, and another on the left fourth leg, which represents a tibial spur. Very likely spurs occur on all legs on each side of the base of the tibia and the basitarsus.

The combs are not well preserved, but a number of detached long and slender teeth were found.

The well-preserved abdominal plates are holosternous and straight across the anterior, with well-rounded posterolateral corners.

No stigmata of any type are present. Since the entire plates are preserved, these structures would be easily preserved and noted if any were present.

On the carapace, no eyes were noted in the position indicated by Lehmann (1944, p. 181), who stated that there were two very small eyes "the size of pin heads" in the posterior part of the carapace, much as occurred in *Proscorpius osborni*. We know now that there are no posterior eyes in *P. osborni* (Kjellesvig-Waering, 1966, and above). I was unable to see any eyes at the posterior part of the carapace in *Palaeoscorpius devonicus* as shown on the cast.

The holotype of *Palaeoscorpius devonicus* Lehmann was studied at the Institut für Paläontologie of the Rhine, Friedrich-Wilhelm Universität, at Bonn, West Germany, on November 16, 1970. Because it is preserved in a thin plate of black slate, both the dorsal and ventral sides can be viewed. Study of the holotype shows that the carapace is not visible in its entirety, although the anterolateral angles are preserved, and these are broadly rounded. Two large median ocelli, which appear elliptical but probably are round in the inflated state, are visible on the anterior part of the carapace. These large eyes are heavily replaced by crystallized pyrite, but the complete outline of the right eye is clearly visible. A median ridge separates the two eyes. No other eyes are visible and there is no evidence whatsoever of eyes toward the back of the carapace as reported by Lehmann. The so-called eyes are rounded lumps of pyrite not connected with any scorpionid structure.

The three-toed terminations reported above were checked on the actual specimen. These are distinct on each leg. Lehmann (p. 182, fig. 4) shows only the two claws and does not recognize the central claw, which actually is the posttarsus.

The sternum, genital operculum, and coxae are of considerable interest. The equilateral, pentagonal sternum has a short spur at the extremities of the base where, apparently, the elliptical genital plates fit.

Family **HYDROSCORPIIDAE**, new family

Palaeoscorpioidea (?) with median eye node located at the first quarter of the carapace; legs with segments as wide or even wider than long; tarsi terminating in two claws. No lateral compound eyes.

Type genus.—*Hydroscorpius,* n. gen.

Remarks.—Since the coxosternal area is not preserved, the superfamily position is uncertain.

Genus **HYDROSCORPIUS**, new genus

Hydroscorpiidae with round, hemicircular carapace; very short, stout legs terminating in two long claws; chelicerae copiously supplied with hairs or setae on the inner side at the junction between the second and third joints.

Derivatio nominis.—*hydro* (Gr.) = water + scorpion.

Type species.—*Hydroscorpius denisoni,* n. gen., n. sp.

Geological range.—Lower Devonian of Wyoming.

Hydroscorpius denisoni, new species

Plate 3, figure 2; Text-figure 20

The species is based on a single nearly complete specimen, FMNH (PE) 6176, collected by Robert H. Denison and E. S. Richardson, Jr. in 1962 at the FMNH excavation site in Cottonwood Canyon, Wyoming.

The specimen is broken, but excellent as to details and original cuticle, with the dorsal side exposed. It is preserved in light-gray, fine-grained, dololutite (dolomite) with the remains of plants, eurypterids, and three other scorpions.

The carapace is incomplete, hemicircular in outline, measuring 4.9 mm in length and an estimated 5.5 mm at the base, which is rounded at the genal angles. The median eye node lies approximately 1.2 mm posterior to the anterior margin, but is too poorly preserved to show the median eyes. Median eyes must have existed because there is no known occurrence of eyeless scorpions in the fossil record. No lateral eyes are present nor seem to have existed, but crucial parts of the carapace are missing.

The chelicerae, measuring 3.4 mm in length from the margin of the carapace, and 2.5 mm in greatest width at the second joint, are preserved nearly whole. The right one reveals the basal joint, and nearly all of the hand and free chela. The free finger is curved to a sharp point and edged with definite, but blunt, serrations (see Text-fig. 20B). The hand is rounded at the base where it articulates with the second joint. At the junction with the second joint, and placed inside the two chelicerae, is a mass of setae (see Text-fig. 20C). No ornamentation occurs on the chelicerae. The color changes from dark brown to black at the extremities. The second joint definitely shows a thin doublure at $\mathbf{d}_2$, suggesting that the base of that joint is there. The third joint, comprising the hand and immobile chela, is the area marked (**3**) on Text-figure 20C. The round area with the thin doublure marking its base is $\mathbf{d}_3$, which is covered over by the transparent cuticle of joint **2**.

The pedipalp measures 3.4 mm in greatest width at the palm, whereas the fixed finger has a width of 0.9 mm at the midsection (it is tapering) and the free finger is 1.1 mm in width at midsection and 4.3 mm in length. Estimated overall length of the pedipalp is 8.5 mm.

Parts of all four walking legs are represented, and they are very short and stout (see Text-fig. 20A). They consist of the usual seven segments plus coxa. The third right walking leg, which is the only leg showing terminal details, ends in a short rounded posttarsus and two long, powerful claws. The thick legs of these scorpions are considered eurypteroid in aspect, and suggest that they were adapted for digging under water. The habitat explains the long sinuous shape.

The ventral side is not revealed, so there is no indication whatsoever of the coxosternal area nor of the pectines. Parts of two displaced abdominal plates show that this scorpion is a holostern.

The preabdominal tergites show a narrow transverse ridge on the anterior margin.

The stinger as preserved is visible from the side. In overall length it measures 3.2 mm on the dorsal side; the actual curved stinger is 1.5 mm long, whereas the bulbous part is 1.7 mm. The bulbous part measures 2.6 mm in length through the midsection, and 2.3 mm through the midsection from top to bottom.

The cuticle does not reveal any sort of ornamentation, except the two carinae on the dorsal side of the last tergite. The color pattern is clearly preserved. The carapace, as well as most of the abdomen, is shiny honey-colored; on the carapace, however, the eye node is darker brown, and the appendages show a gradation from the honey-colored cuticle to progressively darker brown, to end in brownish black to black at the extremities. This is true of all appendages from the chelicerae to the walking legs. The tail also shows this gradation, the increase in brown is progressively darker to end at the stinger, which is dark brown to black. The latter has mainly flaked off, but enough of the original cuticle was present to reveal the color.

Type information.—Lower Devonian, Beartooth Butte Formation, from the FMNH excavation site in Cottonwood Canyon, Big Horn Mountains, WY, U.S.A. The specimen is deposited in the Field Museum of Natural History, Chicago, registered as FMNH (PE) 6176.

Derivatio nominis.—Named in honor of Robert H. Denison, former Curator of Fossil Fishes at the Field Museum of Natural History, Chicago, IL, and one of the collectors of the specimen.

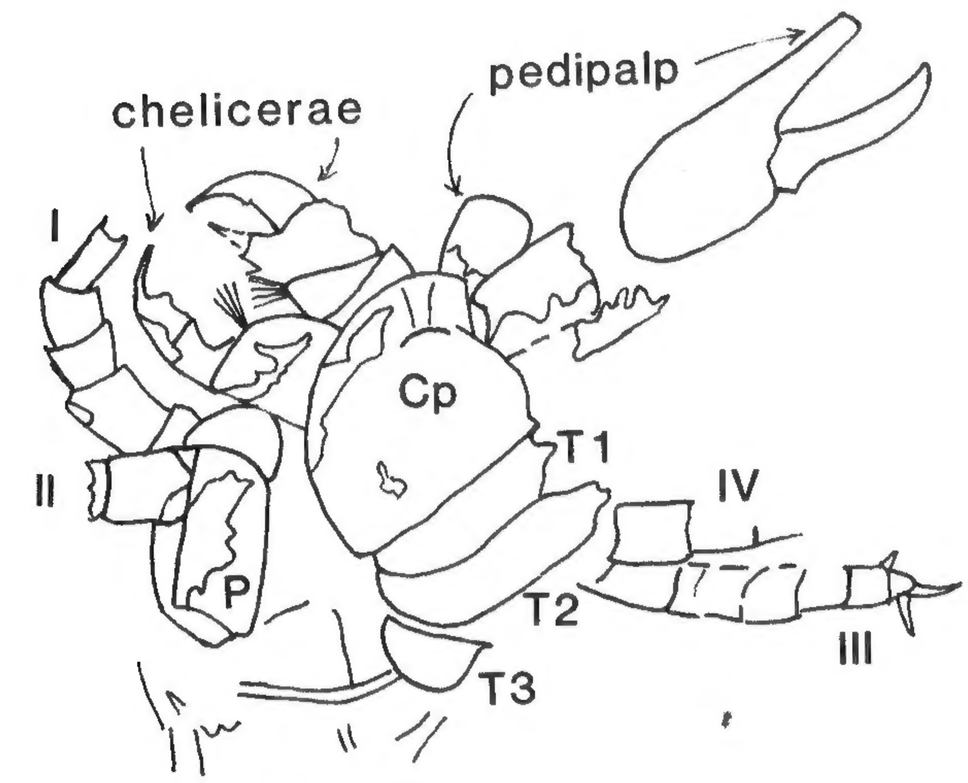
Measurements (in mm) of mesosoma and metasoma of FMNH (PE) 6176.—

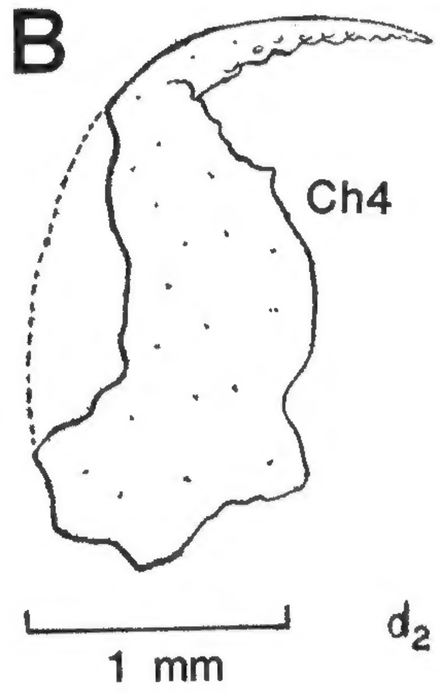
		length	width
Tergite No.	1	1.2	
	2	1.6	
	3	incomplete	
	4	2.1	
	5	2.2	
	6	2.6	5.2
	7	3.6	
	8	incomplete	
	9	missing	
	10	3.9	2.8 (from side)
	11	4.5	2.8 (from side)
	12	4.5	2.3 (dorsal)

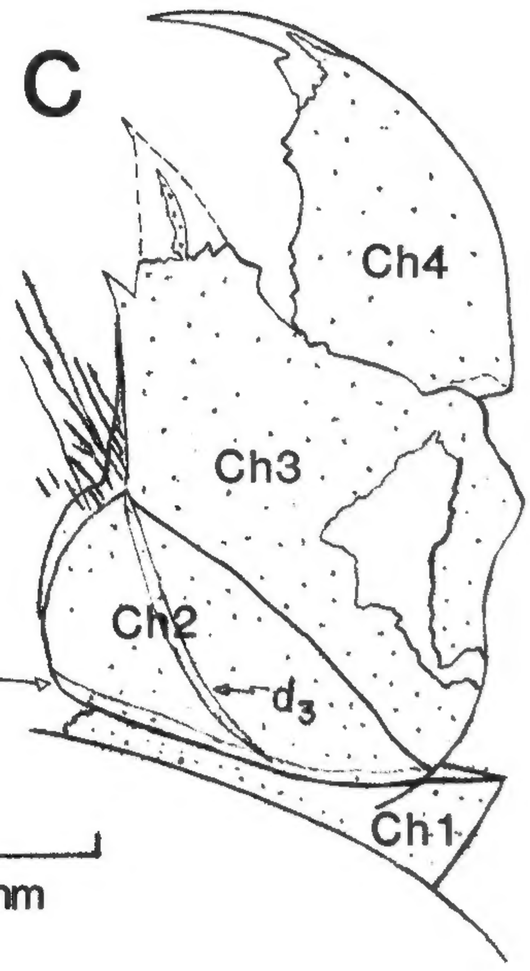
Remarks.—*Hydroscorpius denisoni* is easily differentiated from the other scorpions in the Cottonwood Canyon locale by its short, stout legs and round carapace. It differs from *Palaeoscorpius devonicus* in hav-

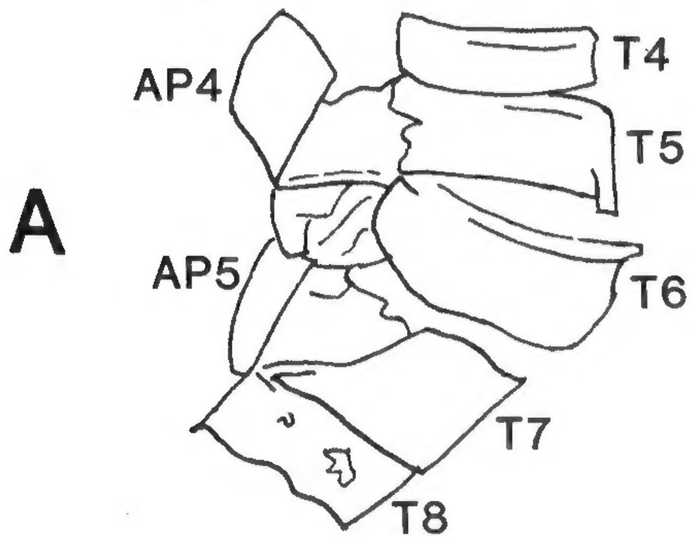
Text-figure 20.—*Hydroscorpius denisoni,* n. gen., n. sp. Holotype, FMNH (PE) 6176. From the Lower Devonian, Beartooth Butte Formation, of Cottonwood Canyon, Big Horn Mts., WY, U.S.A. See foldout inside front cover for explanation of abbreviations.

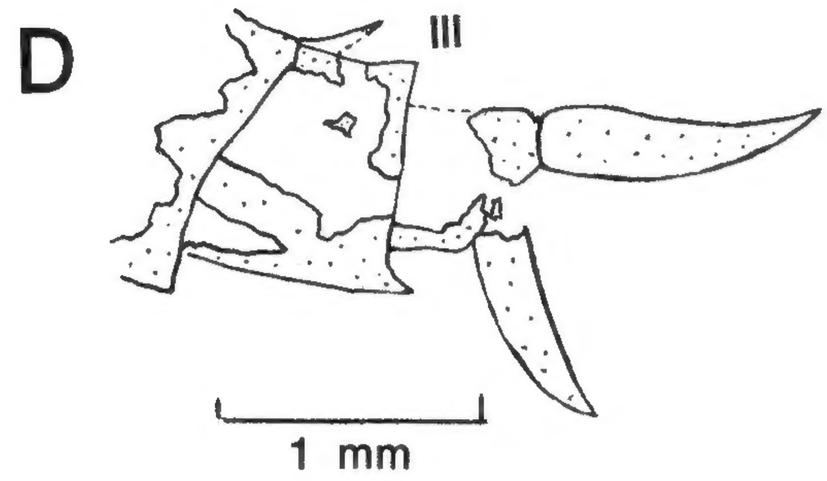
A. Entire specimen. **B.** Free chela of the left chelicera. **C.** Right chelicera showing the four joints. The curved line at the base represents the edge of the cephalothorax. Note the mass of setae. **D.** Terminal end of the third right walking leg. **E.** Detail of left pedipalp and part of the second left walking leg. **F.** First left walking leg. **G.** Carapace with median eye node. **H.** Right pedipalp.

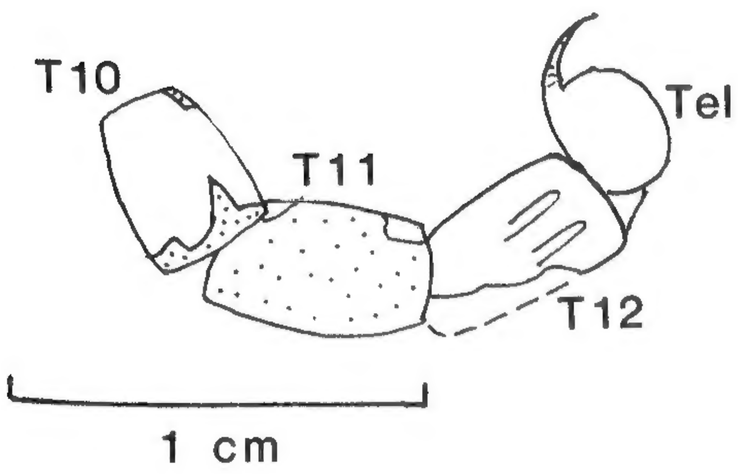

chelicerae
pedipalp
I
II
Cp
T1
IV
P
T2
III
T3

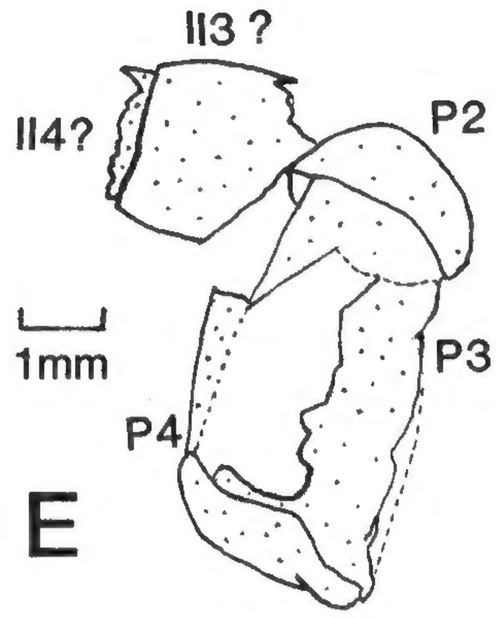

B
Ch4
1 mm

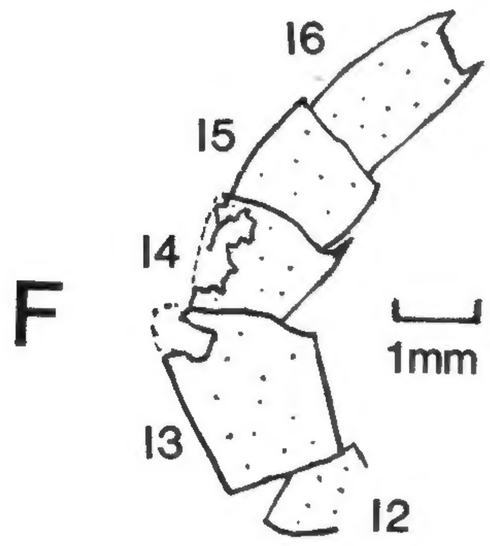

C
Ch4
Ch3
Ch2
d2
d3
Ch1
1 mm


AP4
T4
T5
A
AP5
T6
T7
T8

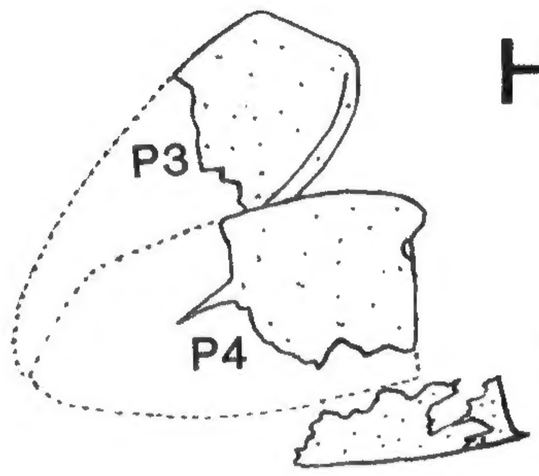

D
III
1 mm

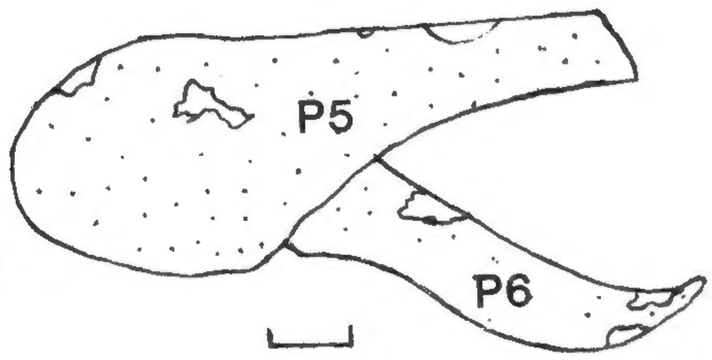

T10
Tel
T11
T12
1 cm


II3 ?
II4?
P2
P3
P4
1mm
E


I6
I5
I4
I3
I2
F
1mm

G
2 mm


H
P3
P4


P5
P6
1mm

ing stubbier walking legs and not so bulbous a pedipalp hand.

Superfamily **ARCHAEOCTONOIDEA** Petrunkevitch, 1949 (emend.)

Holosternina with first pair of coxae meeting in front of the sternum, without maxillary lobes; other three pairs of coxae abutting against the sternum; legs very short.

Type family.—Archaeoctonidae Petrunkevitch, 1949.

Family **ARCHAEOCTONIDAE** Petrunkevitch, 1949 (emend.)

Archaeoctonoidea with sternum large, campanulate, slightly tapering and pointed anteriorly; no lateral compound eyes.

Type genus.—*Archaeoctonus* Pocock, 1911.

Remarks.—There is no family that this very distinct scorpion group could be confused with except the Loboarchaeoctonidae, which is a lobostern, whereas *Archaeoctonus* is a holostern and has many other obvious fundamental differences.

Genus **ARCHAEOCTONUS** Pocock, 1911 (new definition)

Legs very short, not reaching to the posterior of the preabdomen, and in general not very different in length; hand of pedipalp and tibia very short; fingers straight with contact along edge; free finger hooked at distal end. Carapace with anteriorly located median eyes and no lateral eyes.

Type species.—*Eoscorpius glaber* Peach, 1883.

Geological range.—Lower Carboniferous.

Archaeoctonus glaber (Peach, 1883) Text-figures 21, 110K, 113B1

1883. *Eoscorpius glaber* Peach, pp. 400–402, pl. 22, figs. 2, 2a–2l.
1885. *Centromachus glaber* (Peach). Thorell and Lindström, p. 25.
1911. *Archaeoctonus glaber* (Peach). Pocock, pp. 17–18, text-fig. 3.
1913. *Archaeoctonus glaber* (Peach). Petrunkevitch, p. 34.
1949. *Archaeoctonus glaber* (Peach). Petrunkevitch (*partim*), pp. 138–139.
1953. *Archaeoctonus glaber* (Peach). Petrunkevitch, pp. 14–15, figs. 14–17, 126.
1955. *Archaeoctonus glaber* (Peach). Petrunkevitch, p. P73, figs. 40(2), 41(1).
1959. *Archaeoctonus glaber* (Peach). Wills, p. 266.
1960. *Archaeoctonus glaber* (Peach). Wills, p. 328.
1962. *Archaeoctonus glaber* (Peach). Dubinin, p. 428, fig. 1241.

Not *Archaeoctonus glaber* (Peach). Petrunkevitch, 1949, pp. 138–139, specimen BM(NH) In.988, figs. 138, 176 [=*Loboarchaeoctonus squamosus* n. gen., n. sp.].

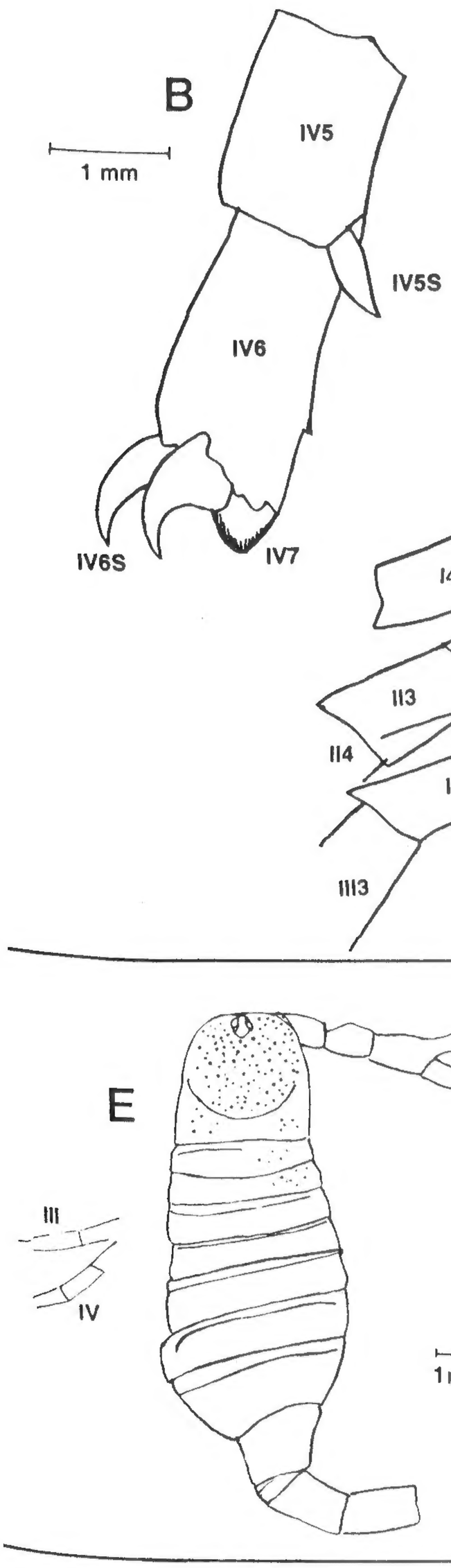
This unusual scorpion was first described by Peach, who did not fully appreciate that only the ventral side was showing. The description lacks the most important feature of this scorpion, namely the coxosternal area, which was preserved in considerable clarity. This fact was also not appreciated by Pocock (1911, pp. 17–18), who apparently worked only from Peach's figures. Petrunkevitch (1953, pp. 14–15) gave a detailed description with four figures. He recognized the coxosternal area and further described several parts, which are here redescribed. I disagree in several important respects with Petrunkevitch's description and figures. The most serious point of disagreement is his statement that a "kidney-shaped stigma (lung opening)" was present on the right side of the fourth "sternite". Wills (1959, p. 266) subjected the holotype to careful review and concluded that no stigmata were present. In my study of the holotype at Edinburgh, I made a special effort to examine the holotype under different types of light and can state without the slightest hesitancy that there are no stigmata present and that the scorpion has holosternous abdominal plates such as are found in countless other fossil forms.

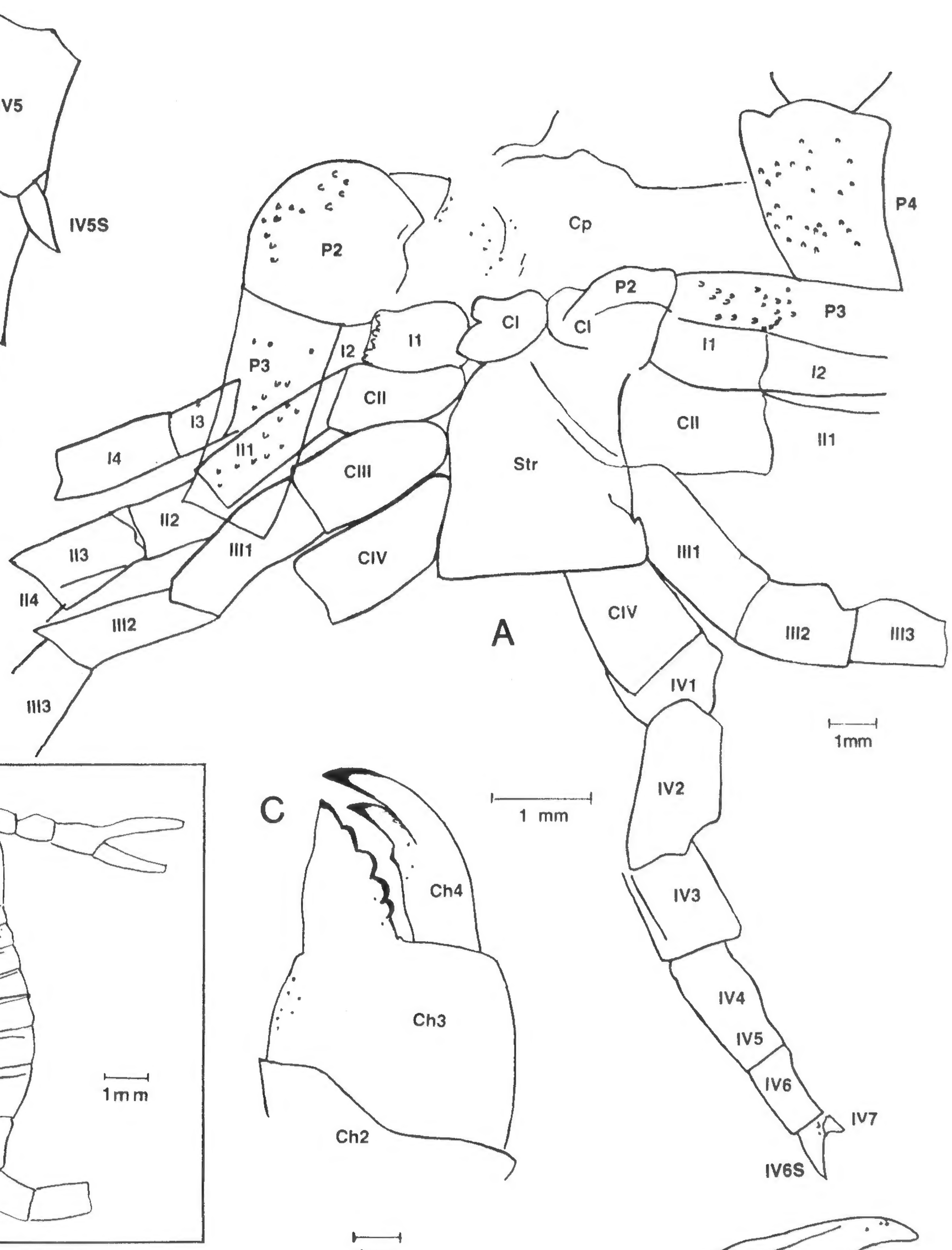
My interpretation of the coxosternal area differs widely from that given by Petrunkevitch (1953, p. 14), although he deserves credit for being the first to describe this region. The sternum is very large, campanulate, straight at the base, with sides slightly tapering anteriorly. The anterior is produced into a point. The first pair of coxae abut each other above the sternum. There are no maxillary lobes present as was stated by Petrunkevitch (1953, p. 15). The coxae are all very short (see Text-fig. 21A).

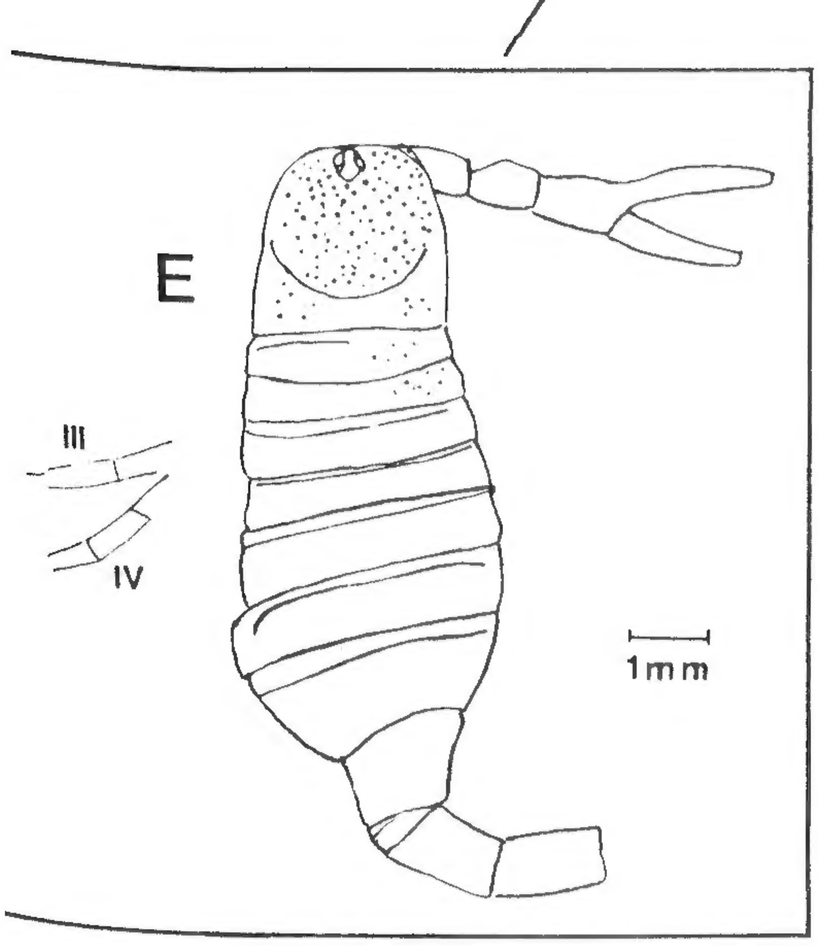
All legs are very short, but they are not tubiform. They resemble, in a great sense, the legs of *Palaeophonus, Allopalaeophonus, Palaeoscorpius* and other older scorpions. The segments are not greatly differentiated in length (see Text-fig. 21A). The right fourth leg is preserved so that the terminal parts are clearly seen. The ungues are short, falcate, without underlying spines, and the posttarsus (**IV7**) is rounded and very short. A short spine or spur occurs in the tissue between the two joints, or at the end of the basitarsus (**IV5S**) (see Text-fig. 21B), which of course is the basitarsal spur.

Text-figure 21.—*Archaeoctonus glaber* (Peach). GSE 5858 and 5859 (part and counterpart) (holotype), and GSE 2039, a juvenile form. From the Lower Carboniferous (lowermost Bernician or S1 of the Viséan), Upper Bradon Group, Cementstone-sandstone Series, Glencartholm Volcanic Beds, River Esk, 5 miles south of Langholm, Dumfriesshire, Scotland. See foldout inside front cover for explanation of abbreviations.

A. Coxosternal organization taken from GSE 5858 and GSE 5859. **B.** Terminal detail of leg **IV,** with two claws (from GSE 5859). **C.** Chela. Free finger and most of palm from GSE 5859, the rest from GSE 5858. **D.** A nearly complete pedipalp from GSE 5858. **E.** Juvenile individual. Drawing made from the original specimen, GSE 2039, and a latex cast thereof.

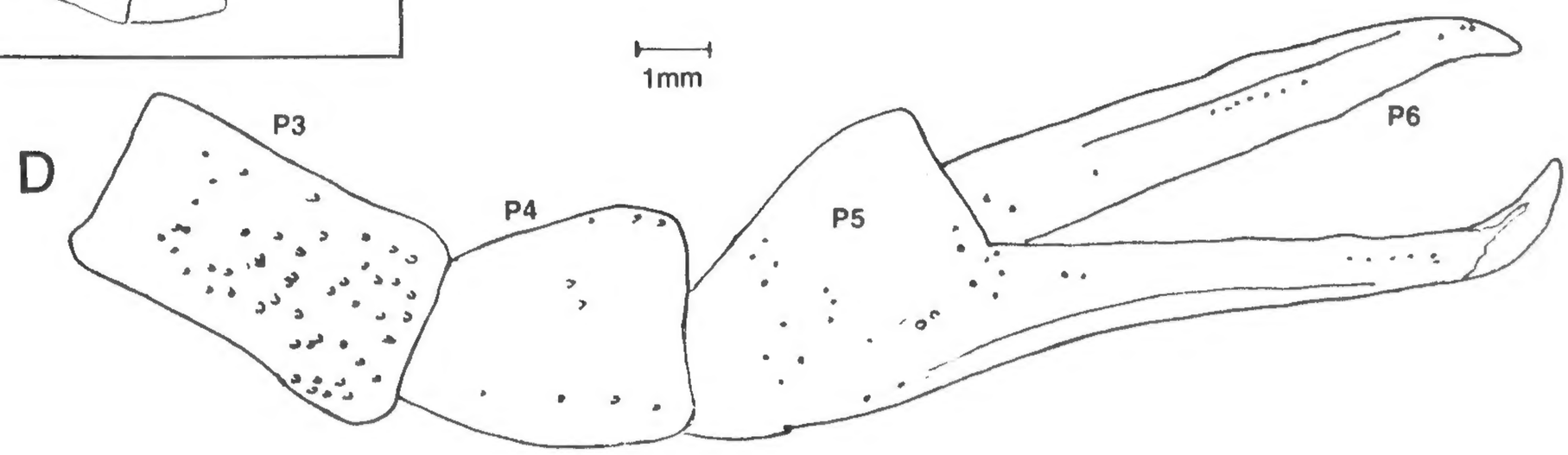

B
1 mm
IV5
IV5S
IV6
IV6S
IV7


P2
P3
I2
I1
CI
CII
I3
I4
II1
CIII
II2
II3
III1
CIV
II4
III2
III3
Cp
P4
P2
CI
P3
I1
I2
CII
II1
Str
III1
CIV
III2
III3
IV1
A
1mm


E
III
IV
1mm

C
1 mm
Ch4
Ch3
Ch2

IV2
IV3
IV4
IV5
IV6
IV7
IV6S


1mm
D
P3
P4
P5
P6

The pedipalps (see Text-figs. 21A, D) have a short femur and tibia, but the chela is composed of a short hand with two very long, rather straight, fingers that are decidedly falcate at the ends. The inner edge is entirely cultrate without the slightest evidence of denticles. The trochanter, femur, and tibia are covered with squamous ornamentation, whereas the hand retains some scattered mucrones and several setal sites. The fingers also show setal sites, and some are in linear series, at least for a limited area (see Text-fig. 21D).

The chelicerae are well preserved, and although only the last three joints were seen, there should be little doubt that four occur. The denticulation is not overly unusual (see Text-fig. 21C), however, the free finger (**Ch4**) is bifid and undoubtedly the teeth straddle the single termination of the fixed ramus.

Another specimen, GSE 2039, in the collection of the Institute of Geological Sciences, Edinburgh, Scotland (see Text-fig. 21E) can safely be included in *Archaeoctonus glaber* (Peach) on the basis of the pedipalp, and I have no hesitance in referring it to *A. glaber.*

The specimen is a juvenile, preserved on dark gray to black shale in a flattened condition; nevertheless it is highly important as it reveals the dorsal side of this important species. The specimen consists of only one piece, with the carapace, most of the opisthosoma, the right pedipalp and fragments of the legs.

The carapace is rather squarish, with an undivided raised cephalic shield, no glossate process, and with small, rounded, median eyes placed on a small, rounded or elliptical, optical mound that is practically so far forward on the carapace as to be marginal. No lateral aggregate or compound eyes are present. The raised cephalic shield is covered with coarse pustules.

The pedipalp reveals the short, stout femur and tibia with a large hand and fingers, which are opposable, incurving so that the inner edges do not meet. The ends undoubtedly must have been falcate.

The prosomal walking legs are only preserved as small fragments of legs **III** and **IV**, but show that they are very short, which is a character of the holotype.

The entire preabdomen is preserved, is widest at the sixth tergite, and except for scattered, fine pustules, devoid of ornamentation. No carinae are present.

Only the anterior half of the cauda is preserved, and shows three unornamented tergites.

Measurements (in mm) of GSE 2039.—

Carapace length:	2.15
Carapace width:	2.2
Length of preabdomen:	4.9
Greatest width at sixth tergite:	3.6
Overall estimated length:	12.0

Type information.—River Esk, 5 miles south of Langholm, Dumfriesshire, Scotland, in the Lower Carboniferous, Cementstone-sandstone Series (lower Viséan) Upper Border Group, Glencartholm Volcanic Beds, on deposit in the Institute of Geological Sciences, Edinburgh. Specimen GSE 2039 is from the same horizon and locality as the holotype (GSE 5858, 5859, part and counterpart).

Remarks.—Peach (1883, p. 402) listed a specimen from the Lower Carboniferous (mid-Viséan), at Redhalls quarry, Water of Leith, near Slateford, Edinburgh, Scotland, which he determined as *Eoscorpius glaber.* I have not been able to locate this specimen and because the ages involved are quite different, it is reason enough to question the determination until the original can be studied and verification made.

Genus **PSEUDOARCHAEOCTONUS**, new genus

Archaeoctonidae with trapezoidal carapace, anteriorly-located median eye node, no lateral eyes and with a raised, partly divided cephalic shield. Pedipalps with very small teeth, apparently on a single row along the inner edge of the fingers. Coxae and legs, long, not tubiform. Pectine, small, long, composed apparently of an undivided rachis, no apparent fulcra and relatively few teeth—less than 15 on each side.

Derivatio nominis.—*pseudo* (Gr.) = false + *Archaeoctonus,* a scorpion genus.

Type species.—*Pseudoarchaeoctonus denticulatus,* n. gen., n. sp.

Geological range.—Lower Carboniferous.

Remarks.—The coxosternal arrangement seems to be the same as in *Archaeoctonus,* but the coxae are much longer, as are the rest of the legs. The pedipalp of *P. denticulatus,* instead of having the fingers opposable and falcate, is recurved on the fixed finger with the free finger adjoining the other along the entire cutting edge. It is also denticulate, as against the cultrate cutting edge of *Archaeoctonus glaber.* The genus *Eskiscorpio* differs in being a Lobosternina and in having lateral compound eyes and cultrate and falcate fingers.

Pseudoarchaeoctonus denticulatus, new species

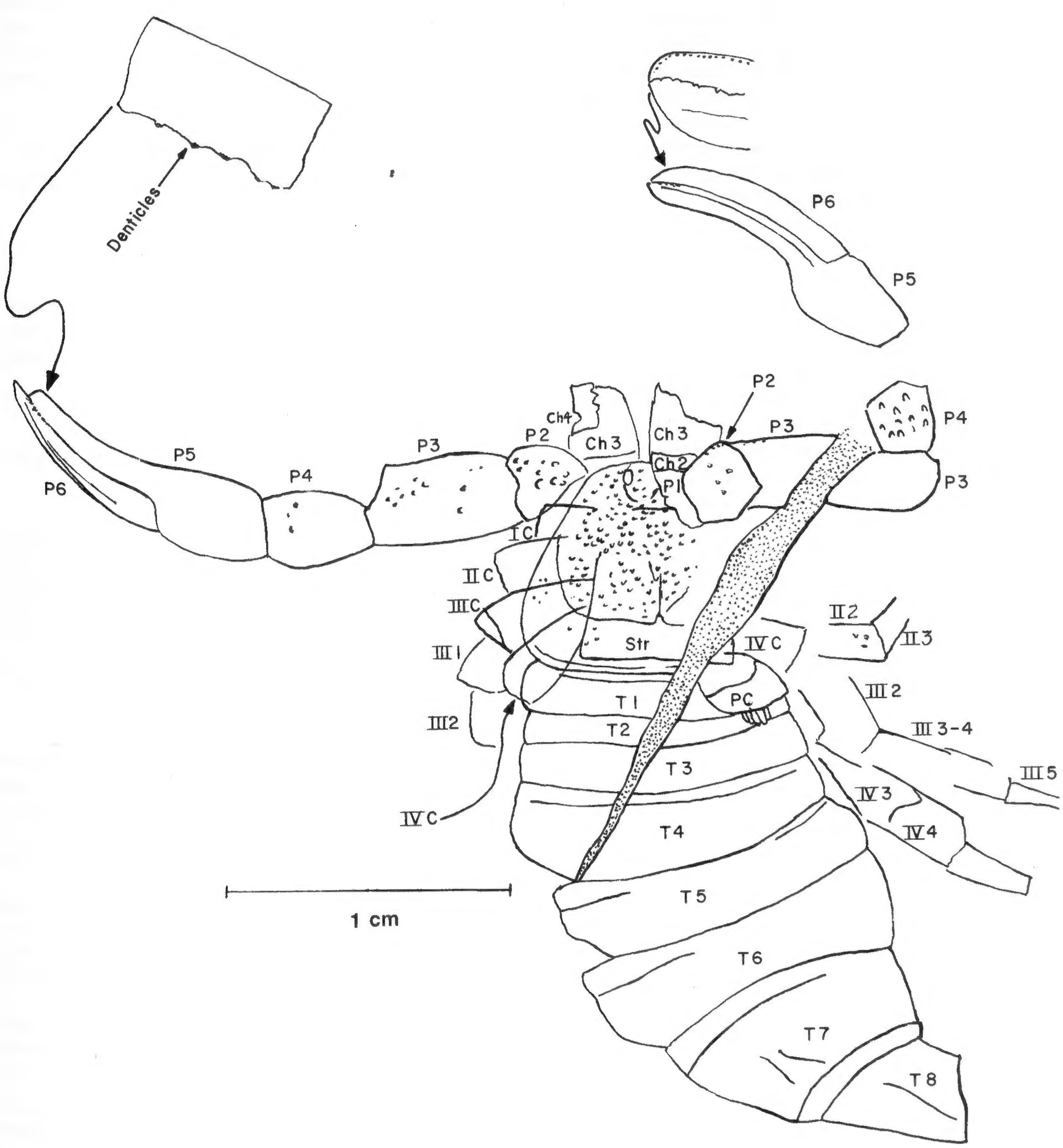
Text-figure 22

The holotype is a specimen preserved in dark gray shale, revealing mainly the dorsal side of the prosoma and parts of the appendages, all of the preabdomen, and one tergite of the cauda. The coxosternal region has been partly impressed through the carapace. The holotype is in the collections of the Institute of Geological Sciences, Edinburgh, Scotland, where it registered as GSE 2038.

The carapace is trapezoidal, without an anterior glossate process, and with a raised cephalic shield that is partly divided at midsection. The lateral margins are convergent anteriorly. The eyes are round, small, lo-

cated on a small, rounded, anteriorly-located ocellar mound. The entire shield is covered by coarse scales. Scattered, but smaller, scales occur in the posterior area of the carapace. The base of the carapace is bounded by a thick marginal rim.

The coxosternal arrangement is visible in part, since it is impressed through the carapace. The entire area is very probably like that in the Archaeoctonidae, although it must be admitted that the possibility exists that, instead, all four coxae abut the very large sternum. If this is so, it would require the establishment of a new family referable to the superfamily Proscorpioi-



Text-figure 22.—*Pseudoarchaeoctonus denticulatus,* n. gen., n. sp. Holotype, GSE 2038. From the lower Carboniferous (lower Viséan), Glencartholm Volcanic Beds, River Esk, Langholm, Dumfriesshire, Scoland. See foldout inside front cover for explanation of abbreviations.

dea. The sternum is very large, the base is square and appears to have straight lateral sides that are abutted by the last three pairs of coxae and possibly also by the first. No maxillary lobes are developed. The anterior of the sternum is unknown.

The chelicerae are large, but are not sufficiently well-preserved to warrant detailed description. The pedipalps are short but stoutly constructed. The femur is particularly thick and considerably longer than the tibia, which is very short. The hand and chela are large, with the fixed or immovable finger recurving, and the free finger incurving forward to fit both cutting edges together. The edges of the fingers are armed with a line of small denticles giving a serrated appearance (see Text-fig. 22). Coarse semilunar to submucronate scales cover the trochanter, femur and tibia.

The rest of the legs are too poorly preserved for description, but are longer than those of *Archaeoctonus glaber* and are flattened as in modern scorpions, and not tubiform. The coxae are relatively long.

The preabdomen is devoid of ornamentation of any kind, each tergite increases in length, is bounded anteriorly by a transverse ridge, and the greatest width is reached at the fourth and fifth tergites. The seventh tergite seems to be smooth, without any carinae.

Only the first tergite of the cauda is preserved.

The pectine of the right side has been preserved and this is a small structure, as long as wide, without any divisions or areoles and without fulcra. The teeth are short, stout, and less than 15 occurred on each pectine. Nothing else is known of the underside.

The specimen is completely flattened on the shale.

Measurements (in mm) of the holotype, GSE 2038.—

Pedipalp:			
Femur	length	**(P3)**	4.71
	width	**(P3)**	2.7
Tibia	length	**(P4)**	3.6
	width	**(P4)**	2.8
Hand	length	**(P5)**	3.12
	width	**(P5)**	3.92
Free finger length			5.7

Type information.—Glencartholm Volcanic Beds, Upper Border Group, Lower Carboniferous (lower Viséan), River Esk, Glencartholm, Langholm, Dumfriesshire, Scotland.

Derivatio nominis.—*denticulatus* (L. dim. of *dens*) = tooth: alluding to the small teeth on the pedipalp.

Remarks.—The ornamentation of raised elongate scales is remarkably like that of mixopteroid eurypterids. The genera *Archaeoctonus* and *Loboarchaeoctonus* have similar scales and occur in the same beds.

Superfamily **ACANTHOSCORPIONOIDEA**, new superfamily

Holosternina with the first pair of legs meeting at the midline, with well-developed maxillary lobes, last three pairs abutting the sternum.

Type family.—Acanthoscorpionidae, new family.

Remarks.—There is not much doubt in my mind that this holosternous scorpion represents a different superfamily than the Archaeoctonoidea, but at our present state of knowledge it seems best to include it in that superfamily. More specimens, perhaps better preserved, will resolve this matter.[11]

Family **ACANTHOSCORPIONIDAE**, new family

Acanthoscorpionoidea with ovoid sternum and lateral compound eyes.

Type genus.—*Acanthoscorpio,* n. gen.

Genus **ACANTHOSCORPIO**, new genus

Acanthoscorpionidae with ovoid sternum and square carapace with lateral compound eyes poorly developed; epidermis covered with small triangular mucrones.

Derivatio nominis.—*acantho* (Gr.) = spiny + scorpion.

Type species.—*Acanthoscorpio mucronatus,* n. gen., n. sp.

Geological range.—Devonian.

Remarks.—There is no scorpion which resembles this one. Because of the robust cauda, as well as the square carapace with compound eyes, it superficially resembles the Scottish *Dolichophonus loudonensis* Laurie, but the latter is a bilobostern, whereas *Acanthoscorpio mucronatus* is a definite holostern.

Acanthoscorpio mucronatus, new species
Text-figures 23, 24, 110N

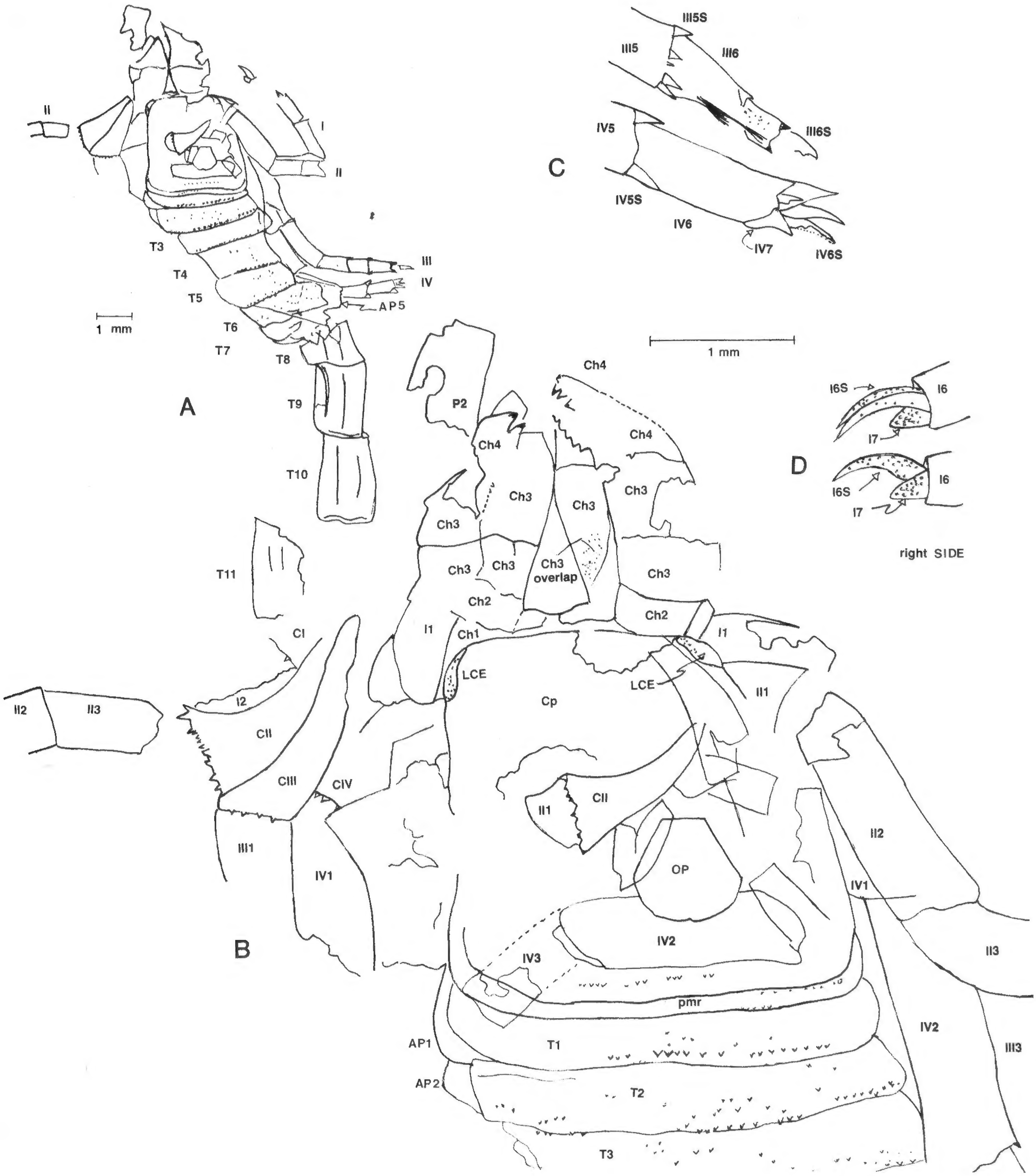
The species is based on a single, nearly complete specimen, which has been split laterally so that each half is composed mainly of dorsal or ventral tissues. The cuticle is unaltered, retaining the original coloration, which is a light brown reminiscent of many of

[11] However, the Acanthoscorpionidae have maxillary lobes and the Archaeoctonoidea do not, and thus cannot be in the same superfamily. Moreover, the huge campanulate sternum of *Archaeoctonus* has no resemblance to the moderately-sized oval sternum of the Acanthoscorpionidae. A.S.C.

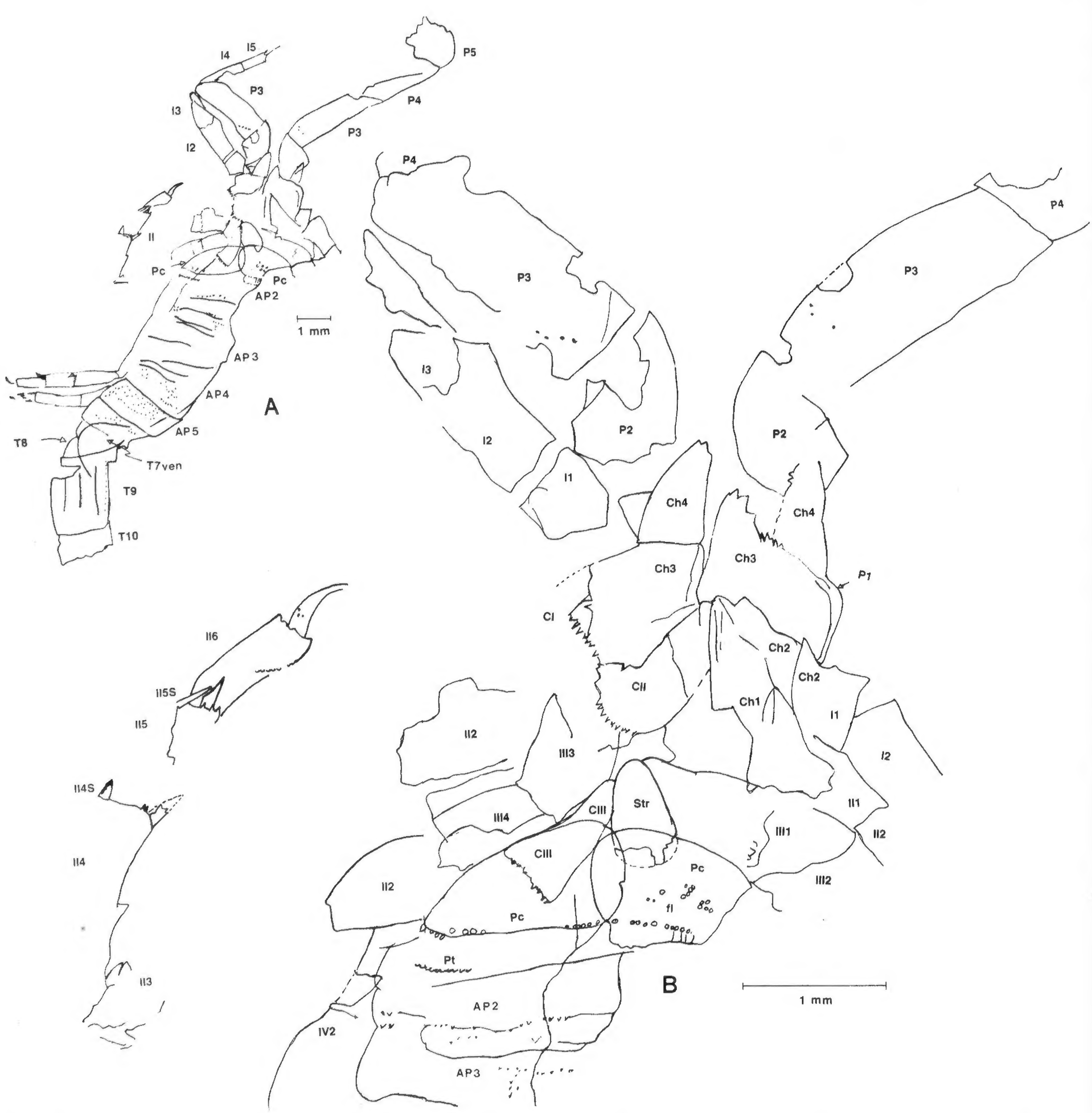
Text-figure 23.—*Acanthoscorpio mucronatus,* n. gen., n. sp. Holotype, FMNH (PE) 6177b. From the Lower Devonian, Beartooth Butte Formation, of Cottonwood Canyon, Big Horn Mts., WY, U.S.A. See foldout inside front cover for explanation of abbreviations.

A. Dorsal aspect of the complete holotype. **B.** Anterior details. **C.** Terminal details of right legs **III** and **IV. D.** Terminal detail of first right leg. Either a single or double claw.

the living Buthidae. The specimen unfortunately has been rolled over to the side, so that interpretation of important morphological details is extremely difficult. This is particularly true of the coxosternal region, and although an attempt at reconstruction has been made, this has been accomplished with considerable misgivings, and I believe firmly that confirmation from other specimens is needed before being fully accepted, as the structures are important phylogenetically, and mistakes in interpretation are easy to make.



The carapace is nearly quadrate, measuring 2.6 mm in length and 2.65 mm at the base. The anterior is completely straight, the base parallel and rounded at the genal angles, which join the straight and parallel lateral margins. The small compound eyes occur at the anterolateral angles and contain facets of very small size. There is no sign of a median eye node nor of the median eyes, although it must be pointed out that this area is not well preserved. There is no doubt, however, that median eyes are present as no scorpion with lateral eyes is known without median eyes. I suspect that these are present and that they are placed well forward on the carapace. The pedipalps are only partly preserved, but enough is present to show that they were slender



Text-figure 24.—*Acanthoscorpio mucronatus,* n. gen., n. sp. Holotype, FMNH (PE) 6177a. From the Lower Devonian, Beartooth Butte Formation, of Cottonwood Canyon, Big Horn Mts., WY, U.S.A. See foldout inside front cover for explanation of abbreviations.

A. Ventral aspect of the holotype, counterpart of Text-figure 23A. Shows the laterally rolled nature of the specimen. **B.** Anterior details.

and elongated. On the outer base of the brachium (**P3**) is a row of four large setal holes, with three other setal holes forming a triangle more toward the center. These are on the ventral side.

The appendages are also poorly preserved, but enough is present for a fairly good description of these structures. The chelicerae are very large, apparently four-jointed, but little can be made out of the denticles or the shape of the chelae. The four walking legs are relatively stout, all armed with at least double basitarsal and tibial spurs, all of which are well developed but not unusually long or robust. The ungues (**I6S**) are very long, slightly bent downward, slender and probably covered with short setae. Setal holes are present. The posttarsus is short, robust and also, very likely, covered with setae (see Text-figs. 23C, D).

Each of the coxae is armed at the end with a row of spines, and these short spines are probably found at the end of each joint of all legs.

The coxosternal region, unfortunately, was broken apart and the interpretation given here needs verification. The sternum is ovoid, wider on the posterior half. Apparently the long triangular coxae of the second, third and fourth pairs of legs abut it. Anterior to this is the first pair which meets at the midline, and medium-sized maxillary lobes adjoin one another. The opercular plate is single, ankylosed, and with a median indentation at the basal midsection. It is truncato-ovoid (see Text-fig. 110N) in shape.

The pectines are large, flipperlike, unjointed, but apparently with a poor development of small rounded areoles, although, for all practical purposes, the pectine may be considered as a single plate. Fulcra are preserved and these are small and rounded. The teeth are very poorly preserved, but are the long type, not as in *Branchioscorpio richardsoni,* and there were probably about 25 on each comb.

The abdominal tergites have been displaced laterally, but show that they are not unusual except for the ornamentation. Each tergite is bordered by a narrow transverse ridge and each increases in size posteriorly. The important seventh tergite cannot be described as it was crushed.

The postabdominal tergites, forming the cauda, are noteworthy for their great thickness, showing that the cauda was very robust.

The abdominal plates are clearly holosternal and, of course, without the slightest indication of stigmata. Each overlaps the succeeding. A narrow, poorly developed, anterior transverse ridge is present on each.

The ornamentation is of extreme interest as it recalls that present in many of the eurypterids. The carapace has at least one row of sharp, pointed, triangular and elevated spines, which normally are referred to as mucrones in eurypterid terminology. These single rows of large mucrones mark the base of each preabdominal tergite and, moreover, each tergite is covered with smaller mucrones. The abdominal plates likewise are covered with scattered mucrones.

The overall length of this scorpion is estimated at 12.5 mm and contrasts with the nearby, enormous, free chela of the chelicera of the eurypterid *Pterygotus mcgrewi* Kjellesvig-Waering and Richardson, where a single denticle is considerably larger than the entire scorpion.

Type information.—Lower Devonian, Beartooth Butte Formation, from the FMNH excavation site in Cottonwood Canyon, Big Horn Mountains of Wyoming, U.S.A. The specimen is deposited in the Field Museum of Natural History, Chicago, and is registered as FMNH (PE) 6177a and b.

Derivatio nominis.—*mucronatus* (L.) = spiny.

Family **STENOSCORPIONIDAE**, new family

Acanthoscorpionoidea with last three pairs of coxae abutting the sternum, which is ovoid. First pair of coxae unknown. Carapace divided into halves, without lateral compound eyes. Abdominal plates with gill chamber opening plain or with sparse spines and setae, opening posterolaterally.

Type genus.—*Stenoscorpio,* n. gen.

Remarks.—It is with considerable confidence that the coxosternal area of Wills coll. specimen No. 164 of *Stenoscorpio gracilis* (Wills, 1947, text-fig. 40D) is reconstructed, revealing that the last three pairs of coxae abut the sternum, inasmuch as the bases of all three coxae are squeezed together naturally and not by preservation. Surprisingly, this is somewhat similar to *Acanthoscorpio* of the Lower Devonian. In itself, this in not as strange as it seems, since the Triassic fauna of England includes such very "primitive" elements as the Spongiophonidae. Unfortunately, the first pair of coxae is unknown, as well as whether or not it and the second pair developed maxillary lobes. By early Devonian, the Acanthoscorpionidae had developed both, so that it is not impossible that the reconstruction made in Text-figure 25B is correct.

There is the possibility that the first pair of coxae developed only poorly formed maxillary lobes such as those found in the Spongiophonidae. At any rate, the Stenoscorpionidae differ from the Acanthoscorpionidae in lacking the compound eyes which were developed in the latter.

Genus **STENOSCORPIO**, new genus

Carapace quadrate; no lateral eyes; anterior margin sharply glossate; round median eyes anteriorly located. Cephalic shield is divided longitudinally by median

groove; opercular plates elongated, subelliptical. Pectines with narrow, undivided rachis and without fulcra.

Derivatio nominis.—*steno* (Gr.) = narrow, + scorpion.

Type species.—*Mesophonus gracilis* Wills, 1910.

Geological range.—Triassic.

Remarks.—The above generic diagnosis is based on the type species, except for the characteristics of the pectines (no fulcra) which are revealed by *S. pseudogracilis.*

Stenoscorpio gracilis (Wills, 1910)
Text-figures 25, 110M

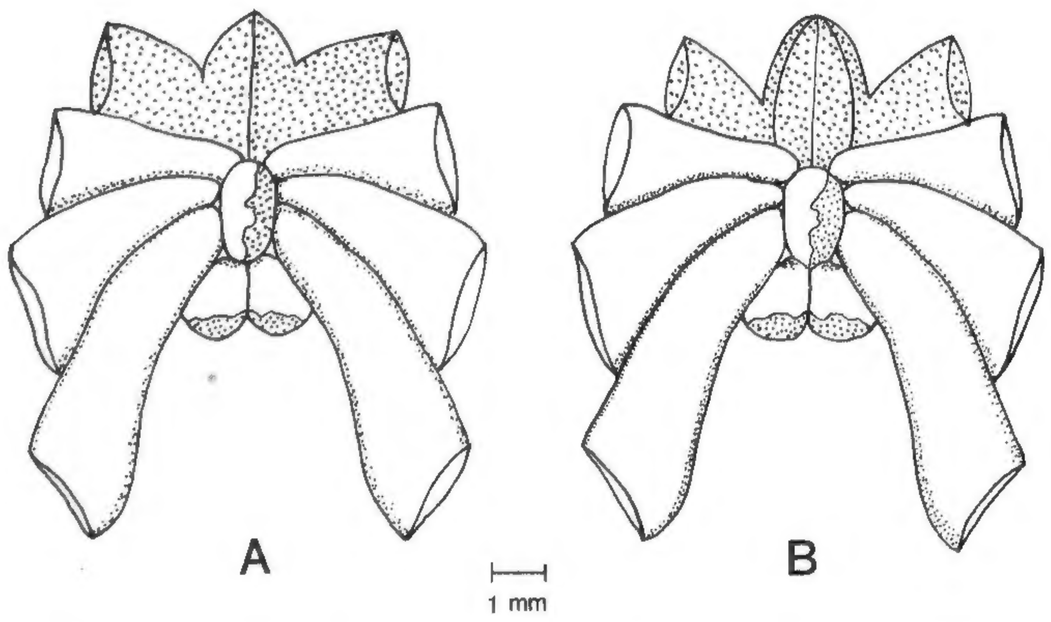
1910. *Mesophonus gracilis* Wills, pp. 317–318, pl. xxv, figs. 2–4; *not* pl. xxv, fig. 10 (specimen 195) = *Willsiscorpio bromsgroviensis* (Wills).
1947. *Mesophonus gracilis* Wills. Wills, pp. 116–120, pl. III, figs. 2–9a; pl. V, fig. 2; pl. VI, fig. 8; pl. VIII, fig. 9; text-figs. 3B, 5G, 20, 23, 24, 40D, 45C, 48A–C; *not* pp. 121–122, pl. V, figs. 6, 9; pl. XI, fig. 4; text-fig. 48, J to M (specimen 0278) = *Stenoscorpio pseudogracilis* (Wills).
1953. *Mesophonus gracilis* Wills. Petrunkevitch, p. 36.

The lectotype (Wills coll. No. 132) is a well-preserved tergite, identified here as the fifth tergite, which has a well-developed anterior median keel ("notch"). Determination of this tergite as the fifth indicates the probability that all the tergites are carinated, as even the seventh tergite has the same dorsal anterior median keel.

Wills coll. specimen numbers included under this species are 132 (lectotype), 11, 025, 102, 137, 147, 164, 185, 0191, 203, 228, 0257, 283, and 327A.

Type information.—Triassic Lower Keuper Sandstone Series, Bromsgrove Quarry, near Birmingham, England.

Remarks.—Specimen numbers refer to Wills' original specimens, which are in the collections of the Sedgwick Museum, Cambridge, England.



Text-figure 25.—*Stenoscorpio gracilis* (Wills). From the Triassic (Lower Keuper) sandstone, Bromsgrove Quarry, near Birmingham, England. Based on specimen SM 164 (of Wills, 1947). Two plausible restorations of the coxosternal area, although that of 25B is preferred in the light of present information. The coarsely stippled areas on the first pair of coxae, maxillary lobes of the second coxae, and parts of the sternum and operculum are restored.

Stenoscorpio pseudogracilis (Wills, 1947)

1910. *Mesophonus* sp. Wills, pl. xxiii, fig. 3; pl. xxvi, fig. 12.
1947. *Mesophonus gracilis* Wills. Wills, pp. 121–122, pl. V, figs. 6, 7; pl. XI, fig. 4; text-figs. 48, J–M.
1947. *Mesophonus infans A* (?) *Mesophonus gracilis* Wills, pp. 122–123, pl. V, fig. 1; pl. XI, fig. 12; text-figs. 48, D–H, 49.
1947. *Mesophonus pseudogracilis* Wills, pp. 123–126, pl. IV, figs. 9, 10; pl. VI, fig. 3; pl. XII, fig. 15; text-figs. 5H, 6, 9, 17, 19, 42C; *not* p. 33, pl. V, figs. 3, 4; text-fig. 13 (specimen 094) = *Mesophonus perornatus* Wills.
1947. *Mesophonus infans D* Wills, pp. 128–130, pl. XI, figs. 2, 3; text-figs. 45B, 50A, B.

One of the pertinent specimens for taxonomy and morphology of this species is the specimen described as *Mesophonus infans D,* the so-called type specimen (Wills, 1947, pp. 128–130, text-fig. 50, A, B). This specimen reveals the important seventh tergite, dorsal and ventral sides, which determines the specimen (0232B) to be *S. pseudogracilis* (compare specimen 012, Wills, 1947, text-fig. 19D). The abdominal plates and tergites are also preserved; the former revealing the gill opening to be small, opening ventrally and placed between the doublure and the posterior edge of the abdominal plate (Wills' Type A2). The fourth tergite (Wills' **tx**) has a part missing along the anterior of the transverse ridge in the form of a notch which very likely represents the slight median carina (Wills' "notch") that characterizes the species.

The species *M. pseudogracilis* lacks fulcra in the pectines. Among the more than 100 genera of living scorpions, this lack of fulcra is of generic importance and is uncommon. The absence of those fulcra, duplicated in Paleozoic scorpions, inclines me to refer this species to the genus *Stenoscorpio.* The seventh tergite, however, retains four well-developed ventral carinae, surmounted with scales, and this is an important generic character, at least among living scorpions. The development of the four carinae is apparently greatly reduced in *S. gracilis,* but nevertheless is present, as attested by the presence of four rows of scales. It seems rather logical at present to consider *M. pseudogracilis* another species of *Stenoscorpio.*

Both species have a central carina (Wills' "notch") on the transverse ridge of the tergites on the dorsal side. The dorsal carina is much more pronounced in *S. gracilis* where, even on the seventh tergite, it is extended in a "V"-shaped, central prolongation of the anterior transverse ridge. In *S. pseudogracilis* the central carina is greatly reduced, being present only on the fourth tergite, possibly slightly on the third.

Specimen 282, the only specimen of *Mesophonus infans A,* which Wills (1947, p. 122) suggested might questionably be a neonate of *S. gracilis,* instead is a

juvenile of *S. pseudogracilis*. Wills, throughout his monograph, refers to "neonates", but all these are much too large to be neonates. They are more properly juveniles, as a neonate would be composed of such fragile cuticle that preservation would be very unlikely. Past the first instar, the scorpion assumes the shape and major characters that are present in the adult. This is not the case in true neonates. The presence of a strong anterior median keel or carina ("notch" of Wills) on the fourth tergite of *M. infans A* clearly indicates that this juvenile is *Stenoscorpio pseudogracilis* (Wills).

Specimen 0278, labelled *Mesophonus gracilis* (Wills, 1947, pl. XI, fig. 4; text-figs. 48J, K, L, M) is an important specimen, revealing much of taxonomic value. There are a number of areas where my study of the original material is not in agreement with Wills (1947, p. 121, and above text-figures). The opercula are elongate-ellipsoidal, but not so long as the restoration on text-figure 48M. I was unable to see any bilobation of the first abdominal plate. The fulcra are not present. The notch, which is so important in the identification of this species, is a slight median keel or carina that occurs on the anterior of the tergite and, when flattened into a single plane, it appears as a "notch" on the posterior of the anterior transverse ridge of the tergite. The presence of the anterior median keel ("notch") on the fourth tergite and its absence on the other tergites is sufficient for the identification of this specimen as *Stenoscorpio pseudogracilis* (Wills).

The specimens which are included under this species are: SM 231 (holotype), 012, 029, 052B, 065, 80, 184, 229, 231, 0232B, 257 (*fide* Wills), 278, 279, 282.

Type information.—Triassic, Lower Keuper Sandstone Series, Bromsgrove Quarries, near Birmingham, England.

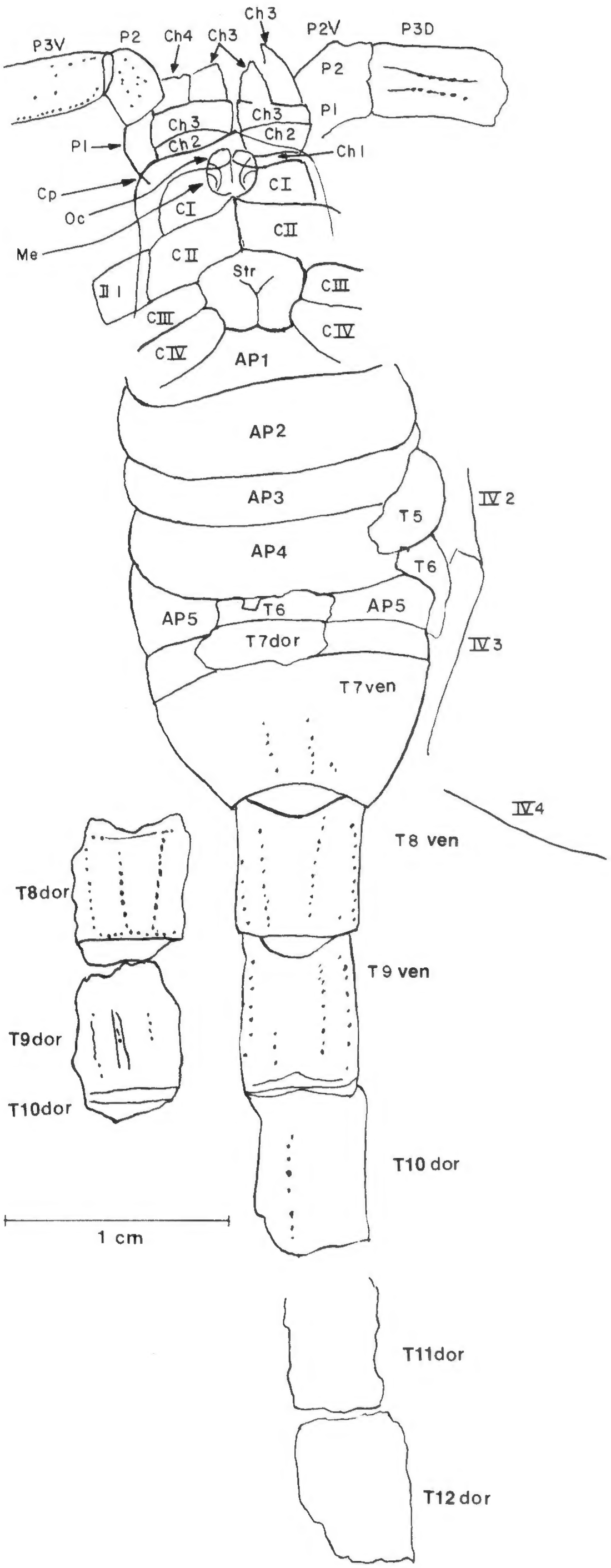
Remarks.—All specimen numbers refer to Wills' original specimens, which are in the collections of the Sedgwick Museum, Cambridge, England.

Superfamily **GIGANTOSCORPIONOIDEA**, new superfamily

Holosternina with last two pairs of coxae abutting the sternum, and first two pairs meeting at the midline in front of the sternum, without the development of maxillary lobes.

Type family.—Gigantoscorpionidae, n. fam.

Remarks.—The lack of maxillary lobes in the superfamily separates it from all other superfamilies of the Holosternina with similar coxosternal arrangements.



Text-figure 26.—*Gigantoscorpio willsi* Størmer. GSE 2137. From the Lower Carboniferous, Eskdale, Scotland. T. S. Stock collection (developed by B. N. Peach). See foldout inside front cover for explanation of abbreviations.

Family **GIGANTOSCORPIONIDAE**, new family

Gigantoscorpionoidea with large, subrounded pentagonal sternum; carapace elongate without lateral compound eyes, but with median eyes anteriorly but intramarginally located.

Type genus.—*Gigantoscorpio* Størmer, 1963.

Genus **GIGANTOSCORPIO** Størmer, 1963

Gigantoscorpionidae with a row of fine denticles on the edges of the pedipalps and with well-developed, long, serrated, flaring tibial and basitarsal spurs.

Type species.—*Gigantoscorpio willsi* Størmer, 1963.

Geological range.—Lower Carboniferous.

Remarks.—The large tibial and basitarsal spurs are of particular importance and are responsible for the identification of this genus in other specimens.

Gigantoscorpio willsi Størmer, 1963
Text-figures 26, 27, 110H, 113B2

1963. *Gigantoscorpio willsi* Størmer, pp. 15–61, pls. 1–3, pl. 4, figs. 1–5, pls. 6–12, pl. 13, figs. 1–4, 7, 8, pl. 14, pl. 15, figs. 1–3, pl. 16; text-figs. 1–3, 5–23.
1972. *Gigantoscorpio willsi* Størmer. Kjellesvig-Waering, p. 39.

Specimen.—GSE 2137 deposited in the Institute of Geological Sciences, Edinburgh, Scotland, consists of a nearly complete specimen showing mainly ventral features, but a few dorsal structures are preserved. In life the specimen must have measured about 75 to 80 mm in length, from the anterior of the carapace to the base of the telson. It is associated with several ostracodes, and a smooth-shelled pelecypod lies on top of the second abdominal plate. The specimen had been "developed" by B. N. Peach, as stated (etched) on the shale slab along with "Eskdale, T. Stock collection". The specimen is in the grayish black shale that characterizes the River Esk fauna.

Unfortunately, the development performed by Peach obliterated many details, although I do not mean any criticism, as optical instruments and the coarse chisels used at that time did not permit delicate work. It is remarkable that development was as good as it was. The description that follows is also based on a latex cast that further brings out certain important details.

The carapace is subquadrate, pointed along the anterior margin, and with a large elliptical eye node surmounted on the sides with two rounded median eyes; the eye node is placed intramarginally but well forward of the center of the anterior half of the carapace. The anterolateral angles are rounded and without lateral eyes.

The pedipalps are developed as stout, strong structures, and, although the first three joints are present (**P1**, **P2**, **P3**), they show that the basal joint could not form part of the oral chamber as it does in present-day scorpions. The chelicerae are large, composed of the usual four joints, and occur above the basal joint of the pedipalps. The pedipalps, at least joints **P2** and **P3**, the trochanter and brachium respectively, contain pustules, which on the ventral side of the brachium occur in a row along the back edge, as do the trichobothria in some living scorpions (for example, some of the Chactidae such as *Broteochactas, Chactas, Teuthrautes, Broteas,* etc.). These pustules were likely setaceous. The dorsal side of the brachium of the pedipalp reveals two carinae surmounted by pustules.

Of particular importance is the coxosternal arrangement. The sternum is very large, round, probably peaked at the anterior, giving it a rounded pentagonal shape. It has a deep median sulcus that seems to bifurcate in the middle part of the sternum. The last two pairs of coxae abut against the sternum. The first and second coxae meet at the midline in front of the sternum and neither pair has developed maxillary lobes, although both project slightly anteriorly to a blunt-pointed inner part that very likely represents a primitive development of the maxillary lobes.

The abdominal plates are holosternous, with rounded epimeral angles.

The last postabdominal tergite, seen only in ventral view, is large with a very well-developed transverse ridge and with two short carinae surmounted with pustules.

The cauda is nearly complete except for the telson. All tergites are long but stout, and in the case of the first two, both sides could be extracted and preserved. The dorsal side has three carinae, all surmounted with coarse granules, or pustules, whereas the venter seems to have only two carinae, also surmounted with coarse granules. There is at least one lateral carina, which also is surmounted by coarse pustules.

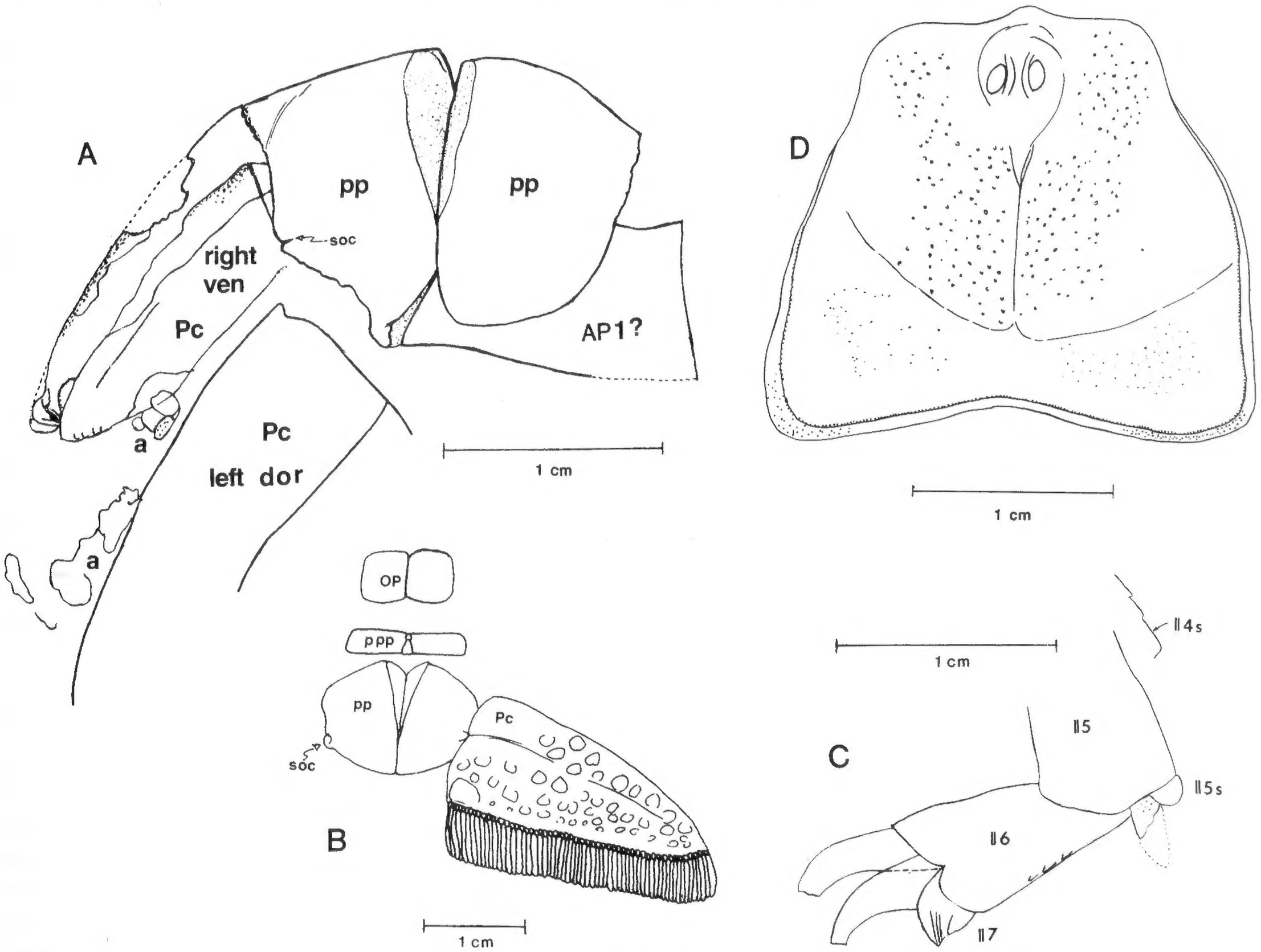
The genital opercula, most of the legs and the pectines were not preserved. The latter undoubtedly were covered by the first and second abdominal plates.

Specimen.—Holotype of *Gigantoscorpio willsi* Størmer. Part of counterpart, BM(NH) In. 42706a in the British Museum (Natural History), London, England.

Several small pieces of black calcareous shale, with parts of a large scorpion, were found while engaging in the study of the fossil scorpion types at the British Museum. I identified these pieces as parts of *Gigantoscorpio willsi* Størmer, and later, Mr. Samuel Morris of the British Museum recognized them as part of the counterpart of the holotype of *G. willsi.* Actually, the pieces represented the entire left half of the specimen as shown by Størmer in his figure (1963, fig. 1). Dr. Størmer and I had discussed several times the possibility of the large oval plate, which had been identified

(Størmer, 1963, fig. 18) as the operculum, being the sternum instead, and the part with the small double plates, which had been identified (Størmer, 1963, fig. 10) as possibly the pregenital tergite, as being the opercular plates. These parts, particularly the so-called "sternum" as well as the terminal portion of the first walking leg are well preserved on the counterpart, and therefore it was anticipated that the question would be settled by the newly-found counterpart. Consequently, the counterpart was borrowed from the British Museum through the kindness of Dr. H. W. Ball, who sent the specimen to me, first in Norway and later in Chicago. In both places I have had long discussions with Dr. Størmer regarding the identification of these parts.

Dr. Størmer and I agreed that the possible pregenital tergite (Størmer, 1963, p. 51, text-fig. 10) represents the two opercular plates, and they occur in their rightful or original position and are seen from the dorsal surface. The part previously identified by Størmer as the operculum is preserved entirely from the ventral surface, and consists of two large semicircular plates, joined at midsection by a deep sulcus. These represent the large pectinal plates, or median anchor plates to which the large pectines were attached by a condyle, socket and intersegmental tissue. These plates are shown here on Text-figure 27A. Attachment is on the lower part of the anterior lamina of the pectines with the above-mentioned condyle and socket, as shown in the restoration (Text-fig. 27B). Traces of the areoles of the middle lamina occur attached to the anterior lamina (see Text-fig. 27A), which prove that the structures in question are the pectines and that one is attached to the pectinal plate.



Text-figure 27.—*Gigantoscorpio willsi* Størmer. From the Lower Carboniferous (lower Viséan), Glencartholm Volcanic Beds (the "River Esk Fauna"), River Esk, Dumfriesshire, Scotland. A–C. Holotype, part and counterpart, BM(NH) In.42706a,b. See foldout inside front cover for explanation of abbreviations.

A. Somewhat problematical impressions of the counterpart surface. **B.** Pectinal area partially revised and restored from Størmer (1963). **C.** Terminal details of leg **II** of the holotype. **D.** Carapace, GSE 2134.

This pectine, therefore, is the one of the right side, while the left pectine is folded over, and preserved with the dorsal side showing. This is the pectine figured by Størmer (1963, text-fig. 18) as the pectine of the right side. In my interpretation, the very small narrow plate, with a median organ (Størmer, 1963, p. 55) is much too fragile to hold the enormous pectines, much less articulate against them, and this plate, therefore, is not the pectinal anchor plate, but the prepectinal plate, greatly reduced. The interrelationship of the plates can be seen in Størmer's (1963, pp. 79–82, text-fig. 32) excellent figure of *Centromachus euglyptus* (Peach) (see Text-fig. 31B) and in *Opsieobuthus pottsvillensis* Moore (see Text-fig. 31A). In Størmer's figure 32, the part labelled as the "basal plate of the combs" which carries the median organ, in my opinion, is the prepectinal plate (**ppp**) whereas the "basal plate of the combs" can be seen directly below, with the combs attached to it (see Text-fig. 31B here for changes). This implies that the opercula are prosomal organs and, because in many primitive scorpions the last pair of legs abuts against them, the possibility is worth considering. It is, however, far from the purpose of this paper to dwell on comparative morphologies other than on the taxonomic levels.

Based on this as well as the parts of the coxosternal area preserved in specimen GSE 2137 (see Text-fig. 26), the coxosternal region can be reconstructed as in Text-figure 110H. The coxosternal area, therefore, comprises a large pentagonal sternum with the third and fourth pairs of coxae abutting against it and with the first and second pairs meeting at midline, but without maxillary lobes, as shown on specimen GSE 2137 of the Institute of Geological Sciences, Edinburgh. The two small squarish opercular plates fit below the sternum (Størmer, 1963, fig. 10).

The terminal joints of the second leg were preserved in an excellent condition (Text-fig. 27C). Two claws are present, which are long and strongly unciform, without ventral denticles as commonly present in many Carboniferous scorpions. One of the claws is slightly larger and this is probably the anterior. Presumably, therefore, the leg is the second of the right side. The posttarsus (**II7**) is short, pointed and triangular. The tarsus (**II6**) is unusually short, with a terminal lobe, or emargination at the terminal part. The entire tarsus widens appreciably, flaring toward the terminal part. The basitarsus is partly preserved and this also is flaring toward the terminal part. It has two spurs at the usual part, and one of these seems to be rounded. The other was broken. A jagged piece of a tibial spur also was preserved, which greatly resembles that figured by Størmer (1963, fig. 16). The presence of this leg of the holotype confirms Størmer's determination that GSE 2174 belongs to *Gigantoscorpio willsi.*

Another specimen which is referred to *Gigantoscorpio willsi* reveals the entire carapace in good condition, but flattened on the black shale. This specimen is GSE 2134 (see Text-fig. 27D) and is deposited in the collections of the Institute of Geological Sciences, Edinburgh, Scotland.

The rim is well developed in the posterior and lower half of the carapace, then narrows anteriorly so that it is not noticeable along the front. The anterior of the carapace is produced into a linguiform process. The eyes are elliptical with strong orbital ridges, but very likely originally round. The eyes occur on a lacrimiform node. They measure about 1.6 mm in the condition they are in (flat). The anterior half is elevated into a cephalic shield, which was divided at midsection. This outline of the cephalic area is accentuated by the coarse pustular ornamentation.

Measurements (in mm) of carapace of GSE 2134.—

Length:	31.5
Width at base:	41.0
Width at midsection:	35.5
Width at anterior (at eyes):	27.0

The entire length of the scorpion from the anterior of the carapace to the end of the cauda is estimated at 240 mm, which is large for a scorpion as compared with modern ones, but is considerably less than half the size indicated by some other fossil specimens.

The holotype of *Gigantoscorpio willsi* Størmer is broken, and lacks the raised cephalic shield. The type of median ocelli, on a mound at the anterior of the carapace, the ornamentation, the glossate process, the outline of the carapace and, significantly, the type of laterobasal rim of GSE 2134 are identical with those of the holotype, and I do not hesitate to identify this specimen with the latter.

Type information.—All the specimens, the holotype and GSE 2134, GSE 2137, and GSE 2174, are from the Lower Carboniferous (lower Viséan) in the Glencartholm Volcanic Beds, Upper Border Group, at River Esk, Glencartholm, Langholm, Dumfriesshire, Scotland.

Remarks.—The large size of this scorpion is spectacular, estimated at 390 to 440 mm (Kjellesvig-Waering, 1972, p. 39), but there is no doubt that these estimates can be doubled, based on the foot of GSE 2174. Nevertheless, other scorpions found in the Upper Carboniferous, *Eoscorpius carbonarius* and *Titanoscorpio douglassi,* as well as *Brontoscorpio anglicus* of the Upper Silurian, and *Praearcturus gigas* of the Devonian, are equally as large or larger.

The most spectacular and taxonomically important aspect of *G. willsi* is the coxosternal arrangement. The

first two pairs of coxae are devoid of maxillary lobes but, surprisingly, this is combined with the condition of having the last two pairs of coxae abut the sternum as in modern scorpions. It was known, however, that the abutment of the last two pairs of coxae against the sternum was a very ancient development, as it was present in the Lower Devonian *Branchioscorpio richardsoni,* which had greatly-developed maxillary lobes. It was a great surprise to have a supposedly advanced condition such as the last two pairs abutting the sternum coupled with a very primitive condition of no development of maxillary lobes in the first two pairs of coxae.

Superfamily **MESOPHONOIDEA** Wills, 1910 (emend.)

Holosternina with first two pairs of coxae meeting at the midline in front of the sternum, and with maxillary lobes. Third pair abuts the sternum and fourth abuts the genital opercula.

Type family.—Mesophonidae Wills, 1910 (emend.).

Remarks.—The superfamily and family bear little or no resemblance to the original definition of Wills (1910, 1947) and Petrunkevitch (1953, 1955) but little can be gained by the introduction of new names when the older ones could be emended without causing any confusion. Mesophonoidea is the holostern "counterpart" of the lobosternous Isobuthoidea.

Family **MESOPHONIDAE** Wills, 1910 (emend.)

Mesophonoidea with narrow, pentagonal sternum; carapace subquadrate; median eyes placed well forward on the carapace, and with small lateral compound eyes.

Type genus.—*Mesophonus* Wills, 1910.

Remarks.—The family Mesophonidae Wills, 1910, is here emended (restricted) and seems to have clear priority over the Mazoniidae Petrunkevitch, 1913, and Centromachidae Petrunkevitch, 1953, both included under the Mesophonoidea. All three families, incidentally, are emended here and bear no resemblance to their original descriptions based on the type of ornamentation. The description of the family Mesophonidae, as emended by Petrunkevitch (1955, p. 78) was meaningless, as most of it was erroneously based on the coxosternal arrangement in the genus *Spongiophonus,* a scorpion that is completely different from *Mesophonus.* Apart from that, the family was based on characters only of species value, as for example, "Comb with 8 to 17 teeth". As restricted here, the family Mesophonidae Wills, 1910, includes only the genus *Mesophonus* Wills, 1910.

Genus **MESOPHONUS** Wills, 1910 (emend.)

Mesophonidae with wide, subquadrate carapace; round median eyes located on prominent median mound that protrudes as a conspicuous, sharp linguiform anterior process; dorsal shield undivided. Abdominal plates with gill openings truncated and located on inner posterior edge of plate.

Type species.—*Mesophonus perornatus* Wills, 1910 (genolectotype by designation, Wills, 1947).

Geological range.—Triassic.

Remarks.—Apart from *Spongiophonus pustulosus,* Wills (1910, 1947) referred all British Triassic scorpions to the genus *Mesophonus.*[12] Petrunkevitch (1953) followed this treatment. However, the genus *Mesophonus* included species with lateral facetted eyes and others without them. This condition was considered by Wills to be sexual dimorphism, although he correctly pointed out that it was unusual for one sex to have lateral facetted eyes and the other to be without them. Although sexual dimorphism is present in scorpions, the differences are of a rather subtle nature; such as the differences in the punctation, color, particularly on the carapace and pedipalps, differences in the thickness of the cauda, relative length of the twelfth tergite, relative width, length and size of the pedipalp, etc. These sex differences seem to have been established early, as some of them have been noted in Silurian scorpions. However, there is never any difference due to sex in the number or type of eyes, even in genera in the Buthidae having the greatest number, or variation, in size or number of lateral eyes. In the Carboniferous, several genera of scorpions have lateral facetted eyes; other genera do not, but these are definitely considered to be separate families and genera. Indeed, in many cases, those that have obvious dorsal similarity are found to belong to different families and superfamilies when the underside is known.

The differences between the type species and *Mesophonus opisthophthalmus* Wills, 1947, are due to secondary sexual characters and therefore both species are identical with the type species, *M. perornatus* having priority. Wills (1947, p. 107) mentioned that this might be the case, but elected to consider them as separate species.

The chelicerae of *Mesophonus* have four joints as in all other Holosternina.

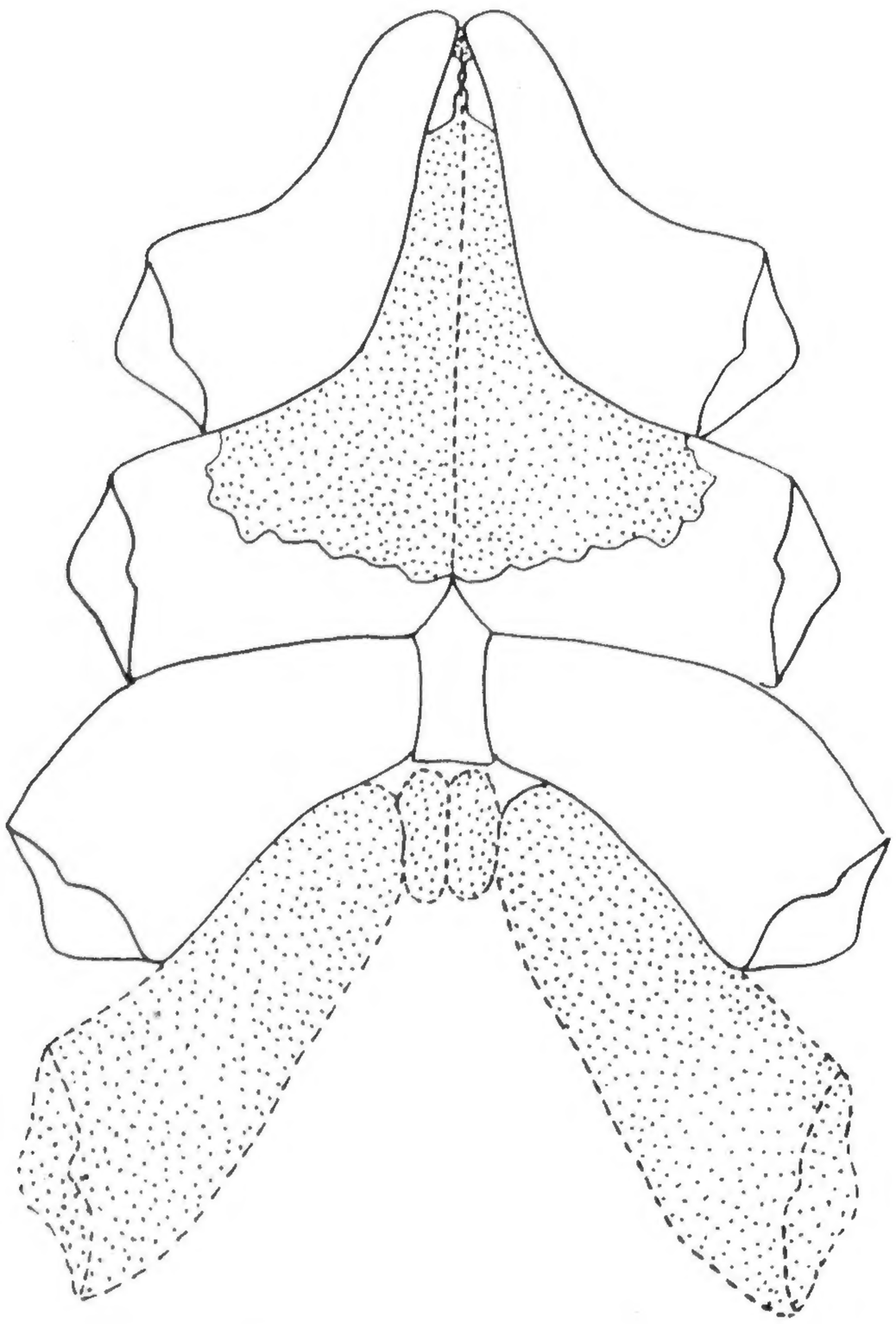
---

[12] Dubinin (1962, fig. 1258) pictures a reconstruction of "*Mesophonus* sp." (Werner, 1934), a scorpion about 42 mm long from the Triassic, with a coxosternal arrangement like that of living scorpions, and holosternous abdominal plates. A.S.C.

Mesophonus perornatus Wills, 1910
Text-figures 28, 110B, 113A3

1910. *Mesophonus perornatus* Wills, pp. 311–313, pl. xxii, figs. 1–3, 5, 7–9; pl. xxvi, figs. 9, 13.
1947. *Mesophonus pseudogracilis* ? Wills, pp. 33, 123, pl. V, figs. 3, 4; text-fig. 13.
1947. *Mesophonus perornatus* Wills. Wills, pp. 102–106, pl. II, figs. 1, 2, 6–8; pl. IV, figs. 3, 4, 7, 8, 11, 12; pl. XII, figs. 1, 7–9, 16; text-figs. 3C, 5C–F, 11, 12, 21, 47D–H.
1947. *Mesophonus opisthophthalmus* Wills, pp. 106–108, pl. II, figs. 3–5, 9; text-figs. 3D, 5J.
1947. *Mesophonus infans E* Wills (*partim*), p. 130, text-figs. 51H–J.
1947. *Mesophonus* sp. Wills, pl. VIII, figs. 1, 2; text-figs. 40A–C, 41.
1962. *Mesophonus perornatus* Wills. Dubinin, p. 432, fig. 1239.

Mesophonus opisthophthalmus Wills, 1947, is a junior synonym of *M. perornatus* Wills, 1910. On Wills', 1947, plate II, figures 3 and 4 (SM spec. Nos. 0107 and 0243) are figured carapaces labelled as *Mesophonus opisthophthalmus,* which show very sparsely scattered scale-tubercles. These two carapaces are considered here to be females and are identical with the female carapace of *M. perornatus,* the lectotype (Wills, 1947, pl. II, fig. 1, SM spec. No. 206). The male of *M. perornatus,* with dense granulation, is shown on Wills' (1947) plate II, figure 2 (spec. No. 011). The type of granulation on the carapace and other areas is a well-known secondary sexual characteristic.



Text-figure 28.—*Mesophonus perornatus* Wills. From the Triassic (Lower Keuper) sandstone, Bromsgrove Quarry, near Birmingham, England. Based on Wills, 1947 (pl. VIII, figs. 1 (SM 040), 3 (SM 0110)). Showing the coxosternal area. Stippled areas are restored.

Specimens referred to *Mesophonus perornatus* Wills are as follows: SM 206 (lectotype), 7, 008, 011, 017, 024, 034, 039A, 040, 85, 094, 095, 0110, 0112, 0122, 125, 0128, 156, 0176, 205, 210, 0212,[13] 213 (*fide* Wills, 1947, p. 36), 0266, 277, 287. Also referred to this species by Wills, but not figured, are SM 050 (p. 42), SM 036 (p. 102), SM 0203 (p. 102) and SM 284 (p. 102).

In addition, the specimens that formed the species *Mesophonus opisthophthalmus* Wills, a junior synonym, may now be added to this list: SM 0107, 0234, and 0161 (*fide* Wills, 1947, p. 107).

Type information.—Triassic, Lower Keuper Sandstone Series, from the quarries at Bromsgrove, near Birmingham, England.

Remarks.—All specimens are in the Sedgwick Museum, Cambridge, England.

Mesophonus (?) **pulcherrimus** Wills, 1910

1910. *Mesophonus pulcherrimus* Wills, p. 318, pl. xxvi, figs. 2, 4, 6, 7.
1947. *Mesophonus pulcherrimus* Wills. Wills, pp. 66–67, 72–74, 126, pl. VII, figs. 5, 9–14; pl. XII, figs. 19, 21, 22; text-figs. 32, 35.

It is not possible to correlate the lectotype (spec. No. 201) or other specimens (all caudal segments) referred to this species with any of the other known British Triassic scorpions and it is here referred questionably to *Mesophonus.*

Type information.—Triassic, Lower Keuper Sandstone Series, Bromsgrove Quarry, near Birmingham, England.

Mesophonus (?) **pulcherrimus** var. **immaculatus** Wills, 1947

1947. *Mesophonus pulcherrimus* var. *immaculatus* Wills, p. 126, pl. III, fig. 12; pl. VII, figs. 8, 15, 16; pl. XI, fig. 7; text-fig. 36.

The "variety" is questionably referred to *Mesophonus,* inasmuch as the caudal segment comprising

[13] Wills (1947) lists spec. SM 0212 twice. On page 102, 0212 (G227) represents *M. perornatus,* thirteenth segment of a young individual, pl. IV, fig. 8, and text-fig. 47F. On page 108, 0212 (G22) represents *M. bromsgroviensis,* "other sternite", pl. VI, figs. 2A and 2B, text-fig. 7. Likewise, 0203 (G230) is listed on page 102 as a thirteenth segment of *M. perornatus,* and on page 116, 0203 (G52) is listed as "tergite with pecten" of *M. gracilis.* A.S.C.

the lectotype cannot be correlated with any of the known Bromsgrove scorpions.

Type information.—Triassic, Lower Keuper Sandstone Series, Bromsgrove Quarry, near Birmingham, England.

Mesophonus (?) **maculatus**
(Brauer, Redtenbacher, and Ganglbauer, 1889)

1889. *Periplaneta maculatus* Brauer, Redtenbacher, and Ganglbauer, p. 12, fig. 14.
1906. ? *Ophismoblatta maculata* (Brauer, Redtenbacher, and Ganglbauer). Handlirsch, p. 527, pl. XLVI, fig. 2.
1928. *Ophismoblatta maculata* (Brauer, Redtenbacher, and Ganglbauer). Grabau, p. 410, fig. 580 b.

Brauer, Redtenbacher, and Ganglbauer (1889) described as a blattoid a single specimen consisting of most of the dorsal side of the prosoma and mesosoma of a scorpion from the Ust-Balei region of the Irkutsk Basin of Siberia. It occurred in Jurassic strata associated with numerous insects and fishes. I have not been able to study the holotype, and presumably only specimen, as it was not available. From the original drawings, there does not appear to be much doubt that the specimen represents a scorpion. It seems from the figure that most of the carapace is present with the succeeding tergites of the preabdomen along with two fragments of the third and fourth legs. The mesosoma shows the increase in width toward the third and fourth tergites, which is common in many scorpions, along with a decrease in width of the tergites from that point, also a common feature in scorpions. The seventh tergite, although incomplete, is revealed as being much longer than the previous tergites. Carinae, a very common feature of the seventh tergite in scorpions, are also present. The attachment of the prosoma to the mesosoma is characteristic of scorpions, not blattoids. All of these features, characteristic of scorpions, are not possible in a blattoid.

Although little can be added to our knowledge from this specimen, while it remains lost, it is important because it is the second known Jurassic scorpion and the only one from the Far East.

Family **MAZONIIDAE** Petrunkevitch, 1913
(emend.)

Mesophonoidea with subequilateral pentagonal sternum, second pair of maxillary lobes reaching halfway the length of the first pair. Median eyes close to anterior edge of carapace; no lateral compound eyes.

Type genus.—*Mazonia* Meek and Worthen, 1868.

Genus **MAZONIA** Meek and Worthen, 1868

Mazoniidae with carapace about as long as wide, with a pointed projection in front; proportionately large chelicera.

Type species.—*Mazonia woodiana* Meek and Worthen, 1868.

Geological range.—Carboniferous.

Mazonia woodiana Meek and Worthen, 1868
Text-figures 29, 110P, 113A2

1868b. *Mazonia woodiana* Meek and Worthen, pp. 563–565, figs. A, D.
1877. *Mazonia woodiana* Meek and Worthen. Miller, p. 224.
1883. *Mazonia woodiana* Meek and Worthen. Peach, p. 409, pl. 23, figs. 24, 25.
1889. *Mazonia woodiana* Meek and Worthen. Miller, p. 571.
1910. *Eoscorpius* (*Mazonia*) *woodiana* (Meek and Worthen). Grabau and Shimer, p. 416.
1911. *Mazonia woodiana* Meek and Worthen. Pocock, p. 11.
1913. *Mazonia woodiana* Meek and Worthen. Petrunkevitch, pp. 54–56, pl. 3, fig. 13.
1944. *Mazonia woodiana* Meek and Worthen. Lehmann, p. 178.
1944. *Mazonia woodiana* Meek and Worthen. Shimer and Shrock, p. 709, pl. 300, figs. 6–9.
1949. *Mazonia woodiana* Meek and Worthen. Petrunkevitch, p. 132.
1953. *Mazonia woodiana* Meek and Worthen. Petrunkevitch, pp. 12–13, figs. 11, 119.
1955. *Mazonia woodiana* Meek and Worthen. Petrunkevitch, p. 70, fig. 38(5).
1960. *Mazonia woodiana* Meek and Worthen. Wills, p. 321.
1962. *Mazonia woodiana* Meek and Worthen. Dubinin, p. 428, figs. 1225, 1227.
1963. *Mazonia woodiana* Meek and Worthen. Størmer, p. 116, fig. 44.
1969. *Mazonia woodiana* Meek and Worthen. Kjellesvig-Waering, pp. 171–190, figs. 91–101.

The holotype, in a typical Mazon Creek ironstone concretion (UI X-491), was thoroughly discussed in Kjellesvig-Waering (1969). That discussion will not be repeated here.

Specimen.—Part and counterpart of a nearly complete scorpion except for part of the cauda and most of the walking legs, preserved as dorsal and ventral impressions in an ironstone concretion from the Middle Pennsylvanian, Francis Creek Shale, collected in ths spoil heaps of Pit 11, on the Kankakee–Will County line, Illinois by Mrs. K. Taelle in 1970. The specimen is in the collection of the Field Museum of Natural History, Chicago, accessioned as FMNH (PE) 39253.

This is an unusually good specimen, which reveals the important underside as well as further confirmation that the preabdomen comprised seven tergites, and not eight, as had been postulated by Meek and Worthen (1868b), and which later was confirmed erroneously by Petrunkevitch (1949, 1955), resulting in his establishment of a suborder and family based on the fictitious presence of an eight-jointed preabdomen (see Kjellesvig-Waering, 1969, pp. 186–189). This specimen is a very welcome addition to our knowledge because of its great taxonomic significance.

Little can be added to our knowledge of the dorsal side as that was fully described (Kjellesvig-Waering, 1969) in the holotype, and that discussion will not be repeated here. However, the cauda is partly preserved and is shown to be thick and surmounted with carinae that are not too clear. The underside also shows carinae.

The pedipalp is unusually long, stout, with a very long manus and long curving fingers. The free fingers are bent forward and, although the fixed fingers are not preserved, these undoubtedly would be recurving backward. No denticles are developed and only small setal openings are present on the cultrate edge.

The chelicerae are preserved and are composed of four joints, are hooklike and proportionately very large. Although teeth are developed, these are not preserved sufficiently for description.

The first walking leg is preserved nearly in its entirety. Basitarsals (**I5**) are well developed, and linear punctations occur on this joint. The other legs are largely unknown except for the tarsus of the fourth leg, which reveals a long (possibly double) tibial spur at the proximal end and two large basitarsal spurs at the distal end. Two rows of spines occur at the posterior. This fragment was dissolved from a piece of the concretion chipped off during cleaning of the specimen and was mounted on a slide (M.W. 1) (see Text-fig. 29F). A small seta is present at the end of the joint.

The end of the fourth leg, consisting of the distal part of the tarsus, two claws and the posttarsus (**IV7**) also was dissolved from chips broken off during the cleaning process. This part was mounted on a slide (M.W. 2) and is shown on Text-figure 29E. The end of the tarsus shows two small setae. The tarsal spurs, which are the curved claws, are long, the anterior one being larger, and are bounded on the bottom edge by evenly spaced small spines. The transtarsus or posttarsus (**IV7**) is small—a short pointed horn with a longer area for the attachment of muscles.

The important coxosternal area is revealed almost in its entirety. The arrangement is clearly that of Mesophonoidea, a pentagonal sternum with the last pair of coxae abutting the genital plates, and the third pair the sternum; the first two pairs meet at midsection in front of the sternum, have well-developed maxillary lobes, but the second pair reaches only halfway the length of the first pair. The anterior part of the tubular area in front of the mouth therefore is made up of the bases of the chelicerae, the first joints of the pedipalps, and the maxillary lobes of the first pair of legs only.

The sternum is pentagonal, with straight sides and a straight base. The opercular plates are elongate, oblong, rounded at the corners, and fit directly below the sternum.

The combs are covered, but enough is impressed through the second abdominal plate to note that they are narrow, small, with small fulcra and many, very small, narrow teeth, which are estimated at about 45 on each comb.

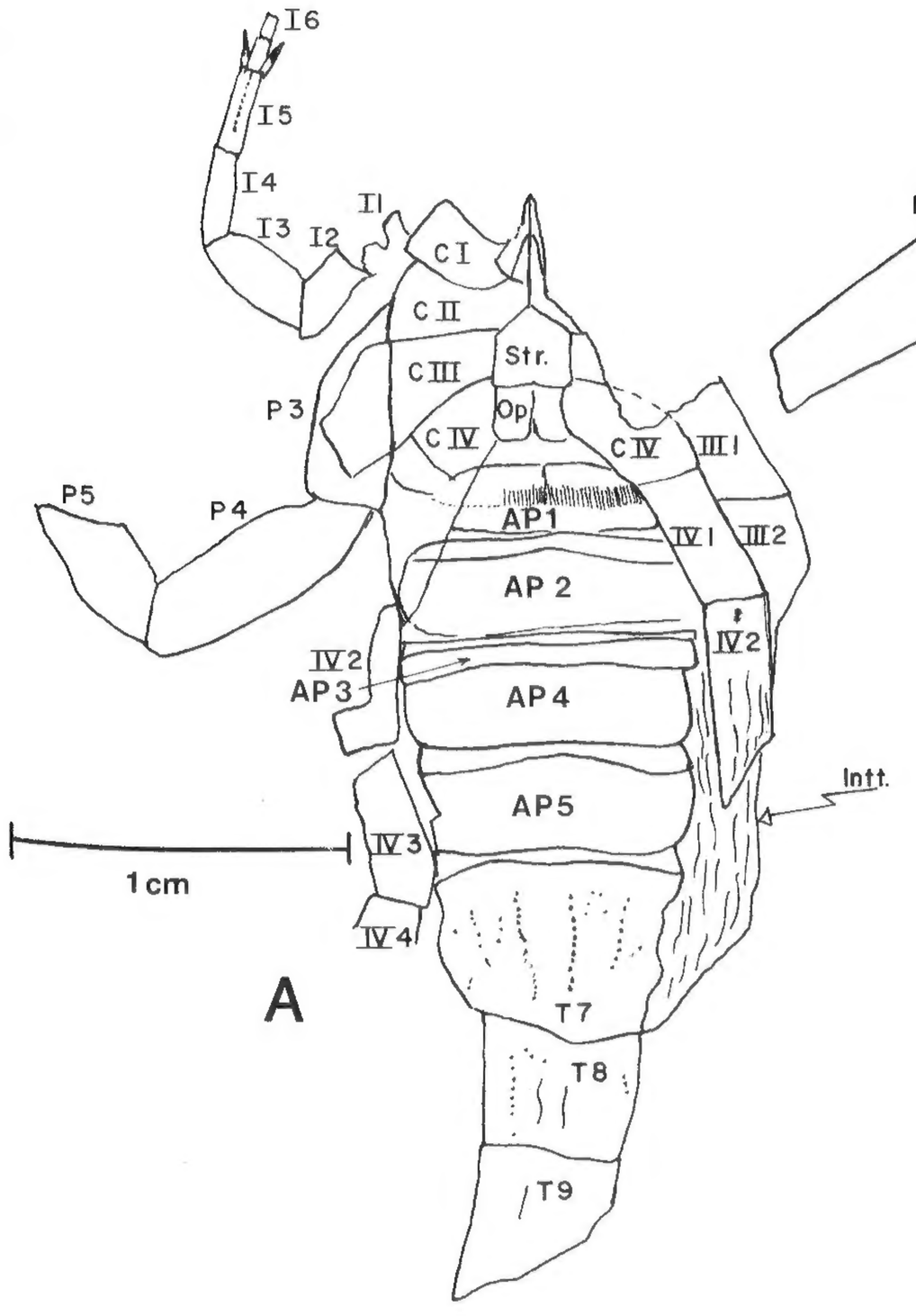
The abdominal plates are distinctly holosternous and not lobosternous, as I reported in 1969 (p. 185), having been misled by the presence of two distinct halves of an abdominal plate. There is no doubt that this was a fortuitous crack, making it appear as if it were a lobostern (or meristostern) plate.

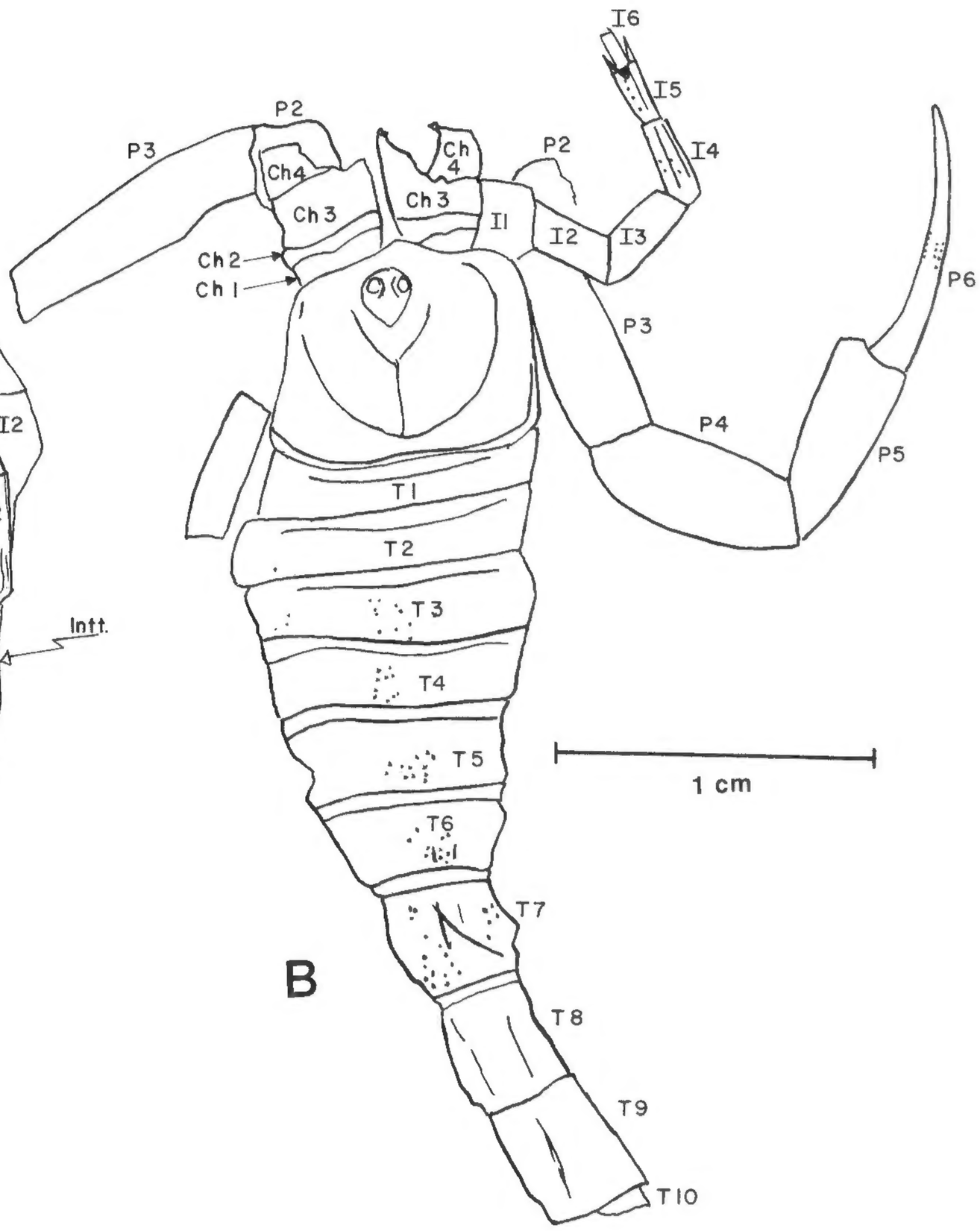
A piece of the ends of a holosternous abdominal plate was extracted; the adhering rock was dissolved in acid with the result that the slitlike opening to the gills, such as is found in some species of Wills' Triassic *Mesophonus,* was clearly discerned. These pieces were mounted on a slide (M.W. 4). The slit is bordered by a few very small spines, the lip being slightly thickened. The integument on the face and on the doublure is reticulated, in a cell-like netting such as is well-known in nearly all scorpions, including the living ones. On the doublure the definite reticulated pattern grades into what is generally known as intersegmental tissue, although this is actually very thin, flexible cuticle and reveals no structure, at least at 200× (see Text-fig. 29C). One of the pieces showing the slitlike opening showed structureless, very thin cuticle that likely represents pieces of the gills (Text-fig. 29C).

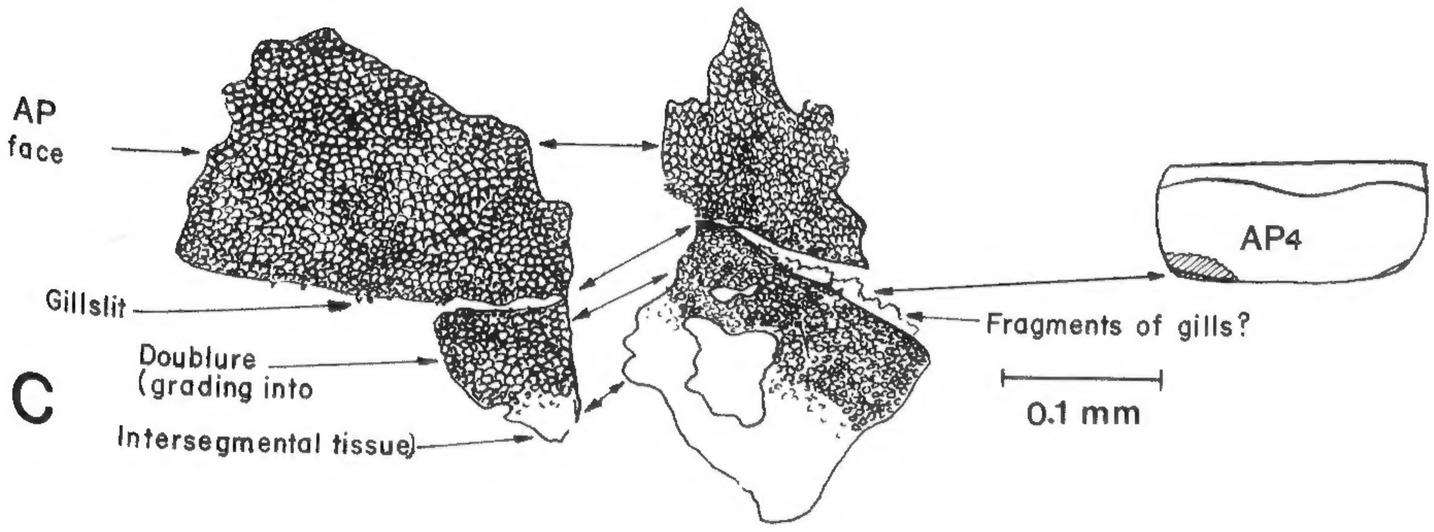
The tergites are covered with distinct ornamentation in the form of pustules along the axis of the mesosoma, with larger pustules on the seventh tergite. Each tergite is bounded by a row of spines at the base (Text-fig. 29D). The ornamentation was of particular diagnostic value in the identification of this species.

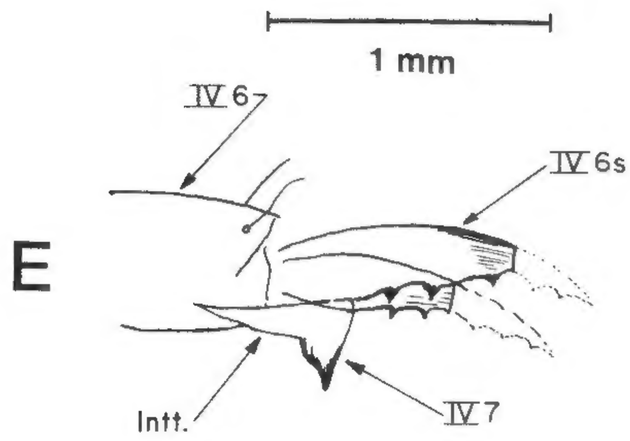
Text-figure 29.—*Mazonia woodiana* Meek and Worthen. Specimen collected by Mrs. K. Taelle (part and counterpart), FMNH (PE) 39253. From the Upper Carboniferous (Pennsylvanian), Carbondale Formation, Lower Francis Creek Shale, at Pit 11, Peabody Coal Co., Will–Kankakee County Line, Illinois. See foldout inside front cover for explanation of abbreviations.

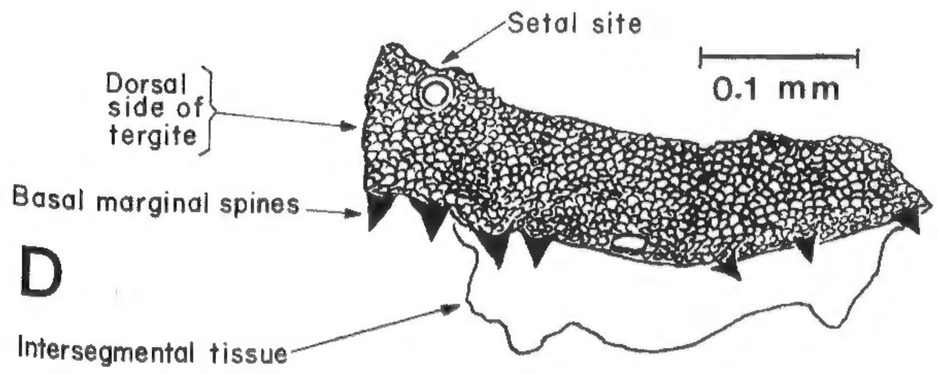
A. Ventral aspect. The third holosternous abdominal plate is almost completely telescoped between abdominal plates two and four. **B.** Dorsal aspect of the specimen, clearly showing seven tergites in the preabdomen, rather than eight as the original authors supposed. **C.** Enlargement of a corner of the fourth abdominal plate posterior margin, which preserves the gill slit, perhaps a fragment of gill tissue, and intersegmental tissue. The integument on the abdominal plate face and the doublure shows the cellular reticulation characteristic of nearly all scorpions. **D.** Tergite surface, showing pustulose surface and basal spines. Based on slide M.W. 3. **E.** Detail of the terminus of the fourth leg. Based on slide M.W. 2. **F.** End of the fourth leg, dissolved out of matrix by acid. Based on slide M.W. 1.

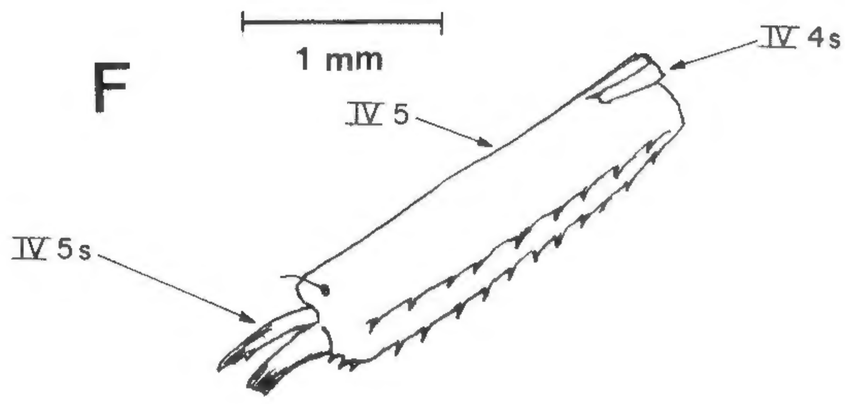

I6
I5
I4
I3
I2
I1
CI
CII
CIII
Str.
P3
Op
CIV
CIV
III1
P5
P4
AP1
IV1
III2
AP 2
IV2
IV2
AP3
AP4
Intt.
AP5
IV3
1cm
IV4
T7
T8
T9
A


I6
I5
I4
P2
P3
Ch4
Ch 4
Ch 3
Ch 3
P2
II
I2
I3
Ch2
Ch1
P3
P6
P4
P5
T1
T2
T3
T4
T5
1 cm
T6
T7
T8
T9
T10
B


AP
face
Gillslit
Doublure
(grading into
Intersegmental tissue)
C
AP4
Fragments of gills?
0.1 mm


1 mm
IV6
IV6s
E
Intt.
IV7


Setal site
0.1 mm
Dorsal
side of
tergite
Basal marginal spines
D
Intersegmental tissue


1 mm
F
IV 4s
IV 5
IV 5s

Measurements (in mm) of the Taelle specimen (FMNH (PE) 39253).—

Carapace:			
Length:			7.26
Width at base:			8.3
Pedipalp:			
Humerus (**P3**):			7.5
Brachium (**P4**):			6.7
Hand length (**P5**):			4.0
Hand width (**P5**):			2.1
Free finger (**P6**):			7.34
Tergite:	length		width
No. 1	1.36		(incomplete)
No. 2	1.66		(incomplete)
No. 3	1.95		(incomplete)
No. 4	2.41		(incomplete)
No. 5	2.7		(incomplete)
No. 6	2.7		(incomplete)
No. 7	3.0 (?) (see underside)		
No. 8	3.3		
No. 9	3.5		
No. 10	3.7		
Abdominal plates:	length		greatest width
No. 2	2.7		7.4
No. 3	2.92		7.6
No. 4	2.92		7.6
Tergite No. 7 (underside)	3.8	anterior:	6.9
		posterior:	4.9

Mazonia wardingleyi (Woodward, 1907)
Text-figure 30

1907. *Eoscorpius* (*Mazonia*) *wardingleyi* Woodward, p. 543, fig. 3.
1953. *Alloscorpius wardingleyi* (Woodward). Petrunkevitch, p. 29, figs. 35, 133.
1969. *Mazonia wardingleyi* (Woodward). Kjellesvig-Waering, p. 188.

Type information.—Holotype of *Eoscorpius* (*Mazonia*) *wardingleyi* Woodward, Carboniferous, Middle Coal Measures, 135′+ above Arley Mine Coal Seam, Sparth Bottoms, Lancashire, England; registered as BM(NH) In.18561 in the collections of the British Museum (Natural History). Presented to the Museum by W. H. Sutcliffe, 1906.

Several important points escaped the descriptions of Woodward (1907, p. 543) and Petrunkevitch (1953, p. 29). The anterior of the carapace is produced into a pointed, triangular area, much as in *Mazonia woodiana* Meek and Worthen. The chelicerae are unusually large, armed with large teeth, and other than noting their presence, preservation does not warrant further description. The pedipalp preserved shows the usual trochanter, followed by an unusually thick femur and tibia. The termination of the first leg on the right side is described for the first time. This ends in two slightly curved claws with spines at the underside; the posttarsus is also produced into a sharp spine. The basitarsal spurs are of two types: a flat, setaceous spur that is serrated at the end, and a flat, short, pointed spur.

Petrunkevitch states that, "There is nothing to recall *Mazonia*" (1953, p. 29), a statement with which this writer does not agree. Both *Mazonia woodiana* and *M. wardingleyi* were well known heretofore only from the dorsal side. Good casts of the holotype of *M. woodiana* in the British Museum collections were compared directly with the holotype specimen of *M. wardingleyi* and nothing could be found on the basis of the dorsal side that would place this scorpion in any genus other than *Mazonia.* The writer has also studied the holotype specimen of *M. woodiana.* The holotype of *M. wardingleyi,* with its inflated aspect, probably denotes a female—that is, if sex criteria are the same for fossils as for living scorpions, and there is no reason to think otherwise.

The cephalic shield shows distinct coarse, short, transverse ridges that should serve as a characteristic of this species. These ridges develop into indistinct large granules toward the base of the cephalic shield.

The intersegmental tissue between the tergites is particularly well preserved. The anterior transverse ridges are also very well developed, recalling again the strong, massive construction of *Mazonia woodiana* (see Kjellesvig-Waering, 1969, p. 171).

Family **CENTROMACHIDAE** Petrunkevitch, 1953 (emend.)

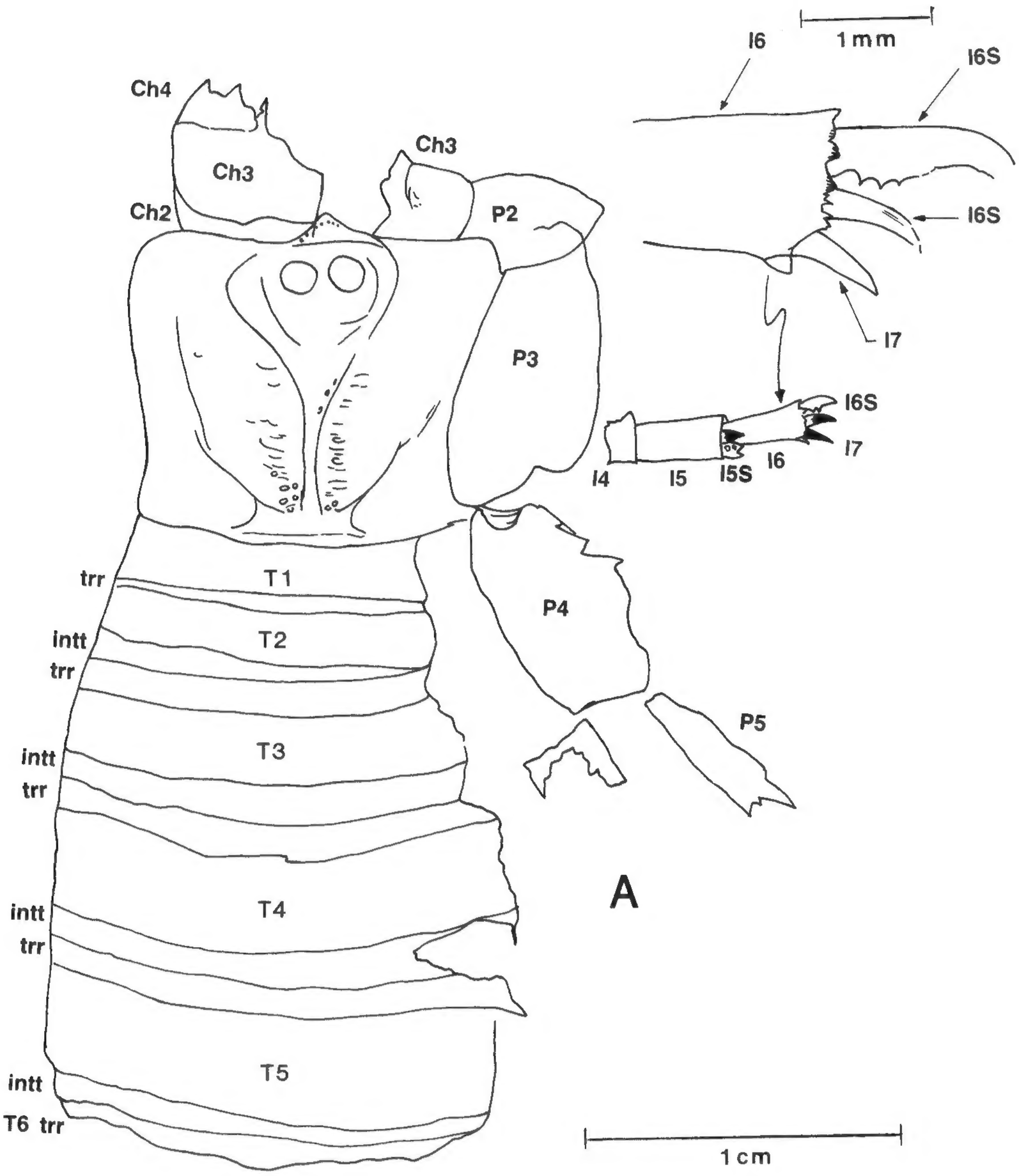
Mesophonoidea with small, subtriangular or subpyriform sternum.

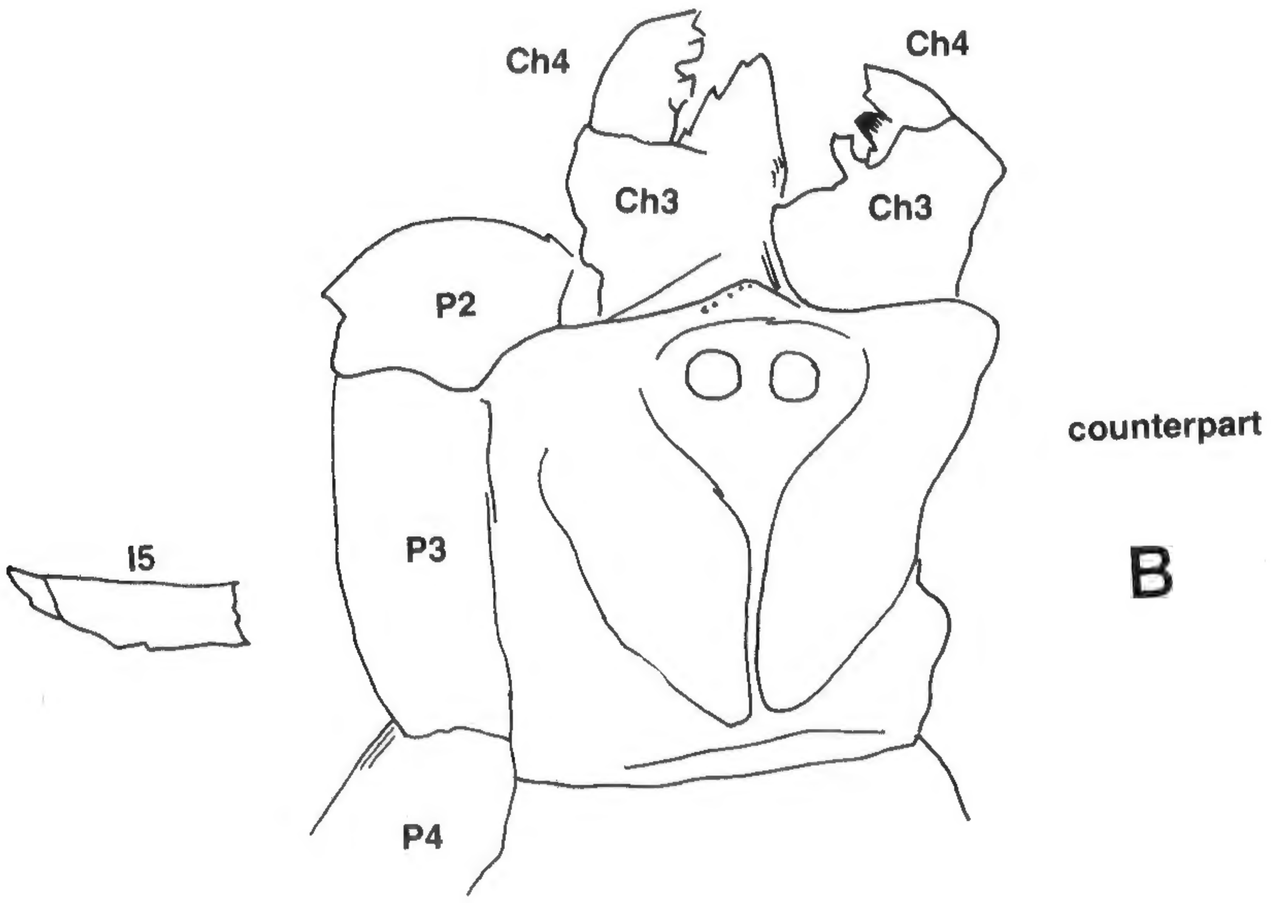
Type genus.—*Centromachus* Thorell and Lindström, 1885.

Remarks.—Petrunkevitch (1953, p. 17) restudied the holotype of *Centromachus euglyptus* (Peach) with the result that the coxosternal region was described as having a pentagonal sternum with only the first pair of coxae having maxillary lobes, whereas coxae II abutted against the sternum and III and IV against the opercula. This led Petrunkevitch to describe the family Centromachidae based on the peculiar arrangement of the coxae, and in 1955 (p. 78) he used the same characters to establish the superfamily Centromachoidea. Størmer (1963, pp. 79–83) made a detailed study of the same specimen and disagreed with the work done by Petrunkevitch. The writer also studied the specimen in 1971 and can verify Størmer's conclusions, namely: The sternum was found to be small and subpyriform, with only the third pair of coxae abutting against it; these coxae had short maxillary lobes that met in front of the sternum. The fourth pair of coxae abutted against

Text-figure 30.—*Mazonia wardingleyi* (Woodward). Holotype, BM(NH) In.18561. From the Carboniferous, Middle Coal Measures, 135′+ above Arley Mine Coal Seam, Sparth Bottoms, Lancashire, England. See foldout inside front cover for explanation of abbreviations.

A. Part. **B.** Counterpart.


Ch4
Ch3
Ch3
Ch2
P2
P3
P4
P5
trr
T1
intt
T2
trr
T3
intt
trr
T4
intt
trr
T5
intt
T6 trr
I6
1 mm
I6S
I6S
I7
I6S
I7
I4
I5
I5S
I6
A
1 cm


Ch4
Ch4
Ch3
Ch3
P2
P3
P4
I5
counterpart
B

the operculum. The second pair of coxae meet in front of the sternum and have well-developed maxillary lobes. The first pair of coxae, not sufficiently well-preserved to show the maxillary lobes, was found to be in normal position. It seems safe to surmise that the first pair of coxae had developed maxillary lobes, since all scorpions with maxillary lobes on the second pair of coxae have the same developed on the first pair. Indeed, maxillary lobes were always first developed on the first pair in the evolution of the scorpions (see *Eoscorpius carbonarius,* Text-fig. 75). A restoration, based mainly on Størmer (1963, pp. 79–82) with slight modification, is given as Text-figure 31B.

Genus **CENTROMACHUS**
Thorell and Lindström, 1885

Centromachidae with elongate, subovoid opercular plates. Pectines large with many teeth (about 70 (Størmer, 1963, p. 82)) anchored to a narrow trapezoidal pectinal plate with a lanceolate median organ.

Type species.—*Eoscorpius euglyptus* Peach, 1883.

Geological range.—Lower Carboniferous.

Centromachus euglyptus (Peach, 1883)
Text-figures 31B, 110J, 113A1

1883. *Eoscorpius euglyptus* Peach, pp. 402–424, pl. 22, figs. 3–3d.
1885. *Centromachus euglyptus* (Peach). Thorell and Lindström, pp. 21, 25.
1911. *Centromachus euglyptus* (Peach). Pocock, pp. 19–20, text-fig. 4.
1913. *Centromachus euglyptus* (Peach). Petrunkevitch, p. 33.
1949. *Centromachus euglyptus* (Peach). Petrunkevitch (*partim*), p. 141, fig. 173; not fig. 136.
1953. *Centromachus euglyptus* (Peach). Petrunkevitch, pp. 17–18.
1955. *Centromachus euglyptus* (Peach). Petrunkevitch, p. 78, fig. 43(3).
1962. *Centromachus euglyptus* (Peach). Dubinin, p. 428, fig. 1242.
1963. *Centromachus euglyptus* (Peach). Størmer, pp. 79–82, text-fig. 32.

Reference is made to Størmer (1963, pp. 79–82) who gives a detailed and excellent description of the holotype, GSE 2142, from the Lower Carboniferous of Langholm, Dumfriesshire, Scotland. I noted, however, the imprint of the middle of the anterior part of the carapace, and this was distinctly bluntly glossate, and also that the only abdominal plate present clearly is holosternous. My identification of part of the morphologies differs from that given, and inasmuch as these determinations have considerable bearing on taxonomy, they are here listed. The area from the opercular plates to the first gill-bearing abdominal plate is preserved undisturbed. In text-figure 32, Størmer shows a wide, divided, trapezoidal plate with a median organ separating the two plates. This plate is identified as the "basal plate of the combs" or the pectinal plate. I believe instead that this is the reduced first plate (of six abdominal plates). This plate occurs anterior to the pectines, and can be seen in other scorpions, for example, the well-preserved underside of *Eochaerilus.*

Family **HELOSCORPIONIDAE**, new family

Mesophonoidea with first and second maxillary lobes narrow, reaching to oral opening, with first pair squeezed away from the midline, leaving only the second pair meeting at the midline. Third pair abuts pentagonal sternum and fourth pair, the opercula. Carapace elongate, subquadrate and divided by a deep V-shaped sulcus. Large median eyes located on an anteriorly-placed ocellar mound. No lateral compound eyes.

Type genus.—*Heloscorpio,* n. gen.

Remarks.—The only family in the Holosternina that bears any resemblance to the Heloscorpionidae is the Buthiscorpiidae, but the latter has median eyes located well within the anterior margin, lacks the deep V-shaped sulcus, and more important, has lateral "compound" eyes, as against the Heloscorpionidae, which has anteriorly-located median eyes, a deep and large V-shaped sulcus, and no "compound" eyes.

Genus **HELOSCORPIO**, new genus

Heloscorpionidae with median eyes located forward on carapace, no lateral "compound" eyes; prominent median carina throughout the preabdomen with a linear depression on each side of the carina resulting in trilobation of the preabdomen.

Derivatio nominis.—*helo* (Gr.) = marsh-dwelling.

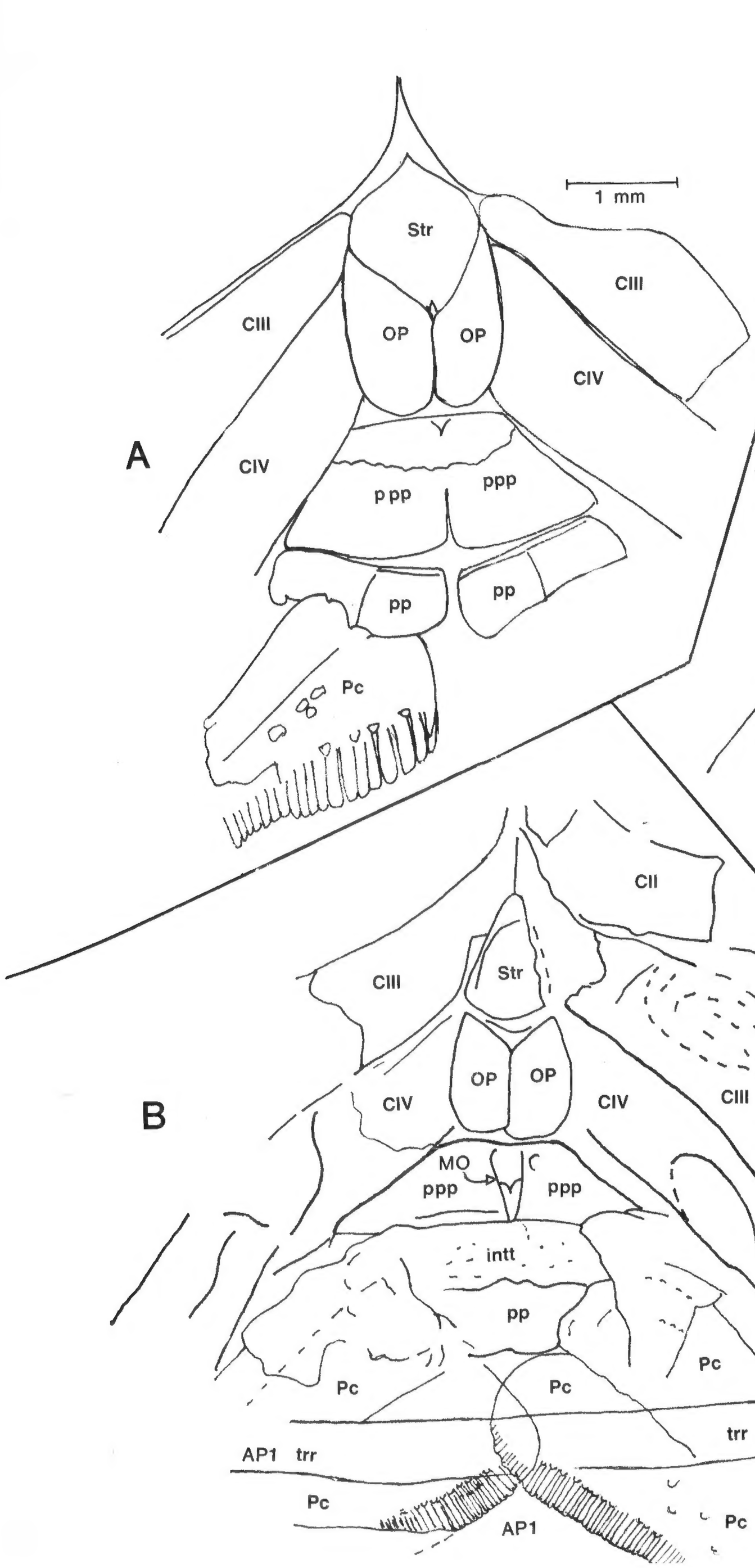
Type species.—*Geralinura*? *sutcliffei* Woodward, 1907.

Geological range.—Carboniferous.

Remarks.—The great central carina and rough trilobation are sufficient to distinguish this genus from any other scorpion, and were the specimen more fully preserved, it would almost surely have to be placed in a new superfamily. There is a possibility that this scorpion is a Meristosternina as the abdominal plates do

Text-figure 31.—Details of the organization of the coxosternal and pectinal regions. See foldout inside front cover for explanation of abbreviations.

A. *Opsieobuthus pottsvillensis* (Moore). From the Upper Carboniferous (Pennsylvanian) of Indiana. Holotype, FMNH 37984. Showing the coxosternal area and right pectine. **B.** *Centromachus euglyptus* (Peach). Holotype, GSE 2142. From the Lower Carboniferous (lower Viséan), River Esk, Scotland. After Størmer, 1963, text-figure 32, with some changes in morphologic interpretation. **C, D.** *Tityus trinitatus* Pocock. From Mayaro, Trinidad. Showing sexual differences in coxosternal organization. **C.** Male. FSU Vial 778, E. N. Kjellesvig-Waering collection. Note presence of prepectinal plate (**ppp**). **D.** Female. FSU Vial 779, E. N. Kjellesvig-Waering collection.


A
1 mm
Str
CIII
CIII
OP
OP
CIV
CIV
p pp
ppp
pp
pp
Pc
B
CII
CIII
Str
OP
OP
CIV
CIV
CIII
MO
ppp
ppp
intt
pp
Pc
Pc
Pc
trr
AP1
trr
Pc
AP1
Pc
C
1mm
Str
CIII
CIII
OP
OP
pp
ppp
Pc
right Pc
removed
CIV
CIV
♂
D
♀
CIII
Str
CIII
OP
OP
CIV
Pc
pp
CIV
right Pc
removed

show a possible separation, which here has been interpreted as an impression of the dorsal central carina.

Heloscorpio sutcliffei (Woodward, 1907)
Text-figures 32, 110I, 113A4

1907. *Geralinura*? *sutcliffei* Woodward, p. 545, fig. 4.
1953. *Trigonoscorpio*? *sutcliffei* (Woodward). Petrunkevitch, pp. 31–32, figs. 29, 121 (*Trigonoscorpio sutcliffei* in text, p. 31).

The holotype was first considered a Thelyphonida by Woodward (1907, p. 545), but was correctly identified by Petrunkevitch (1953, p. 31) as a scorpion and was referred to the genus *Trigonoscorpio* Petrunkevitch, 1913, an American genus of highly doubtful standing, as it was based on dubious characters (it is known here as a male specimen of *Eoscorpius carbonarius* Meek and Worthen). The reference to *Trigonoscorpio* was, however, considered with question by Petrunkevitch. The figures made by Petrunkevitch, as well as the main parts of his description, are highly erroneous and due entirely to misinterpretation of preservational factors, and failure to develop the specimen.

The holotype is composed of two parts revealing only the dorsal side, with only a triangular piece of the carapace exposed. The coxosternal region is, however, impressed on the part. The coxae abutted this triangular piece, which Petrunkevitch mistakenly accepted for the entire carapace, resulting in his drawing of an improbable scorpion with a very elongated, triangular, narrow and small carapace (1953, fig. 29). Actually, this "carapace" was the triangular corner of the right side of the carapace, from the diagonal formed by the median sulcus, surrounding the median eyes, to the genal angles of the carapace—less than one-third of the actual carapace. Development revealed that this was the case, for it was obvious that such a small carapace simply could not support the great pair of pedipalps and coxae, not to mention the lack of room for the chelicerae. A complete pedipalp was also uncovered with the development of this side. A quite accurate description of this scorpion is now possible.

The carapace is distorted, but shows a triangular depression or sulcus surrounding the median ocellar node. Only a small part of the latter is preserved, but the eyes are impressed through the carapace, revealing that they are round and large. These eyes can be perfectly seen on a rubber cast. A reconstruction (see Text-fig. 32B) shows an elongate rectangular carapace with a deep triangular sulcus and median eyes located on a mound at the anterior. There are no traces of lateral eyes. The coxosternal region is present so that it is possible to reconstruct the entire region (see Text-fig. 32D). The sternum is clearly impressed through the carapace and can be seen under alcohol. It is pentagonal, large, and has only the third pair of coxae abutting it. Petrunkevitch is incorrect in assuming that the fourth pair abuts it. The fourth pair is faintly visible below the third pair, and can be seen abutting the genital plate, which can be outlined faintly under light at a low angle. The second pair of coxae, however, can clearly be seen to curve upward from the anterior of the sternum. These are the maxillary lobes of the second pair of coxae, which means that the second pair met at midsection and that the first pair abutted the second pair. A reconstruction of this important area is therefore possible (see Text-fig. 32D) without danger of error.

The pedipalp shows a short tibia, which is ornamented with a spine anteriorly. The hand is large, with two narrow ridges on the face of the hand on the dorsal side.

The tergites are noteworthy for the conspicuous central carina. No other ornamentation was noted, in fact the bald aspect of the dorsal side is a feature that instantly attracts attention, as few scorpions are like that. Small scales are, however, noted at the base of the carapace and along the posterior of the first tergite and it must be assumed that the other tergites also had this single row of scales along the basal edge. The cauda is represented by fragments of two tergites. The venter of the seventh tergite is ornamented with at least a central carina composed of coarse pustules or granules.

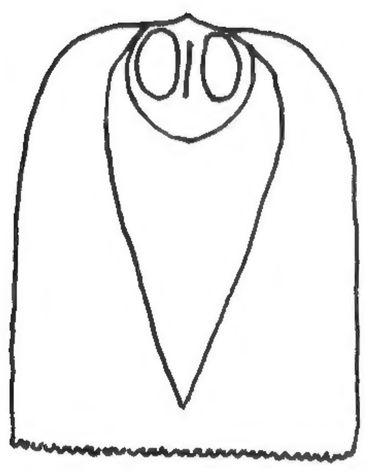
The narrow linear depression running on each side of the central carina, midway between the carina and the lateral edges of the preabdomen, means that this scorpion had a rough trilobation of the preabdominal tergites as is present in some eurypterids such as the genera *Mixopterus* and *Megalograptus* (see Størmer, 1955, pp. 34–36).

The abdominal plates, at least four of which are well-preserved, reveal that they are holosternous, with a well-developed anterior transverse ridge. It is possible that a central carina is present, although it is believed that the apparent carina is an impression formed by the dorsal carina.

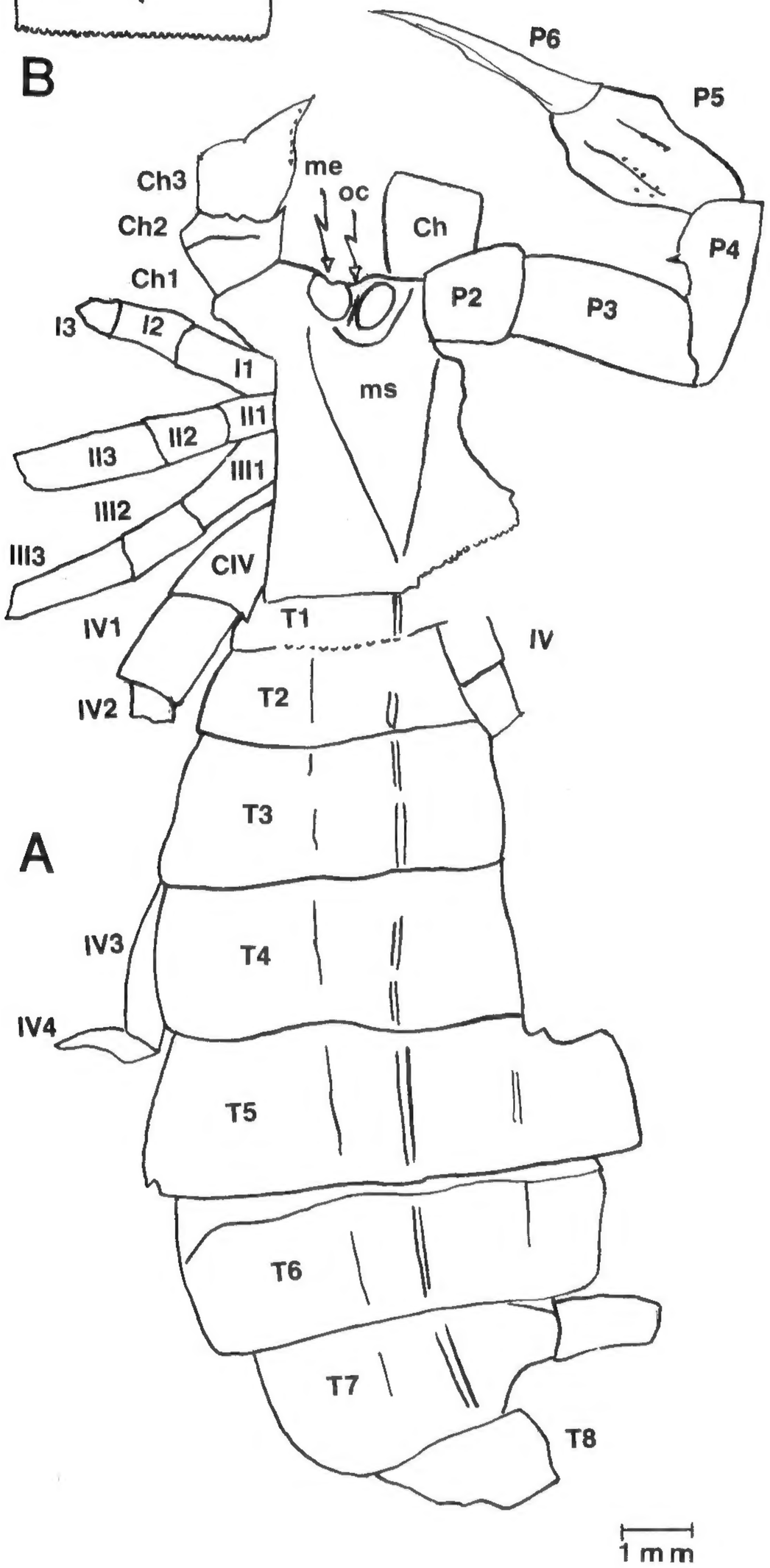
Type information.—Carboniferous, Middle Coal Measures, about 135 feet above the Royley coal, half a mile south of Rochdale Town Hall, Sparth Bottoms, Rochdale, Lancashire, England, and deposited in the

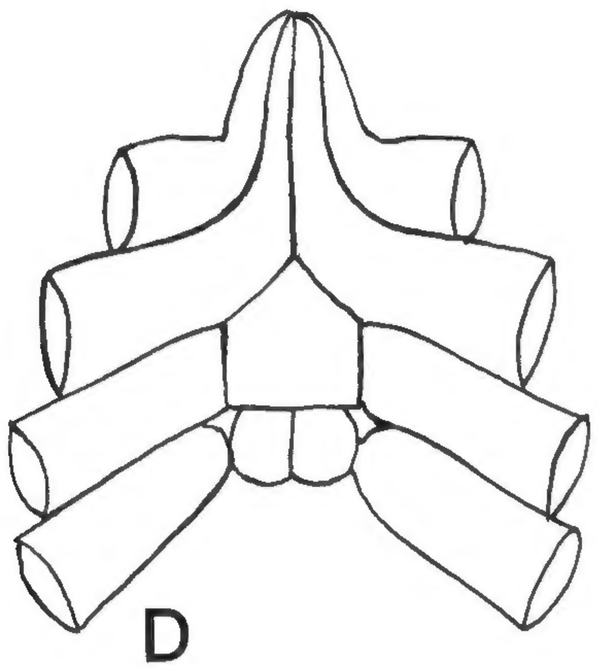
Text-figure 32.—*Heloscorpio sutcliffei* (Woodward). Holotype, BM(NH) In.18564, part and counterpart. From the Carboniferous, Middle Coal Measures, Sparth Bottoms, Rochdale, Lancashire, England. See foldout inside front cover for explanation of abbreviations.

A. Dorsal aspect of the holotype. **B.** Reconstruction of the prosomal carapace. **C.** Ventral counterpart. Note that the abdominal plates might be considered meristosternous. **D.** Reconstruction of coxosternal area.

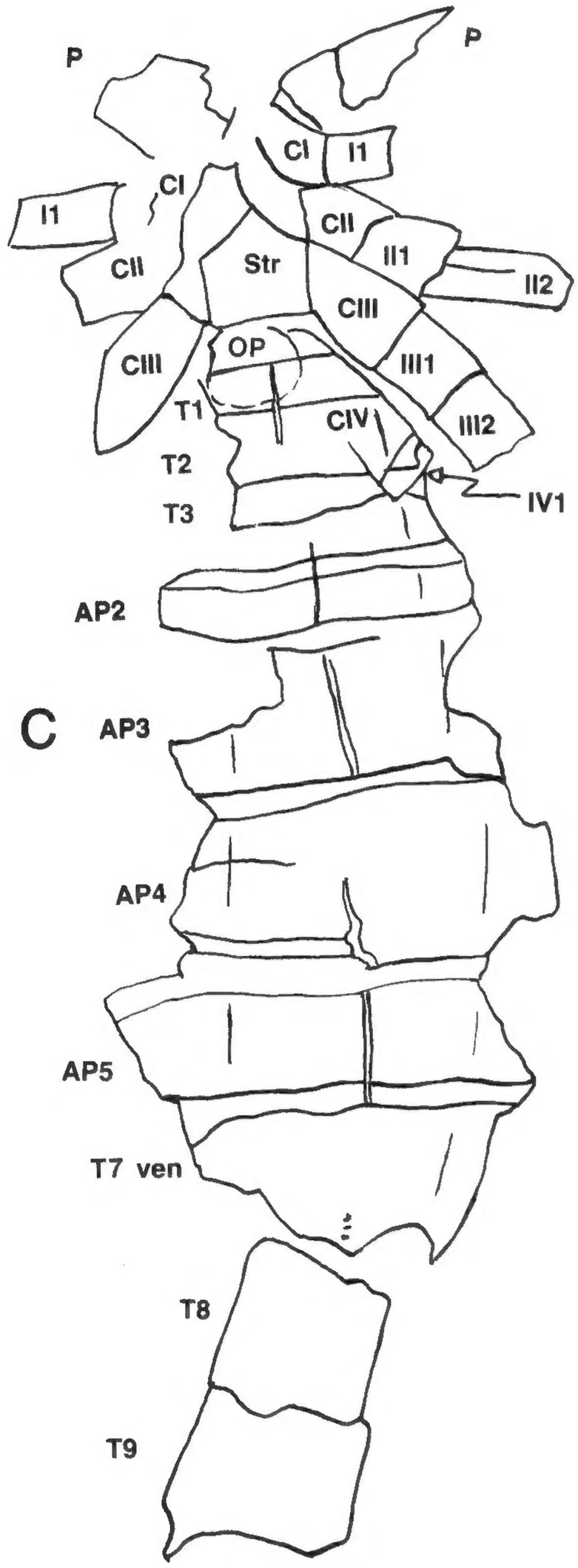


B


P6
P5
P4
P3
P2
Ch
me
oc
Ch3
Ch2
Ch1
I3
I2
I1
II3
II2
II1
III3
III2
III1
CIV
ms
IV1
T1
IV
IV2
T2
T3
A
IV3
T4
IV4
T5
T6
T7
T8
1 mm



D


P
P
CI
I1
CI
I1
CII
CII
Str
II1
II2
CIII
CIII
OP
III1
T1
CIV
III2
T2
IV1
T3
AP2
C
AP3
AP4
AP5
T7 ven
T8
T9

collections of the British Museum (Natural History) where it is registered as BM(NH) In.18564.

Remarks.—There is no scorpion that may be confused with this species. The central carina and trilobation of the preabdomen are sufficient for identification and comparisons are thereby superfluous.

Family **LIASSOSCORPIONIDAE**, new family

Mesophonoidea with carapace having nearly centrally-located median eyes; lateral schizochroal eyes, bulging, elliptical and with narrow rim; gill openings without fringe of large spines, but covered with very small, blunt, spinelike pustules.

Type genus.—*Liassoscorpionides* Bode, 1951.

Remarks.—Details of the above morphologies are given under the new description of *L. schmidti* Bode, which follows. It differs from the rest of the Mesophonoidea in the nearly centrally-located median eyes compared with the anteriorly-located eyes of all the Mesophonidae. Perhaps it is not too speculative to suggest that the Jurassic genus *Liassoscorpionides* is directly descended from forms like *Mesophonus* with its extremely forwardly-located eyes. The type of large glossate process of the carapace, and the large gill openings also point to that development.

Genus **LIASSOSCORPIONIDES**, Bode, 1951 (emend.)

Liassoscorpionidae, devoid of ornamentation and with very large chelicerae.

Type species.—*Liassoscorpionides schmidti* Bode, 1951.

Geological range.—Jurassic.

Remarks.—The large chelicerae, composed of four distinct joints, have a development of the cheliceral flange suture or slot which is also present in the British Triassic *Stenoscorpio gracilis* (Wills) (*fide* Wills, 1947, pp. 76–77). I do not recall seeing the suture or slot, which always occurs on the dorsal side of the second joint of the chelicera, in any other scorpion. Perhaps the comparatively great size of the chelicerae of the Mesozoic scorpions required a suture or slot for greater flexibility, or muscle attachment.

Liassoscorpionides schmidti Bode, 1951
Text-figure 33

1951. *Liassoscorpionides schmidti* Bode, pp. 58–65, fig. 1.
1953. *Liassoscorpionides schmidti* Bode. Petrunkevitch, pp. 38–39 (Scorpiones *incertae sedis*).
1955. *Liassoscorpionides schmidti* Bode. Petrunkevitch, p. 79 (Genera *incertae sedis*).
1962. *Liassoscorpionides schmidti* Bode. Dubinin, p. 433, figs. 1259A–D (Scorpionida *incertae sedis*).

Bode's (1951, pp. 58–65) original description is incorrect in many major points, and this was followed by Petrunkevitch's (1953, pp. 38–39) analysis of Bode's description and figure, which was equally erroneous in assuming a short tail, leading to his incorrect determination that the scorpion was possibly "related to either *Palaeopisthacanthus* or *Typhlopisthacanthus*". No three scorpions could differ more, notwithstanding the fact that all three had fictitious short tails. *Palaeopisthacanthus* is a pulmonate orthostern (a Neoscorpionina), whereas "*Typhlopisthacanthus*" is a junior synonym of the gilled lobostern *Eoscorpius* (Branchioscorpionina). *Liassoscorpionides schmidti* Bode is clearly a Holosternina, belonging to the superfamily Mesophonoidea, for which a new family, the Liassoscorpionidae, has been erected. The specimen is not by any means so poorly preserved as stated (Bode, 1951, p. 58) and all parts, mainly dorsal, are clearly and incontrovertibly preserved.

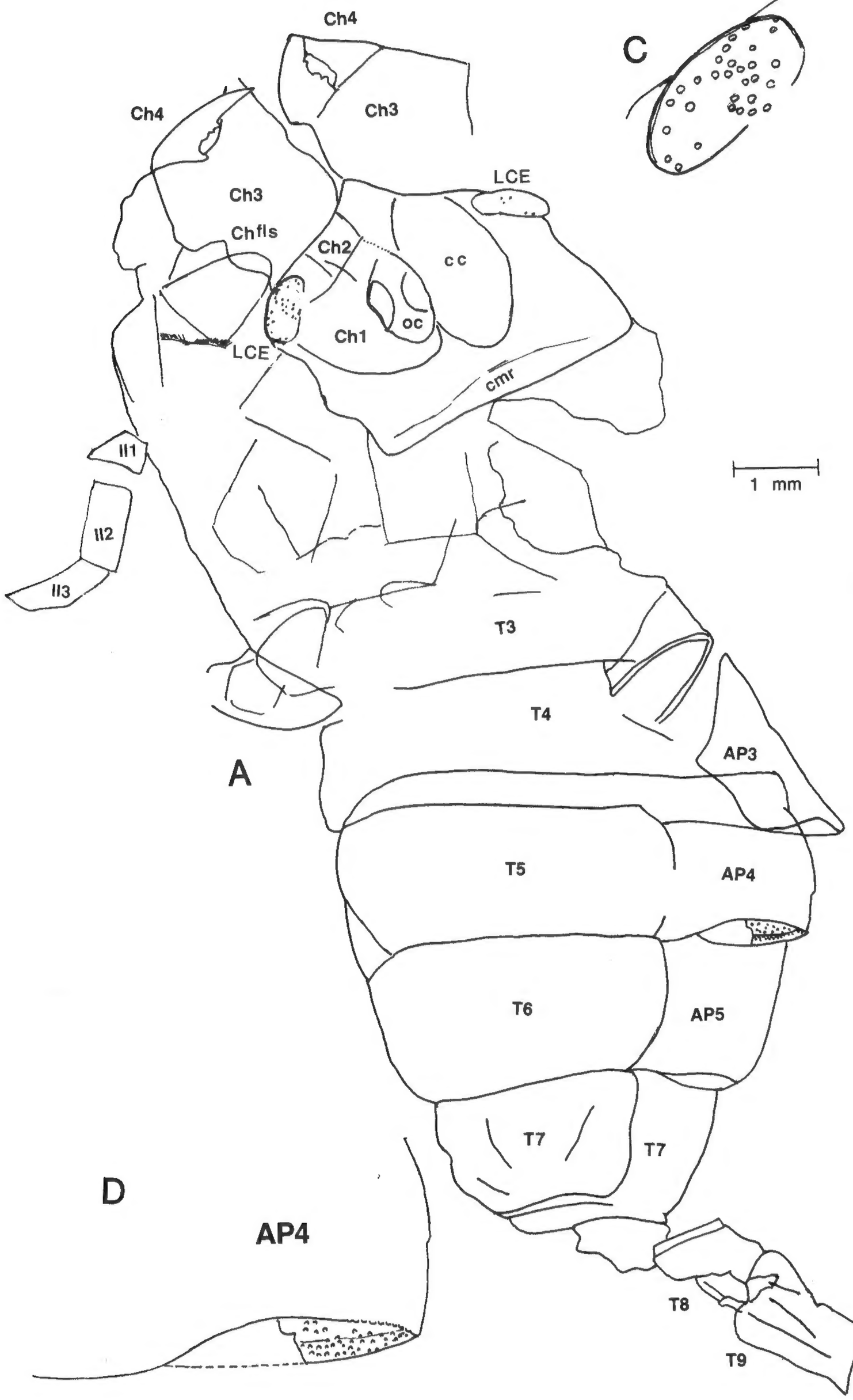
This becomes one of the most interesting scorpions known, as it is a further development of the "*Mesophonus* fauna" of the Triassic and gives us an insight, although limited, into the Jurassic forms, at least the aquatic Branchioscorpionina. The specimen is associated with marine fossils on the same level. The limestone is slightly oolitic.

Studies of this scorpion were made both in the dry state and under alcohol, revealing many morphological details. The original colors were preserved and are shiny dark brown throughout.

Bode (1951, p. 68, fig. 1) shows morphological features that are not present, and were erroneously determined. These include: 1) The alimentary canal: The right edge of the tergites, in part, was mistaken for the canal, and I confess that the upper part shown is inexplicable. It is not present. 2) According to Bode, the pulmonate type of stigmata occur on the last three preabdominal tergites. This is completely erroneous as the scorpion retains abdominal plates and not sternites,

Text-figure 33.—*Liassoscorpionides schmidti* Bode. Holotype, GUM 525-1, part and counterpart. From the Jurassic (Lias epsilon), marl pit at Hondelage b. Braunschweig, West Germany. See foldout inside front cover for explanation of abbreviations.

A. One side of the two-piece holotype. The organism was squashed during fossilization so as to expose both dorsal and ventral features on the same surface of the specimen. In Bode's description (1951), the right edge of the posterior tergites (**T4–7**) of this complex preservation were mistaken for evidence of the gut, and the presence of both tergites and abdominal plates (**AP**) in the preservation was not realized. He extended the "gut" forward without any evidence for the extension being present on the specimen. He also erroneously identified stigmata, although gill openings are present at the base of each abdominal plate (**AP3–5**). **B.** A reconstruction of the holotype showing the slim mesosoma (rather than broad, as Bode thought), and the extraordinary prosomal carapace and gigantic chelicerae, which are faithfully drawn. **C.** Showing the facetted left lateral eye of the holotype, with some of the lenses preserved. **D.** Detail of the fourth abdominal plate (**AP4**) showing the gill opening on the right side of the specimen.


Ch4
Ch4
Ch3
Ch3
LCE
Chfls
Ch2
cc
oc
Ch1
LCE
cmr
II1
II2
II3
T3
T4
AP3
T5
AP4
T6
AP5
T7
T7
T8
T9
A
1 mm
C
D
AP4
B

and gill openings (not stigmata!) are perfectly developed at the base of each abdominal plate. It is sufficient to note that stigmata were also placed on the seventh tergite (ventral), an impossibility in any scorpion, fossil or living. 3) Only two tergites of the cauda are preserved. Obviously these two tergites have been crushed laterally, but are not narrow, as attested by the basal attachment to the preabdomen (No. 7 tergite), which is normal and not as previously thought (Bode, 1951, p. 65; Petrunkevitch, 1953, p. 38; 1955, p. 79).

With these changes, and others noted, a new description of the holotype is possible, which assigns the genus to the Mesophonoidea.

The holotype is preserved so that most of the dorsal side is present with the interior of the venter of the right side exposed.

The carapace is known for the first time in detail. It is subquadrate, wider than long, with a large anteriorly-pointed glossate process and with a raised basal marginal rim that is wide at midsection and tapers to either side. Located on the central part of each half are raised, elliptical, cephalic cheeks. The median eyes are located on the prominent median eye node. These eyes appear elliptical and are only faintly preserved, but entirely visible under alcohol. In life, the eyes were probably round and became elliptical by compression. At the anterolateral corners are the many-facetted, bulbous, elliptical eyes, which are bordered by a slight ridge surrounding the eyes. This margin is seen on the left eye (see Text-figs. 33A, C) and the eye proper is composed of about 200 round, certainly biconvex, lenses.

Unfortunately the coxosternal area is not known, occurring in an area that consists of a mish-mash of cuticle that is impossible, at least for me, to unravel with any degree of certainty. Only the second leg of the left side is preserved, and this consists of the trochanter, femur and patella (see Text-fig. 33A).

The last five tergites of the preabdomen are preserved and show a gradual increase in size posteriorly. The last (T7) is complete and reveals a large, wide, attachment area for the cauda. Two carinae are present. What remains of the cauda consists only of two segments out of the five, but it should not be mistaken for a thin or short tail. It is merely distorted.

The chelicerae are noteworthy both for their good preservation and for their enormity. They are, in fact, longer than the carapace, and clearly consist of four joints, as in all Holosternina. The first joint, or coxa, is rounded, distinctly calathiform, and truncated at the anterior. The second joint consists of a band-like segment, sutured at the dorsal side, although this suture-like structure may represent the junction of a slot. In either case it is interesting to see that some of the British Triassic forms also have this development. The third and fourth joints are like other scorpions, with teeth developed on the chelae, but not good enough for description (see Text-figs. 33A, B).

The venter reveals the third to fifth abdominal plates of a holosternous scorpion from the inside. The gill openings of each abdominal plate are perfectly preserved. These consist of large slits at the junction between the abdominal plate and the doublure; the edges of both, and the inside, are covered with very small, triangular mucrones. No spines were developed (see Text-fig. 33D).

The ventral side of the seventh tergite is devoid of any carinae in the preserved part.

The first two tergites of the cauda are preserved and, other than to note that two superior crests surmount each tergite, no further description is possible. The tergites have obviously been distorted laterally, giving a superficial and incorrect aspect of being thin rather than of normal thickness (see Text-figs. 33A, B).

Measurements (in mm) of GUM 525-1.—

Estimated total length restored (chelicerae to end of cauda):	18.0
Length of carapace at midsection:	3.1
Lateral eye length:	0.8
Lateral eye width:	0.3

Type information.—Jurassic: Upper Lias, Lias epsilon, Mergelgrube, Hondelage b. Braunschweig, Germany. It is registered as No. 525-1 in the Geological-Paleontological Institute and Museum, Georg-August University, Göttingen, Germany [abbreviated herein as GUM].

Remarks.—This species, being the last known record of the Branchioscorpionina, and in particular, the Holosternina, is important in showing the gradual backward displacement of the median eyes to a nearly central position such as is present in modern scorpions. The holosterns very likely never left the water for extended periods as the gills had to be bathed with water.

On the same surface with the holotype are a number of fragments of scorpion integument and joints. None is identifiable, but they indicate that if the exact horizon could be located again, further specimens of scorpions could be obtained. The importance of further finds is assuredly of great interest, and I urge any collector to try to determine the exact horizon. I know of few stratigraphic levels which could furnish anything as interesting as these Jurassic scorpions. The locality promises much and could surpass the British scorpion localities in interest, uniqueness, and the possibility of finding further important evolutionary data. These specimens will be found to be composed of original cuticle and therefore the Holm–Wills technique (see Wills, 1910, p. 303; Wills, 1947, pp. 136–137) is possible, thus freeing the scorpionid parts from the matrix.

Complete specimens, or those showing the important coxosternal areas, should not be subjected to dissolution in acids, as they come apart, in many cases making reconstruction quite difficult. Nevertheless, slabs with obvious scorpion parts can be dissolved in the hope of freeing other and better specimens, as Wills did with specimens from the British Triassic (1947).

Family **PHOXISCORPIONIDAE**, new family

Mesophonoidea with elongate hexagonal sternum. Carapace without lateral compound eyes. Enormously developed pectinal plate without median organ.

Type genus.—*Phoxiscorpio,* n. gen.

Remarks.—The only family with which the Phoxiscorpionidae may be confused is the Centromachidae. At one time (not published) I had included both in an emended superfamily Centromachoidea, but the presence of maxillary lobes developed on the third pair of coxae not only abutting the sternum, but meeting in front of the sternum, is a major development and taxonomic consideration in the Centromachoidea, which the Phoxiscorpionidae does not show.

Genus **PHOXISCORPIO**, new genus

Phoxiscorpionidae with subquadrate carapace, glossate on mid-anterior margin, and large anteriorly-located median eyes. Pectines large with unusually narrow and small teeth.

Derivatio nominis.—*phoxos* (Gr.) = pointed, peaked.

Type species.—*Phoxiscorpio peachi,* n. gen., n. sp.

Geological range.—Lower Carboniferous (middle Viséan).

Phoxiscorpio peachi, new species
Text-figures 34, 110E

A poorly-preserved specimen approximately 60 mm in length when alive. Most of the underside is revealed and, dorsally, patches of the carapace, some tergites, and all of the basal three joints of the right pedipalp.

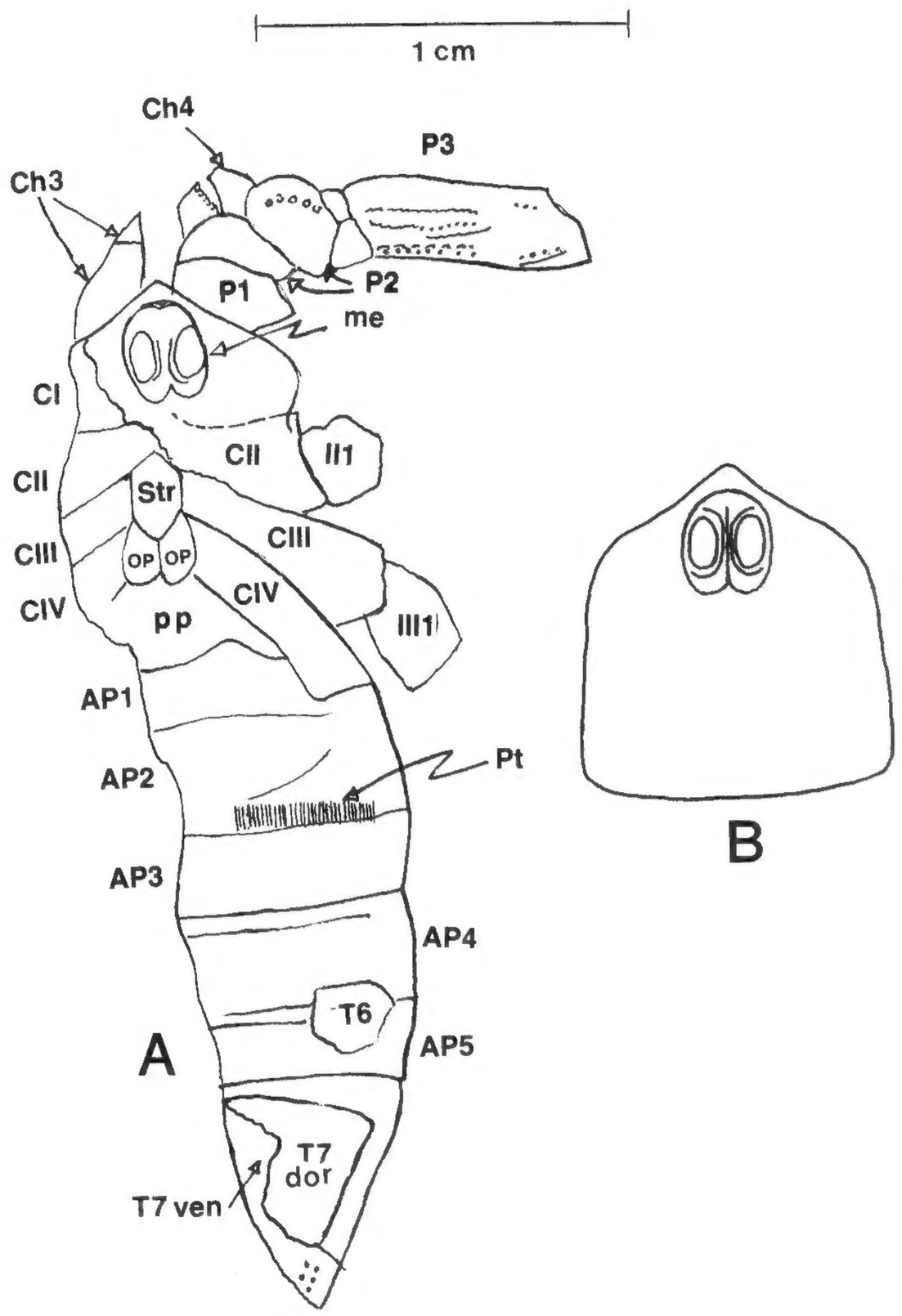
Although most of the dorsal side of the carapace was not preserved, much can be interpreted from the parts present (see Text-fig. 34A). The eye node occupies a frontal median position, is elliptical, with large elliptical eye sockets, bounded above by rather heavy orbital ridges. The median eyes are elliptical, but probably were round in life, as they are now in a compressed state. The large median eyes indicate that there should be no lateral compound eyes, nor does the right lateral angle of the carapace reveal any. It doesn't seem speculative to consider the carapace to be subquadrate, rounded at the anterolateral angles, produced to a median point anteriorly, and truncated at the base, as in most scorpions. A restoration is given in Text-figure 34B.

The pedipalp (Text-fig. 34A) is preserved in dorsal aspect and undoubtedly is a stout appendage. Only the first three joints are preserved.

The trochanter (**P2**) is noteworthy for being very large, and seems to be divided into two joints. This is a common condition in many living scorpions, and I have always believed that the pedipalp trochanter was composed of two ankylosed joints. This may be the case here, but it is difficult to ascertain whether it is two separate joints or one. A ridge of granules occurs across the uppermost part of the "second" trochanter.

The femur (**P3**), also seen in dorsal aspect, reveals a line of setaceous granules at the back and at least one row of setaceous granules along the central part.

The coxosternal region shows an elongate hexagonal



Text-figure 34.—*Phoxiscorpio peachi,* n. gen., n. sp. Holotype, GSE 2140. From the Lower Caroniferous (middle Viséan), Dalmeny railway cutting, near Edinburgh, Scotland. See foldout inside front cover for explanation of abbreviations.

A. Carapace, entire right chelicera and right pedipalp seen from the dorsal side; the rest seen from the inside of the ventral side. Note: the pectinal plate has not been described in the text. **B.** Restored prosomal carapace.

sternum and two long, rather elliptical, opercular plates that fit at the base of the sternum. The fourth pair of coxae abuts the opercular plate whereas the third pair abuts the sternum. The first two pairs of coxae meet at midsection and there are indications of a slight maxillary lobe on the second pair. This would indicate that both the first and second pairs of coxae have short maxillary lobes. Both almost certainly meet at the midline.

Mainly the ventral side of the postabdomen is preserved, and it is important to record that the abdominal plates are holosternous. All abdominal plates have a narrow transverse ridge along the anterior margin.

The pectines were covered by the abdominal plates and are seen from the dorsal side of the plates, but the teeth of the pectines are impressed through and are very narrow and small, like those shown by Størmer (1963, p. 60), for the holotype of *Centromachus euglyptus* (Peach). The pectinal plate, devoid of a median organ, is enormously developed.

Type information.—It is preserved in dark gray-black shale, along with ostracodes, in the Lower Carboniferous (middle Viséan) at Dalmeny railway cutting near Edinburgh, Scotland, and is registered as GSE 2140 in the collections of the Institute of Geological Sciences at Edinburgh, Scotland.

Derivatio nominis.—Named in honor of B. N. Peach, whose contributions to Scottish paleontology, particularly his early fossil scorpion work, need no further comment here.

Remarks.—At first I had mistaken this specimen for *Centromachus euglyptus* (Peach), but the differences became apparent, particularly in the shape of the sternum. The sternum in *Phoxiscorpio peachi* is hexagonal rather than subtriangular, and the coxae of the last three pairs of legs are distinctly longer. More important is the presence of maxillary lobes on the third pair of coxae and the presence of the trapezoidal pectinal plate with median organ in *Centromachus euglyptus* (Peach), in contrast to the lack of maxillary lobes on the third pair of coxae, and the extremely large pectinal plate without a trace of a median organ in the new species.

The specimen had been badly developed by chisels and, although what is left is fragmentary, much can be revealed in the dry state, by the use of various types of light, by immersion in alcohol, and from a latex cast.

Family **WILLSISCORPIONIDAE**, new family

Holosternina, possibly referable to the superfamily Mesophonoidea, without lateral facetted eyes, and with anteriorly-located median eyes in line with or anterior to the anterior margin of the carapace. Gill chamber opening slitlike, located on the doublure and opening internally and dorsally to the abdominal plate. Gill lamella bounded by small spinelets.

Type genus.—*Willsiscorpio,* n. gen.

Genus **WILLSISCORPIO**, new genus

Willsiscorpionidae with quadrate carapace with large median eyes placed on a large anterior, rounded glossate process. Elevated dorsal, shieldlike, undivided cephalic area is well-delineated by the ornamentation.

Derivatio nominis.—Named in honor of Leonard J. Wills, who discovered and so ably described the British Triassic scorpions.

Type species.—*Mesophonus bromsgroviensis* Wills, 1910.

Geological range.—Triassic.

Remarks.—Although included in the genus *Mesophonus* by Wills (1910, 1947), the new genus differs greatly in the lack of lateral facetted eyes and in the undivided cephalic shield of the carapace, which in *Mesophonus* is divided into two elevated cheeks separated by a median sulcus. The presence or absence of lateral facetted eyes, as stated above, is not a secondary sex character as proposed by Wills (1947, pp. 20–21), but a fundamental character of at least family level.

Willsiscorpio bromsgroviensis (Wills, 1910)

1910. *Mesophonus bromsgroviensis* Wills, pp. 313–314, pl. xxiii, figs. 1, 2, 4, 5, 7; pl. xxvi, fig. 11.
1910. *Mesophonus gracilis* Wills (*partim*), p. 318, pl. xxv, fig. 10.
1910. *Mesophonus* sp. Wills, pl. xxii, figs. 6, 10; pl. xxvi, figs. 3, 10.
1947. *Mesophonus bromsgroviensis* Wills. Wills (*partim*), pp. 108–115, pl. I, figs. 1–6; pl. III, fig. 1; pl. IV, figs. 1, 2; pl. VI, figs. 1, 2, 4–7; pl. XI, figs. 9, 10; pl. XII, figs. 12–14; text-figs. 3A, 5A, B, 7, 10, 46A–C, E, F; not *Mesophonus bromsgroviensis* ? Wills, pp. 35, 39, 110; pl. VI, fig. 9; text-fig. 14 (specimen 0163).

The Wills coll. specimens which are included under this species are: SM 158 (lectotype), 9, 13, 18, 23, 35, 47, 074, 080, 098, 101, 195, 208, 212, 213 (*fide* Wills, 1947, p. 108), 215, 220, 0235, 270, 273, 275, 0280, 295.

Type information.—This fine species is known from the Triassic Lower Keuper Sandstone Series, Bromsgrove, near Birmingham, and from a boring at Messrs. Southalls (B'ham) Ltd. works at Charford Mills, Birmingham, England.

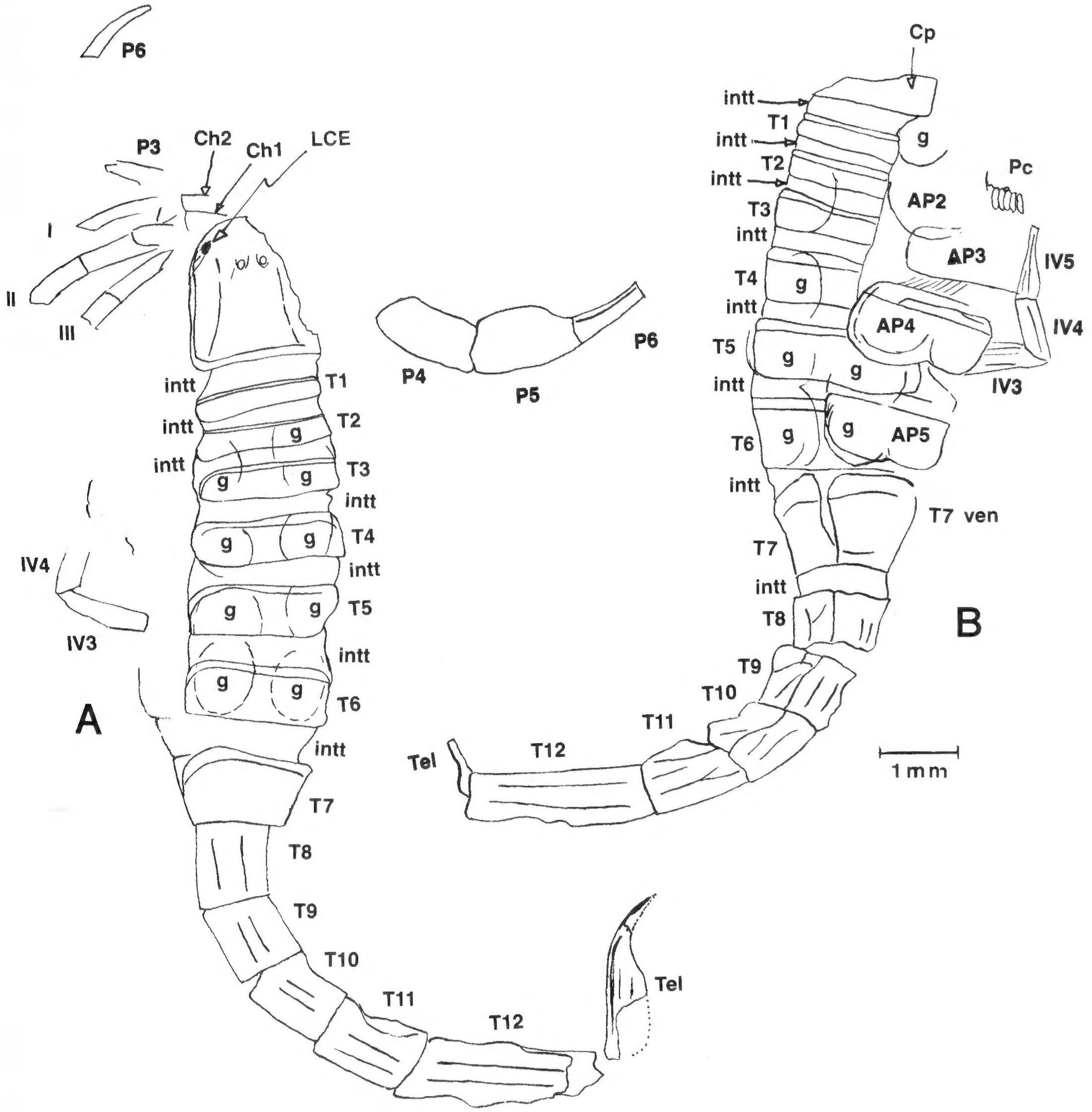
Superfamily **EOCTONOIDEA**, new superfamily

Holosternina with the first two pairs of coxae in front of the sternum and with maxillary lobes developed; first pair extends further anteriorly than the second pair; third and fourth pairs abut the sternum.

Type family.—Eoctonidae, new family.

Remarks.—This superfamily is an intermediate group between the Lobosternina and the Holosternina.

It is closer to the Holosternina, whereas the superfamily Pseudobuthiscorpioidea is closer to the Lobosternina. In my opinion, these two superfamilies connected the two suborders, namely through the Eoctonoidea into the Pseudobuthiscorpioidea. The development of the coxosternal areas bears this out. These intermediates are therefore among the most important and interesting of the fossil scorpions.



Text-figure 35.—*Eoctonus miniatus* Petrunkevitch. Holotype, YPM 131. Upper Carboniferous (Pennsylvanian), presumably from the Carbondale Formation, Lower Francis Creek Shale, Mazon Creek area of Grundy Co., IL. This specimen is of particular interest since it proves that the gills were attached to the body wall, rather than to the abdominal plates, just as the lungs are in living scorpions. It is a male as indicated by the extra-long twelfth tergite (**T12**). See foldout inside front cover for explanation of abbreviations.

A. Dorsal side. **B.** Counterpart, showing ventral features. Note the lobate abdominal plates which, although posteriorly lobate, appear at be at a grade intermediate between holosternous and lobosternous condition.

Family **EOCTONIDAE**, new family

Eoctonoidea with intramarginal, small, lateral schizochroal eyes and with median ocelli placed in the center of the anterior half of the carapace.

Type genus.—*Eoctonus* Petrunkevitch, 1913.

Remarks.—See remarks under description of *Eoctonus miniatus* Petrunkevitch (below).

Genus **EOCTONUS** Petrunkevitch, 1913

Eoctonidae with elongate subrectangular lanceolate carapace with indistinct lateral, longitudinal ridges.

Type species.—*Eoctonus miniatus* Petrunkevitch, 1913.

Geological range.—Upper Pennsylvanian.

Eoctonus miniatus Petrunkevitch, 1913
Plate 4; Text-figures 35, 37–39, 110G

1913. *Eoctonus miniatus* Petrunkevitch (*partim*), pp. 51–52, pl. 3, fig. 14, text-fig. 15; not p. 52, pl. 3, fig. 15 (paratype No. 132) (=*Paraisobuthus virginiae,* n. gen., n. sp.).
1949. *Eoctonus miniatus* Petrunkevitch. Petrunkevitch, p. 137.
1953. *Eoctonus miniatus* Petrunkevitch. Petrunkevitch, p. 16, figs. 40–43.
1955. *Eoctonus miniatus* Petrunkevitch. Petrunkevitch, p. 73, fig. 41(2).
1962. *Eoctonus miniatus* Petrunkevitch. Dubinin, p. 428, fig. 1229.

The holotype, YPM 131, is preserved in a nodule consisting of two halves showing most of the dorsal and ventral sides. The part showing the coxosternal region is not preserved, nor are most of the appendages. The cephalothorax is very elongate. The genal corners form right angles and the anterolateral margins are rounded. The anterior margin is also rounded. In general aspect it is lanceolate.

The median ocelli are prominent, round, and about one-third of the length from the anterior edge, or located midway in the anterior half of the carapace, and with strong interocular ridges.

The lateral eyes are schizochroal, intramarginal and on the anterolateral margins. Although individual facets cannot be described exactly as to shape (they are rounded in another specimen), approximately eight of these facets or individual eyes occur in a roughly reniform cluster or aggregate. The long axis of the kidney-shaped lateral eye is obliquely located on the carapace. The individual eyes are much smaller than the simple lateral ocelli, such as occur in modern scorpions or in the terrestrial Carboniferous scorpion *Palaeopisthacanthus schucherti* Petrunkevitch.

The only ornamentation on the carapace consists of faint traces of two longitudinal linear ridges running from the lateral eyes to the base. A definite wide marginal and basal rim occurs. The entire preabdomen is preserved, although the last segment has been partly turned over. Each tergite had been pulled apart at burial to reveal a considerable expanse of intersegmental skin, indicating great flexibility in life. All the tergites are progressively longer posteriorly, and each is bounded anteriorly by a well-developed marginal ridge. There is no ornamentation on the tergites.

The appendages of the prosoma are not well enough preserved, except at their bases, to merit description. The pedipalp, however, is largely preserved. The tibia of the pedipalp is relatively short and stout, and is covered with cuticle that might best be described as very finely rugose, although not punctate, on the dorsal side. The hand of the palp is relatively wide and rounded. Enough of the free finger was preserved to show that it has a well-developed dorsal ridge. There are no denticles preserved on the inner edge of the fingers.

The combs are almost obliterated and approximately six teeth are noted on the left side of the nodule. These are of the long, slender type and probably represent only a small part of what actually existed. Fulcra occur in this species as at least one of these plates was noted.

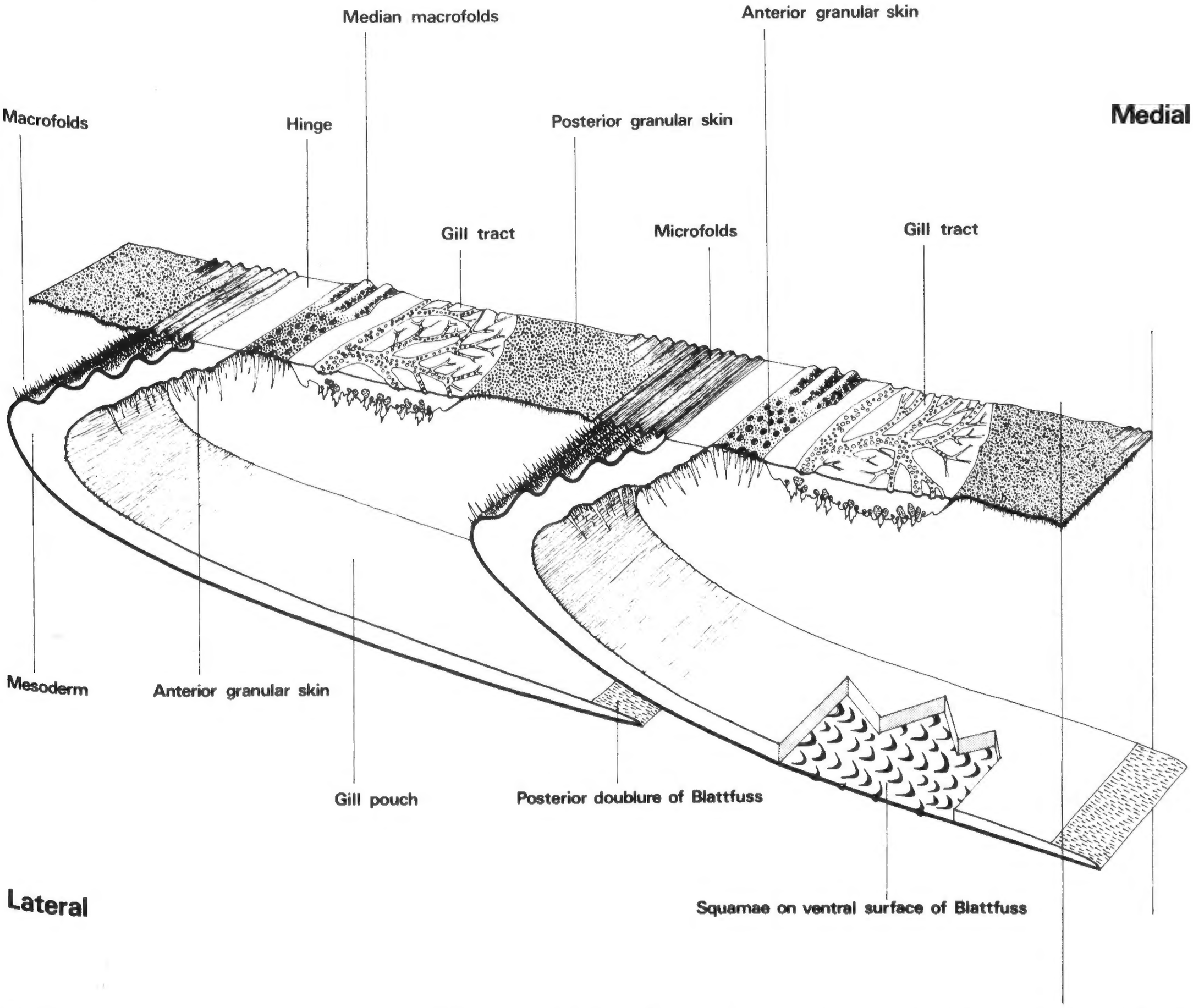
By far the most interesting thing about this scorpion is the presence of large, paired, oval areas that are impressed as rounded ridges through the dorsal side of the tergites. These oval areas occur along the trunk of the scorpion in the area where the respiratory organs should be located. The abdominal plates have been displaced to the left side of the specimen and thus these areas would have to be structures that are not connected to the plates. It appears that these oval structures are the remains of the gills and that nine of them were preserved in this particular specimen. There can be no doubt that there were five pairs originally. It therefore seems that the gills were, in part at least, rounded or oval structures, almost as large as an individual half or lobe of the holosternous plate. The ventral part of the holotype, which is preserved as an impression of the inner side, clearly reveals these structures as deep, rounded depressions on the abdominal plates, exactly as in the Eurypterida (see Text-fig. 36). In other scorpions, such as *Eoscorpius, Palaeobuthus,* etc., identical structures have been described where they occur as impressions on the inner side of the lobostern and meristostern abdominal plates. As shown by the holotype of *E. miniatus,* the structures were not attached to the abdominal plates, but to the body, and floated free from the abdominal plates. The covering abdominal plates have a round pouch or gill chamber to accommodate the large gills. The abdominal plates are holosternous, with a very slight emargination in the middle of the posterior margin, and with well-developed anterior marginal ridges.

The complete postabdomen is preserved and, at the upper part, the tergites have been turned on their sides; therefore it is not possible to determine the number of ridges. On the last two tergites, two well-formed carinae can be noted on the dorsal surface. The vesicle was exposed for the first time (although Petrunkevitch shows a drawing of this, which he undoubtedly took from YPM 132, a small specimen which is described herein as *Paraisobuthus virginiae,* n. sp.). The vesicle is very long, with the aculeus slightly curved and with a well-formed carina on each side of the telson. Two other indefinite ridges were noted below this but were not of the prominent type found toward the dorsal part of the long vesicle. The only ornamentation occurs in the form of punctations, which are probably setaceous, along the carinae. The long twelfth tergite indicates, without a doubt, that the holotype is a male.

Measurements of this specimen are given in Petrunkevitch (1913, p. 51). The vesicle, which was unknown at the time, is approximately 2 mm long.

Type information.—Upper Pennsylvanian from the Francis Creek Shale, at Mazon Creek, Illinois, registered as YPM 131 in the Yale Peabody Museum of Natural History.

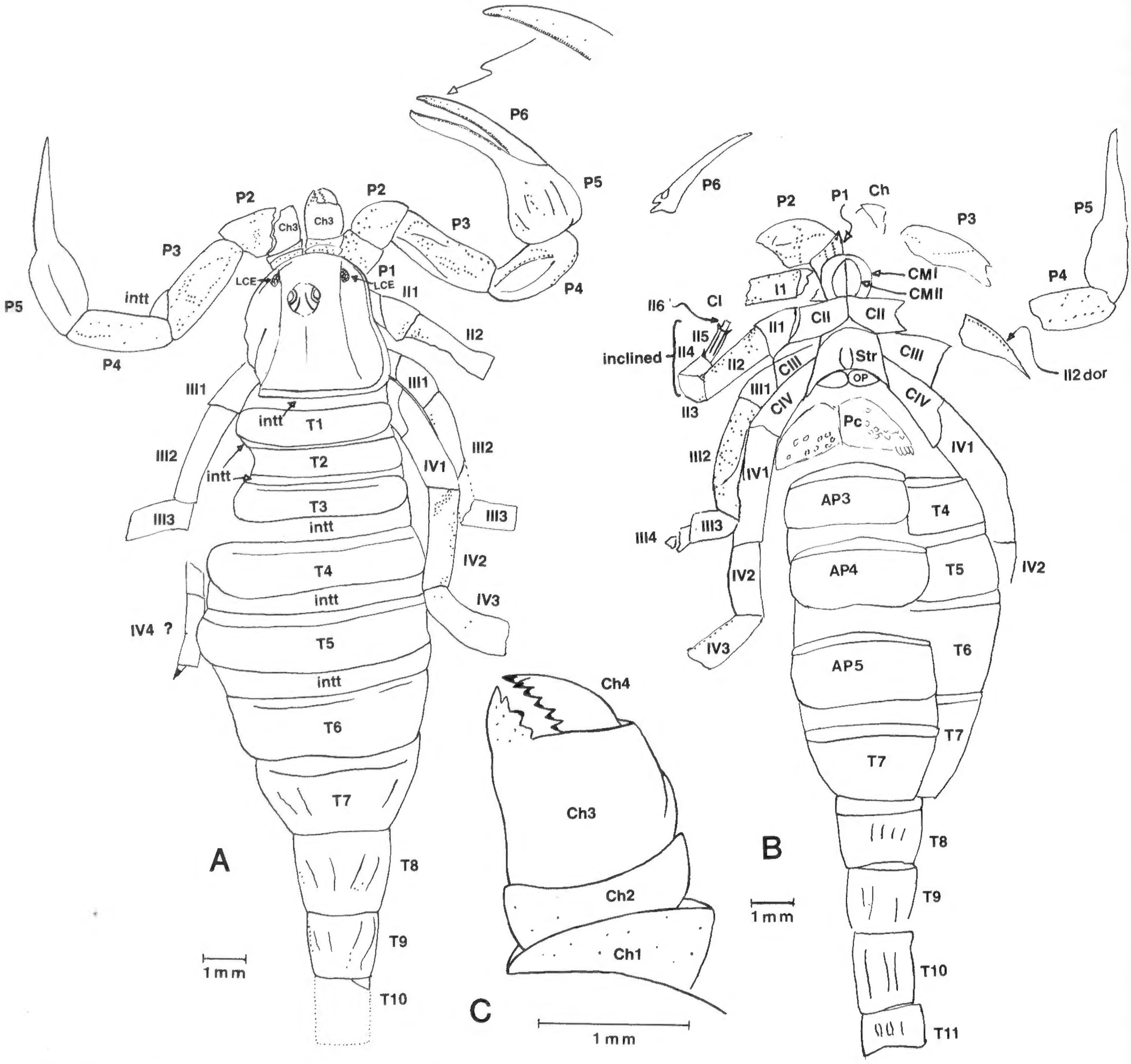
Another specimen (see Pl. 4; Text-fig. 37) consists of an ironstone concretion preserved in two parts, one of which contains the dorsal side and the other the ventral side. Both sides are very well preserved, show-



Text-figure 36.—*Tarsopterella scotica* (Woodward). An eurypterid from the Devonian of Scotland. This reconstruction of the gill chamber by Charles E. Waterston (1975, fig. 3) is introduced for comparison. This type of gill apparatus is thought to be the same in primitive scorpions of the infraorders Lobosternina and Holosternina. Reproduced by kind permission of C. E. Waterston, and Stefan Bengtson, editor, *Fossils and Strata.*

ing excellent detail. The specimen has been studied mainly in a dry state, although some structures were visible under alcohol. It was collected by Ray Bandringa from Pit 11 (Essex Fauna), Upper Pennsylvanian, Francis Creek Shale, on the Will Co.–Kankakee Co. line, Illinois, commonly considered as part of the Mazon Creek area. The specimen is now in the collections of the Field Museum of Natural History where it is registered as FMNH (PE) 16498 (part and counterpart).

The carapace is broadly rounded on the anterior, truncated at the posterior and with the sides converging anteriorly. A prominent marginal rim occurs along the posterior and lateral sides. Two suturelike ridges separate the carapace diagonally and a narrow sulcus is present directly behind the ocellar node. The ocellar



Text-figure 37.—*Eoctonus miniatus* Petrunkevitch. Ray Bandringa collection, FMNH (PE) 16498 (part and counterpart). Upper Carboniferous (Pennsylvanian), Carbondale Formation, Francis Creek Shale, Mazon Creek area, Pit 11 (Essex fauna), Will Co.–Kankakee Co. line, IL. See foldout inside front cover for explanation of abbreviations.

A. Dorsal view from the inside. Note the fine denticulation of the pedipalp fingers. **B.** Counterpart, showing ventral features seen from the inside and dorsal components from the outside. The abdominal plates are essentially holosternous. **C.** Restored right chelicera seen from the dorsal side.

node is nearly round and is located in the center of the anterior half of the carapace, much as occurs in living scorpions.

The median eyes are round and are separated from each other by prominent ocular ridges. Of particular interest is a verification of the lateral compound eyes. These are located well within the margin of the carapace and anterior to the median eyes. These lateral eyes are roughly reniform and approximately eight small rounded eyes occur within the confines of the reniform area. The greatest length is 0.11 mm and the width is about half that.

The chelicerae are small, much as in living scorpions, but consist of four joints instead of three. The first two are very short, whereas the third comprises the hand with the immovable chela, which is armed with several large teeth. The free finger, armed with denticles, is curved much like in living scorpions. The preservation of the denticles did not permit a clear definition of their structure or arrangement other than to know that they were present.

The pedipalp is a massive structure with a rather long and stout chela, and in all respects resembles that of many living scorpions. The trochanter is triangular in general outline, whereas the femur and tibia are stout with some ridges apparently present. These three joints are covered with numerous setal holes which may have been trichobothria. These trichobothrialike openings occur in distinct rows much as found in some of the living scorpions.

The chela has a wide hand and again evidence of ridges is present. The two fingers are very long, the immovable finger being curved slightly backwards, whereas the free finger has a slight forward bend. Definite small denticles in the shape of linear structures occur along both edges. The hand also is covered with some setal openings that appear to be in series.

The four walking legs are preserved only in part, and must have been highly hirsute. Only one spur, apparently the basitarsal spur, was noted, and that occurred on the third leg. However, little can be said about spurs on the legs as preservation did not permit description. The second leg, however, does have two tarsal spurs and one basitarsal spur present. It is quite possible that two basitarsal and two tarsal spurs were present in life on all four pairs of legs.

The coxosternal region is of unusual interest. The sternum is very large, pentagonal in shape with an inverted rounded area at the posterior, and the first coxa extends forward with a rounded, elongate maxillary lobe. Maxillary lobes are also present on the second coxa, which extends almost to the end of the first pair of maxillary lobes. The third and fourth coxae abut against the large pentagonal sternum.

The pectines are small, not very wide, but are quite long, making each pectine appear triangular with a rounded anterior edge. They were not very clearly preserved, but enough was noted to ascertain that rounded sclerites cover the rachis and that the teeth were small and elongate, and about sixteen teeth probably occurred on each pectine. The genital operculum lies directly posterior to the wide sternum and is composed of two teardrop plates that fit in the inverted circular part at the base of the sternum.

The preabdomen consists of the usual seven tergites dorsally, with each tergite increasing in length posteriorly to reach the greatest width at the fifth tergite. All tergites are smooth and without any ornamentation. Each of the tergites is bounded anteriorly by a transverse ridge. One of the peculiarities about this scorpion, which was also noted on the holotype, is that a considerable area of intersegmental tissue occurs between each of the tergites. It is thought that this is actual and not a condition of ecdysis, and that this scorpion was particularly elongated along the preabdomen, was quite sinuous in life, and had a highly flexible body. This characteristic is present in living Chactidae and Diplocentridae.

The abdominal plates are entirely holosternous; each is quite long and bounded along the anterior by a transverse ridge. The abdominal plates also do not have any ornamentation whatsoever. The postabdomen was only partly preserved; only the anterior tergites were present. These show that all had numerous ridges, although it was not possible to ascertain how these ridges were in life. Nevertheless, their presence has been noted toward the lateral parts, and on the dorsal side, at least, there are a few setal openings. No other ornamentation has been noted.

The wide mesosoma indicates that this specimen is a female.

Measurements (in mm) of FMNH (PE) 16498.—

Prosoma:	
Width at base:	3.8
Greatest width:	3.2
Length:	3.4
Median eyes:	
Distance from anterior margin:	0.8
Distance from posterior margin:	2.0
Distance from lateral margin:	1.5
Diameter:	0.11
Chela length:	4.7
Hand width:	1.1
Hand length:	1.8
Femur length (dorsoventral):	2.8
Tibia length (dorsoventral):	2.5
Free finger length:	3.2
No. of rows of denticles:	
Present but not possible to determine if more than one row occurs	

Measurements of FMNH (PE) 16498 (cont'd.)

Pectine:

No. of teeth: 16 (estimated from the ones present)

Mesosoma and metasoma:

	length of tergite	greatest width of tergite
No. 1	0.5	3.6
No. 2	0.6	(covered)
No. 3	0.7	4.2
No. 4	1.0	4.6
No. 5	1.3	5.0
No. 6	1.6	4.4
No. 7	1.9	3.5 (anterior) 1.8 (posterior)
No. 8	1.8	1.8
No. 9	1.8	1.5
No. 10	2.0	1.3

Abdominal plate:

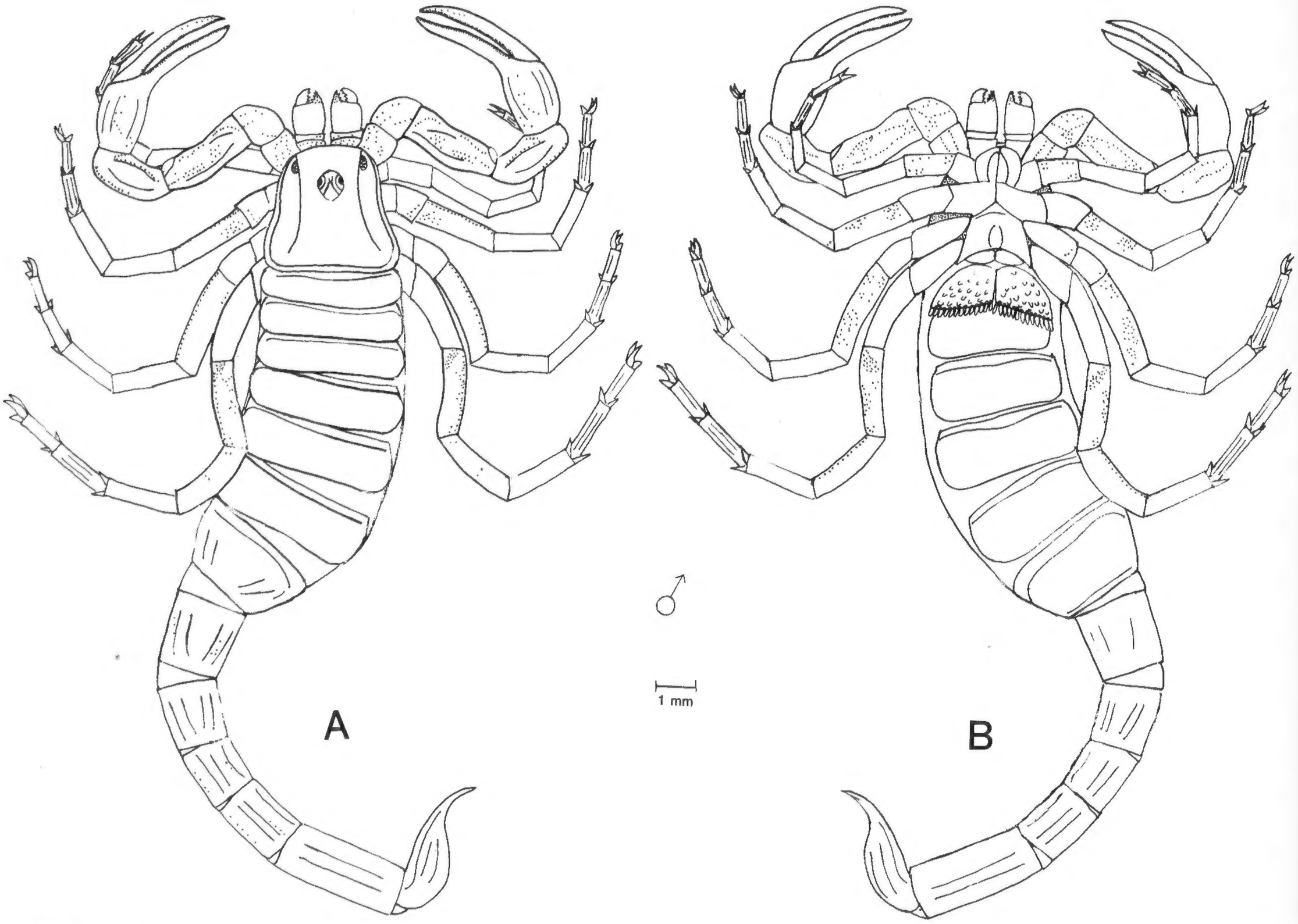
	length (covered)	width (covered)
No. 1		
No. 2	1.4	3.1
No. 3	1.7	3.25
No. 4	1.7	3.3

Total body length (including chelicerae): 27.0 (estimated)

Remarks.—My description of the holotype differs greatly from that of Petrunkevitch (1913) and nothing is to be gained by detailing the differences. Originally the species was based on a holotype and paratype, but later (1953, p. 15) Petrunkevitch noted that the paratype was not the same species and relegated it to *Alloscorpius granulosus* (Petrunkevitch), which here is considered to be a junior synonym of *Eoscorpius carbonarius* Meek and Worthen. Actually, the paratype is the holotype of *Paraisobuthus virginiae,* n. sp. (see below).

These two specimens of *Eoctonus miniatus* Petrunkevitch fortunately reveal both ventral and dorsal sides so that a reconstruction of the species was possible (Text-fig. 38). Again, fortunately, it appears that these two specimens represent both sexes.

This is a very unusual scorpion. The median eyes are rather small and have receded back from the anterior margin to a position not unlike that of some of the living scorpions (*Chaerilus, Calchas*). The small lateral compound eyes are noteworthy too, because



Text-figure 38.—*Eoctonus miniatus* Petrunkevitch. From the Pennsylvanian of Illinois (Mazon Creek). The last three joints of legs **I, III and IV** are inferred; the rest is taken from actual specimens. **A.** Dorsal reconstruction. **B.** Ventral reconstruction of a male.

they occur a considerable distance from the anterolateral margin of the carapace rather than marginally as in other fossil scorpions.

The most important fact revealed by the holotype specimen is that the large elliptical gills are attached to the underside of the body and are free of the abdominal plates. This is in contrast to the book-lungs, which in living scorpions develop in the embryo by invagination of a small section of the external face of the sternite. Therefore in living scorpions the lungs are attached to the sternite, and during ecdysis the entire chitinous part of the lung books is cast off, attached to the sternite.

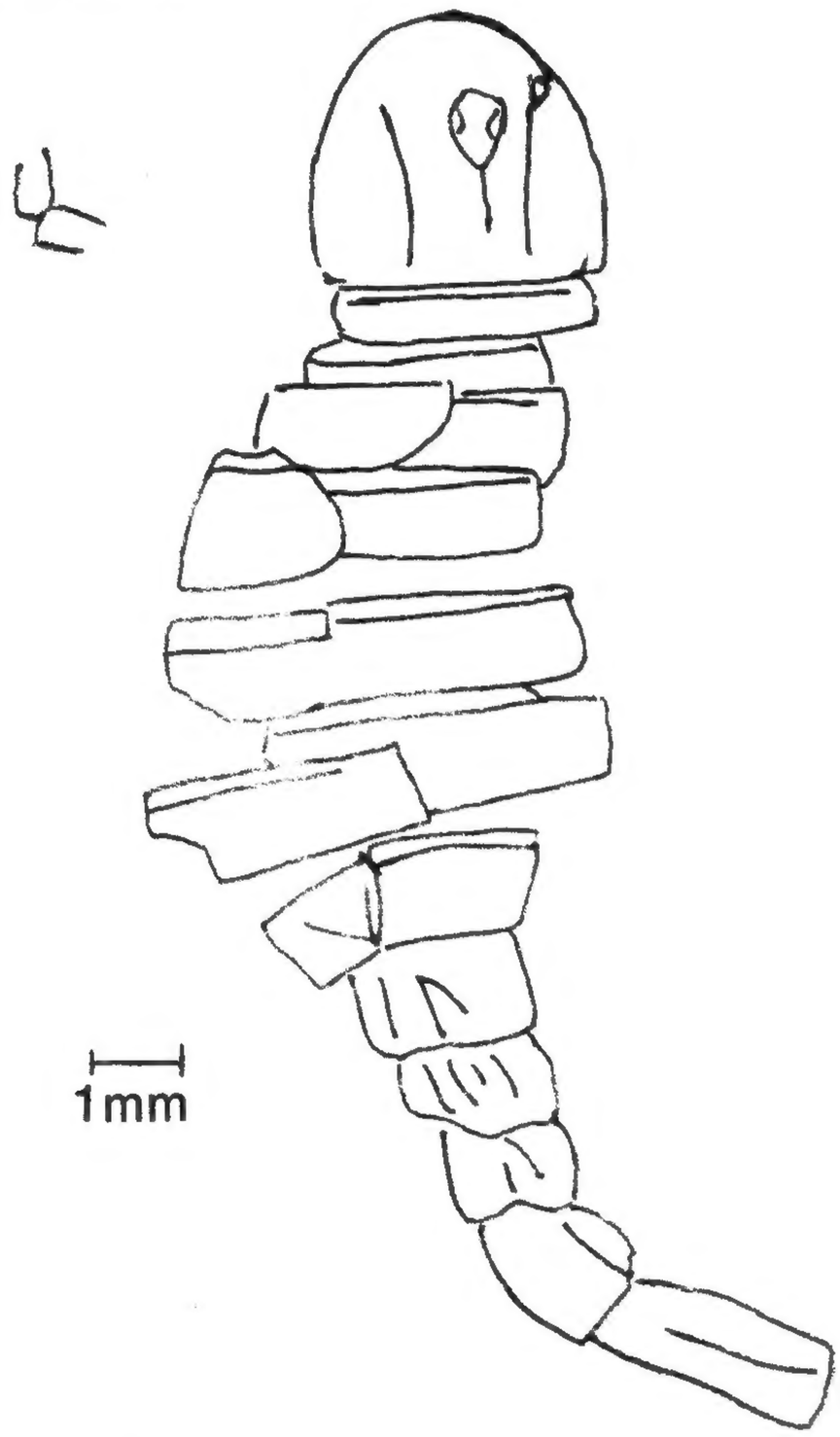
A third specimen, FMNH (PE) 32202 in the Field Museum of Natural History, Chicago, consists of one-half of an ironstone concretion collected at the Strip Mines (Braidwood fauna) in Will Co.–Grundy Co., IL, from the lower Francis Creek Shale. The specimen is poorly preserved, but merits illustration of this rare species. The eye node as well as undoubted holosternous abdominal plates are preserved. The typical facial grooves are also revealed, as well as a lateral eye which is composed of several rounded lenses, very likely schizochroal. The last tergite of the cauda is greatly elongated as in the holotype and indicates a male. Overall length is approximately 18 mm (see Text-fig. 39).

Family **BUTHISCORPIIDAE**, new family

Eoctonoidea with first and second pairs of coxae having well-developed, narrow, maxillary lobes; second pair meeting at midline, with first pair of maxillary lobes behind the second pair and extending anteriorly together. Last two pairs abutting against the sternum. Sternum pentagonal, large, longer than broad, with lateral margins and base emarginate, anterior obtuse. Elliptical intramarginal schizochroal eyes are present.

Type genus.—*Buthiscorpius* Petrunkevitch, 1953.

Remarks.—*Buthiscorpius* Petrunkevitch, 1953, with *Anthracoscorpio buthiformis* as type species, represents a genus of holosternous scorpions that Petrunkevitch had included with the Eoscorpiidae in the *Treatise of Invertebrate Paleontology* (1955). Petrunkevitch had incorrectly diagnosed the coxosternal arrangement because he erroneously used the coxosternal arrangement of a protolobosternous scorpion (BM(NH) In.1555), which is described here as *Pseudobuthiscorpius labiosus,* and Wills, in his elaborate description (1960, pp. 277–290) confirmed Petrunkevitch's interpretation of this area. However, Wills (1960, p. 277) believed that *Anthracoscorpio* Kušta, *Buthiscorpius* Petrunkevitch (including all paratypes of *B. buthiformis* erroneously referred to it by Pocock, 1911) and *Eoscorpius* Meek and Worthen undoubtedly belonged to the Eoscorpiidae, but he recognized that until the diagnosis of the family Eoscorpiidae was properly defined, the problem could not be settled. Had either Petrunkevitch or Wills recognized that the holotype of *Buthiscorpius buthiformis* had lateral schizochroal eyes, it is possible that neither would have included this scorpion with several others that were referred to it. The coxosternal region of *Eoscorpius* is now known and it differs from *Buthiscorpius,* therefore the two cannot belong to a common family nor even in the same superfamily. *Eoscorpius* is a lobostern with large compound lateral eyes, and with the last pair of coxae abutting against the genital opercula. It is an isobuthoid of the suborder Lobosternina. The paratypes of *Buthiscorpius buthiformis* (Pocock) have been referred to several other genera and species. For example, the important specimen BM(NH) In.1555 is now the holotype of *Pseudobuthiscorpius labiosus,* which is also the type of a new family and superfamily. Paratype specimen BM(NH) In.31262 is the holotype of *Coseleyscorpio lanceolatus,* n. gen., n. sp., and paratype specimen BM(NH) In.22832 is the holotype of *Leioscorpio pseudobuthiformis,* n. gen., n. sp. An almost identical species of *Buthiscorpius* was

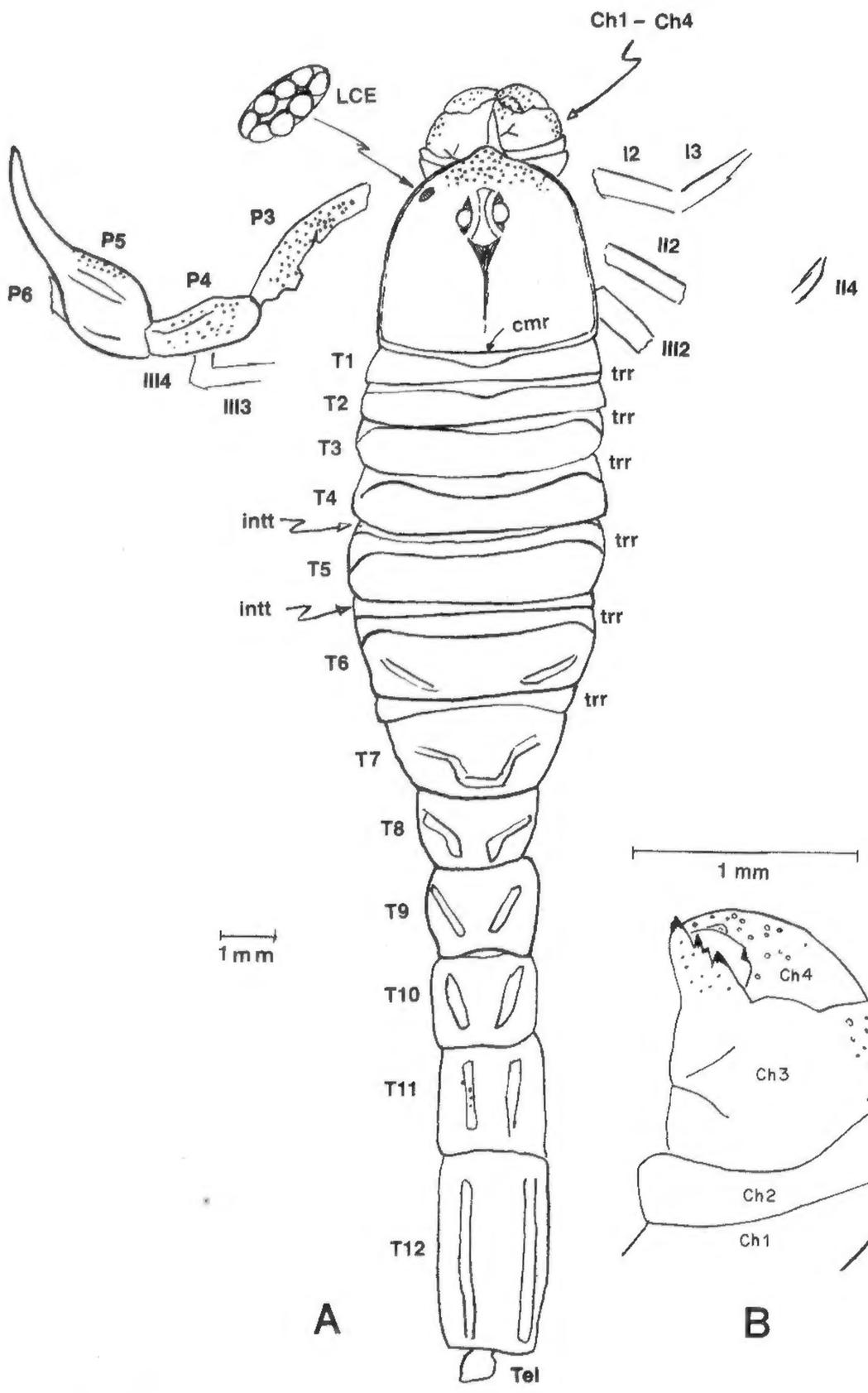


Text-figure 39.—*Eoctonus miniatus* Petrunkevitch. FMNH (PE) 32202. From the Upper Carboniferous (Pennsylvanian), Carbondale Formation, lower Francis Creek Shale, collected at the strip mines (Braidwood fauna) in Will Co.–Grundy Co., IL. This is a complex mold that preserves the inside of some dorsal features and the exterior of ventral ones.

recently found in the Mazon Creek beds of Illinois. This important specimen, which was named *Buthiscorpius lemayi,* shows the ventral side and furnishes the solution to many of the problems concerning *B. buthiformis* and others that had been referred to it.

Buthiscorpius buthiformis is holosternous, with lateral, intramarginal, schizochroal eyes. The first two pairs of coxae are quite similar to those of living scorpions, inasmuch as both have well-developed maxillary lobes, the second pair of which extends anteriorly to crowd out the first pair, which therefore does not meet at the median line. The sternum is roughly pentagonal, large, with the lateral sides and base emarginate. The last two pairs of coxae abut the sternum.

The family Eoctonidae differs from the family Buthiscorpiidae in that the second pair of coxae does not reach to the anterior of the first pair, and in having the second pair of coxae developed as spatulate lobes. The sternum in the Eoctonidae is broader than long and has lateral margins that converge anteriorly, in contrast to the longer-than-broad sternum with emarginate sides in the Buthiscorpiidae.



Text-figure 40.—*Buthiscorpius buthiformis* (Pocock). Holotype, BM(NH) In.18596. From the Carboniferous (Westphalian A), Middle Coal Measures, *Carbonicola communis* beds, Sparth Bottoms, Rochdale, Lancashire, England. See foldout inside front cover for explanation of abbreviations.

A. Complete specimen. **B.** Showing the terminus of the chelicera.

Genus **BUTHISCORPIUS** Petrunkevitch, 1953 (emend.)

Buthiscorpiidae with lanceolate carapace, median eyes in center of anterior half of carapace, and lateral schizochroal eyes anterior to median eyes. Carapace divided by a median sulcus into two cephalic cheeks. Sternum longer than wide, pentagonal and with emarginate lateral margins.

Type species.—*Anthracoscorpio buthiformis* Pocock, 1911.

Geological range.—Carboniferous.

Remarks.—The differences between the genera *Buthiscorpius* and *Anthracoscorpio* are numerous and of higher category than generic. For example, they belong to different families as the maxillary lobes of the second pair of coxae in *Anthracoscorpio* have not reached full development—that is: they do not reach the same level as the first pair. On the generic level, the sternum is wider than long in *Anthracoscorpio* and the opposite is true in *Buthiscorpius.*

Buthiscorpius buthiformis (Pocock, 1911) Text-figures 40, 110F

1911. *Anthracoscorpio buthiformis* Pocock (*partim*), pp. 24–28, pl. 2, fig. 1; text-fig. 6; not pp. 26–27, text-fig. 8 (paratype BM(NH) In.22832 = *Leioscorpio pseudobuthiformis,* n. gen., n. sp.); not p. 26, text-fig. 7 (paratype BM(NH) In.7883 = *Compsoscorpius elegans* Petrunkevitch); not pp. 27–28, pl. 1, fig. 2 (paratype BM(NH) In.1555 = *Pseudobuthiscorpius labiosus,* n. gen., n. sp.).

1913. *Eoscorpius buthiformis* (Pocock). Petrunkevitch, p. 35.

1949. *Eoscorpius buthiformis* (Pocock). Petrunkevitch, p. 153.

1953. *Buthiscorpius buthiformis* (Pocock). Petrunkevitch (*partim*), p. 32, figs. 31–33; not p. 32, fig. 34 (paratype BM(NH) In.1555 = *Pseudobuthiscorpius labiosus,* n. gen., n. sp.).

1955. *Buthiscorpius buthiformis* (Pocock). Petrunkevitch, p. 74, fig. 43(3).

1960. *Buthiscorpius buthiformis* (Pocock). Wills (*partim*), pp. 277–290; not pp. 278–284, pl. 46, 47; text-figs. 1–5 (BM(NH) In.31262 = *Coseleyscorpio lanceolatus,* n. gen., n. sp.); not pp. 284–290, pl. 48; text-figs. 6–9 (BU 720 = *Allobuthus macrostethus,* n. gen., n. sp.).

1962. *Buthiscorpius buthiformis* (Pocock). Dubinin, p. 431, figs. 1233, 1252.

The holotype consists of two parts showing the dorsal surface only, BM(NH) In.18596a and b.

The original description of Pocock (1911, p. 24) is essentially correct, therefore my comments will be restricted to features either not described or overlooked,

some of which are highly important and which necessitate a redefinition of the genus.

1. On the anterolateral angles, the presence of small, elliptical, schizochroal eyes were first noted on latex casts and verified on the actual specimen. The presence of lateral eyes was also verified in the American species *B. lemayi.* The individual eyes are rounded, and approximately seven to eight eyes occur in an elliptical cluster at the same spot where the lateral eyes of present-day scorpions are found. The eyes are therefore intramarginal and schizochroal.

2. Pocock (1911, p. 24) mentions that the dorsal surface is finely- to closely-granulated. This does not seem to be the case, although it was on other specimens incorrectly referred to this species. In fact, the dorsal surface is quite smooth except for the anterior part of the carapace where it is granular.

3. The carapace is elliptical or oval in general outline, with a distinct but slight prolongation at the anterior midsection (see Text-fig. 40A). The marginal rim is very narrow. The basal rim is narrow but well marked, slightly protruding over the adjoining tergite.

4. The dorsal keels or carinae are surmounted by granules, each of which seems to be setaceous.

5. The pedipalps show numerous setaceous granules, not in any apparent order, on the femur and tibia as well as the anterior of the hand. The edge of the fixed finger of the pedipalp seems to be cultrate, without granules or denticles.

6. The twelfth tergite or last caudal segment was developed for the first time and revealed an unusually long tergite. The overall aspect of the tail is very thick, and does not decrease in size posteriorly. The last segment measures 3.3 mm in length. The great length of this segment is indicative of a male; the coarse granulation on the anterior of the carapace also verifies that the holotype is a male. This sex determination is further strengthened by the presence of a very short corresponding tergite in the closely related American species *B. lemayi,* which would be indicative of the female.

Type information.—From the Carboniferous (Westphalian A) *Carbonicola communis* beds, Middle Coal Measures, Sparth Bottoms, Rochdale, Lancashire, England.

Remarks.—As restricted here, the species *Buthiscorpius buthiformis* (Pocock) is at present known only from one specimen (part and counterpart) exhibiting the dorsal side only. The other specimens that had been referred to this species have here been relegated to different families, genera and species (see generic description above).

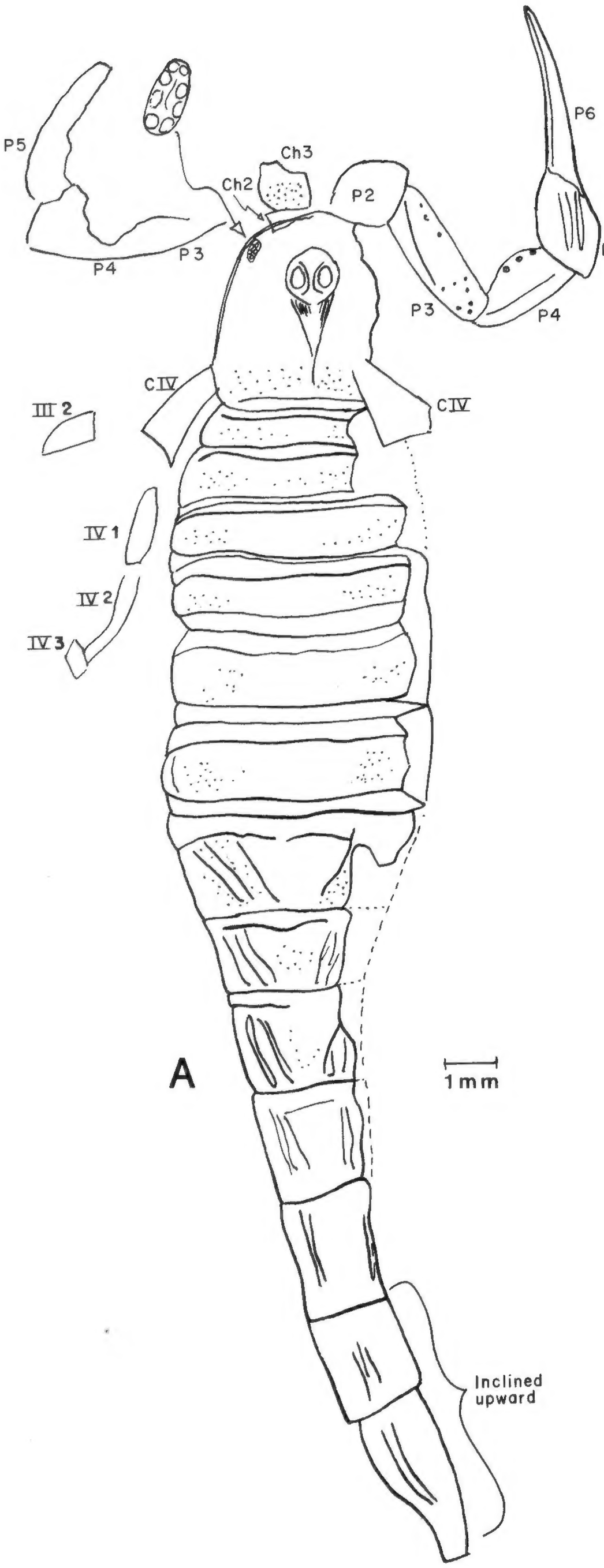
Buthiscorpius lemayi, new species
Text-figure 41

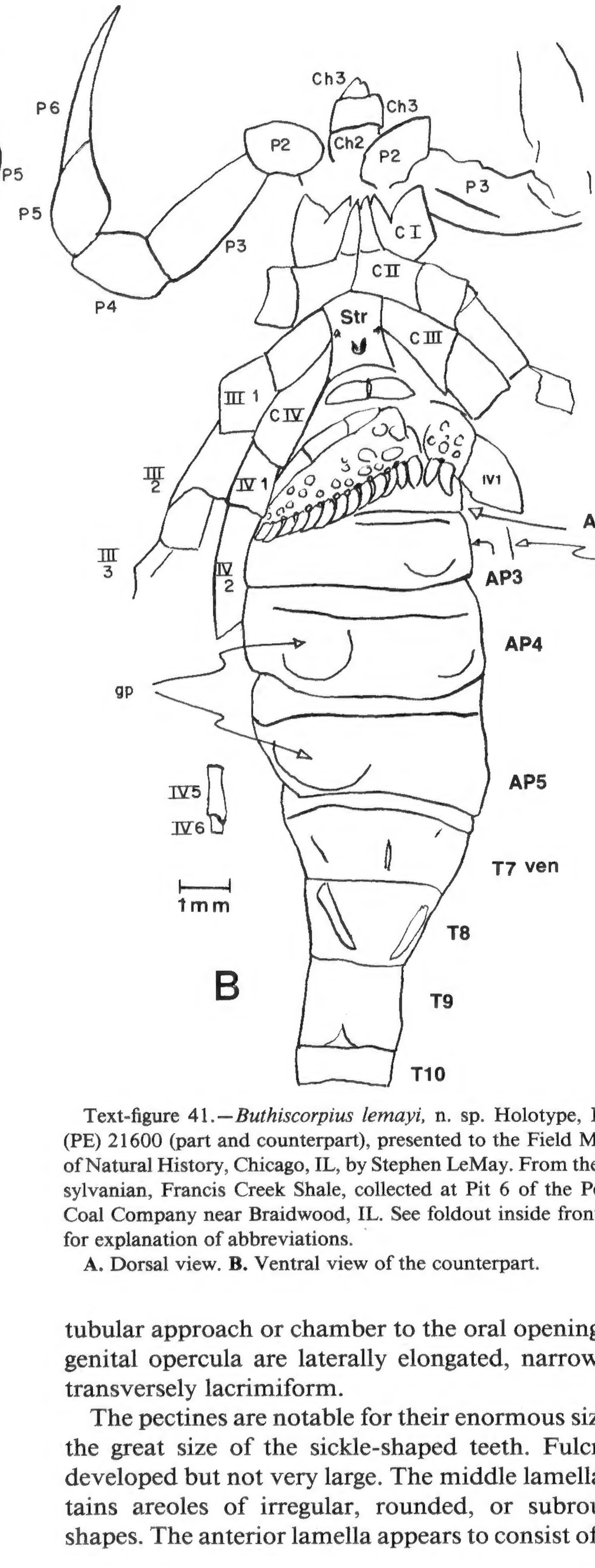
Morphologically and taxonomically this is one of the most important specimens known, as the underside of an undoubted *Buthiscorpius* is preserved. The type species, *B. buthiformis* (Pocock) from England, was known only from the dorsal side, albeit a very well-preserved form. It further verified the presence of lateral compound eyes, which previously had not been known in this genus despite the studies by Pocock, Petrunkevitch, and Wills. Preservation in both the British holotype and the new American species is so perfect that the setal openings, or sites, on the pedipalps can be used for the first time as specific differences, in much the same manner as the trichobothria of the pedipalps are used in descriptions of modern scorpions. It may be that the setal openings are trichobothria, as they occur in precisely the same areas as the modern trichobothria, although, of course, the trichogen cells developed at the base of each seta have not been fossilized.

The carapace is lanceolate, with well-developed round median eyes located on a prominent eye node slightly behind the center of the anterior half of the carapace. A deep median sulcus divides the carapace behind the eye node. Supraorbital ridges are well-developed. The lateral compound eyes are reniform and probably enclose eight small, rounded lenses. A few punctae occur along the base of the carapace, which is bounded by a transverse basal ridge and a very thin marginal rim. The anterior is not as noticeably protruding as in *B. buthiformis.*

The legs are not well preserved except for the important pedipalps, which are stout, with long curved fingers. Setal openings are present in the humerus (**P3**), brachium (**P4**) and most likely the chela (**P5**, **P6**). In their distribution, these are in marked contrast to those present in *B. buthiformis* (Pocock) (see Text-fig. 41). The rest of the legs and the chelicerae are not sufficiently well preserved for a meaningful description.

The important coxosternal region is preserved in its entirety and reveals an arrangement much as in living scorpions. The sternum is elongate-pentagonal, the base being incurved with the anterior triangular part hardly projecting forward. A deep sulcus, no doubt for the attachment of muscles, occurs in the posterior half of the plate, and two other indentations occur at the sides at midsection, also for the attachment of muscles. The third and fourth pairs of coxae abut against the sternum, whereas the maxillary lobes of the second coxae meet at midsection and crowd out the maxillary lobes of the first coxae, as happens in living scorpions. The maxillary lobes of both the first and second coxae are narrow and reach to the anterior, thus forming the





Text-figure 41.—*Buthiscorpius lemayi,* n. sp. Holotype, FMNH (PE) 21600 (part and counterpart), presented to the Field Museum of Natural History, Chicago, IL, by Stephen LeMay. From the Pennsylvanian, Francis Creek Shale, collected at Pit 6 of the Peabody Coal Company near Braidwood, IL. See foldout inside front cover for explanation of abbreviations.

A. Dorsal view. **B.** Ventral view of the counterpart.

tubular approach or chamber to the oral opening. The genital opercula are laterally elongated, narrow, and transversely lacrimiform.

The pectines are notable for their enormous size and the great size of the sickle-shaped teeth. Fulcra are developed but not very large. The middle lamella contains areoles of irregular, rounded, or subrounded shapes. The anterior lamella appears to consist of three

well-defined joints. About 13 teeth occur on the great pectines, which had to spread beyond the margins of the opisthosoma in life.

The opisthosoma is lanceolate without great contraction at the eighth tergite. Measurements (given below) show a gradual increase in length in the mesosoma, and the greatest width is reached at the fifth tergite. Double keels are very prominent on the metasoma. Apparently these are also developed on the venter. The abdominal plates are holosternous and have well-developed gill chambers (see Text-fig. 41B).

The telson is not preserved in its entirety but it is very long and not unduly curved.

The holotype is no doubt a female, which is revealed by secondary sexual characters, such as the short twelfth tergite (in contrast to the long male segment in the holotype of *B. buthiformis* (Pocock)), the lack of coarse granulation (in contrast to the coarse granules in the male of *B. buthiformis*) and the wide mesosoma.

Measurements (in mm) of the holotype, FMNH (PE) 21600.—

Carapace:		
Length:		3.35
Width at base:		3.4
Median eyes:		
Distance from anterior margin:		0.8
Distance from posterior margin:		2.26
Tergite:	length	greatest width
No. 1	0.7	(incomplete)
No. 2	0.9	(incomplete)
No. 3	1.0	3.1
No. 4	1.24	4.0
No. 5	1.4	4.7
No. 6	1.5	4.0
No. 7	1.6	anterior 2.8
		posterior 2.16
No. 8	1.6	posterior 2.0
No. 9	1.7	posterior 1.7
No. 10	1.8	posterior 1.6
No. 11	2.2	posterior 1.56
No. 12	2.2	posterior 1.56
Telson	2.1	(incomplete) 1.5
Pedipalp:		
Length of **P3**:		2.4
Length of **P4**:		2.3
Hand width (**P5**):		1.0
Hand length (**P5**):		2.0
Free finger length (**P6**):		3.0

Type information.—Holotype is an adult female preserved in an ironstone concretion, comprising part and couterpart of a nearly complete specimen. It is from the Pennsylvanian, Francis Creek Shale, collected at Pit 6 of the Peabody Coal Company near Braidwood, Illinois.

Derivatio nominis.—Named in honor of Stephen LeMay, who kindly alerted the author to the specimen and graciously presented the specimen to the Field Museum of Natural History, Chicago, where it is registered as FMNH (PE) 21600.

Remarks.—In contrast to *Buthiscorpius buthiformis* (Pocock) which is known only from the dorsal side, the differences, other than those considered due to sexual dimorphism (granulation, short twelfth tergite, and mesosomatic width), consist of the presence of a much more delicate and longer pedipalp, the different setal distribution on the humerus and brachium, the lack of the pronounced anterior prolongation of the carapace, and the double rows of dorsal carinae on the postabdominal tergites. These dorsal characters are sufficient to separate *B. lemayi* from the British *B. buthiformis*. It is an interesting addition to the famous Mazon Creek fauna.

Family **ALLOBUTHISCORPIIDAE**, new family

Eoctonoidea (?) apparently without lateral compound eyes.

Type genus.—*Allobuthiscorpius,* n. gen.

Remarks.—Since the single specimen is known only from the dorsal side, its higher taxonomic position is in doubt.

Genus **ALLOBUTHISCORPIUS**, new genus

Allobuthiscorpiidae with lanceolate carapace, divided by a median sulcus into two cephalic cheeks; median eyes in center of anterior half of carapace.

Derivatio nominis.—*allo* (Gr.) = another, different + *Buthiscorpius.*

Type species.—*Buthiscorpius major* Wills, 1960.

Geological range.—Carboniferous.

Remarks.—*Buthiscorpius major* Wills cannot remain in *Buthiscorpius* as it seemingly lacks lateral eyes.

Allobuthiscorpius major (Wills, 1960)

1960. *Buthiscorpius major* Wills, pp. 300–305, pl. 51, figs. 1–3; pl. 52; text-figs. 14–16.

Holotype (GSM Za 2926) on deposit in the Institute of Geological Sciences, London, from the Coal Measures (Ammanian), base of *communis* zone, Kilburn Coal, Trowell Colliery, Nottinghamshire, England. The specimen was in a half nodule revealing only the ventral surface of the dorsal side of a large scorpion (to quote Wills, p. 301):

about twice the size of *Buthiscorpius buthiformis* Pocock; carapace ornamented with granules, some being large, mimicking lateral eyes which are absent; median eyes small and near to one another on an eye-tubercle without visible ridges between the eyes; eye tubercle about two-fifths of carapace length from the front; tergites with mucronate posterior margins; tail short and relatively shorter than in *B. buthiformis*; caudal ring XVIII not much longer than the previous one, and shorter than the flask-shaped sting. Pedipalp hand with fingers longer in proportion to the palm than in *B. buthiformis.*

For dimensions and detailed description that cannot be improved upon, see Wills (1960).

Remarks.—Wills felt that the hairs actually still attached to the chelicera of *B. major* (pp. 287–288) suggested that some of the Carboniferous scorpions employed the same method of feeding as do their present-day descendants, and one that would appear more appropriate in terrestrial than in aquatic animals, but the undoubtedly aquatic *Hydroscorpius* from the Devonian of Cottonwood Canyon was copiously supplied with hairs or setae on the chelicerae (see Text-figs. 20A, C) and couldn't possibly have had maxillary lobes.

Genus **ASPISCORPIO**, new genus

Allobuthiscorpiidae with oval carapace, small round median eyes located in central part of the anterior half of the carapace; well-developed, raised cephalic shield, with raised median glabellalike ridge behind eyes, and raised posterior genal areas. No lateral compound eyes.

Derivatio nominis.—*aspis* (Gr.) = shield.

Type species.—*Aspiscorpio eagari,* n. gen., n. sp.

Geological range.—Carboniferous.

Remarks.—This scorpion has a superficial resemblance to *Buthiscorpius* and is associated with it in the type locality. It can readily be distinguished from that genus by the lack of a frontal protuberance, the development of the strong cephalic shield, and no lateral schizochroal eyes. I had placed it in the Buthiscorpiidae with considerable misgivings as the underside is not known, but the lack of lateral compound eyes makes a position within the Buthiscorpiidae untenable.

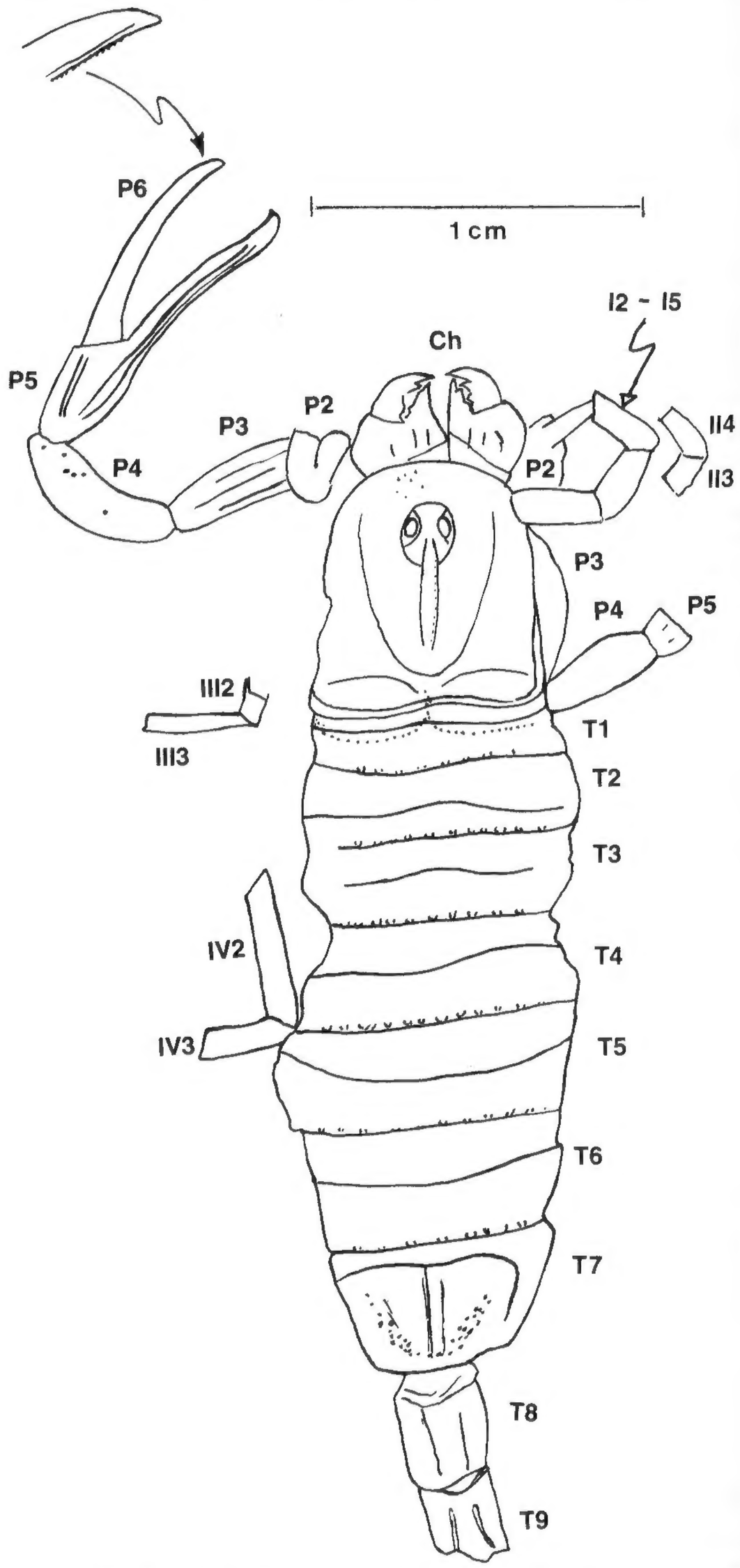
Aspiscorpio eagari, new species
Text-figure 42

1953. *Eoscorpius sparthensis* Baldwin and Sutcliffe. Petrunkevitch (*partim*), p. 28.

Based on a single specimen showing the inside of the dorsal part of the carapace, mesosoma, and anterior two tergites of the postabdomen. The chelicerae are preserved from the dorsal part, and the right (in life) ventral side of the entire pedipalp. Inconclusive fragments of the walking legs are present.

Carapace relatively long, oval in front, without traces of an anterior protrusion. It is rimmed by a very narrow marginal rim, which is very prominent on the basal and basilateral margins. There are no lateral eyes and the median eyes are very small, round, located on a rather round ocellar mound, about in the center of the anterior half of the carapace. Orbital ridges are negligible. A raised, elongate cephalic area is very prominent, and this is divided by a medial raised ridge that extends to the median eyes, and has the form of the glabellar ridge in eurypterids. Two raised areas occur in the pleural part.

The mesosoma is noteworthy for the unusually long transverse ridges on the tergites. Undoubtedly these transverse ridges include the intersegmental tissue between tergites, but nevertheless the ridges are very well developed. Slight, but noticeable, crenulations ornament the basal margins of the tergites, and it is due to



Text-figure 42.—*Aspiscorpio eagari,* n. gen., n. sp. Holotype, UMM L 8182. From the Carboniferous (Westphalian A), *Carbonicola communis* beds, Sparth Bottoms, Rochdale, Lancashire, England. Note that the rachis of the pectines is reflected as an imprint (dotted lines). See foldout inside front cover for explanation of abbreviations.

the presence of these crenulations that the tergites can be easily separated.

The last tergite has a raised low carina in the central part and two diagonal carinae marked by pustules on the sides. The central carina is marked by two depressed thin lines. The cauda, or postabdomen, is represented by only two tergites, which reveal well-developed double carinae.

The pedipalp is preserved in its entirety, showing it to be very long, with a very short hand, and very long fingers. The fingers contain very small denticles, but it is not possible to determine the pattern. They may be in a straight line along the cultrate edge. Two very thin carinae, which continue into the hand, occur on the ventral side of the fixed finger.

Except for the crenulations noted, and some sparsely distributed pustules in the front of the carapace, the rest is very smooth. Some setal openings were noted on the pedipalp tibia.

Measurements (in mm) of the holotype, UMM L 8182.—

Carapace:		
Length:		6.5
Width at base:		6.2
Eyes:		
Diameter:		0.25
Distance from anterior margin of carapace:		1.35
Distance from posterior margin of carapace:		2.6
Distance from lateral margins of carapace:		1.65
Pedipalp:	length	width
Femur:	6.5	1.3
Tibia:	5.0	1.7
Hand:	3.5	2.0
Free finger:	6.4	
Tergites:	length	width
No. 1	1.2	7.0 (estimated)
No. 2	2.0	7.2 (estimated)
No. 3	2.6	7.3 (estimated)
No. 4	2.6	8.6 (estimated)
No. 5	3.0	7.4
No. 6	3.8	7.0
No. 7	3.5	5.4 (anterior) 2.7 (posterior)
No. 8	3.3	2.65
No. 9	(incomplete)	2.50

Type information.—Preserved in an ironstone concretion from the Carboniferous (Westphalian A) *Carbonicola communis* beds at Sparth Bottoms, Rochdale, Lancashire, England (pers. commun., M. Eagar). Deposited in the Manchester University Museum, where the holotype is registered as L 8182.

Derivatio nominis.—Named in honor of Dr. Michael Eagar of Manchester University.

Remarks.—As stated in the remarks regarding the genus, the only scorpion with which this scorpion might be confused is *Buthiscorpius buthiformis* (Pocock), which also occurs at Sparth Bottoms. The prominent raised cephalic shield of *Aspiscorpio eagari* is sufficient for identification, as well as the lack of lateral schizochroal eyes.

Family **ANTHRACOSCORPIONIDAE**, new family

Eoctonoidea with large pentagonal sternum, long maxillary lobes on the first and second pairs of coxae; the second pair meets at the midline from the sternum almost to the anterior of the first pair of maxillary lobes; no lateral compound eyes.

Type genus.—*Anthracoscorpio* Kušta, 1885.

Genus **ANTHRACOSCORPIO** Kušta, 1885

Carapace semicircular anteriorly with slightly concave posterior edge; median eyes sessile, sitting in advance of middle.

Type species.—*Anthracoscorpio juvenis* Kušta, 1885.

Geological range.—Carboniferous.

Anthracoscorpio juvenis Kušta, 1885
Text-figures 43A, B, 110D, 113B3

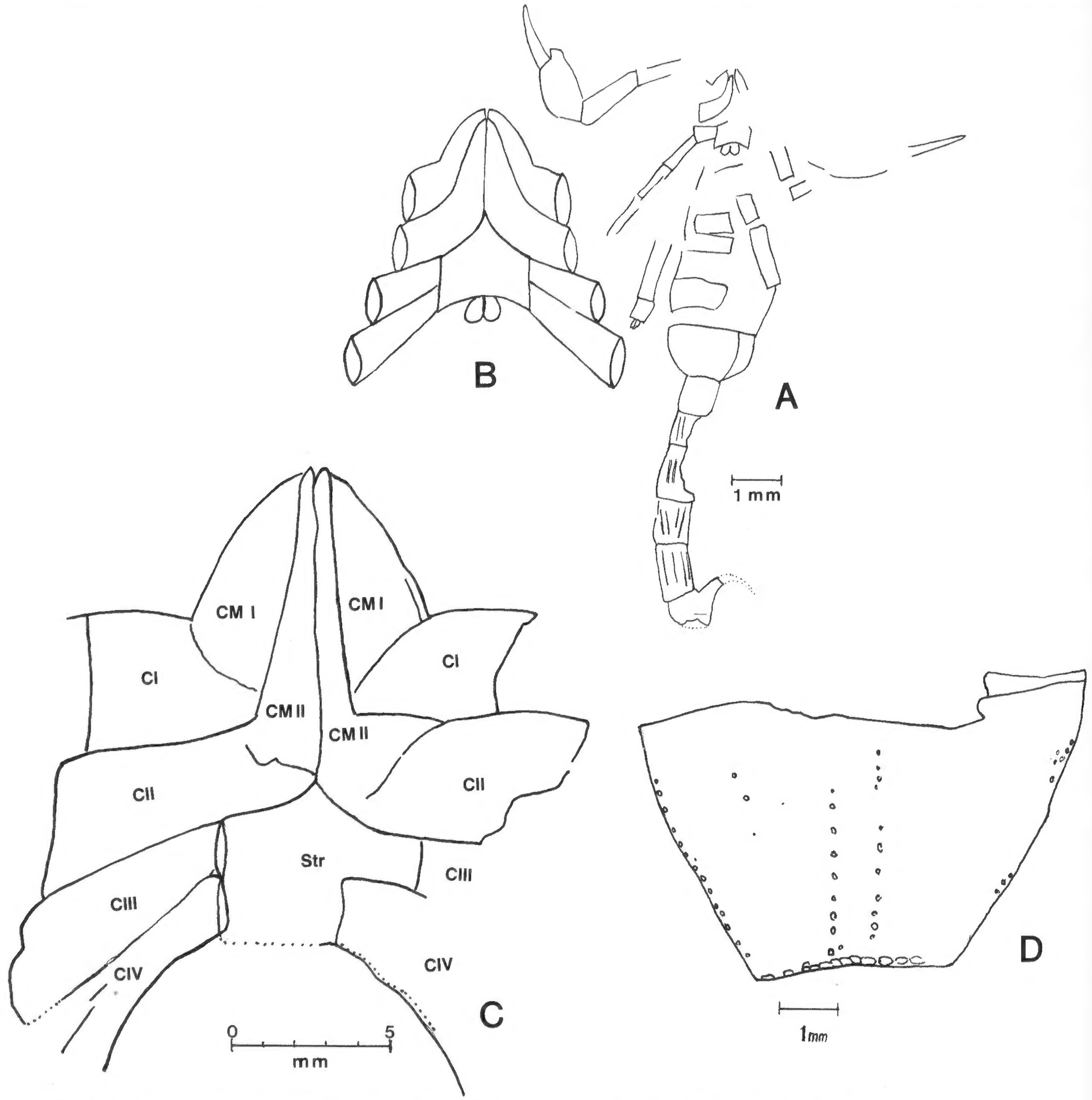
1884. *Cyclophthalmus senior* Corda. Kušta (*partim*), p. 48.
1885. *Anthracoscorpio juvenis* Kušta, p. 7.
1904. *Anthracoscorpio juvenis* Kušta. Frič, pp. 75–76, text-fig. 94.
1949. *Anthracoscorpio juvenis* Kušta. Petrunkevitch, p. 143.
1953. *Anthracoscorpio juvenis* Kušta. Petrunkevitch, p. 30, figs. 30, 130.
1955. *Anthracoscorpio juvenis* Kušta. Petrunkevitch, p. 74, fig. 43(4).
1962. *Anthracoscorpio juvenis* Kušta. Dubinin, p. 431, fig. 1250.

Type information.—Holotype, No. 836 (Frič's Inv. P. 3520) in the National Museum at Prague, Czechoslovakia, from the Upper Carboniferous (Westphalian B/C) Radnice Member of the Radnice Group, at Rakovnik (about 45 km west of Prague), Czechoslovakia.

Holotype consists of one half only, which is flattened, complete, and preserved in light greenish-gray, slightly sandy shale. The cuticle has no doubt deteriorated since Kušta (1884) and Frič (1904) worked on this specimen, but enough is left to reveal some very interesting points of structure. Kušta did not figure this specimen, but Frič (1904) and Petrunkevitch (1953) did, and both showed the dorsal side. However, this is not possible, since the scorpion is preserved on the ventral side. The anterior maxillary lobes of the first two pairs of coxae were mistaken by Frič (1904, fig. 94) for the chelicerae. I am unable to determine what prompted Petrunkevitch (1953) to make the drawing that he did, showing a wide carapace with two eyes. This is not to be taken seriously as the outline of the carapace is not present and almost certainly would not

have been as shown by Petrunkevitch. In fact, the outline of the carapace drawn by Frič is probably correct. It is assumed, of course, that the outlines were present and that today the specimen has deteriorated.

The discovery of parts of the coxosternal area is a welcome addition to our knowledge of this scorpion and, although fragmentary, enough is present to make a good restoration possible (see Text-fig. 110D). The



Text-figure 43.—Species of *Anthracoscorpio* Kušta, 1885. See foldout inside front cover for explanation of abbreviations.

A, B. *Anthracoscorpio juvenis* Kušta. Holotype, NMP Inv. 836. From the Upper Carboniferous (Westphalian B-C), Radnice Member of the Radnice Group, Rakovnik, Czechoslovakia.

A. Holotype after Kušta, 1885, text-figure 94. **B.** Restoration of coxosternal region.

C. *Anthracoscorpio dunlopi* Pocock. Holotype, RSM 1957.1.4995a and b. From the Carboniferous, Upper Coal Measures, shale above Drumgray Coal, Longrigend, Airdrie, Lanarkshire, Scotland. Coxosternal area.

D. *Anthracoscorpio dunlopi* (?) Pocock. RSM 1957.1.5000 through 5002. From the Carboniferous of Airdrie, Scotland. Seventh tergite. Note that this is the venter, because the carinae are close together (see *Paraisobuthus duobicarinatus* and *Eoscorpius carbonarius*).

sternum is large and pentagonal in shape. The first pair of coxae has well-developed, narrow but long, maxillary lobes that abut against the maxillary lobes of the second pair, as in modern scorpions. The second pair meets at midsection, anteriorly to the sternum, extending almost to the anterior part of the first maxillary lobes. The last two pairs of coxae abut the sides of the sternum. This arrangement therefore is like that found in the Eoctonoidea, particularly in the Buthiscorpiidae and in modern scorpions. The genital opercula are very small, rather elliptical and adjoin the base of the large sternum.

The scorpion is a holosternous form and the plainly visible abdominal plates confirm this.

The pedipalp does not show any denticles on the edge of the fingers, which appear to be cultrate. The palm and fingers are narrow and long. The preabdomen narrows abruptly into the cauda, which shows well-defined double carinae that may be ventral and lateral carinae. The vesicle is large and bulblike, followed by an aculeus that likely was long.

Anthracoscorpio dunlopi Pocock, 1911
Text-figures 43C, D

1911. *Anthracoscorpio dunlopi* Pocock, pp. 21–24, pl. 1, fig. 1; text-fig. 5.
1913. *Eoscorpius dunlopi* (Pocock). Petrunkevitch, p. 34.
1949. *Eoscorpius dunlopi* (Pocock). Petrunkevitch, p. 153.
1953. *Eoscorpius dunlopi* (Pocock). Petrunkevitch, p. 28, fig. 131.
1962. *Eoscorpius dunlopi* (Pocock). Dubinin, p. 429, fig. 1247.

The two parts of the holotype, preserved in black shale, reveal only the dorsal side and counterpart of the same surface. The important coxosternal region can be faintly made out as it is impressed through the dorsal surface, and is therefore described for the first time.

The first two pairs of coxae have well-developed maxillary lobes. The maxillary lobes of the second pair of coxae are very narrow and extend anteriorly to squeeze the first pair of maxillary lobes away from the midline, as in living scorpions. The sternum is large, pentagonal, and the last two pairs of coxae abut against it.

Pocock's (1911) description of the dorsal side is quite adequate, and little can be gained by repetition here. The development of the coxosternal region in the genotype *Anthracoscorpio juvenis* Kušta (Text-figs. 43A, B) reveals that Pocock was correct in referring the holotype to that genus. The scorpion cannot be referred to *Eoscorpius,* as Petrunkevitch (1913, 1949, 1953) thought, since it is not a lobostern, but a holostern, a major difference among many others.

Type information.—Holotype is from the Upper Coal Measures, shale above Drumgray Coal, Longrigend, Airdrie, Lanarkshire, Scotland. It consists of part and counterpart, showing only the dorsal side, and is registered as No. 1957.1.4995a and b, in the collections of the Royal Scottish Museum, Edinburgh, Scotland.

Remarks.—Royal Scottish Museum Nos. 1957.1.5000 through 5002, part and counterpart, here illustrated as Text-figure 43D, may be a specimen of *A. dunlopi* Pocock. It consists of a single seventh tergite preserved in dark gray micaceous shale from Airdrie. The tergite (No. 7) of the preabdomen, reveals two closely-set median carinae, each of which is surmounted by rounded tubercles. Similar tubercles, but larger and longer, occur along the base. The anterior is bounded by the usual transverse ridge.

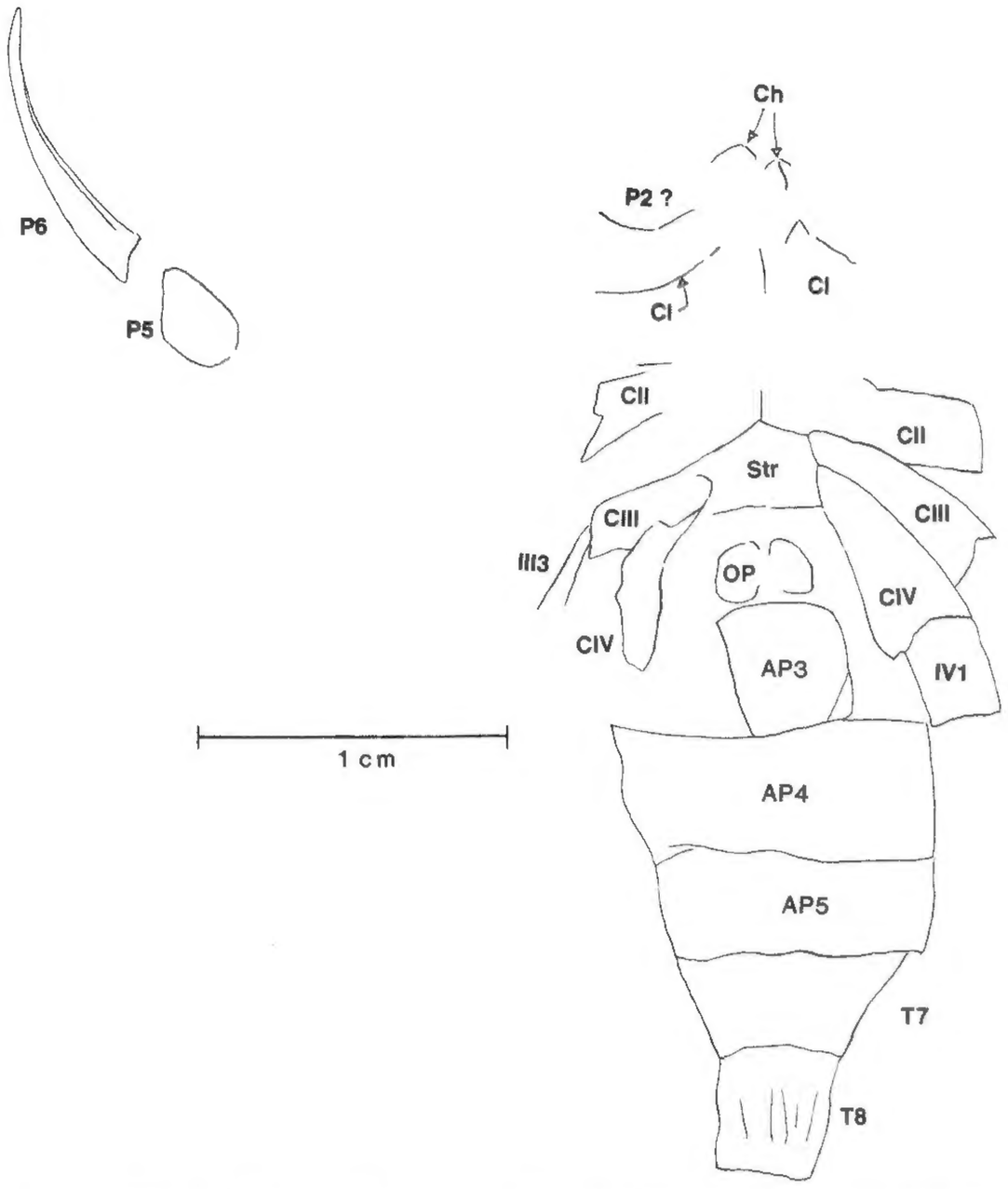
Measurements (in mm) of RSM 1957.1.5000 through 5002.—

Anterior width:	9.9 (estimated)
Posterior width:	4.0
Length:	6.6 (estimated)

Anthracoscorpio (?) species
Text-figure 44

1913. *Eoscorpius typicus* Petrunkevitch (*partim*), pp. 39–43, pl. 1, fig. 1.

Specimen No. YPM 126, in a typical Mazon Creek



Text-figure 44.—*Anthracoscorpio* (?) sp. YPM 126, designated as a paratype of *Eoscorpius typicus* Petrunkevitch. From the Upper Carboniferous (Pennsylvanian), Carbondale Formation, Mazon Creek area. See foldout inside front cover for explanation of abbreviations.

ironstone concretion, one of the paratypes of *Eoscorpius typicus* Petrunkevitch, 1913, was assigned to *Mazonia woodiana* Meek and Worthern in a note Kjellesvig-Waering left, and illustrated as Text-figure 44. No description was found. The specimen is obviously not a *Mazonia,* which is a Mesophonoidea, in which, by definition, the fourth pair of coxae abuts against the operculum, whereas, in this illustration, the fourth pair abuts against the sternum, so that YPM 126 seems to fit in the Eoctonoidea. The specimen is preserved with only the ventral side showing on half the nodule. The sternum is pentagonal, and the genital opercula appear to be elongate and ovoid, thus sternum and opercula resemble the Anthracoscorpionidae. The abdominal plates are holosternous, without any sign of stigmata. The free finger of the pedipalp is fairly well preserved, shows a ridge for its entire length, and lacks denticles (A.S.C.).

Genus **LICHNOSCORPIUS** Petrunkevitch, 1949 (emend.)

Anthracoscorpionidae with parabolic carapace, two small median eyes anteriorly placed on a wide lacrimiform eye node, and with the preabdomen tapering into the cauda without an abrupt attenuation, and with the cauda tapering posteriorly.

Type species.—*Lichnoscorpius minutus* Petrunkevitch, 1949.

Geological range.—Upper Carboniferous.

Remarks.—The genus *Anthracoscorpio* Kušta was established in 1885 for a small scorpion from the Middle Bohemian Coal Basin. In 1949, Petrunkevitch described another small scorpion from the Upper Coal Measures at Coseley, England, as *Lichnoscorpius minutus.* In 1953, Petrunkevitch, based on a wrong interpretation of both species, decided that his genus *Lichnoscorpius* was a junior synonym of *Anthracoscorpio.* I am at a loss to understand how Petrunkevitch (1953) could have made a drawing of the dorsal side of the carapace when only the ventral side is preserved.

It is not possible to include two scorpions such as *Anthracoscorpio juvenis* Kušta and *Lichnoscorpius minutus* Petrunkevitch in the same genus, when the preabdomen of one (*A. juvenis*) is abruptly constricted into a slender cauda with parallel sides, and the other (*L. minutus*) has a preabdomen that tapers into a tapering cauda. *Lichnoscorpius* has an opisthosoma much like that of the more sinuous genera of the Chactidae, such as *Broteochactas,* and likely was a burrower or a true cryptozoan in a water medium. *Anthracoscorpio juvenis,* on the other hand, has the slender aspect of the buthids, such as *Tityus* and *Centruroides,* which led a more active or less cryptozoan life.

Lichnoscorpius was proposed by Petrunkevitch (1949) because the genus *Anthracoscorpio* was not considered to have median eyes, whereas the genotype of *Lichnoscorpius* had well-developed eyes. On studying the holotype of *Anthracoscorpio juvenis* Kušta, the genotype, Petrunkevitch decided that it had a pair of small "sessile" eyes, and therefore considered his genus *Lichnoscorpius* to be a junior synonym of *Anthracoscorpio* Kušta, 1885 (Petrunkevitch, 1953, p. 30).

The holotype of *Lichnoscorpius minutus* clearly shows large rounded eyes located on a definitely-outlined, anteriorly-located eye node that is surrounded by a narrow sulcus, and where the eyes are also separated by a sulcus. Petrunkevitch (1949, p. 148) stated, "The eyes are visible only on the piece representing the mold and the interocular ridges appear therefore as depressions, but with perfectly sharp outlines. There is no eye-tubercle, the level of the eye-circumference being the same as that of the carapace". A rubber cast of the mold would have given the correct relief, namely, a very well-developed eye node, quite normal on Paleozoic scorpions, with a narrow sulcus separating the eyes. There are strong supraorbital (interocular?) ridges, and it would be surprising, if not impossible, to find a scorpion with "the level of eye circumference being the same as that of the carapace". Compaction and consequent flattening of thin tissues is not a difficult process to understand in fossils. The position of the eyes on the carapace, as shown here for *Lichnoscorpius minutus,* and the purported eyes shown by Petrunkevitch for *Anthracoscorpio,* do not mean that the two belong to the same genus. Other much more important differences occur, as given below.

Inasmuch as the generic name *Lichnoscorpius* Petrunkevitch, 1949, is available and is in truth a valid name, the generic description has been emended. The holotype is known from both dorsal and ventral surfaces and shows that the abdominal plates are holosternous. It is considered here that, although the coxosternal arrangement is not entirely preserved, enough is present to show that it is typical of the Eoctonoidea. The same is true of *Anthracoscorpio* Kušta, 1885, and a detailed restudy of the two genotypes proves the point.

Lichnoscorpius minutus Petrunkevitch, 1949
Text-figure 45

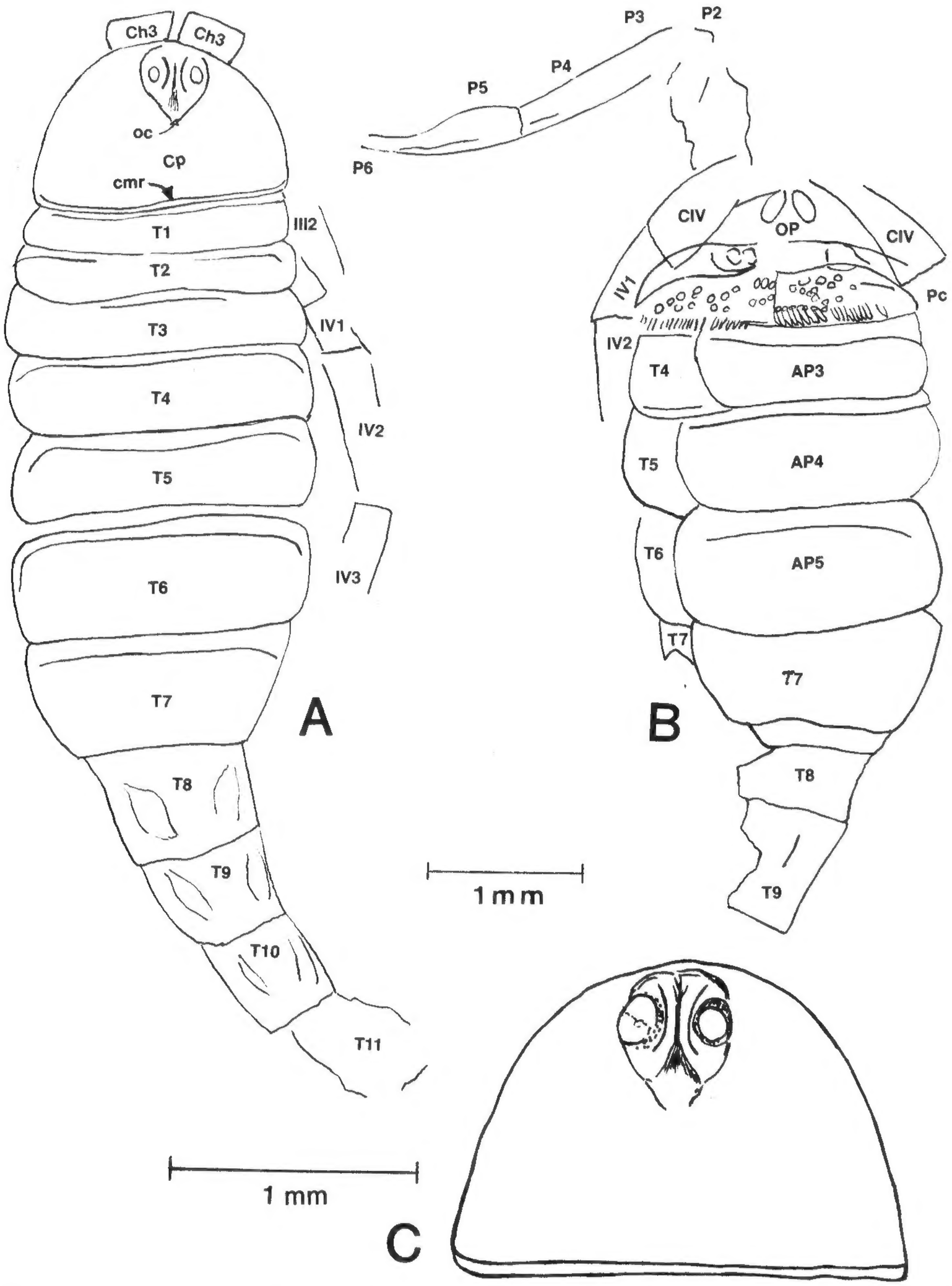
1949. *Lichnoscorpius minutus* Petrunkevitch, pp. 148–149, figs. 144, 145, 181.
1953. *Anthracoscorpio minutus* (Petrunkevitch). Petrunkevitch, pp. 30–31.
1962. *Anthracoscorpio minutus* (Petrunkevitch). Dubinin, p. 431, fig. 1249.

Type information.—Holotype from the Upper Coal Measures in the *Modiolaris similis* and *pulchra* Zones, ten feet above the Thick Coal of Coseley, in the South

Staffordshire Coalfield, England, and deposited in the British Museum (Natural History) as BM(NH) In.31266.

The original description and figures of the holotype are erroneous. Petrunkevitch (1949, p. 148) states that the holotype consists of two parts, both showing "the dorsal surface without any traces of the ventral surface". The ventral surface is shown on one of the specimens, thus revealing several very important structures. The restudy requires a full redescription, which is given here.

The carapace is broadly semicircular with a narrow marginal rim at the base, which is straight, and a well-developed lacrimiform median eye node surmounted by two small round eyes with well-developed supraorbital ridges. No visible rim is present. The tergites increase slightly in size posteriorly. Therefore the last three preabdominal tergites are approximately the same size. A strong transverse ridge occurs at the anterior of each preabdominal tergite. The cauda, the anterior four tergites of which are present, is stoutly constructed—two high carinae, diagonally placed, surmount each



Text-figure 45.—*Lichnoscorpius minutus* Petrunkevitch. Holotype, BM(NH) In.31266. From the Upper Carboniferous, Upper Coal Measures (*Modiolaris similis* and *pulchra* zones), Coseley, Staffordshire, England. See foldout inside front cover for explanation of abbreviations.
A. Dorsal side. **B.** Ventral side, counterpart. **C.** Outline of the carapace and ocular details. From a rubber cast.

tergite dorsally. The cauda tapers posteriorly and there is no great constriction at the eighth tergite.

The underside shows the abdominal plates to be holosternous, rounded at the genal angles, and with a slight transverse ridge on the anterior. The coxosternal region has largely been broken away, but the genital opercula are present and are elongate, subtriangular, and rounded at the posterior part. More important is that the anterior of the operculum lies below the level of the last pair of coxae. Therefore this pair had to abut the sternum, and it seems probable that the coxosternal arrangement was typical of the family Anthracoscorpionidae.

The pectines are faintly preserved and are narrow, long, containing approximately 25 to 30 teeth, with fulcra and the rachis divided into irregular-sized rounded sclerites or areoles, which are coarser toward the center than at the edges. The anterior lamella also has rounded sclerites.

Measurements and description of the opisthosoma were given in the original description (Petrunkevitch, 1949, pp. 148–149).

Remarks.—It can easily be separated from *Pseudobuthiscorpius labiosus* Kjellesvig-Waering by the different opercular plates, as well as the holosternous abdominal plates as against the lobosternous plates in the latter. Both species probably had rather similar coxosternal arrangements.

Genus **ALLOBUTHUS**, new genus

Anthracoscorpionidae having a square carapace, slightly emarginate or straight anterior margin, and median eyes located one-third of the distance from the anterior, without elevated cephalic shield. No lateral compound eyes.

Derivatio nominis.—*allo* (Gr.) = another + *buthus* (Gr.) = a scorpion genus.

Type species.—*Allobuthus macrostethus,* n. gen., n. sp.

Geological range.—Carboniferous.

Remarks.—It differs from *Buthiscorpius* in having a quadrate carapace as against a nearly semielliptical one, and in the lack of compound eyes. The semicircular carapace of *Anthracoscorpio* is sufficient to distinguish it from the quadrate form of the new genus.

Allobuthus macrostethus, new species
Text-figures 110C, 113B4

1960. *Buthiscorpius buthiformis* (Pocock). Wills (*partim*), pp. 284–289, pl. 48, text-figs. 6–9.

Type information.—Holotype, Birmingham University BU 720, "almost certainly obtained from the Coal Measures of South Staffordshire, probably from above the Thick Coal at Coseley" (Wills, 1960, p. 284), England.

Included by Wills (1960, p. 284) under the description of *Buthiscorpius buthiformis* (Pocock) is a scorpion from a different locality and very likely different age than the holotype of that species. The specimen BU 720 was successfully extracted from the matrix, but it cannot properly be assigned to *Buthiscorpius buthiformis* (Pocock) nor even to the same genus. The differences are much too great to include BU 720 and the holotype of *B. buthiformis* (Pocock) in the same genus, and these differences cannot be ascribed to secondary sexual characters. Moreover, there seems to be no doubt that both specimens are males. This is based on the generally slender mesosoma of BU 720 and on the equally slender mesosoma and the great length of the fifth caudal segment of the holotype of *B. buthiformis.* Both of these characters are used for determining sex in living scorpions, and are quite reliable. Even if the sex determination were not correct, there are many other differences unrelated to possible sex differences.

The differences between *Allobuthus macrostethus* and *Coseleyscorpio lanceolatus,* n. gen., n. sp., which Wills had successfully developed (1960, p. 277) as a paratype (BM(NH) In.31262) of *Buthiscorpius buthiformis* (Pocock) are listed below:

	A. macrostethus (BU 720)	*C. lanceolatus* (BM(NH) In.31262)
Carapace:	nearly square	semielliptical
	anterior margin slightly emarginate	anterior margin oval
	slightly wider than long	considerably longer than wide
	eyes smaller	eyes larger
	eyes close-set without interocular ridge	eyes much farther apart with interocular ridge
Sternum:	sides nearly straight, base straight	sides converging forward, base deeply notched
	proportionately wider	proportionately narrower, particularly anteriorly
Coxa 1:	much wider maxillary lobe	much narrower maxillary lobe
Coxa 2:	not divided by "joint line" from the maxillary lobe	well-developed "joint line" separating maxillary lobe from coxa
Coxa 3:	less than half as long as coxa 4	more than half as long as coxa 4
Trochanter of pedipalp:	flaring at distal end	rounded at distal end
Seventh tergite:	carinae not present, apparently smooth	well-developed sharp, double carinae and strong median spine

The sternum of the holotype of *Allobuthus macrostethus* is not complete along the base, but enough is present to show that this part had to be straight rather than deeply-notched as in *Coseleyscorpio lanceolatus.*

Detailed descriptions and figures of the holotype of *Allobuthus macrostethus* have been given by Wills (see synonymy) and little can be gained by repetition here.

Derivatio nominis. —*macro* (Gr.) = long, large + *stethos* (Gr.) = breast.

Genus **COSELEYSCORPIO**, new genus

Anthracoscorpionidae of small size; carapace lanceolate, without lateral eyes, small rounded eyes located at the base of the anterior quarter of the carapace, poor development of eye node and orbital ridges. Sternum pentagonal, converging anteriorly, deeply-notched or flared at posterior and with genital opercula fitting into notch. First two coxae with well-developed, narrow maxillary lobes. Pedipalp fingers straight.

Derivatio nominis. —Named for Coseley, where the holotype was found.

Type species. —*Coseleyscorpio lanceolatus,* n. gen., n. sp.

Geological range. —Carboniferous.

Remarks. —This is another genus developed from a paratype of *Buthiscorpius buthiformis* (Pocock).

Coseleyscorpio lanceolatus, new species

1911. *Anthracoscorpio buthiformis* Pocock (*partim*), p. 27, pl. 1, fig. 2a.
1953. *Buthiscorpius buthiformis* (Pocock). Petrunkevitch, p. 32.
1960. *Buthiscorpius buthiformis* (Pocock). Wills (*partim*), pp. 278–284, pls. 46, 47; text-figs. 1–5.

The above synonymy refers to specimen BM(NH) In.31262 only. The description and illustrations given by Wills (1960) cannot be improved upon.

Type information. —From concretionary shale about ten feet above the ten-foot-thick bed of coal in the Coal Measures, Coseley near Dudley, South Staffordshire, England. The specimen is deposited in the British Museum (Natural History) as BM(NH) In.31262.

Derivatio nominis. —Named for the lanceolate carapace.

Remarks. —This specimen differs from the holotype of *Buthiscorpius buthiformis* as follows:

1. The median eyes of BM(NH) In.31262 are further forward than in the holotype.

2. Specimen BM(NH) In.31262 lacks the ornamentation along the anterior of the carapace of *B. buthiformis,* although both are males, and also lacks the anterior prolongation.

3. No lateral compound eyes are present in BM(NH) In.31262.

The many points in which it differs from *Allobuthus macrostethus* have already been enumerated in the discussion of that species (see above).

Family **GARNETTIIDAE** Dubinin, 1962 (emend.)

Eoctonoidea with compound lateral eyes; maxillary lobes unknown; last two pairs of legs abutting pentagonal sternum; first two pairs meet in front of the sternum; anterior pair of legs fossorial, flattened, and with large spurs and serrations; highly-serrated rachis of comb, unsegmented.

Type genus. —*Garnettius* Petrunkevitch, 1953.

Genus **GARNETTIUS** Petrunkevitch, 1953

Garnettiidae with small, anteriorly-located, median eyes and large, bulbous, lateral eyes on a nearly square carapace, which is much narrower on central part than anteriorly or posteriorly; chelicerae very large, and with short, stout pedipalps; opercular plates elongate, asymmetrical, lacrimiform.

Type species. —*Mazonia hungerfordi* Elias, 1936.

Geological range. —Missourian Series of the Pennsylvanian.

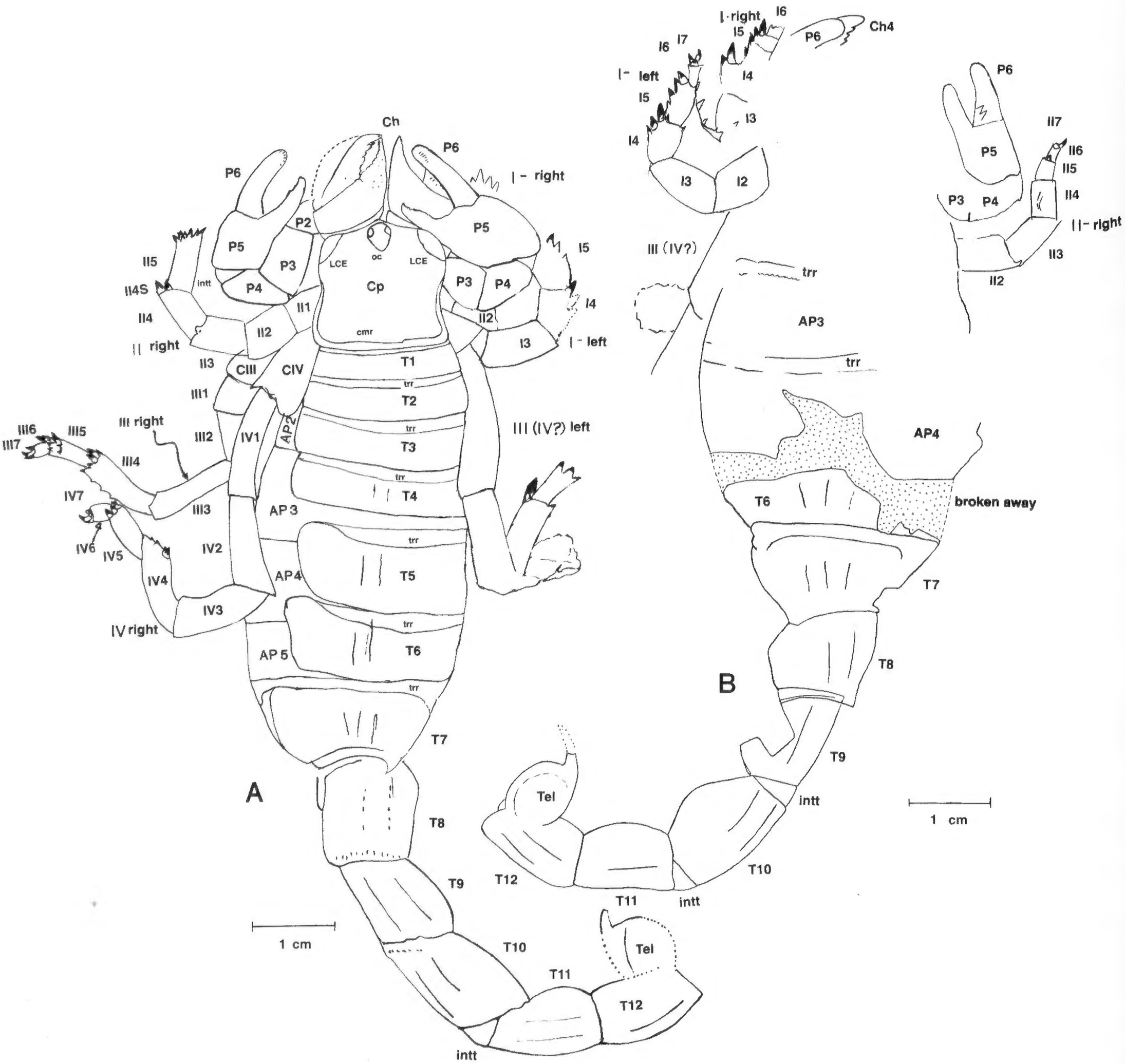
Distribution. —Kansas.

Remarks. —There is little to be gained by comparing this peculiar and unique scorpion with any fossil or living genus. It is distinct on many counts, as a glance at the figures will show. The most surprising feature of this scorpion is the anterior pair of legs, which is adapted for digging. Inasmuch as it is a gill-bearing or holosternous type, it must be assumed that digging had to occur in water or at least in very moist areas. The last three pairs of legs are also adapted for a digging existence, as they are encircled at the basitarsus and tarsus with a ring of spines that opened when pressure was applied, and thereby gave more stability and traction to any digging action by the front legs. This combination of fossorial legs and "stabilizers" is known in many other arthropods, such as the mole cricket, and countless beetles, particularly the coprophagous scarabs (*Phanaeus, Copris, Canthon*), but is totally unknown in any of the scorpions, fossil or living. The living scorpions that burrow do not have legs developed into fossorial types, but do have a development of setae which enables them to dig in soft or unconsolidated sands and soft soils.

Garnettius hungerfordi (Elias, 1936)
Text-figures 46, 47B–K, 48

1936. *Mazonia hungerfordi* Elias, p. 13, fig. 6; p. 15, fig. 8.
1937. *Mazonia hungerfordi* Elias. Elias, pp. 335–336.
1949. *Mazonia hungerfordi* Elias. Petrunkevitch, p. 133.
1953. *Garnettius hungerfordi* (Elias). Petrunkevitch, pp. 34–35, figs. 36–39, 125.
1955. *Garnettius hungerfordi* (Elias). Petrunkevitch, p. 75, fig. 44(8).
1962. *Garnettius hungerfordi* (Elias). Dubinin, p. 432, figs. 1240, 1257a, b.

Type information.—Holotype, USNM 125453a and b, in the collections of the National Museum of Natural History, Washington, DC, formerly KU 220.1 and 220.2 in the University of Kansas Geological Museum. Pennsylvanian, Rock Lake Shale Member of the Stanton Limestone Formation of the Lansing Group, Missourian Series, in Section 32, T. 19 S., R. 19 E., six miles northwest of Garnett, Anderson County, Kansas. Associated on the same slab with articulated brachio-



Text-figure 46.—*Garnettius hungerfordi* (Elias). Holotype, USNM 125453a,b; part and counterpart (formerly KU 220.1, 220.2). From the Upper Carboniferous (Pennsylvanian) Stanton Group, Missouri Series, 6 mi northwest of Garnett, Anderson Co., KS. See foldout inside front cover for explanation of abbreviations.

A. Showing dorsal features only. **B.** Counterpart showing some suggestions of ventral features.

pods, bryozoa, crinoid stems and plants.

The specimen is preserved as a flattened skin that retains original coloration and numerous details such as setae and setal sites. A considerable part of the original cuticle has flaked off but much can be discerned from the imprint left on the fine-grained, buff-colored, highly calcareous shale. This paleobiotype is known as the *Garnettius* Assemblage (Moore, 1964, p. 297), which is considered to be a marine lagoon or bay with an admixture of marine and terrestrial animals and plants.

It is important to understand how this scorpion is preserved. The rock has been split along the bedding plane, revealing numerous fossils on each surface. The scorpion is composed of cuticle, and both sides of the bedding plane retain parts of the cuticle or the imprints of the cuticle, which, on the edges, are of considerable value in revealing the structure. Thus each half of the fossil may retain the imprint of the ventral or the dorsal surfaces, along with parts of either the dorsal or ventral side of the original cuticle, or both, depending on how the cuticle broke when both sides of the bedding were exposed. For example, one half may contain the dorsal imprint of the anterior part of the carapace and the edges, as well as part of the ventral side, as shown by the cuticle. This is precisely the case with the anterior part of the holotype seen in Text-figure 46B. The cuticle of the legs represents the anterior ventral side, whereas the back legs are revealed mainly as imprints of the posterior side, except where the original cuticle is present on the end of the fourth leg, and there the anterior side is preserved.

The imprint of this fossil reveals fine details in various types of lighting, particularly a light source from a very low angle. The specimen has been studied dry, without the preservative covering necessary to prevent the remaining cuticle from flaking off. It has also been studied immersed in alcohol, a method which reveals much from the cuticle. By all these methods it was possible to discern many morphological structures not previously noted.

The holotype, and still the only known specimen, is remarkable for the large size of the chelicerae, the lateral compound eyes, and the unusual, highly-serrated, anterior legs, resulting in the differentiation of the legs, a factor not encountered in other scorpions. The specimen was described by Elias in 1936 and later was studied by Petrunkevitch (1953, pp. 34–35, figs. 36–39), who gave descriptions and figures that are not in agreement with the description given here. Major points of disagreement or of total omission will be pointed out in the description. The overall coloration of this scorpion is dark reddish-brown, shiny and very much like that of living scorpions such as *Broteochactas, Euscorpius, Opisthacanthus* and *Hadogenes.*

The carapace is nearly square, rounded at the anterolateral angles and with the anterior margin produced into a pointed process. The lateral margins are incurving, so that the area at the base and at the anterolateral angles is wider than along the narrowed middle. The base is straight and the genal angles form rounded right angles. A wide, raised marginal rim extends along the base and halfway around the lateral margins. There is no anterior marginal rim such as Petrunkevitch (1953) shows in figures 36 and 37. The part which Petrunkevitch misinterpreted as an anterior rim is the first segment of the two chelicerae, which almost meet in front of the carapace.

The most prominent features of the carapace are the small median eyes and the very large lateral compound eyes. The median ocelli are small, elliptical in shape, and are located laterally on a small, cordated, raised ocellar mound that is placed anteriorly on the carapace, close to the anterior projection of the anterior margin. The lateral eyes, previously undetected, are bulbous, very large, and located at the rounded anterolateral corners. No facets were noted as all of the original cuticle has been stripped away, but the outlines of the compound eyes are very clearly revealed. The small median eyes together with large compound eyes is a common combination in Paleozoic scorpions.

The prosomal appendages are known in almost all detail, and they are among the most unusual in any scorpion. The enormous chelicerae (see Measurements) are features that are unknown in other scorpions. The chelicerae are very well preserved and were noted in part by Elias (1936) in his figure, but were completely omitted by Petrunkevitch (1953). These structures are nearly as large as the chelae of the pedipalps or almost half as large as the carapace. It is not known whether there are three or four joints as the carapace covers everything but the last three joints. Because other related Paleozoic scorpions have four-jointed chelicerae, it must be assumed that four joints were present. The very wide chelicerae have a very large free finger that is hooked and armed with several large teeth; the fixed finger is concave along the edge and also is armed with teeth. It was not possible to determine the actual arrangement of these teeth as the chelicerae were compressed into a single plane and little of the original cuticle was left. However, it is certain that the distal end of the free finger ends in a single hooklike tooth and not in a double tooth, an arrangement present in some scorpions such as the living Buthidae. To stress the great size of these chelicerae, they extend 9.8 mm beyond the frontal edge of the carapace, whose total length is only 16.7 mm. The chelicerae are 6.8 mm wide at midsection.

The pedipalps are known in their entirety (see Mea-

surements) and are stout short structures characteristic of burrowing scorpions such as some of the living Chactidae and Scorpionidae. The femur and tibia are very short, stout, and slightly longer than wide. The chelae are short, stout, with a rather quadrate hand, and fingers that are quite unusual. The free finger is stout, but much longer than the immovable one, and is slightly bent inward with a very blunt, rounded end. The immovable finger is also incurving and very stout. Numerous setae occur on the ends of the fingers, in particular as a fringe along the dorsal side of the fingers, near the edge. No teeth are discernible along the edge, but this may be due to preservation and should not be discounted.

This is the only known scorpion where differentiation of the legs occurs. Other scorpions have the four legs similarly developed except, of course, for relative length of the individual segments, or at the coxae. Some differentiation does occur in scorpions in the presence or absence of certain tarsal or basitarsal spurs, but this is minor in comparison to the differentiation of the first leg of *Garnettius hungerfordi* into a scooping, flattened, serrated organ admirably suited for digging, as against the other legs which, although varying in length, are similar to each other. In modern insects, the *Garnettius* type of front legs can be duplicated in many groups, as mentioned above. In these groups the front legs are curved inwardly and are not employed in walking, but are specialized for burrowing.

The first pair of legs is well preserved and almost entirely known. The right leg has been displaced and is present on the left anterior part alongside the left leg. This leg is preserved in its original cuticle with the dorsal side showing. The left leg is also preserved in its original cuticle and is shown ventrally. The exact podomere count is not known, but it is assumed that eight joints, coxa and posttarsus included, make up the entire leg. If this is correct, then in Text-figure 47J the long joint labelled **I3** would be the femur, **I4** tibia, **I5** basitarsus, **I6** tarsus, and **I7** the posttarsus. All joints are naturally flattened, and only the tibia and basitarsus are serrated along the posterior edge, which would be carried ventrally in life, bowed inwardly, and with the dorsal side facing the anterior. It is interesting to note that in this leg, although far removed by specialization from the normal plan, the basitarsal and tarsal spurs are developed as in many other fossil scorpions. It is certain that at least two very large movable spines are present on the distal part of the tibia. These definitely appear to be in sockets of the tibia and not in the intersegmental skin between the tibia and basitarsus as in other scorpions. It may be possible that they are present in the intersegmental skin in a cove or depression at the end, but this does not seem to be the case as definite sockets have been observed. The spines are flattened in conformity with the flattened and serrated edge of the rest of the tibia. A short spine, which definitely occurs in the intersegmental skin between the tibia and tarsus, was noted, and this may be the actual basitarsal spur.

The basitarsus, as stated above, is constructed along the same plan as the previous joint, being flat and with very large serrations along the posterior side. This edge would be ventral in life.

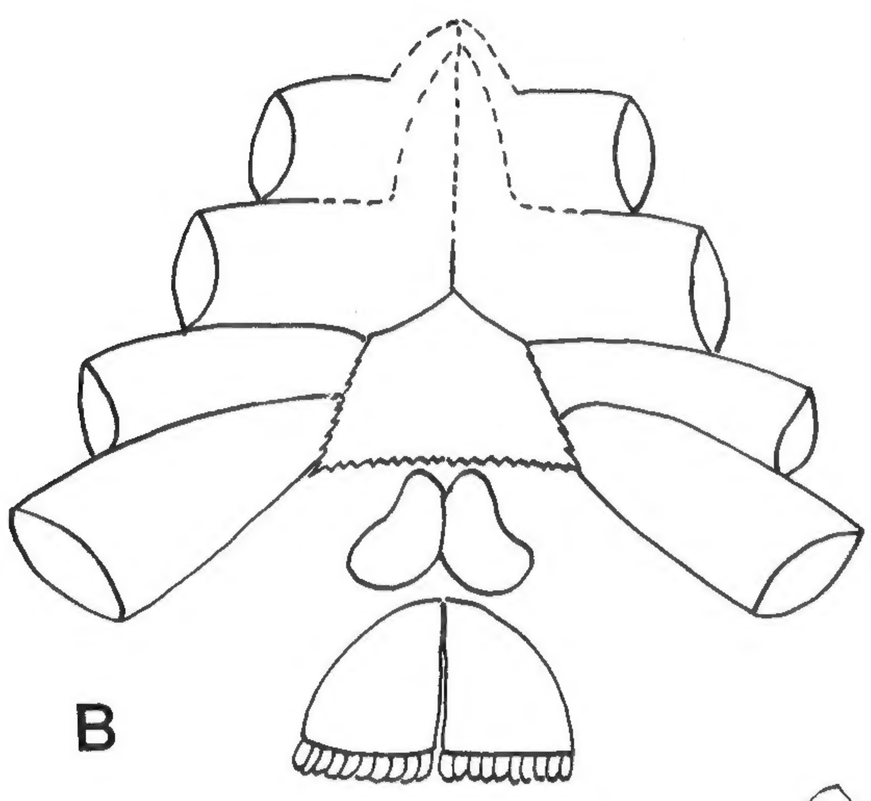
The tarsus, surprisingly, is a joint of "normal" nature and not spinous as the previous one. Two short claws, slightly bent and hooklike, terminate the leg. The anterior claw is slightly larger. Immediately below is the posttarsus, which is rounded, short, and unusually stout.

The second walking leg is rather tubular and without the development of the spurs present in the first leg. This leg has eight short tubular joints. Basitarsal and tarsal spurs are developed, two in the basitarsus and an unknown number in the tarsus. Preservation was not very good in this part. The tarsus, with the terminal claws, and the posttarsus are very well preserved from the ventral side, in their original cuticle. The tarsus is very short, devoid of spines except at the intersegmental anterior part. Two claws are present, of which only the shorter posterior one is fully preserved. This is tapering and not hooklike. The anterior claw is presumably longer, but only the base is preserved, which shows that it is considerably larger at the base than the posterior one. The posttarsus is a short, padlike, rounded structure that occurred in life under the claws. It is ornamented with a definite semicircle of large, rounded holes that very likely represented setal sites.

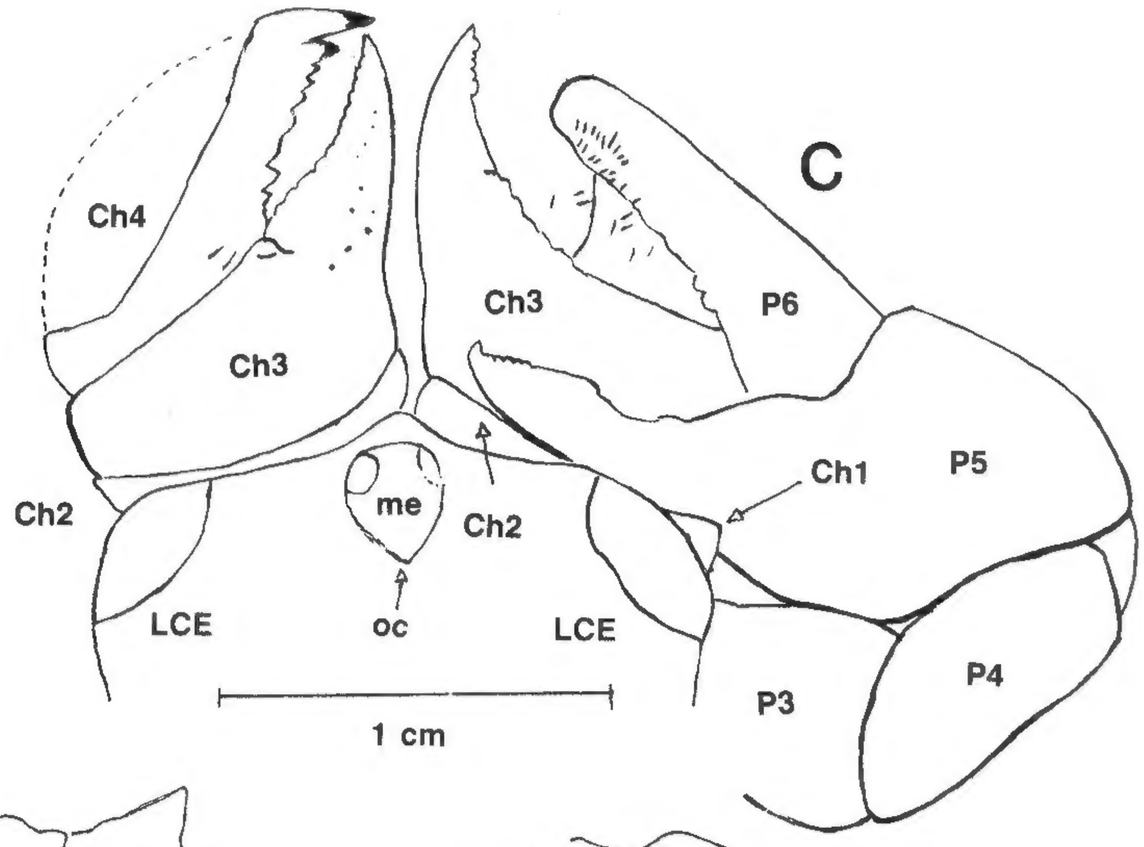
The third leg of the right side is preserved in its entirety and in posterior view. Eight joints are present and appear not to be flattened, but mainly tubular. In Petrunkevitch's drawings (1953, figs. 37 and 38) the

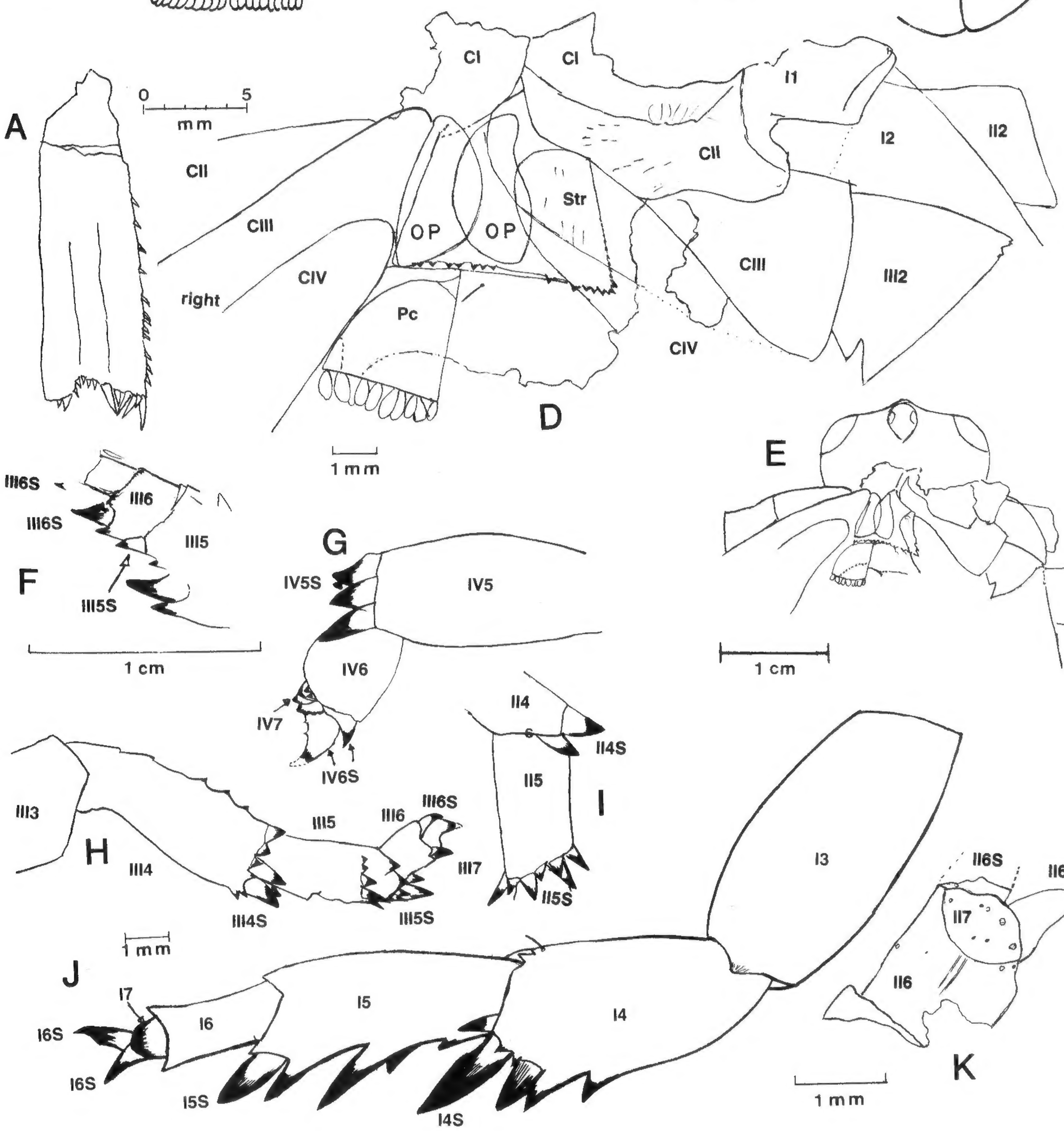
Text-figure 47.—Species of *Garnettius* Petrunkevitch, 1953. See foldout inside front cover for explanation of abbreviations.

A. *Garnettius* (?) sp. RSM 1957.1.5007 (Dunlop coll.). From the Lower Coal Measures (Westphalian A), Airdrie, Scotland. The basitarsus or tarsus of a large scorpion. The posterior striated spines recall the fossorial scorpion *Garnettius hungerfordi* (Elias). **B–K.** *Garnettius hungerfordi* (Elias). Holotype, USNM 125453a,b; part and counterpart. From the Upper Carboniferous (Pennsylvanian) Stanton Group, Missouri Series, 6 mi northwest of Garnett, Anderson Co., KS. **B.** Diagrammatic interpretation of the coxosternal-opercular pectinal area. Based on Text-figure 47D. Dotted areas not seen. **C.** Chelicerae and powerful chela of right pedipalp. **D.** Enlargement of ventral features shown in Text-figure 47E. **E.** Showing ventral features only of coxal arrangement, and anterior dorsal aspect of the prosoma. **F.** Third right leg from dorsal side; had been turned over and shifted to the left side. **G.** Fourth leg showing basitarsus, tarsus and posttarsus. **H.** Third leg, showing the extraordinary distal spinosity. **I.** Joint 5 of the second leg, also unusually spinose. **J.** First right walking leg from ventral side. **K.** Distal part of second right leg, ventral view, preserved with original cuticle.



B


Ch4
Ch3
Ch3
P6
C
Ch1
P5
Ch2
me
Ch2
LCE
oc
LCE
P4
P3
1 cm


A
0 5
mm
CII
CIII
CIV
right
CI
CI
II1
II2
I2
CII
Str
OP
OP
CIII
III2
Pc
CIV
D
1 mm
E
1 cm
III6S
III6
III6S
III5
F
III5S
1 cm
G
IV5S
IV5
IV6
IV7
IV6S
II4
II4S
II5
II5S
I
III3
H
III4
III5
III6
III6S
III7
III4S
III5S
1 mm
J
I7
I6S
I6
I6S
I5S
I5
I4
I4S
I3
II6S
II6S
II7
II6
K
1 mm

first leg, with its characteristic serrations, was unfortunately placed in the position of the third leg. The same specimen is shown in Petrunkevitch's figures 37 and 38 respectively, as in Text-figures 46A and 47J herein, but this leg does not occur where he shows it to be, but in the anterior part of the specimen. This dislocation must have occurred when Petrunkevitch assembled the various parts of the drawing, as he stated,

> In studying the details for a drawing, I was forced to make camera lucida drawings at a magnification of ten diameters, piece them together on a large sheet of paper and then reduce the drawing to the present size photographically.

The third leg, therefore, is relatively uncomplicated, although a fringe of numerous spines occurs on the distal part of the basitarsus and tarsus. At least two basitarsal spurs are present and the same number of tarsal spurs, but it must be admitted that this may only be a small part of the actual spurs (see Text-figs. 46A, 47F, H).

The tarsus is short, and the terminal claws are short, hooklike, and with a short, spinelike posttarsus. The entire end of the leg appears to be admirably suited for pushing, as the spines on the distal ends would open to give the leg added traction. This can be found in many of the burrowing insects (*Phanaeus, Pinotus,* etc.).

The complete fourth leg is known from the posterior side of the right leg. It has eight joints and is relatively uncomplicated. As in the previous leg, the joints appear to have been mainly tubular, without noticeable compression, and it also had a very spinous distal end (see Text-figs. 46A and 47G). At least two basitarsal spurs are known and several serrations that might be spurs are present at the distal end. These spurs appear to fit into sockets of the tibia, and not in the intersegmental skin below the tibia and above the basitarsus as in other scorpions.This fact was also noted in the first leg. The distal end of the basitarsus shows at least four spurs and these could well be in the intersegmental skin and thus would correspond to the tarsal spurs. All spurs seem to be the same size. The tarsus is very stout and rounded at the edges and has two small terminal hooklike claws, the anterior one being larger. The posttarsus is short and is hidden from view by the presence of several short spines. A possible interpretation, taken from an imprint, is shown on Text-figure 47G.

The coxosternal region, with operculum and pectines, is largely preserved in the original cuticle. This is shown in ventral view in Text-figures 47D, E. The region, however, is badly preserved, displaced to the right side, and the coxae are squeezed partly one above the other, whereas the opercular plates have been dislocated so that they rest on top of the sternum. The mass of cuticle is therefore very difficult to untangle, and without a doubt other interpretations are quite possible. In fact, the writer tried various interpretations, but the most reasonable one is that given in Text-figures 47B, D. Because of the complexity of the preservation, the coxosternal arrangement must be verified by other specimens as, admittedly, I have no overwhelming confidence in the correctness of the interpretation given here. It appears that the third and fourth coxae abut against a large pentagonal sternum that has a fringe of short spines along the posterior of the lateral margins. These spines also form a prominent fringe at the base of the sternum where they are stout and triangular. The other two coxae apparently lie anterior to the sternum and it is assumed that they meet at the median line and have maxillary lobes developed (not seen). The operculum is well preserved and consists of two elongate asymmetrical lacrimiform plates. Both plates have been pushed over the sternum and are slightly overlapping. This was clearly seen in the wet state under alcohol.

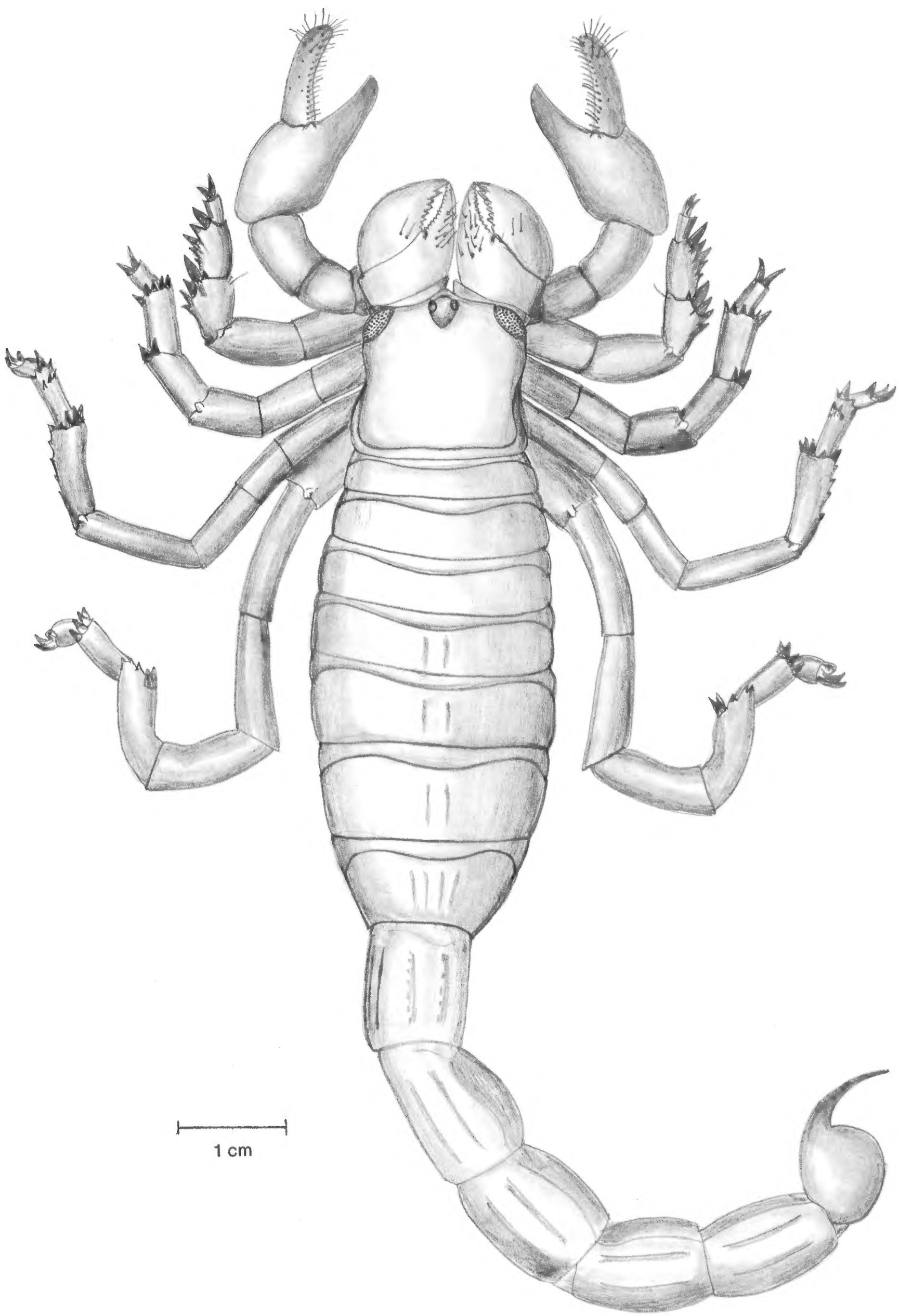
The pectines are relatively small and, as seen under alcohol, are rather well preserved. The rachis is devoid of any segmentation or of the small rounded sclerites common to the Carboniferous scorpions. There are also no fulcra. The teeth, approximately 10 on each comb, are small, stout, and rather elongate-ellipsoidal. I have also noted this type of comb in the Lower Devonian genus *Branchioscorpio,* n. gen.

The preabdomen is composed of the usual seven tergites, and these increase in size progressively. Each tergite is bounded by the usual anterior transverse ridge, presumably raised. Two central carinae occur on the fourth to sixth tergites, whereas the seventh appears to have three carinae.

The abdominal plates are preserved to the side and, although not completely exposed, there is no doubt that they are holosternous. Therefore, no stigmata are present; enough of the abdominal plates were exposed to determine this fact.

The cauda is unusually thick. The first tergite has two dorsal carinae surmounted by elongate punctations. The rest of the tergites, seen in lateral view, show two lateral carinae. The telson is very stout, short, and powerfully constructed. The vesicle is nearly round and devoid of a subaculear tubercle. The aculeus is only preserved as an impression, but appears to be of the usual shape, curved and tapering to a point.

The integument of the holotype is mainly smooth and without noticeable granules or any other ornamentation not already noted. It is, however, highly hirsute and numerous setae were found on many parts of the cuticle, although it was not possible to determine any pattern, as not enough of the original cuticle was preserved. The area around the fingers of the pedipalps was particularly setaceous.



Text-figure 48.—*Garnettius hungerfordi* (Elias). Restoration based on the holotype, USNM 125453a,b.

Measurements (in mm) of the holotype (USNM 125453a,b).—

Prosoma:		
Length		16.7
Width at base		16.8
Width at lateral eyes:		16.8
Width at midsection:		14.2
Median eyes:		
Length:		1.0
Width:		0.6
Distance from anterior margin:		0.7
Distance from posterior margin:		14.6
Distance from lateral margin:		6.9
	length	width
Compound eye:	4.2±	2.0±
Pedipalp:		
Chela	17.0	
Hand	7.5	5.7
Free finger	5.0	
Femur	6.0	
Tibia	6.8	
Tergite:		
No. 1	2.5	
No. 2	3.7	
No. 3	3.8	
No. 4	5.0	
No. 5	6.2	
No. 6	7.4	
No. 7	10.0	
No. 8	10.2	
No. 9	11.1	
No. 10	12.6	
No. 11	11.0	
No. 12	12.0	
Telson:		
Vesicle	9.7	6.7
Aculeus	4.0 (estimated)	
Greatest width of tergites at base of fourth tergite:	23.0	
Total length of scorpion:	about 125.0	

Remarks.—This is one of the most peculiar scorpions known. Obviously the first pair of legs is typical of a burrower as they are structurally similar to those found in many burrowing arthropods. The second to fourth legs, with their fringe of numerous side spines, also denote a burrower as these legs seem to be admirably suited for pushing or giving the animal more traction along the burrow. It is the only scorpion in which such great differentiation occurs in the legs. Dubinin (1962) was correct in forming a family for this scorpion, although only a small amount of the information was then available in the literature and, part of this, erroneous. Certainly the many other unique characters of this scorpion, including the enormous chelicerae, could also have served to form a distinct family.

The nature of the habitat of this scorpion can, of course, only be surmised. On the same slab, and same surface, are numerous articulate brachiopods, fragments of bryozoa, and pieces of crinoid stems. Obviously the specimen was buried in a marine environment, possibly of lagoonal nature. As noted elsewhere, the pointed anterior margin is characteristic of water-dwelling chelicerates such as the eurypterids, and is considered to be used for the same function in scorpions inhabiting a water environment. There is no question regarding the presence of stigmata—there are none, and the scorpion is clearly holosternous. Therefore it is considered to be a water-dwelling scorpion. Of course, it is not possible to determine whether or not the specimen was swept in from a fresh-water source. However, the specimen is complete and it is known that appreciable transportation is quite destructive to these frail skins. The indications are that the scorpion lived in or near the burial site. I see no good reason why the scorpion could not have been a marine form, inhabiting a lagoonal environment, as suggested by the burial site.

Garnettius (?) species
Text-figure 47A

Specimen data.—A single joint, probably the basitarsus or tarsus (No. 5 or 6) of a large scorpion, preserved in dark gray micaceous shale, from the Lower Coal Measures (Westphalian A), possibly from the "Fern bed", 20′ above the Upper Drumgray Coal, Airdrie, Scotland, deposited in the Royal Scottish Museum (Dunlop Collection), as RSM 1957.1.5007.

The single joint is important because it reveals a row of movable, striated spines along the posterior part, and numerous movable spines at the end of the joint, such as are present in *Garnettius hungerfordi* (Elias), which was an obvious fossorial scorpion. If this relationship is correct, the joint could be in the third or fourth leg and probably would correspond to the basitarsus, or less likely, the tarsus (5 or 6), and the movable spines would open to push the animal forward when burrowing, much as is found today in fossorial insects. Length of joint, incomplete, is 15 mm, and width is 4.3 mm.

Superfamily **SPONGIOPHONOIDEA**, new superfamily

Holosternina (?) with coxosternal area having last two pairs of coxae abutting the sternum, second pair partly abutting the sternum and each other and without maxillary lobes. First pair with short maxillary lobes and adjoining one another at the midline.

Type family.—Spongiophonidae, n. fam.

Remarks.—This is a highly primitive superfamily, which surprisingly occurs in the Triassic. The lack of development of maxillary lobes on the second pair of coxae is unique and would indicate a relict from the

Paleozoic. It is obvious that our knowledge of scorpions is meager, otherwise a development such as indicated by *Spongiophonus* would not be such a surprise. No other superfamily known, regardless of the infraorder, has the characters listed for the coxosternal area.

Family **SPONGIOPHONIDAE**, new family

Spongiophonoidea having large, mainly triangular, sternum with anterior developed as a small subpentagonal area. The ornamentation is coarsely pustulose in the form of polygons.

Type genus.—*Spongiophonus* Wills, 1947.

Genus **SPONGIOPHONUS** Wills, 1947

1955. *Spongiotarsus* Wills. Petrunkevitch (in error—not Wills), p. 79.

The generic description includes the characters listed above for the superfamily and family.

Type species.—*Spongiophonus pustulosus* Wills, 1947.

Geological range.—Triassic.

Spongiophonus pustulosus Wills, 1947
Text-figure 110L

1947. *Spongiophonus pustulosus* Wills, pp. 133–135, pl. 3, figs. 13–15; pl. 11, figs. 8, 13; text-fig. 53.
1953. *Spongiophonus pustulosus* Wills. Petrunkevitch, p. 37, fig. 47.
1955. *Spongiotarsus pustulosus* Wills. Petrunkevitch (in error—not Wills), p. 79.
1962. *Spongiotarsus pustulosus* Wills. Dubinin (in error), p. 432.

Four specimens of this important and peculiar form are known. The holotype (SM 280), consisting of the superb specimen that forms the basis of the higher taxa described above, comes from a borehole at Messrs. Southalls (B'ham) Ltd. works at Charford, Birmingham, England, whereas three tergites, SM 0286, 276, and 059, come from the Bromsgrove Quarry, near Birmingham, England. All are from the Triassic, Lower Keuper Sandstone Series, and are in the Sedgwick Museum, Cambridge, England.

Family **PRAEARCTURIDAE**, new family

Spongiophonoidea of large size with very narrow, greatly-elongated, lanceolate sternum, with deep median infolded sulcus; coarsely tuberculate dorsally; smooth ventrally.

Type genus.—*Praearcturus* Woodward, 1871.

Remarks.—Surprisingly the coxosternal arrangement is the same as the Triassic *Spongiophonus* Wills, 1947 (and so far unknown elsewhere), namely: only the first pair of coxae has maxillary lobes, which are poorly developed, and the second pair is without maxillary lobes, meeting at midsection and also abutting the anterior part of the sternum. The last two pairs of coxae abut the sternum. The completely different sterna relegate the genera to separate families.

Genus **PRAEARCTURUS** Woodward, 1871
(new definition)

Praearcturidae having very poor development in size of the first tergite (or considerable development of the pregenital tergite). Carapace anterior unknown, but with well-developed lateral cheeks and raised posterior area. Chela of pedipalp cultrate.

Type species.—*Praearcturus gigas* Woodward, 1871.

Geological range.—Lower Devonian.

Distribution.—England; Wyoming, U.S.A.

Remarks.—The tuberculate ornamentation is very distinct and is responsible for the recognition of this genus in the Lower Devonian of Wyoming.

Praearcturus gigas Woodward, 1871
(new description)
Text-figures 49, 110A

1871. *Praearcturus gigas* Woodward, pp. 266–270, 5 text-figs.
1872. *Praearcturus gigas* Woodward. Woodward, p. 166.
1877. *Praearcturus gigas* Woodward. Woodward, p. 65.
1900. *Praearcturus gigas* Woodward. Kingsley *in* Zittel–Eastman, p. 668.
1922. *Praearcturus gigas* Woodward. Hennig, p. 144.[14]
1969. *Praearcturus gigas* Woodward. Hessler, Treatise R(1), p. 393.
1969. *Praearcturus gigas* Woodward. Rolfe, Treatise R(2), p. 622, fig. 395.
1980. *Praearcturus gigas* Woodward. Rolfe *in* Panchen, p. 147.

This interesting and spectacular scorpion is based on a number of large fragments from the Dr. D. M. McCullough Collection in the British Museum, and two other specimens in the collections of the Institute of Geological Sciences, Edinburgh, Scotland. All fragments represent different body parts, and although there is no documentation to settle the matter, I believe all may represent one individual. At any rate, all are similarly preserved in light-gray, calcareous micaceous sandstone, and are uncrushed.

The dorsal side of the carapace is known only in part from the lectotype, BM(NH) I.534. Less than half of the carapace is preserved; only the posterior part. The parts that are preserved are in excellent condition. The lateral cheeks are present as raised structures surmounted with coarse tubercles. A median raised ridge, a structure not seen in other scorpions, separates the cheeks. At the base of the lateral cheeks (see Text-fig. 49A) are two shallow, but quite noticeable, large pits which are similar to but larger than those of the first

[14] Apparently, Kjellesvig-Waering got this reference from the *Treatise on Invertebrate Paleontology, part R, Arthropoda 4(2)* (1969, p. 618), but the entry does not appear in the bibliography of the *Treatise* and we have been unable to locate it. A.S.C. & K.E.C.

tergite. These shallow pits are interpreted as marking the site for muscles.

The basal area of the carapace also is raised and surmounted with coarse tubercles, with remnants of the raised median ridge present. The posterior margin is emarginate with the genal angles rounded.

The carapace is uncrushed and the lateral margins converge slightly anteriorly. A very good width measurement is possible by doubling the complete right side. Width at nearly midsection of the carapace is 100.0 mm; at the posterior margin 102.0 mm.

The first tergite is known in its entirety from the lectotype. It is a very unusual first tergite, and the possibility of this being an internal tergite, namely, the pregenital tergite, is a possibility that must be considered. The fact that the plate lies below the level of the carapace, is much narrower than the adjoining carapace, and lacks coarse tubercles (except for small ones at the lateral edges) greatly enhances the possibility. It cannot be a ventral structure, such as the prepectinal plate, which has been thrust upward during ecdysis, since the small tubercles on the margins of the plate show distinctly that the plate is a dorsal structure (these tubercles are dorsally located). If it is not the pregenital tergite, I am inclined to consider this to be the inside of the first tergite. The plate is straight anteriorly, rounded at the posterior angles, considerably narrower than the carapace, and rounded along the posterior edge. It is surmounted by a raised coarse transverse ridge at the usual position. The plate is entirely smooth except for small scattered tubercles at the lateral margins. Intersegmental membrane is seen to join this tergite to the carapace. The anterior of the tergite, above the transverse ridge, grades gradually into the intersegmental tissue. Length of tergite is 23.0 mm; the greatest width is 78.8 mm. Two well-defined large, but shallow, pits, closer together but nearly in line with the "facial pits", are present in the anterior of the tergite, above the transverse ridge on either side of the midsection. As stated above for the "facial pits", these pits are considered sites (dorsal) for muscle attachment (see Text-fig. 49A).

The chelicerae are only partially preserved, namely, the first two joints (**Ch1**, **Ch2** in Text-fig. 49A) and the dorsal side of most of the hand of the third joint. There are four joints in this scorpion, since it must be assumed that the chelicerae were normal and included the free ramus of the chela, which would be the fourth joint. The first joint is annular ventrally, and only the distal end is preserved, and was, no doubt, largely covered by coxae of the first pair of legs. It is devoid of ornamentation. The second joint is also devoid of ornamentation, both ventrally and dorsally, and seems to be considerably longer on the ventral side than on the dorsal, where it seems to be a narrow band. The third joint is preserved, although known only from the dorsal side of the hand. The chelae are not preserved. All that can be said about this joint is that it is covered with very coarse raised tubercles, mainly round to elliptical of variable sizes, some of which measure nearly 3 mm in greatest diameter.

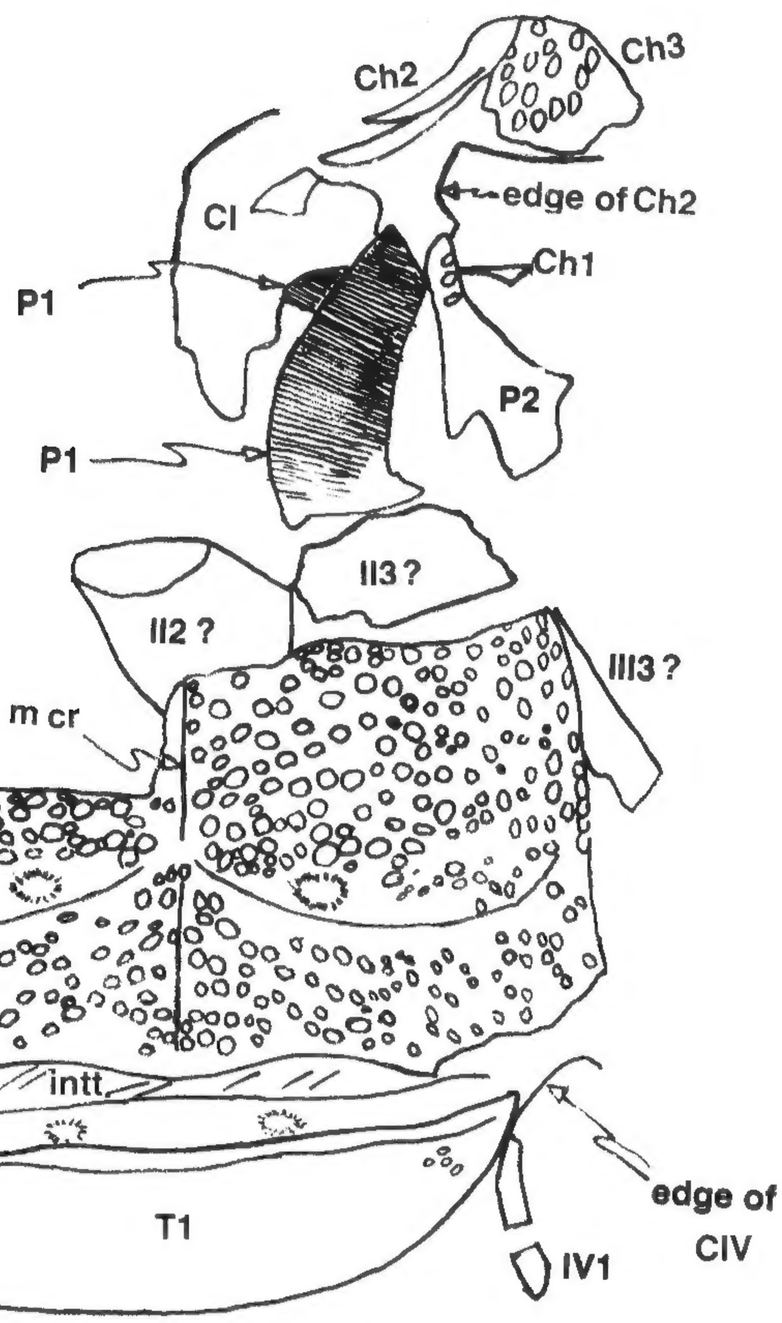
The pedipalp is preserved nearly complete in BM(NH) I.534, In.60443, and In.41782. In this ponderous animal over 300 mm in total length, the basal or first joint (see Text-fig. 49A, **P1**) is of particular interest because it contains a large area on the dorsal side that is covered by fine grooves, resulting in ridges of cuticle, which undoubtedly is a stridulating organ. This is an unusually large organ, consisting of almost the entire dorsal surface of the first joint, or coxa, of the pedipalp. Stridulating organs are known in the Triassic *Mesophonus perornatus* Wills (1947, pp. 82–84, pl. 8, figs. 1–5; text-figs. 40A–C, 41A–C) where they consist of spinules on the first three pairs of coxae. In *Praearcturus gigas,* the stridulating organs are grooves at the right angle from the inner edge. The grooves gradually become less pronounced in the posterior of the joint (**P1**).

The location of the corresponding or opposite stridulation organ presents some problems as the known "sounding boards" are dorsally located on the coxae. They could occur on the opposing pedipalp coxae or first two pairs of legs, which apparently can be brought to bear on the stridulating organs. There are no scleritic organs above the pedipalps. The grooves are very fine and consist of four grooves or three ridges to the mm. The entire first coxa measures 30 mm by 17 mm, but these are incomplete measurements.

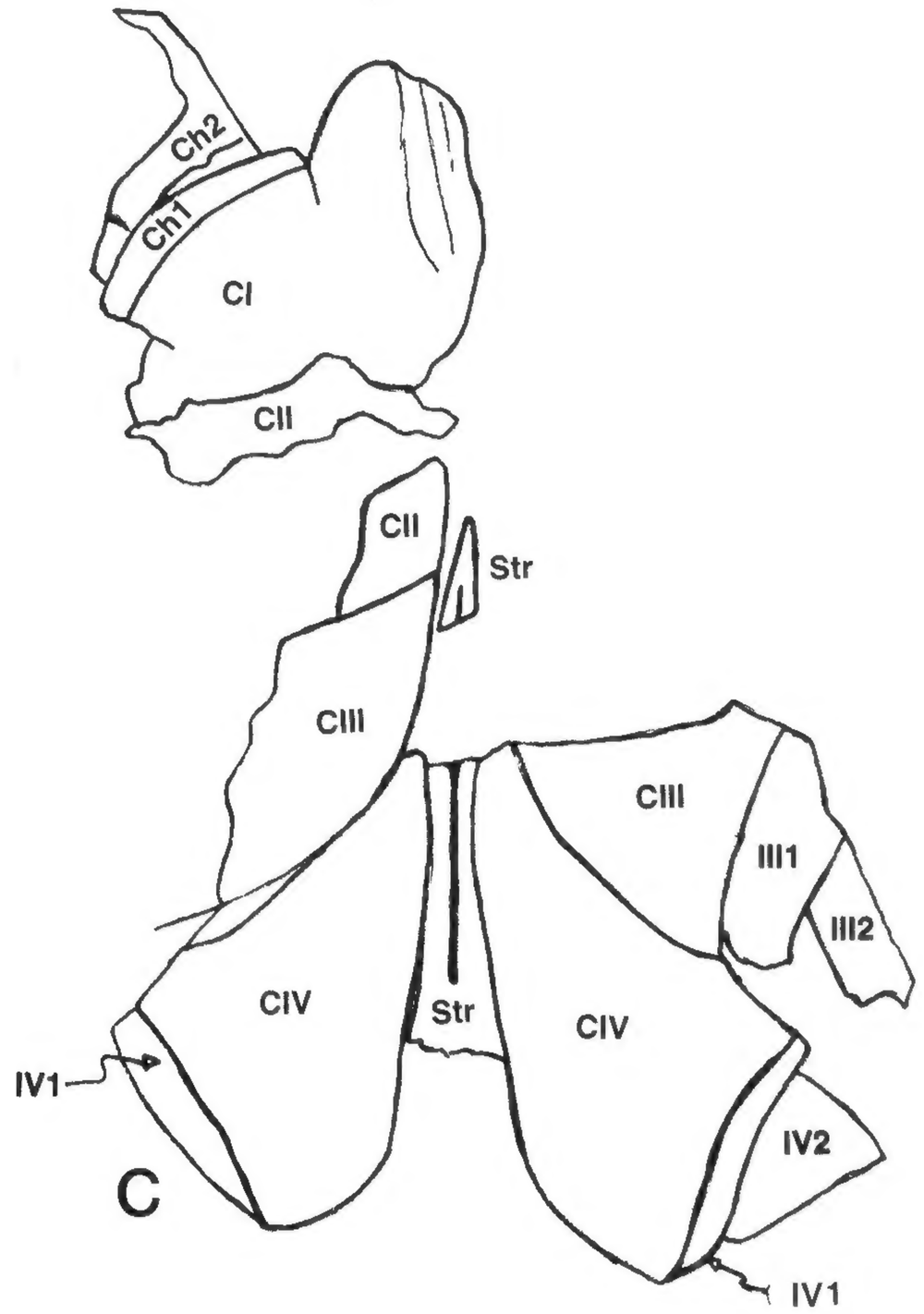
Regardless of where the opposing stridulating organ was located, it is interesting and perhaps significant, that adjacent to the coxa of the right side, described above, is a small piece of the coxa of the left side, which also shows the same stridulating organ. The close

Text-figure 49.—*Praearcturus gigas* Woodward. Lectotypes in the collections of the British Musuem (Natural History). From the Lower Devonian (XI), Old Red Sandstone (Cornstones) of Rowlestone, Herefordshire, England. See foldout inside front cover for explanation of abbreviations.

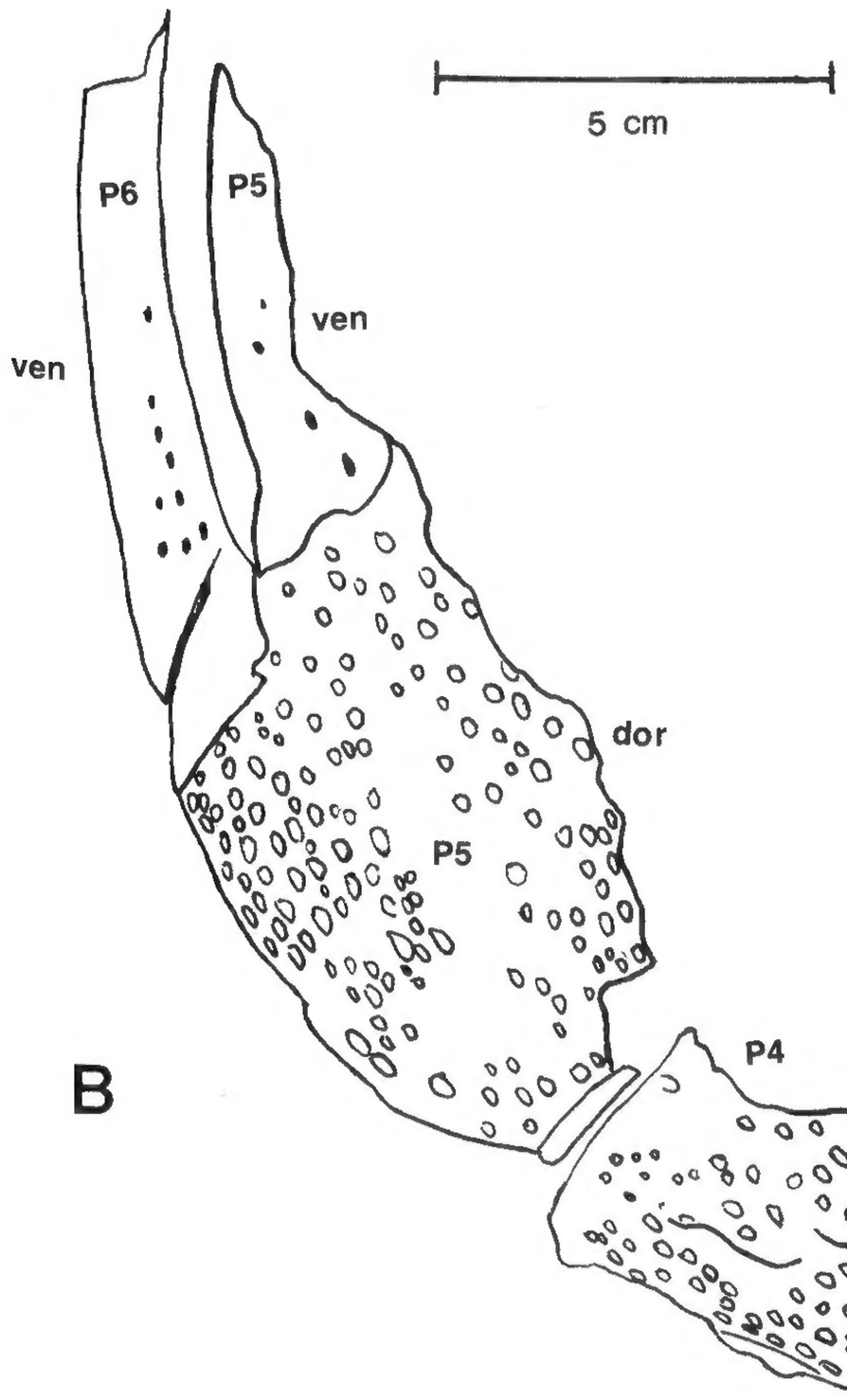
A. Dorsal side of posterior region of the carapace (**Cp**) of lectotype BM(NH) I.534, showing rugged pustulation, the first tergite (**T1**) and bases of prosomal appendages (as indicated) where anterior prosoma is lost. The very fine parallel grooves (much finer than drawn) on the first joint of the pedipalp apparently represent a stridulation organ. There are four grooves per mm. **B.** Pedipalp from BM(NH) In.60443, showing the dorsal side of the manus and **P4** joint. The coarse nodes or granulation are apparently restricted to this side. At any rate, the ventral surface of the fingers (**P5**, **P6**) preserved as external ventral molds, is smooth with scattered elliptical pits. **C.** Counterpart of BM(NH) I.534, showing parts as labelled. **D.** Restoration of the coxosternal area of *Praearcturus gigas* Woodward based on the lectotype, BM(NH) I.534.


Ch2
Ch3
edge of Ch2
CI
Ch1
P1
P2
P1
II3?
II2?
III3?
m cr
Cp
intt
T1
edge of CIV
IV1

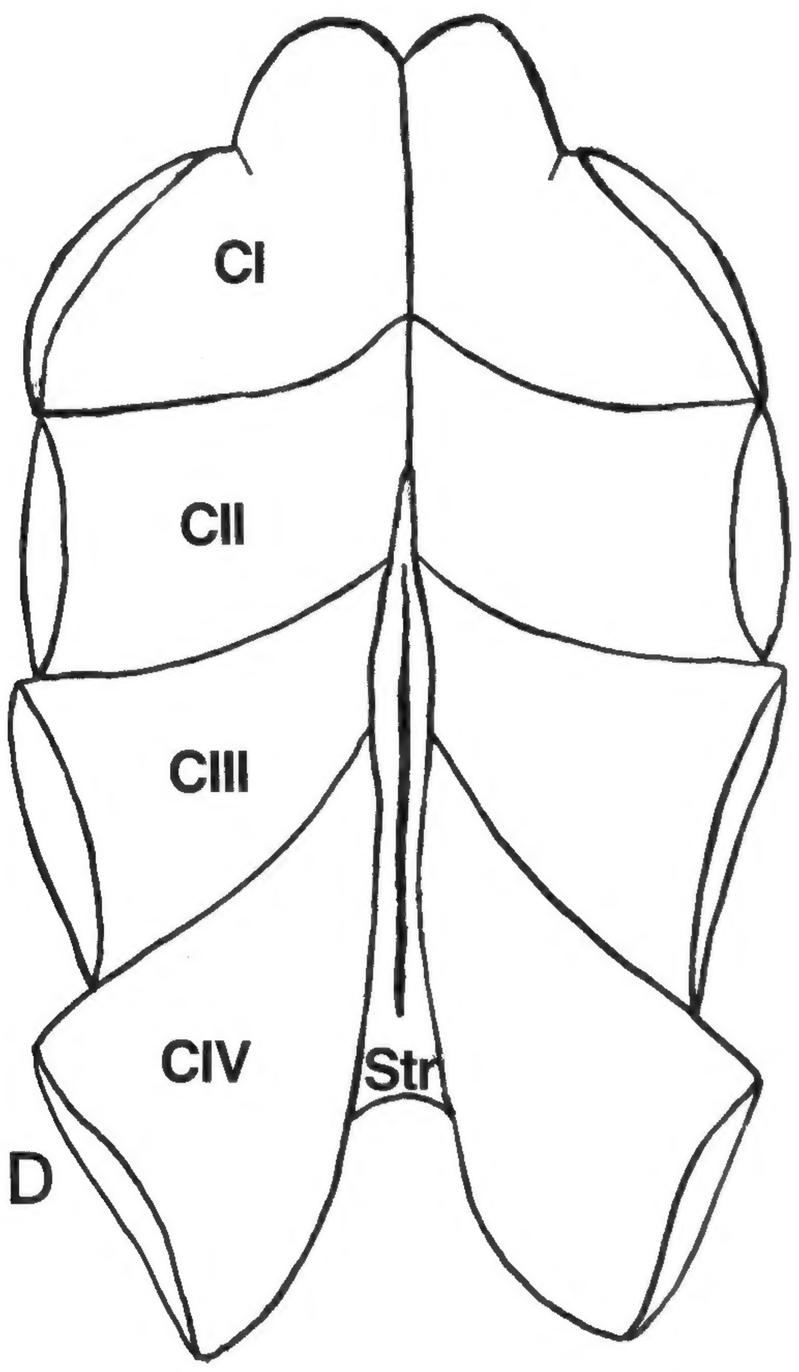
A


Ch2
Ch1
CI
CII
Str
CIII
CIII
III1
III2
CIV
Str
CIV
IV1
IV2
IV1

C


5 cm
P6
P5
ven
ven
dor
P5
P4
dor
P3

B


CI
CII
CIII
CIV
Str

D

proximity, in fact the two coxae are touching, means that the two organs could be brought together, thus effecting stridulation.

If the stridulation organs are placed on the dorsal side of the coxa, it would mean that these coxae would have to be rotated so that the stridulating boards were opposite each other. This is possible even with the pedipalp coxae of present-day scorpions, where the side of the coxae are adjacent to one another. The type shown here is the oldest known, being Lower Devonian in age, but it is known in various living arachnids (see Lawrence, 1953, pp. 166–168, text-figs. 61, 62), including living scorpions.

The trochanter of the pedipalp is only partly preserved, showing that it is mainly smooth on the ventral side, with only a few coarse pustules anteriorly (see Text-fig. 49A, **P2**).

The femur is known from specimen BM(NH) In.60445, from the same locality and horizon. It is a short stout structure, terete toward the junction with the tibia. The dorsal side is covered with the same round and elliptical coarse pustules. Some of the pustules, particularly the round ones, appear to be surmounted with a setal opening. The length through the midsection is 57.0 mm; the width at the base (junction with **P2**) is 27.7 mm; the width at the distal end (junction with **P4**) is 31.0 mm; the greatest width is 41.5 mm.

The rest of the pedipalp, tibia, hand and fingers, are known from BM(NH) In.60443 from the same locality and horizon. The pedipalp, except for the fingers, is preserved on the dorsal side; it is therefore the pedipalp of the right side.

The tibia, preserved dorsally, is short and stout, covered with large pustules (see Text-fig. 49B) and apparently with a deep sulcus in the central part. It is not complete, except lengthwise, but measurements are as follows: Length: 51.7 mm; greatest width *preserved*: 34.2 mm; greatest width (estimated): 45.0 mm.

The hand is preserved only dorsally, but incomplete as to width. It is a very stout, massive structure, covered dorsally with large pustules, either round or elliptical, but I have not been able to determine that any were piliferous. I do not rule out the possiblity, however. Measurements are as follows: Length of the hand through midsection to the junction of the fingers: 81.0 mm; greatest width *preserved*: 53.0 mm; greatest width (estimated): 60.0 mm.

The two fingers are preserved from the ventral side. The free finger (**P6**) curves inward, whereas the fixed finger is recurving. Both are smooth but sparsely pitted with shallow elliptical pits. The inner edges of the fingers are cultrate, in keeping with other Lower Paleozoic scorpions. The fingers are not complete, but the major part of each is present. Measurements are as follows: from the inner junction of the two fingers, the *preserved* length of **P5** is 65.4 mm; estimated length of **P5** is 80 mm; *preserved* length of **P6** is 76.5 mm; estimated length is 82.0 mm; width at approximate midsection: 12.3 mm.

The coxosternal area is preserved (in the lectotype, BM(NH) I.534) so that all parts are seen mainly from the ventral side, but some, as for example the first pair of coxae, can also be seen from the dorsal side (see Text-figs. 49A, C). An accurate reconstruction, therefore, is possible (see Text-fig. 49D).

The sternum is unusual, being very elongate, lanceolate-triangular, with the third and fourth pair of coxae, as well as nearly half of the second pair, abutting against it. Although part of the upper midsection is not preserved, the forward edge is preserved as well as the entire lower half, which shows that the sternum expands slightly. Thus a rather accurate restoration is possible. The anterior half is very slender, shaped like a slender spear point or dagger, which expands posteriorly. The base is indicated by a short line on the right side of the sternum, which apparently marks the posterior limits (see Text-figs. 49C, D). The sternum is deeply infolded in midsection.

The entire sternum measures 68.5 mm in length; the base is 14.4 mm in width and 11.8 mm in width at midsection. At the middle of the posterior half, the sternum is 9.9 mm in width. The midgroove of sulcus is 50.6 mm in length.

The first pair of coxae is preserved on both ventral and dorsal sides. They are large thick structures that meet each other at the midline. Maxillary lobes are definitely developed, but are blunt and represent an early attempt at forming the oral tube. The coxa measures 42.4 mm in greatest length, 50.7 mm in estimated width (47.0 mm are preserved), and 19.4 mm in width approximately in the center of the coxa. The maxillary lobe is 15.0 mm in length (greatest length) and 20.0 mm in width at the base of the lobe.

The second pair of coxae is poorly preserved, but well enough to determine that there were no maxillary lobes developed and that the anterior half of each coxa meets at the midline whereas the posterior half abuts the narrow point of the sternum.

The third pair of coxae is sufficiently well-preserved that the coxae can be reconstructed. The coxa, a flaring structure, abuts the sternum in the anterior half. Measurements are as follows: length: 50.0 mm along the anterior line; 60 mm and 31.0 mm at the juncture with the trochanter (see Text-fig. 49C, **CIII** and **III1**).

The trochanter is ringlike, unusually short, and at midsection measures 11.2 mm in length and 30.6 mm in width. A rather close estimate can be made of the

thickness at the junction with the femur (**III2**), which is 16.8 mm.

The femur (**III2**) is preserved only at the basal part, but shows that the joint is rather elliptical in cross-section. It is 14.2 mm thick ventrally and 25.7 mm thick horizontally.

The coxae of the fourth pair of legs are preserved almost in their entirety, both having the trochanters attached. The coxae are long, flaring, and abut the sternum from slightly anterior to the midsection to the base of the sternum. The coxae measure 57 mm along the anterior edge and 74 mm along the posterior margin (both straight-line measurements, not following the curve). The anterior edges of the coxae are also seen from the dorsal side, which reveals that the anterior part tapers to a rather cultrate edge. The terminal end, at the junction with the trochanter, measures 36.3 mm.

The trochanters (see Text-fig. 49C, **IV1**) are unusually short; in fact, considerably shorter than those of the third pair of legs. The trochanter is ringlike and measures 6.7 mm in greatest length and 34.7 mm in greatest width.

The femur of the fourth leg is only preserved as a fragment at its anterior end. The thickness is 26.0 mm in horizontal measurement and 19.6 mm in vertical measurement, thus elliptical in cross-section.

The coxae, sternum, and ventral side of the trochanter (dorsal side not known) are completely smooth, contrasting with the extremely coarse pustules that characterize most of the dorsal side of this scorpion.

The measurement of the entire coxosternal area from the tip of the maxillary lobes of the first pair of coxae to the end of the fourth pair of coxae is 155 mm, whereas the width at the anterior of the third coxae is 86 mm. The thickness of the scorpion, measured in the middle of the carapace to the sternum is 47.0 mm.

Type information.—Lower Devonian, Old Red Sandstone (Cornstones) of Rowlestone, Herefordshire, England, collected by Dr. D. M. McCullough of Abergavenny.

Remarks.—*Praearcturus gigas* Woodward was first considered to be a gigantic isopod. Rolfe (1969, p. R622) considered the fossils to be "Doubtful taxa formerly attributed to Arthropleurida".[15] In Norway, in 1971, Dr. Leif Størmer asked me to study the specimen registered as BM(NH) I.534 for the possibility of its being a scorpion. For reasons (mainly the unusual tergite) not entirely clear to me now, I did not think the specimen represented a scorpion. It was due to Dr. Rolfe's persistence, however, that we are finally able to determine that this spectacular fossil is a gigantic scorpion.

In 1979, Dr. Rolfe wrote to me and asked me to review the photographs (Rolfe, 1969, p. R622, fig. 395) in the *Treatise on Invertebrate Paleontology.* Reorientation of the photographs clearly showed that the specimen BM(NH) I.534 represented a scorpion, a determination that was easily and conclusively proved by the photograph of the enormous pedipalp chela (specimen BM(NH) In.60443). Later Dr. Rolfe advised me that Dr. Størmer had identified these fossils as a scorpion as early as 1971. I gladly credit both my friends, Leif Størmer and Ian Rolfe for the final determination of this spectacular animal.

In total size, *Praearcturus gigas* must have measured a full meter in length. It therefore rivals the Downtonian *Brontoscorpio anglicus* Kjellesvig-Waering and the Lower Carboniferous *Gigantoscorpio willsi* Størmer. Comparison with these is superfluous as the cultrate pedipalp fingers of *Praearcturus* are sufficient to indicate an altogether different scorpion.

A single tergite of a *Praearcturus* was found among the material from the Devonian of Cottonwood Canyon, Wyoming. A name would have been given to this North American representative of the genus, for not only is the tergite perfectly preserved in its original flexible cuticle, but it is easily recognized by the distinctive tuberculate type of ornamentation, had it been possible to locate the specimen again. It may still be found in the material at the Field Museum of Natural History in Chicago.[16] Indeed, because of the unusual ornamentation, it is more easily recognized from small fragments than are the other scorpions present in the same horion: *Branchioscorpio richardsoni, Hydroscorpius denisoni* and *Acanthoscorpio mucronatus,* which are preserved almost in their entirety. The specimen consists of a single tergite, very likely the second mesosomatic, which was dissolved out of the limestone with the use of weak hydrochloric acid.

There are further specimens of *Praearcturus*[17] available.

---

[15] *Praearcturus gigas* has long been a classic "*Incertae Sedis*". Hessler (1969), in the *Treatise on Invertebrate Paleontology,* considered it to be a peracaridan malacostracan. K.E.C.

[16] Dr. Derek E. G. Briggs, in November, 1983, located a slide of cuticle material from the Beartooth Butte Formation, Cottonwood Canyon, Wyoming, FMNH (PE) 26080 B, which might well be the specimen Kjellesvig-Waering referred to. The tergite is tuberculate, but only 8 mm across. A.S.C.

[17] Dr. Ian Rolfe (written commun., April 13, 1984) quoted a letter from Kjellesvig-Waering, dated December 1, 1978. ". . . with regard to *Praearcturus,* I forgot to mention Størmer's Ringerike paper, 1934, pl. 12, fig. 2, "genus *indet* 1" is another *Praearcturus* and I remember it again in the paper I wrote on the eurypterids of the Downtonian at Stoke Edith, 1951, pl. 2, figs. 3 and 4. So we have two others—different species, but same genus. I will have to rework these. Nice! I'll start thinking about any specimens with smallpox [*i.e.* the tubercles of *P.*] in America." A.S.C.

Brontoscorpio anglicus[18]
Kjellesvig-Waering, 1972

1972. *Brontoscorpio anglicus* Kjellesvig-Waering, pp. 39–42, 2 text-figs.

Specimens BM(NH) In.31403, In.31404 and In.31405, the entire free finger and counterparts of an enormous scorpion from the Siluro-Devonian conglomeratic sandstone referable to the Downtonian 1-9 bed, at the Birmingham Water Works, NNE of Eastham Bridge, Trimpley, Worcestershire, England.

Infraorder **MERISTOSTERNINA**, new infraorder

Branchioscorpionina with abdominal plates divided by a median suture, and retaining well-developed gill chambers and doublures, with the gill slit opening between the doublure and the abdominal plate.

Remarks.—The infraorder Meristosternina has been characterized throughout its known history by the small number of genera and species so far discovered. In contrast to the other infraorders of the Branchioscorpionina, which are rich in genera and species, the Meristosternina are represented by only four genera: *Tiphoscorpio* from the Upper Devonian of New York State, *Cyclophthalmus* and *Microlabis* from the Carboniferous of Czechoslovakia, and *Palaeobuthus* from the Carboniferous of Illinois, with only six species in all. These are too few forms to establish lines of evolution.

Superfamily **TIPHOSCORPIONOIDEA**, new superfamily

Meristosternina with lateral schizochroal eyes.

Type family.—Tiphoscorpionidae, new family.

Remarks.—The trilobed ribbed gills probably should be considered a familial or even superfamilial character, but not enough is known about these structures to merit their use as a major taxobase. The posteriorly-slit meristosternous plates are considered to be of infraorder importance.

Family **TIPHOSCORPIONIDAE**, new family

Tiphoscorpionoidea with pectines composed of a single undivided plate on each side.

Type genus.—*Tiphoscorpio,* new genus.

Genus **TIPHOSCORPIO**, new genus

Tiphoscorpionidae with smooth carapace, median eyes on rounded eye node placed anteriorly on carapace, and schizochroal eyes marginal, round and very large; no ornamentation on the carapace. No fulcra on the pectines. Tarsus with fringe of movable spines.

Derivatio nominis.—*tiphos* (Gr.) = marsh or swamp + *scorpio.*

Type species.—*Tiphoscorpio hueberi,* n. gen., n. sp.

Geological range.—Lower Upper Devonian.

Tiphoscorpio hueberi, new species
Plates 5–8; Text-figure 50

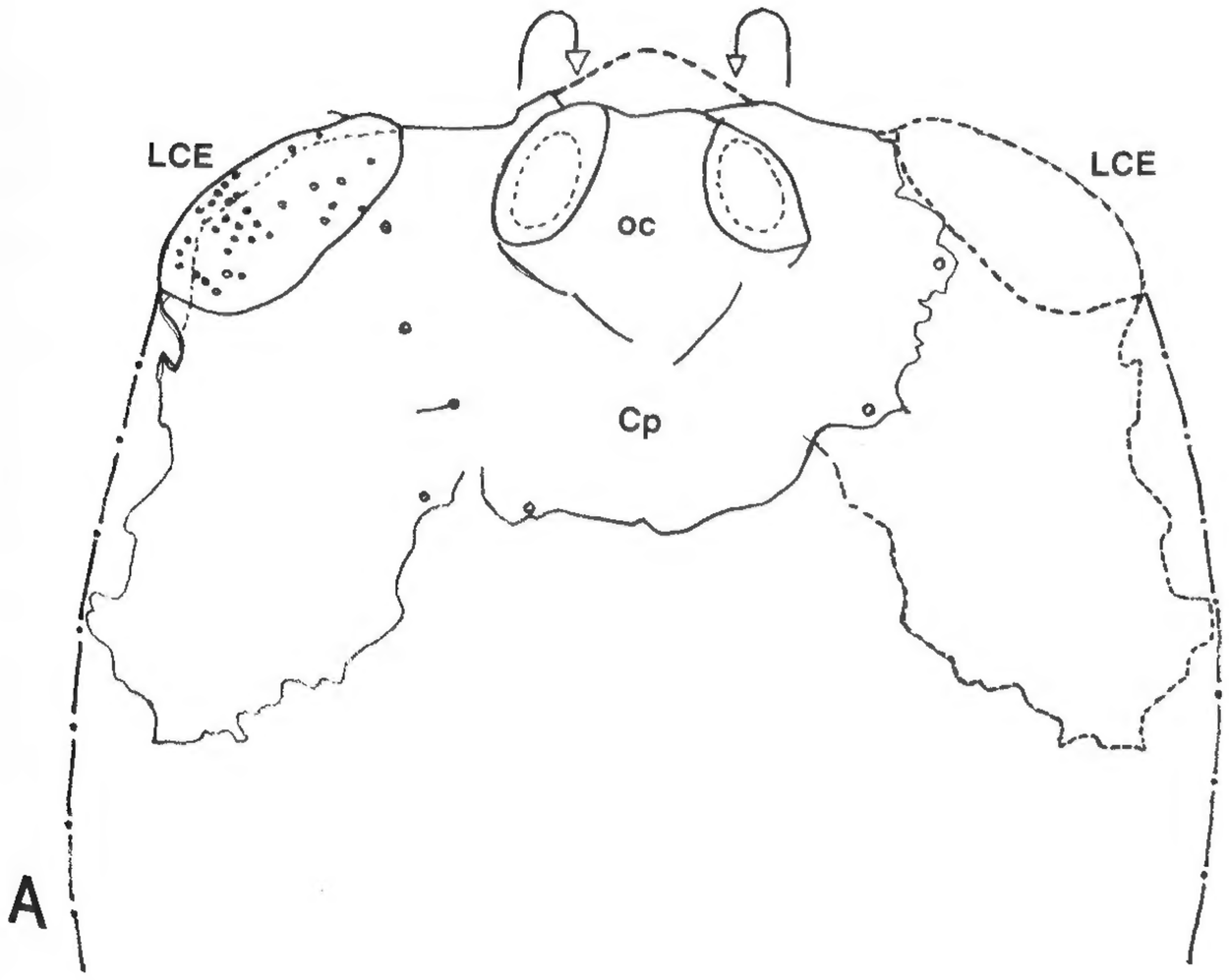
This is one of the most interesting of all scorpions because of its unusual preservation. Although known only from a few fragments, these fragments fortunately represent important structures of considerable taxonomic value. The holotype consists of half a specimen, as only the carapace, ventral part of the abdomen, the seventh tergite, and a walking leg were recovered. The dorsal side of the abdomen and all of the cauda are missing, as well as the prosomal limbs, except for a tarsus. But of greatest importance is the remarkable preservation of a great many of the gills.

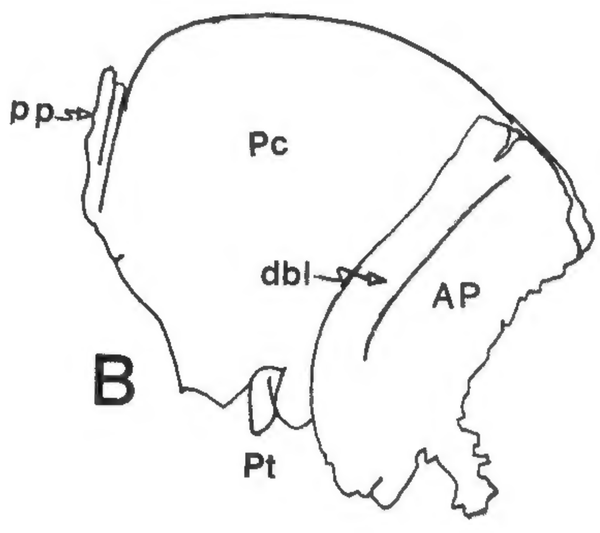
Dr. Francis Maurice Hueber, in his study of the flora from the Onteora "red beds" (lower Upper Devonian) of New York State, recognized the fragments as part of an arachnid (Hueber, 1960). Dr. John Wells of Cornell University advised me of these fragments, which were promptly and kindly lent to me by Dr. Hueber.

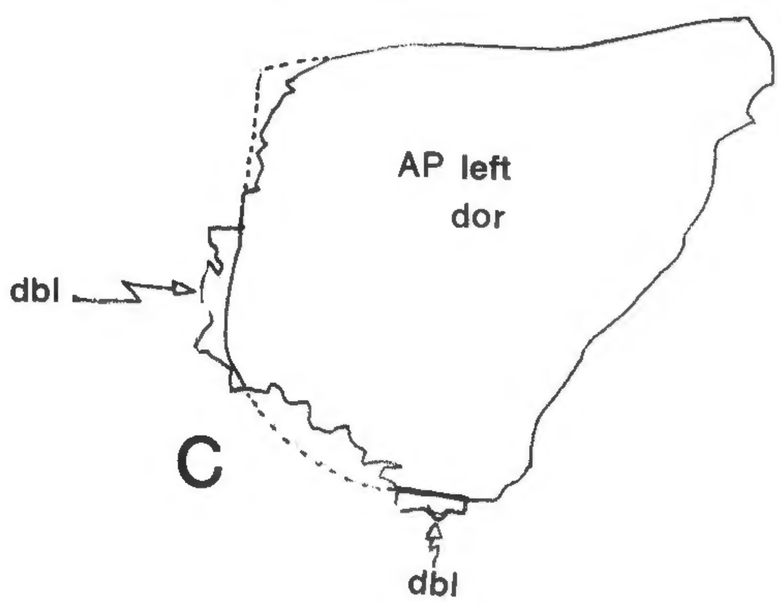
Text-figure 50.—*Tiphoscorpio hueberi,* n. gen., n. sp. Holotype (USNM 252629). From the lower Upper Devonian (Lower Frasnian), lowermost Onteora Formation ("Onteora red beds"), Schoharie Co., NY. Drawn from slides of macerations. See foldout inside front cover for explanation of abbreviations.

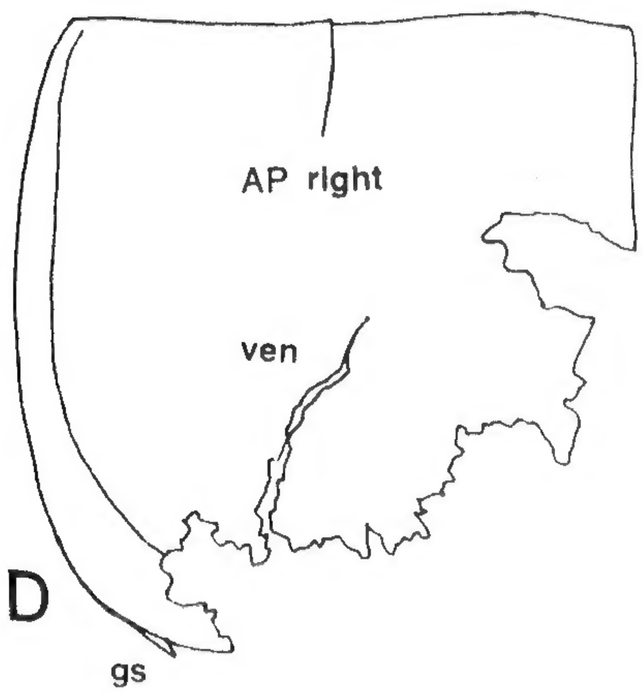
A. Anterior of carapace (see Pl. 5, figs. 1–3). The glossate process, which is turned under on the specimen, has here been restored, by dash-line, to its original position. The median eye sockets were drawn by reflected light, whereas the lateral eye details came from transmitted light. Postorbital margin inferential (dot-dash lines). **B.** The pectine of the right side showing an attached abdominal plate with doublure. One or two pectinal teeth (**Pt**) and a small portion of the pectinal plate (**pp**) can be seen. **C.** A left abdominal plate of a meristosternous pair seen from the dorsal side. **D.** Showing the ventral surface of the right plate of a paired meristosternous abdominal plate (**AP**) with gill slit showing at the base. Note the doublure. **E.** Showing the ventral surface of the left plate of a paired meristosternous abdominal plate (**AP**). This was very likely paired with the plate in Text-figure 50D to complete the "sternite". Note doublure and gill slit. See Text-figures 50F, G. **F, G.** Dorsal and ventral sides of part of the doublure shown in Text-figure 50E, which bear small mucrones. **H.** Ventral surface of a right meristosternous abdominal plate inclined downward. **I.** The dorsal (internal) side of one of a pair of meristosternous abdominal plates (**AP**), left side, showing a wide doublure and part of a gill slit. **J.** Gill with attached abdominal plate (**AP**), which shows the doublure. **K.** Small outer anterior portion of an abdominal plate.

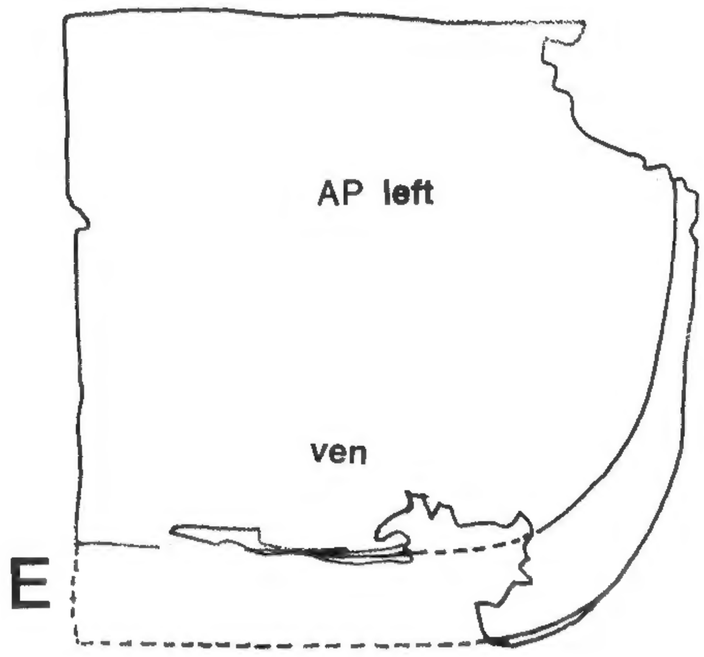
[18] *Brontoscorpio anglicus* is being listed after *Praearcturus gigas* merely because its age and unusual size suggest comparison. In 1972, Kjellesvig-Waering placed *B. anglicus* in the Eosocorpiidae, which seems meaningless, now that the ventral surface of *Eoscorpius carbonarius* is known. It probably belongs in Genera Incertae Sedis. A.S.C.

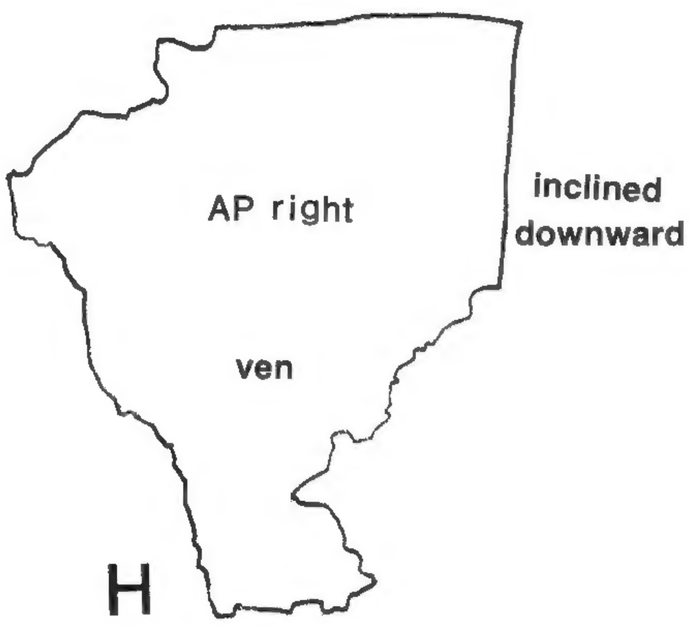

LCE
LCE
oc
Cp
A

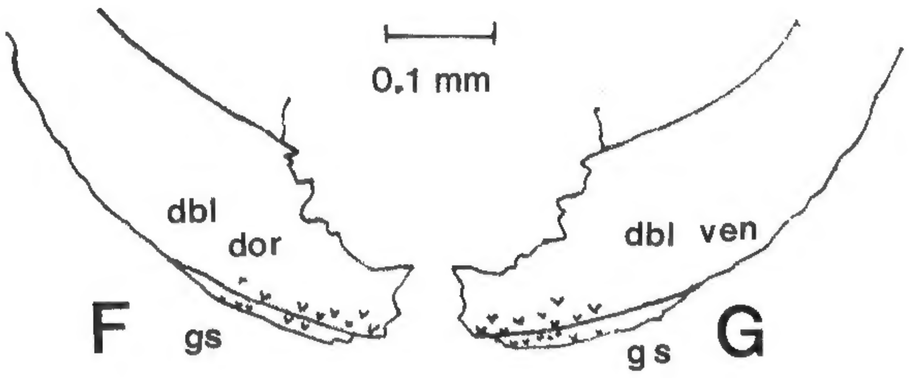

pps
Pc
dbl
AP
B
Pt

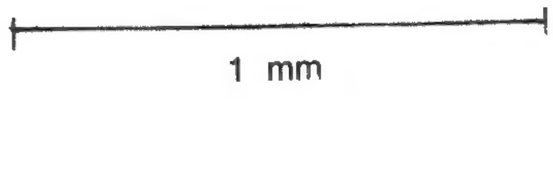

AP left
dor
dbl
C
dbl

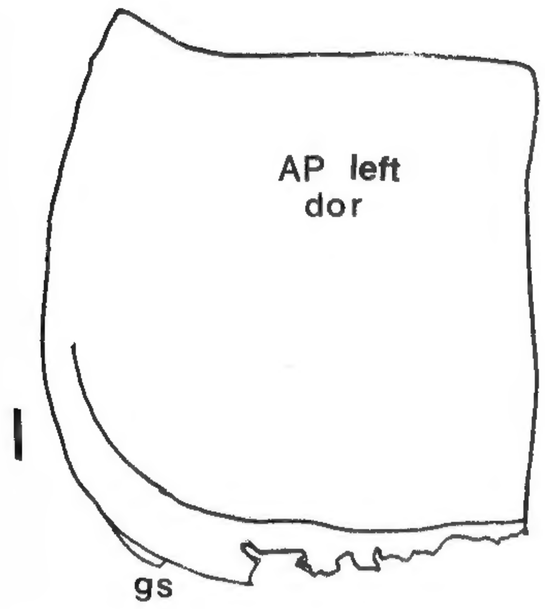

AP right
ven
D
gs

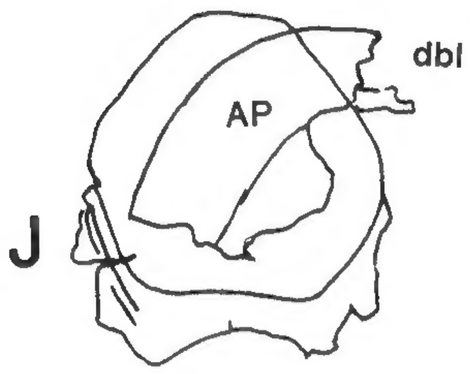

AP left
ven
E

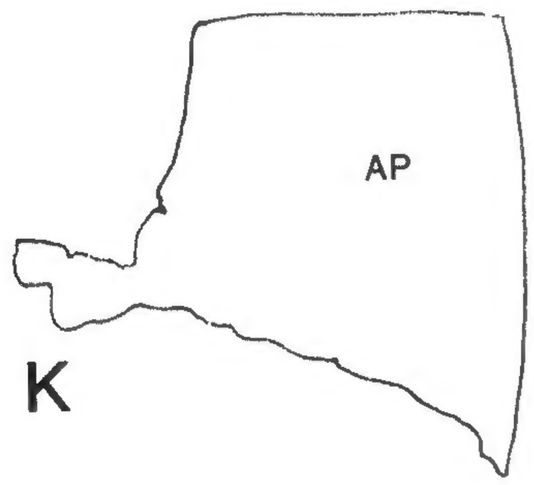

AP right
inclined
downward
ven
H


0.1 mm
dbl
dor
F
gs
dbl ven
gs
G


1 mm


AP left
dor
I
gs


dbl
AP
J


AP
K

The specimens occurred in shale and there seem to be only two individuals, which are here designated holotype and paratype. The latter, although represented by only one lamella of a gill, is approximately twice the size of the holotype.

All specimens are mounted in Canada Balsam on glass slides. They were macerated out of the shale by Dr. Hueber using concentrated (48%) hydrofluoric acid and the residues were washed through ten changes of water (Hueber, pers. commun., Nov. 1, 1965). Each of the samples of shale macerated averaged 3 × 4 × 0.5 in.

Only the anterior half of the carapace is preserved, but this is preserved in such detail that even the setae and eye facets of the lateral eyes are clearly revealed. The part preserved is sufficient to provide a good description (see Pl. 5, figs. 1–3; Text-fig. 50A). The anterior margin of the carapace is straight, with a well-developed median glossate process which, in the Canada Balsam mount, has been turned under the eye node. The median eyes are relatively small, located on a wide lacrimiform eye node that nearly touches the anterior margin. The lateral schizochroal eyes are composed of about 250 lenses, appearing as a pebbly surface on the lateral eyes. They are marginal, large and bulbous. The width of the carapace is probably 2.5 mm. The surface of the carapace is smooth, without any ornamentation except for small setae or open setal sites that seem to form a circular area around the eye node. These setae could therefore demarcate the sulcus, or the shoulders of the inflated cheeks of the cephalic shield that surround the eye node.

The pectine is very poorly preserved, but enough is present to show that the pectines were composed of an unjointed plate, without rounded sclerites or fulcra, and with small, rather stout teeth (see Text-fig. 50B). Judging from the whole tooth preserved, it appears that 20 to 25 teeth were present on each comb. The pectine is preserved attached to an abdominal plate and its doublures (see Text-fig. 50B).

One small piece of a prosomal leg was preserved. This is the tarsus and shows a posterior fringe of strong movable spines.

The abdominal plates are almost completely preserved; unfortunately, the inner posterior parts on each are missing. However, the preserved parts reveal a meristosternous plate, bounded by a wide doublure. Each of these plates is split along the basal margin between the doublure and the abdominal plate face. The slit probably extends to the middle part. The inner parts are covered with small triangular scales pointing to the posterior (see Text-figs. 50F, G). There are eight parts (or halves) of the double abdominal plates preserved (see Text-figs. 50B–E, H–K) out of the original ten halves. There is no ornamentation on the plates.

The seventh tergite is preserved and this is considered to be the ventral side. It is a triangular plate, with a posterior doublure and with four rather smooth carinae. No ornamentation other than scattered setal hairs occurs.

The remarkable gills are preserved in unusual condition. There are three types of gills, which are described as follows:

1. *Rounded type* (Pl. 6, figs. 1–4, 6–8; Pl. 8, figs. 1, 2, 4–7). These are oval bodies composed of white, spongy material in a single lamella with ribbing on the anterior parts. This ribbing consists of turned-in folds, some of which are anastomosing. The surface of the gills is covered by small subtriangular spines, rather indistinctly formed, but pointing toward the rounded area that does not contain the ribbing, thereby proving that the posterior of this type of gills is the rounded, non-ribbed part. There are a total of six of the rounded type.

2. *Subrectangular type* (Pl. 6, fig. 7; Pl. 7, figs. 1–7; Pl. 8, figs. 3, 8). These gills are long, straight along the inner edge, and bowed on the outer. Along the outer edge are at least three large, thick spines. These also show that the anterior part has the anastomosing ribs, whereas the subrounded posterior does not have the ribbing. The gill consists of a single lamella covered with small indistinct subtriangular spines that point to the rounded end, thus revealing the orientation of the gill. All are composed of white spongy material. There are five of these subrectangular gills preserved in the holotype, and one in the paratype (from the same horizon and locality), which is twice as large as the five described above. The paratype (USNM 252630) measures 3 mm in length (see Pl. 7, fig. 1).

3. *Irregular type* (Pl. 6, fig. 8; Pl. 7, figs. 6–7; Pl. 8, fig. 1). These gills are smaller and rounded with the same ribbing as described for the other gills, but either with large thick spines at the posterior end (Pl. 7, figs. 6, 7) or a fringe of serrations as in Plate 8, figure 1. These gills are also composed of white spongy material, and are covered with short indistinct triangular spines which reveal that the coarse spines represent the posterior of the gill.

The three types of gills are found associated or even attached together. The gills are also found associated with the abdominal plates. Although the preservation is perfect, it is not possible to develop any ideas on how all three types fitted together in the gill chamber. It seems clear from the ornamentation of small spines that the three types of gills occurred together, all with the rounded or spinous ends facing the gill slit, or posterior end of the abdominal plates.

Type information.—Lower Upper Devonian (Lower Frasnian), lowermost Onteora Formation, in a dark, fine-grained shale lens at Quarry on northwest slope of South Mountain, Schoharie County, NY. 1.1 miles west of Schoharie Co.–Green Co. line (Livingston 7½′ quad.) at 74°16′30″E, 42°23′55″N. Collected by Francis Maurice Hueber. The scorpion is associated with numerous plants and scales of a crossopterygian fish[19] (see Hueber, 1960). The specimens are on deposit at the National Museum of Natural History, Washington, DC, as USNM 252629 for the holotype, and USNM 252630 for the paratype.

Derivatio nominis.—Named in honor of Dr. Francis Maurice Hueber, who collected the specimens and successfully macerated them out of the shale.

Superfamily **CYCLOPHTHALMOIDEA** Thorell and Lindström, 1885 (emend.) (*nom. transl.* Kjellesvig-Waering, herein) (*ex* Cyclophthalmidae Thorell and Lindström, 1885 *not* Petrunkevitch, 1913)

Meristosternina with two pairs of coxae abutting one another in front of the sternum, the third pair abutting the sternum and the fourth pair abutting the opercular plates.

Type family.—Cyclophthalmidae Thorell and Lindström, 1885.

Remarks.—Petrunkevitch (1913) apparently was unaware that Thorell and Lindström had established the family Cyclophthalmidae in 1885, and this error was carried throughout his monographs to the *Treatise* (Petrunkevitch, 1955, p. 77). The superfamily Cyclophthalmoidea, as envisioned by Petrunkevitch (1955, p. 77), was furthermore wrongly diagnosed, as he mistook the basal segment of the chelicera (see **Ch1** in Text-fig. 52) for the first coxa, thus his count of "three pairs of coxae in front of sternum". There are only two pairs of coxae anterior to the sternum.

The main reason for retaining the superfamily Cyclophthalmoidea within the Meristosternina is the presence of the detached meristosternous abdominal plate on the holotype. In this respect it is important to keep in mind the preservation of this scorpion. It is mainly uncrushed, but only the dorsal side of the abdomen is present on both halves of the specimen. In one half (Text-fig. 51), the carapace and the dorsal side of the abdomen are preserved as a counterpart, whereas on the other half, the ventral part of the prosoma and the same dorsal side of the abdomen are preserved as the part with relief. The underside of the abdomen is not preserved.

The determination of the meristosternous plate, however, needs further confirmation. My determination was made because both halves of the plate are connected by a suture and are without carinae, both are rounded at the posterior corners, and both are of approximately the same width. Nevertheless, it could well be that this plate actually represents two tergites of the cauda. I do not consider this probable, but nevertheless, it needs confirmation as this determination results in an important conclusion.

Family **CYCLOPHTHALMIDAE** Thorell and Lindström, 1885 (emend.)

Cyclophthalmoidea with no maxillary lobes on the first two pairs of coxae, or at most, only a slight lobate extension. Median eyes large, placed on a scutelliform eye node in the middle of the anterior half of the carapace. No evidence of lateral eyes.

Type genus.—*Cyclophthalmus* Corda, 1835.

Remarks.—I can see no reason not to credit Thorell and Lindström with the family, albeit much emended, for their original description was far more correct than the later ones.

Genus **CYCLOPHTHALMUS** Corda, 1835 (emend.)

Cyclophthalmidae with carapace having a ring of large bosses surmounting the cephalic shield, and with pedipalp chela with round denticles, probably four deep along the edge, arranged in a row. Ventral side of pedipalp smooth but very hirsute.

Type species.—*Cyclophthalmus senior* Corda, 1835.

Geological range.—Carboniferous.

Cyclophthalmus senior Corda, 1835 Text-figures 51–52, 111I

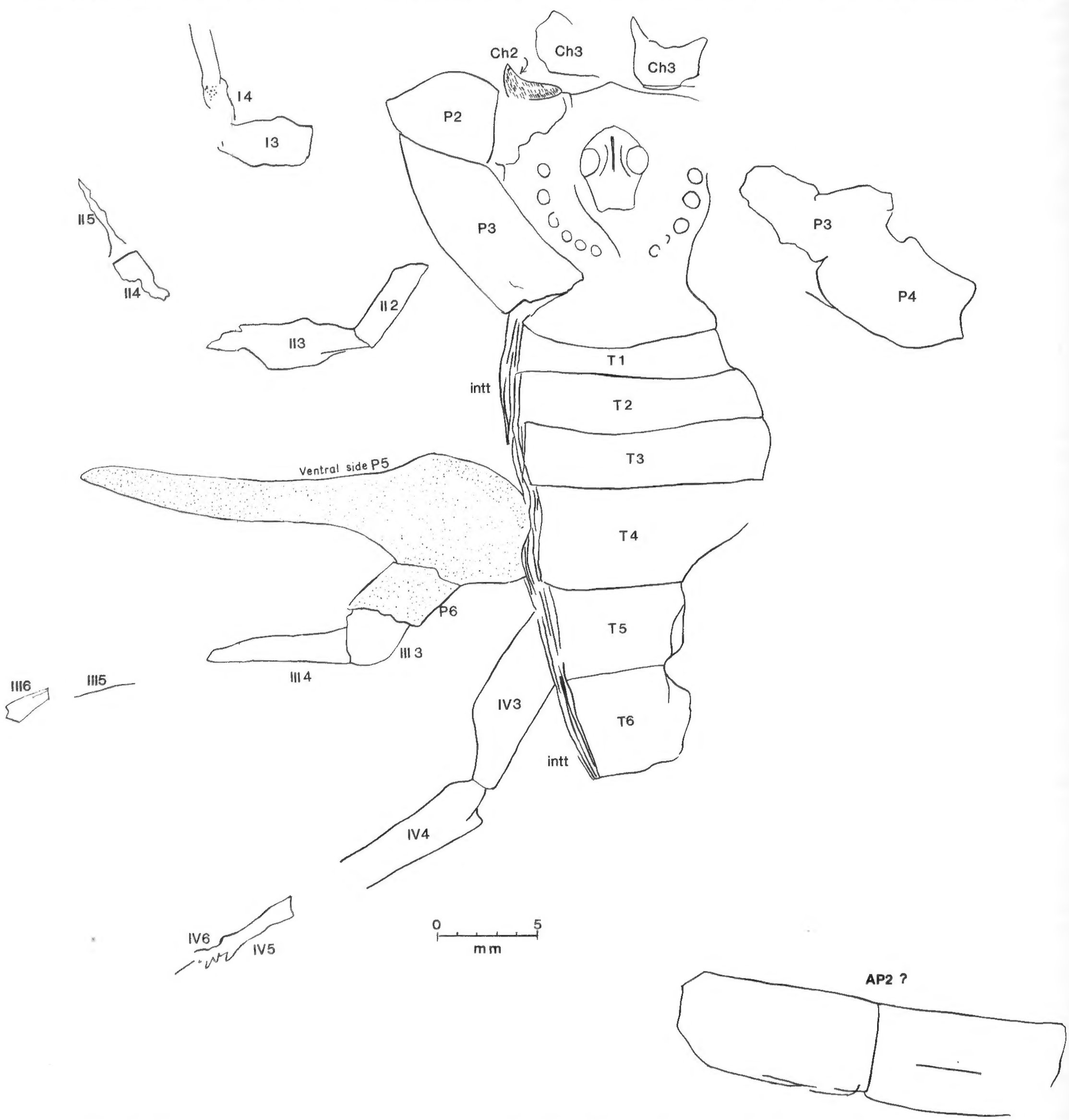
1835. *Cyclophthalmus senior* Corda, p. 36, figs. 1–13.
1873. *Cyclophthalmus senior* Corda. Frič, pl. III, fig. 4.
1885. *Cyclophthalmus senior* Corda. Thorell and Lindström, p. 24.
1902. *Cyclophthalmus senior* Corda. Frič, p. 483.
1904. *Cyclophthalmus senior* Corda. Frič, pp. 66–68, pl. 7, figs. 1–4; pl. 8, figs. 3–5; text-figs. 84–86.
1913. *Cyclophthalmus senior* Corda. Petrunkevitch, p. 33.
1949. *Cyclophthalmus senior* Corda. Petrunkevitch, p. 141.
1953. *Cyclophthalmus senior* Corda. Petrunkevitch, pp. 24–25, figs. 22–26, 128, 129.
1955. *Cyclophthalmus senior* Corda. Petrunkevitch, p. 77, text-fig. 44(4).
1962. *Cyclophthalmus senior* Corda. Dubinin, p. 429, figs. 1234, 1246.

[19] According to Dr. Harlan P. Banks of Cornell University (written commun., April, 1983) the Onteora red bed association in the "first greening" of the continents, also contains centipedes, a tarantula-like arachnid, and a mite that can be put in a Recent family (these are apparently Givetian in age). There is also an arthropod fragment that may be a silverfish (machilid), which would be the first-known record of the Insecta. This information is confirmed by Rolfe (1982). K.E.C.

It is important to determine how the holotype is preserved. It consists of two parts, one of which consists of the carapace, appendages and mesosoma in dorsal aspect. The counterpart shows the dorsal (inside) side of the coxosternal region, the ventral side of the appendages, the dorsal side of the mesosoma and the first two tergites of the metasoma. The abdominal plate is preserved from the dorsal side.

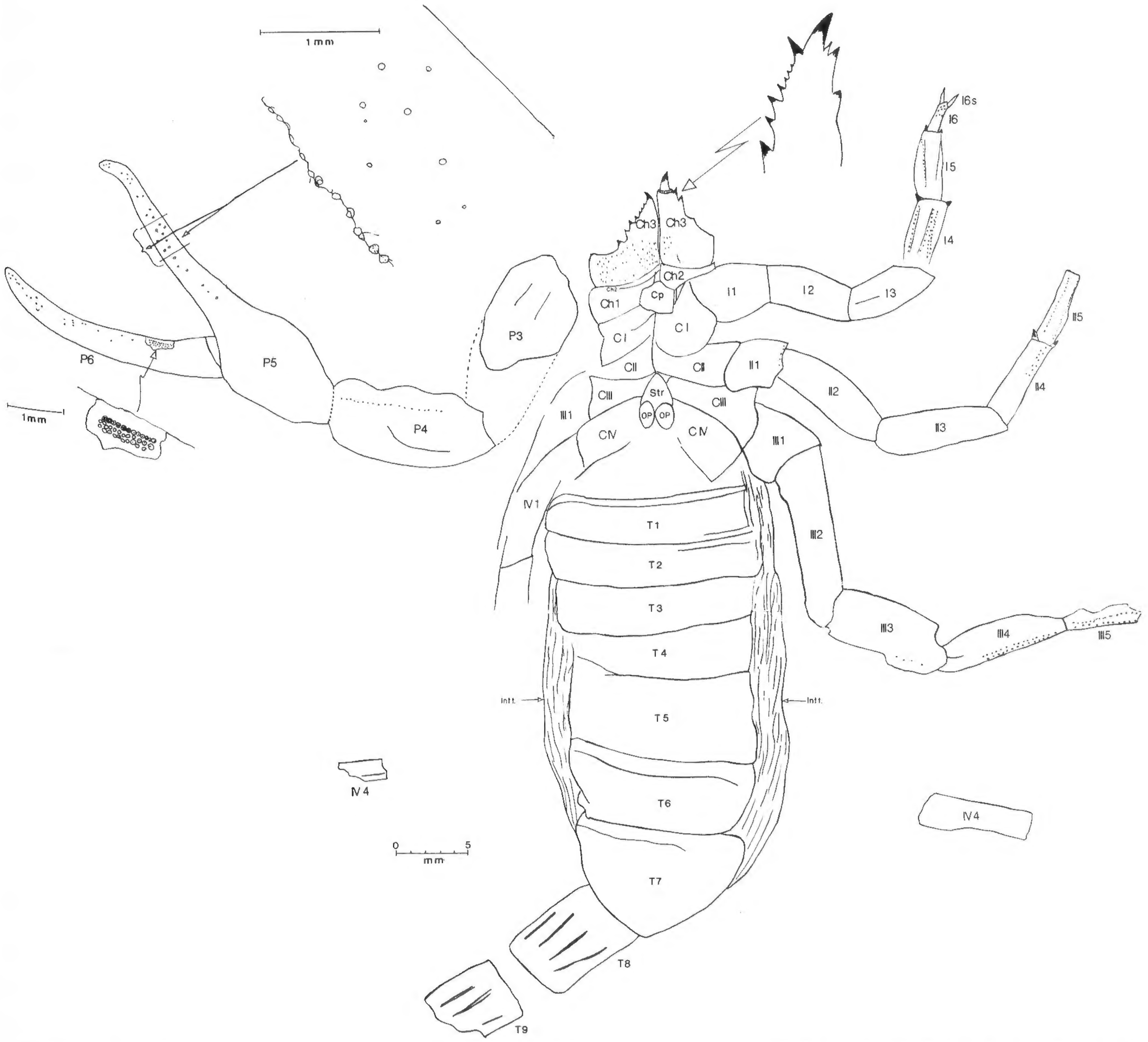
The holotype is a well-preserved scorpion of approximately 100 mm in overall length. It is preserved so that all the structures are in an inflated state.

The carapace is preserved on the counterpart, but



Text-figure 51.—*Cyclophthalmus senior* Corda, 1835. Holotype, NMP Inv. 801. From the Upper Carboniferous (Westphalian B-C), Radnice Member of the "Lower Gray" Formation, Chomle, near Radnice, Czechoslovakia. The dorsal part of the two-part holotype slab. A dissociated meristosternous abdominal plate (**AP2** ?) is exposed on this surface below. See foldout inside front cover for explanation of abbreviations.

the entire outline cannot be seen. It is obvious, however, that Petrunkevitch's (1953, pl. 9, fig. 22) depiction of an unusually long, narrow carapace, is erroneous. The most prominent feature is the well-defined lacrimiform, highly-elevated eye node, with a rounded anterior and emarginate posterior, and two round eyes with well-developed orbital ridges and a deep sulcus between them. It was not possible to see if this scorpion had lateral compound eyes, as the part where they would occur, if present, was covered on one side by the pedipalp base, and the carapace was incomplete on the other (see Text-fig. 51). The cephalic portion of the carapace is surrounded by a ring of prominent bosses. The anterior margin of the carapace protrudes, as is common in other Paleozoic scorpions. A description of the outline is not possible, but on the left side of the counterpart, an edge of the carapace is present. This would mean that the carapace is long, as in *Mazonia,* probably rounded at the anterolateral corner, and that the base is straight, as noted by the basal edge which is largely preserved (see Text-fig. 51). This would result in a carapace with the eye node well within the margin, about in the center of the anterior half, and the outlines would reveal a carapace slightly wider than long.



Text-figure 52.—*Cyclophthalmus senior* Corda, 1835. Holotype, NMP Inv. 801. From the Upper Carboniferous (Westphalian B-C), Radnice Member of the "Lower Gray" Formation, Chomle, near Radnice, Czechoslovakia. The ventral part of the holotype slab. See foldout inside front cover for explanation of abbreviations.

The mesosomatic tergites show a well-preserved raised anterior transverse ridge, and increase in size to the posterior. The seventh tergite of the preabdomen does not show any carinae of prominence which would have been preserved if present. The imprint of the intersegmental tissues on the sides is particularly well preserved with all the longitudinal creases (see Text-figs. 51, 52).

The coxosternal region is seen from the inside and is well preserved. The sternum is small and subtriangular with the elongate elliptical opercular plates fitting at the base. The first two pairs of coxae meet at midsection and each has very slight, short maxillary lobes developed. The third pair of coxae abuts the sternum and the fourth abuts the genital opercula. Petrunkevitch (1953, pl. 9, fig. 24) correctly shows the sternum and genital opercula, but mistakes the third coxae for the fourth. He further mistakes the base of the left chelicera for the first coxa. Thus his restoration of the coxosternal area (1955, fig. 3) is wrong, and the diagnosis of the superfamily as having three pairs of coxae in front of the sternum is also wrong.

Also erroneous is Petrunkevitch's determination of "lung slits" (1953, p. 24, fig. 26) at the end of a supposed "sternite". The latter is the fourth coxa, as can be proven by the arrangement of the legs. The so-called "lung slit" is nothing more than the open end of the coxa.

The appendages are well preserved and those present on the counterpart reveal the ventral side, whereas the dorsal side is shown on the part. It is important to keep this relationship in mind. The chelicerae are also in an inflated state, so that it is possible to make a complete restoration of both dorsal and ventral edges of the fixed ramus (see Text-fig. 52). The lower row contains two large teeth that jut outward, nearly on a plane with the edge of the ramus. The tip clearly must end in a bifid point, although the upper point was broken off. The rest of the dorsal edge is armed with four small sharp teeth followed by a large central tooth and two smaller ones. Both sides of the chelicerae are hirsute, the ventral side more so.

The pedipalps are preserved on both dorsal and ventral sides. These are massive structures having large, well-developed trochanter, femur and tibia. The tibia retains a row of granules, each of which is surmounted by a seta. The chela is long, with a bulbous hand and long fingers. Both fingers are covered with many large setaceous granules on the dorsal side. The ventral side is very smooth but extremely hirsute, as the setal bases are still present, embedded in the skin. The edges of the pedipalp are armed with round denticles, probably several thick, along the edge. Near the posterior part of the fixed finger, a row of crowded setaceous denticles or granules was noted. These occur close to the edge, but likely occurred at the edge, as they were on a part of the finger that formed a narrow platform close to, if not at the edge.

The walking legs may show the usual eight joints (the posttarsus is covered). The first leg is complete and this, as well as the second, shows well-developed double tarsal and basitarsal spurs. The dorsal side reveals rows of well-developed setal granules, but the ventral side is smooth and very hirsute.

The entire ventral side of the chelicerae, pedipalps and walking legs is very hirsute, which is in marked contrast to the dorsal surface. It is therefore very likely that all of the ventral side was hirsute. The coxosternal area has been seen only from the dorsal side.

The abdominal plates were not wholly preserved, except for a single detached one which is complete. It is meristosternous and probably represents the second abdominal plate.

Only two segments of the cauda are preserved, the first two tergites in dorsal aspect. These reveal the presence of three very strongly-developed superior carinae.

Measurements are given by Frič (1904) and Petrunkevitch (1953, pp. 24–25).

Type information. —The holotype, consisting of part and counterpart, is from the Upper Carboniferous (Westphalian B-C) Radnice Member of the Lower Gray Formation at Chomle, near Radnice, Czechoslovakia, preserved in white, hard, kaolinized, volcanic tuff with considerable quartz of magmatic origin, associated with many plants. NMP Inv. 801 in the National Museum, Prague, Czechoslovakia.

Cyclophthalmus robustus, new species
Text-figure 53

1949. *Palaeomachus* sp. Petrunkevitch, p. 138, pl. 48, fig. 156; pl. 55, fig. 180.
1953. Not *Palaeomachus* sp. Petrunkevitch. Petrunkevitch, p. 38 (incorrectly referred to as In.3976 instead of In.13976).
1962. *Palaeomachus* sp. Petrunkevitch. Dubinin, p. 433, fig. 1260.

In 1949, Petrunkevitch referred the specimen, In.13976, consisting of a hand and fingers of a scorpion, to *Palaeomachus* sp. Later in 1953 he stated that the specimen was not congeneric with *Palaeomachus* Woodward. In either case, the chela was incorrectly described, his having omitted diagnostic details that would have permitted good generic separation. The row of setal openings on the fixed finger shows that this is undoubtedly close to *Cyclophthalmus,* and it is here described as the only British representative of that well-known, but rarely encountered, genus.

The holotype, BM(NH) In.13976, consists of an ironstone concretion, retaining dorsal and ventral sides of a well-preserved pedipalp chela of the right side.

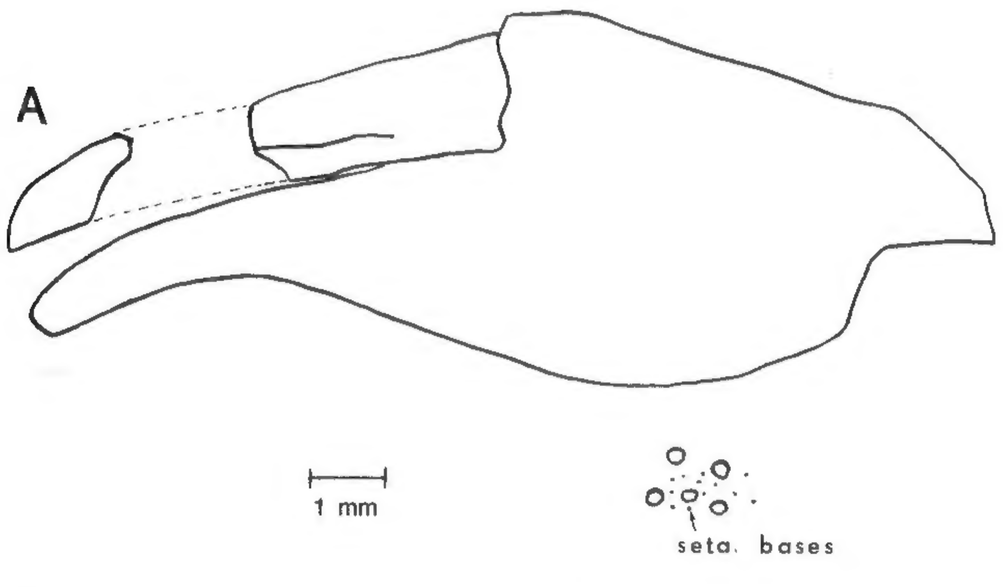
The main diagnostic feature of the chela is the thick row of setal openings on the inner half of the fixed finger, which was unnoticed prior to this study. This conspicuous row of setal openings is five to six openings wide at the base of the finger and gradually narrows to a double row at midsection. The fixed chela is broken here so that it is not possible to determine whether or not the double row continues or narrows further to a single row. The setal row probably also occurs on the free finger, but this is covered by the fixed finger because of a scissorlike action. The hand is robust, about as long as the fingers, and no carinae are present. The fingers are relatively short, with the free finger falcate and incurving, and with the fixed finger recurved. The fingers are cultrate. Measurements in mm of the holotype (BM(NH) In.13976) are as follows: hand length, 7.4; hand width, 5.3; free finger length, 8.2.

Type information.—The holotype is from the Upper Carboniferous, Upper Coal Measures, at Coseley, Staffordshire, England, and is registered in the collections of the British Museum (Natural History) as BM(NH) In.13976.

Derivatio nominis.—*robustus* (L.) = robust (referring to the overall robust aspect of the holotype chela).

Remarks.—I agree with Petrunkevitch that this specimen is not congeneric with *Palaeomachus,* although it is difficult to understand why the two were ever considered to be the same genus in the first place. It differs greatly from the Czechoslovakian *Cyclophthalmus senior* Corda on the species level in having short fingers with a long hand, just the opposite of the combination in the genotype.

Cyclophthalmus senior shows some small denticles on the edge of the pedipalp, which are not present in the British form. This may require a new genus for the British form, but until more is known of the species, it is not considered judicious to separate them. It is, however, a distinct possibility that should be resolved in the future.



Text-figure 53.—*Cyclophthalmus robustus,* n. sp. BM(NH) In.13976 (=*Palaeomachus* sp. Petrunkevitch, 1949, XXXVII, p. 138, pl. 55, fig. 180; 1953, p. 38). From the Upper Carboniferous, Upper Coal Measures, Coseley, South Staffordshire Coalfield, England. Showing two aspects of the pedipalp manus. The long concentration of setal bases along the fixed finger (**P5**) is very characteristic of the genus.

Cyclophthalmus (?) **sibiricus**
Novojilov and Størmer, 1963[20]

1963. *Cyclophthalmus* (?) *sibiricus* Novojilov and Størmer, pp. 84–87, pls. I and II.

Holotype No. 638/1 of the collection of Palaeontological Institute, Academy of Sciences, Leningrad, U.S.S.R. A single specimen lying on its back, with ventral sclerites to a large extent dislocated or removed exposing the impression of the dorsal surface; total length 32.5 mm. The holotype occurs in a dark argillite, probably from the lower part of the Stephanian, in a drill-core, borehole 3, depth 71 m, from the Tomjusinsky District, Kemerov Region, Kuznetsky Basin, U.S.S.R.

Family **MICROLABIIDAE**, new family

Cyclophthalmoidea with a pentagonal sternum and quadrate opercular plates. All five abdominal plates approximately of the same size, without reduction of the anterior plates.

Type genus.—*Microlabis* Corda, 1839.

Remarks.—The genus *Microlabis* had previously been included in the family Isobuthidae by Petrunkevitch (1955, p. 78), but this is no longer possible as *Microlabis* is a Meristosternina, not a Lobosternina. Until something is learned about the maxillary lobes, the family must remain in the Cyclophthalmoidea.

Genus **MICROLABIS** Corda, 1839
(emend.)

Microlabiidae having an anteriorly-rounded carapace, with two large median eyes anteriorly located on a lacrimiform eye node, probably no facetted lateral eyes, very slender, short pedipalps with long, well-developed chelicerae. All legs are unusually short and slender.

---

[20] The only reference to this species found in Kjellesvig-Waering's papers was this note to himself, "For Scorpion opus; do not forget Novojilov's and Størmer's". Although it was not mentioned in the description, the median line on the fifth abdominal plate, shown in plate I, fig. a, and also visible on photograph 1 in plate II, strongly suggests a meristostern. There is a slight indication of a similar median line on the second abdominal plate. A.S.C.

Type species.—*Microlabis sternbergii* Corda, 1839.
Geological range.—Carboniferous.

Microlabis sternbergii Corda, 1839
Text-figure 54

1839. *Microlabis sternbergii* Corda, pp. 14–18, pl. 1.
1873. *Cyclophthalmus sternbergii* (Corda). Frič, p. 2, pl. II, fig. 3.
1885. *Cyclophthalmus sternbergii* (Corda). Thorell and Lindström, p. 24.
1904. *Microlabis sternbergii* Corda. Frič, pp. 69–70, pl. 9, figs. 1–4; text-fig. 87.
1913. *Microlabis sternbergii* Corda. Petrunkevitch, p. 35.
1953. *Microlabis sternbergii* Corda. Petrunkevitch, pp. 23–24, figs. 21, 127.
1955. *Microlabis sternbergii* Corda. Petrunkevitch, p. 78, fig. 44(6).
1962. *Microlabis sternbergii* Corda. Dubinin, p. 428, fig. 1245.

The holotype is preserved so that the entire mesosoma on the dorsal side has been removed except for a small amount on the right side. The ventral side is shown in its entirety from the inside. The carapace as well as the prosomal appendages are seen from the dorsal side. It is not preserved as Petrunkevitch (1953, p. 23) states, "The specimen really lies on its back . . .". It is a *dorsal* impression of both the dorsal and ventral sides. Thus the "ridges" described by Petrunkevitch (1953, p. 23) separating the "sternites" are in reality grooves (sutures).

The carapace is very indistinct and only the central part is present. The outline as shown by Petrunkevitch (1953, fig. 21) does not exist. The median eyes, however, are present, flattened and apparently elliptical and very large. Petrunkevitch states that it is not possible to show what parts of the dorsal side were removed by Frič (1904, p. 70), but it does not seem to have been much as the only fresh break on the specimen is in the region of the operculum.

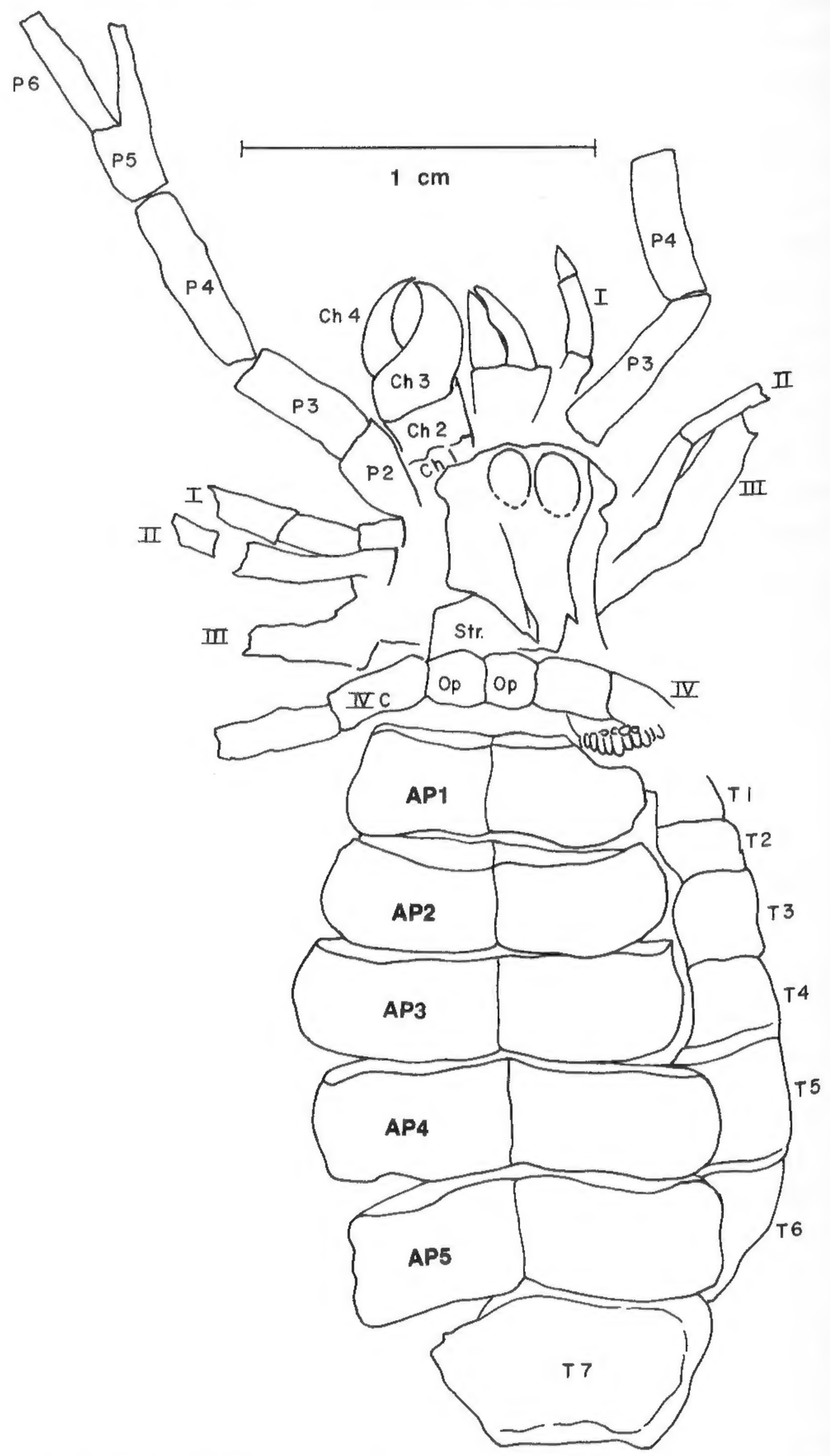
Nothing can be said about the coxosternal arrangement except that it is clear that the fourth pair of coxae abuts the genital opercula, the third pair abuts the sternum and the first two pairs are above the sternum. The sternum is short but large and pentagonal in shape. The maxillary lobes are not known.

The legs are relatively short and small and the pedipalps are unusually slender and small. The chelicerae are large and long, hooklike and undoubtedly armed with teeth, although they were insufficiently well-preserved for description. The chelicerae are composed of four joints, exactly as found in most other Paleozoic scorpions. The comb contains few teeth, probably about ten, and these are large and well inflated. The rachis is small, but the fulcra are comparatively very large.

The venter is noteworthy for the meristosternous abdominal plates. There are five plates, very wide, and jointed by a suture at midsection. A transverse ridge occurs along the anterior edge and this ridge is also cut by the suture, which is groovelike. The last ventral preabdominal tergite is not cut by a suture and has no carinae. No ornamentation of any kind occurs on the parts of the tergite preserved to the right of the specimen nor on the abdominal plates of the venter.

The dorsal side has been preserved on the right side of the specimen showing the right side of the abdomen. The first to sixth tergites are preserved and are progressively longer toward the posterior; nothing more can be described. There is no ornamentation on the tergites.

Type information.—The holotype is a single piece registered as No. 583 Sternberg collection, Inv. No.



Text-figure 54.—*Microlabis sternbergii* Corda. Holotype, NMP Inv. 802 (Sternberg Coll. 583). From the Upper Carboniferous (Westphalian B-C). Lower Gray Formation, Chomle, near Radnice, Czechoslovakia. The ventral side seen from the inside, or dorsal side. Note the characteristic meristosternous abdominal plates (**AP1-5**). See foldout inside front cover for explanation of abbreviations.

802 in the National Museum at Prague, Czechoslovakia, preserved in white, fine, volcanic tuff that has been kaolinized and "contains quartz of magmatic origin. The ash had been deposited in fresh water" (according to label). Small specks of carbonaceous material are on the same slab. Collected from the Radnice Member of the Lower Gray Formation of Upper Carboniferous (Westphalian B-C) age at Chomle (a town situated 65 km southwest of Prague) in the neighborhood of Radnice, Czechoslovakia.

Remarks.—Judging from the great size of the median eyes, it might not be too great a speculation to suspect that this scorpion had not developed lateral eyes. The correlation of large median eyes and small lateral eyes, or vice versa, has been noted throughout this study.

This is an important specimen that shows all of the abdominal plates in place, without having been jammed forward as occurs during ecdysis.

Superfamily **PALAEOBUTHOIDEA**, new superfamily

Meristosternous scorpions with the first and second pairs of coxae meeting at midsection anterior to the sternum, and with the third and fourth pairs of coxae abutting the sternum.

Type family.—Palaeobuthidae, new family.

Family **PALAEOBUTHIDAE**, new family

Palaeobuthoidea with sternum pentagonal and with the first two pairs of coxae having well-developed, narrow, maxillary lobes; second pair meeting at the median line and with first pair on each side abutting the maxillary lobes of the second pair; last two pairs abutting the sternum. No lateral eyes.

Type genus.—*Palaeobuthus* Petrunkevitch, 1913.

Remarks.—Petrunkevitch (1913, p. 53, and continuing through to the *Treatise on Invertebrate Paleontology* in 1955 [p. 78, fig. 44(7)]) erroneously diagnosed the sternum as being triangular, and the coxae of the last pair of legs as abutting the opercula. This was taken from the holotype, which shows instead that the supposed triangular sternum was nothing more than the junction of the base of the second pair of coxae. The actual sternum, which was mistaken for the opercula, is clearly pentagonal with a deep cleft in the posterior midsection, and with both third and fourth pairs of coxae abutting the sides of the sternum. This is a rather advanced scorpion, considerably more so than the Cyclophthalmoidea (or the true Isobuthoidea).

The determination of the sternum, and its correct relationship to the genital opercula and the coxae in *Palaeobuthus distinctus* Petrunkevitch, means that the genus can no longer properly be in the superfamily Isobuthoidea Petrunkevitch, 1913. Inasmuch as this is a meristosternous scorpion, with well-developed maxillary lobes of the first two pairs of coxae and having the last two pairs abutting against the large pentagonal sternum, it is essential that a new family and superfamily be created to accommodate this genus under the Meristosternina.

The genus *Palaeobuthus* Petrunkevitch, 1913 with *P. distinctus* Petrunkevitch, 1913, type species, reveals a coxosternal arrangement much like the living scorpions, with a well-developed oral tube. Of course it differs greatly from living scorpions in being meristosternous rather than orthosternous.

Genus **PALAEOBUTHUS** Petrunkevitch, 1913 (new definition)

Palaeobuthidae with square carapace, small median eyes, anteriorly located; no lateral eyes; coarsely punctate; pedipalps finely denticulate on the edge; opercula subcuneate; telson very large, scimitarlike aculeus.

Type species.—*Palaeobuthus distinctus* Petrunkevitch, 1913.

Geological range.—Pennsylvanian.

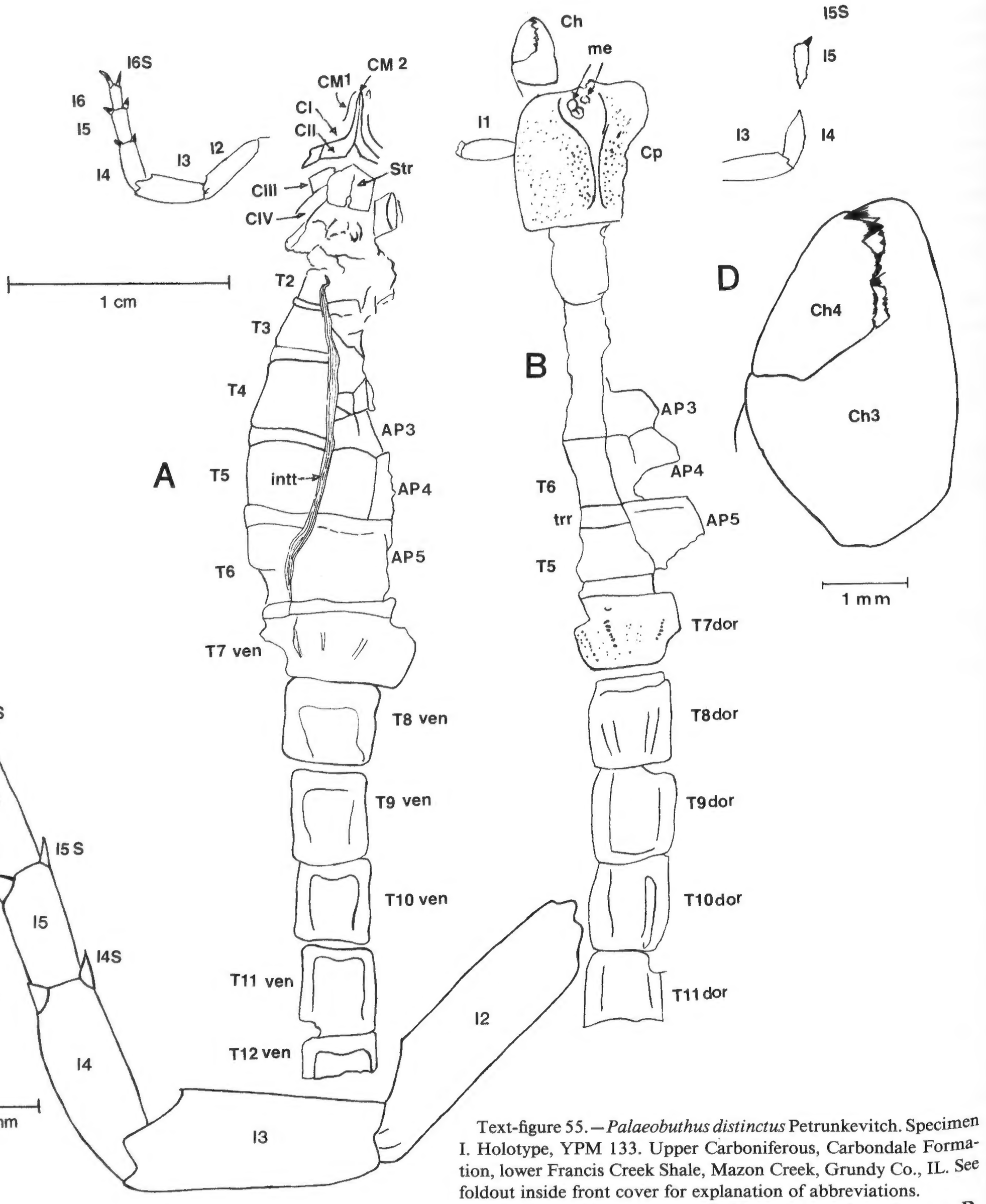
Remarks.—The description of this genus is now based on three female specimens and one male and is, therefore, one of our better known fossil scorpions (see restorations, Text-fig. 58).

Palaeobuthus distinctus Petrunkevitch, 1913 Text-figures 55–58, 111H

1913. *Eoscorpius typicus* Petrunkevitch (*partim*), pp. 39, 42.
1913. *Eoscorpius granulosus* Petrunkevitch (*partim*), p. 46.
1913. *Palaeobuthus distinctus* Petrunkevitch, p. 53, pl. 1, fig. 5; text-fig. 16.
1949. *Palaeobuthus distinctus* Petrunkevitch. Petrunkevitch, p. 136.
1953. *Palaeobuthus distinctus* Petrunkevitch. Petrunkevitch, p. 22.
1955. *Palaeobuthus distinctus* Petrunkevitch. Petrunkevitch, p. 78, fig. 44(7).
1960. *Mazoniscorpio mazonensis* Wills, pp. 290–300, pls. 49, 50, 51, figs. 4–6; text-figs. 10–13.
1962. *Palaeobuthus distinctus* Petrunkevitch. Dubinin, p. 428.

Specimen I.—The holotype of *Palaeobuthus distinctus* Petrunkevitch, 1913 (YPM 133), is preserved in a nodule consisting of two halves, neither of which had been properly cleaned. Most of the carapace and the coxosternal arrangements are revealed, as well as parts of the dorsal and ventral sides of the mesosoma and the dorsal side of the cauda. It is a poorly-preserved specimen, consisting of an ironstone concretion showing most of the dorsal and ventral sides respectively on each part of the concretion.

The carapace is subquadrate, forming a right angle at the genal angles, rounded at the anterolateral angles, and with the anterior nearly straight except at the middle where a triangular glossate anterior process occurs.



Text-figure 55.—*Palaeobuthus distinctus* Petrunkevitch. Specimen I. Holotype, YPM 133. Upper Carboniferous, Carbondale Formation, lower Francis Creek Shale, Mazon Creek, Grundy Co., IL. See foldout inside front cover for explanation of abbreviations.

A, B. Part and counterpart. **C.** Ventral side of the first leg. **D.** Dorsal side of the left chelicera retaining the last two joints.

A deep, narrow, median sulcus separates the carapace into two parts and continues anteriorly to form a Y-shaped sulcus on the carapace, with the anterior median ocellar node in the open part of the Y-shaped area. At least one median eye is barely visible, but it is so badly preserved that description is not warranted except to note that it is relatively small. Coarse granules occur on both sides of the narrow median sulcus, and also along the other parts of the carapace, although not so well nor so coarsely developed. In the pleural parts of the carapace the pustules are very small. Most of them seem to be setaceous as each is surmounted by a round hole indicating the site for a seta (see Text-fig. 55B).

The well-preserved chelicerae (see Text-fig. 55D) are very long and unusually large for a scorpion this size. Numerous denticles occur, but it has been impossible to determine whether or not they occur in two rows, as only an impression of the dorsal side is visible. The free ramus is particularly massive and very wide in contrast to the much narrower fixed ramus. The first walking leg (see Text-figs. 55A–C), known almost in its entirety, has double tibial and basitarsal (pedal) spurs, whereas the claws are two short spines that probably are slightly curved. The posterior spine appears longer than the anterior one (see Text-fig. 55C). I was unable to see a posttarsus, but this is probably present.

The coxosternal region is of considerable interest (see Text-fig. 55A). The sternum is definitely pentagonal, very wide, large, and with a deep median sulcus at the posterior half and continuing anteriorly as a suturelike division. The base is straight, the sides are parallel, the anterior forms an obtuse triangle and it is slightly wider than long. The genital opercula are composed of two long plates, but these have been compressed to an almost unrecognizable form. The first and second pair of coxae have long and well-developed narrow maxillary lobes. The second pair of coxae meets at the midline, in front of the sternum, whereas the first pair abuts against the maxillary lobes of the second pair of coxae, having been squeezed away from the midline. The third and fourth pair of coxae abut against the sternum.

The "triangular sternum" that Petrunkevitch (1913) described is merely the filling in by sediments of the space between the bases of the second pair of coxae, and the long "anterior process" of the sternum is merely the matrix or filling-in by sediments of the narrow space between the maxillary lobes of the second pair of coxae. The rounded genital plates, which Petrunkevitch (1913) revealed, are merely the large sternum with the edges covered and therefore appearing as a rounded, sutured plate that was interpreted to be the genital plates. The genital opercula are so badly preserved that description is not merited.

Little can be said of the tergites except that all have well-developed anterior ridges. The ventral abdominal plates cannot be described as preservation is very poor, but they are definitely meristosternous, each half being rather square and joined by a median suture. The last preabdominal tergite shows two very prominently developed ridges with knobby pustules arranged on the crest. Coarse pustules are present on the extremities of the lateral angles in no particular pattern, although there is a faint linear arrangement on part of the pustules. Some fairly coarse pustules occur along the center of the tergite.

The cauda is known only from the dorsal surface, and only the first four tergites are preserved. The tergites show the cauda to be massive, with two crests developed on the dorsal surface. These two linear crests are widely separated and do not appear to be surmounted with knobby pustules, such as occur on the two crests of the last preabdominal tergite. Intersegmental tissue from the lateral part of the mesosoma obscures part of the venter.

The robust and wide mesosoma and metasoma suggest that this specimen is a female.

Measurements (in mm) of Specimen I, holotype, YPM 133.—

Total body length:	55.0 (estimated)
Length of tergite No. 7:	4.0
Length of tergite No. 8:	3.9
Length of tergite No. 9:	4.0
Length of tergite No. 10:	4.1
Length of tergite No. 11:	4.5
Sternum length:	1.9
Sternum width:	2.0

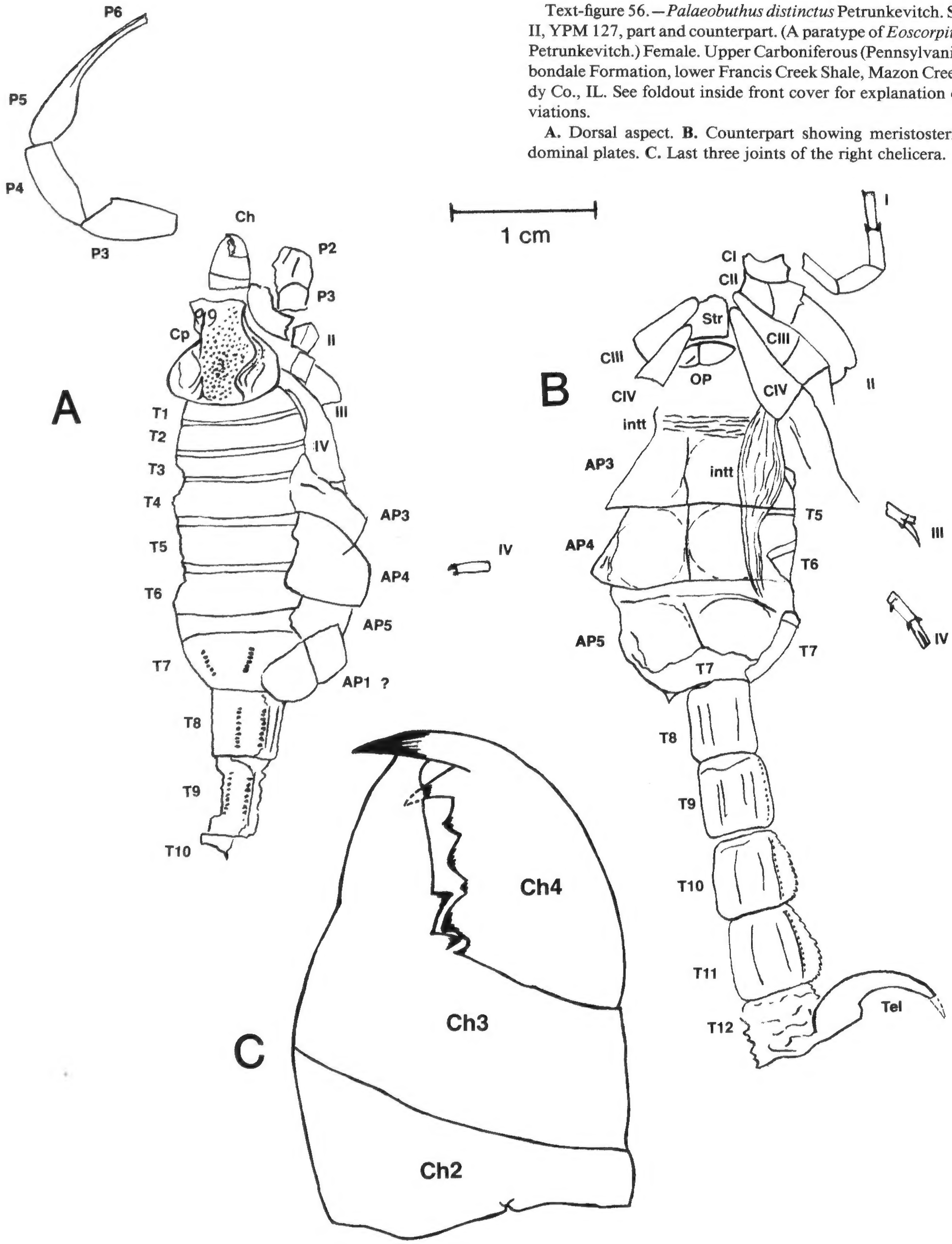
Specimen II.—Paratype of *Eoscorpius typicus* Petrunkevitch, 1913 (YPM 127). The specimen is in two parts containing the dorsal and ventral sides of a well-preserved scorpion in a typical ironstone concretion.

The carapace is badly crushed but reconstruction was possible. The anterior margin has a slight glossate process at the middle. On either side of the process, the anterior is slightly emarginate. The base was probably straight in life with the sides slightly tapering anteriorly. On the midsection is a narrow sulcus at the end of which occurs a small ocellar node, with the sulcus separating two small, round median eyes. The cephalic part of the carapace is covered with coarse pustules, some of which are rather tuberculate. The pleural areas of the carapace have a few scattered pustules of much lesser size (see Text-figs. 56A, B).

The chelicera is known from the dorsal side (see Text-fig. 56C), revealing a double tooth arrangement at the apical end of the free ramus, much as in living Buthidae. It was impossible to determine whether the chelicera was made up of three or four joints. However, four joints appear to be the correct number as there is a small condyle present on the basal segment, which I interpret to be the second joint, for the articulation against another (basal) joint which presumably existed but is covered.

The pedipalp is almost completely known, showing a stocky femur that may not be complete, followed by a tibia that is narrower and slightly longer (see Text-fig. 56A). Only the hand and the free finger were preserved and reveal a crest or groove running along the length of both finger and hand. It is probable that this groove is only cuticular folding. No denticles were discovered on the edges of the fingers.

The coxosternal arrangement is not entirely known. Only the base and one of the lateral margins of the



Text-figure 56.—*Palaeobuthus distinctus* Petrunkevitch. Specimen II, YPM 127, part and counterpart. (A paratype of *Eoscorpius typicus* Petrunkevitch.) Female. Upper Carboniferous (Pennsylvanian), Carbondale Formation, lower Francis Creek Shale, Mazon Creek, Grundy Co., IL. See foldout inside front cover for explanation of abbreviations.

A. Dorsal aspect. **B.** Counterpart showing meristosternous abdominal plates. **C.** Last three joints of the right chelicera.

sternum are known. This shows that it was probably large and hexagonal. The third and fourth pairs of coxae abut against the sternum. It is presumed, from the position of the parts of the first and second coxae, that the second coxae meet along the midline and should have long maxillary lobes developed, which extend to the anterior. From their position, the first coxae appear to abut against the maxillary lobes of the second, very much as in present-day scorpions. In fact, the entire arrangement would be very similar to the living scorpions. The genital plates are long and subcuneate.

The dorsal side is almost complete and shows that the tergites increase progressively in size toward the posterior. They are almost devoid of ornamentation, except on the seventh preabdominal tergite, which shows two obliquely-placed crests with very coarse knobby pustules surmounting each crest.

The abdominal plates are well shown and are of the meristostern type. It is interesting to note that large round depressed areas occur in the middle of each of these plates. No structure is discernible within the round areas, but presumably they are the impressions of pouches or gill chambers for the large gills. Intersegmental tissue from the lateral sides of the mesosoma has been preserved on the right side of the specimen.

The first two tergites of the dorsal side of the cauda are present and show two crests surmounted by knobby pustules. The rest of the cauda is known from the ventral surface, which appears to have two crests without ornamentation. The last two tergites show what appear to be lateral crests, or very high carinae, increasing in size from the third to the fourth tergite, and presumably also increasing in the fifth caudal segment, which is not well developed, but shows a serrated edge. It is probable that these high crests are lateral crests on each side of the tergite, much as in some of the "fat-tailed" scorpions of North Africa and South America. The telson is almost complete and is unusually large, having a rather short vesicle and a very long, curved aculeus. I know of no scorpion, other than the British *Eoscorpius pulcher* (Petrunkevitch), that has a stinger as large as this one.

The anterior joints of the walking legs are almost unknown. However, parts of the terminalia of these legs were successfully exposed and show that the tarsus has two long claws. Double pedal (basitarsal) spurs also occur and, at least on the fourth leg, a single tibial spur occurs. However, preservation was not too clear at this point, and it is highly possible that double tibial spurs also occur. The walking legs themselves are not well preserved, except for the first, where measurements were possible. This leg retains two tibial and two pedal spurs. The terminations of the second and third walking legs were successfully exposed and show that the scorpion had a tarsus that terminated in two long, slightly curved, claws. It also appears that the other legs, as shown by the fragment of what seemed to be the fourth walking leg, had two basitarsal and two tibial spurs, although in the fourth leg itself only one of the tibial spurs is preserved. From the wide and robust size of the body, this specimen appears to be a female. The posttarsus was not seen but undoubtedly should be present in better preserved specimens.

Measurements (in mm) of Specimen II, YPM 127.—

Total body length:	67.0
Total abdomen length:	20.8
Total caudal length:	35.2
Carapace length:	7.5
Median eyes:	
Distance from anterior margin:	0.6
Distance from posterior margin:	5.7
Pedipalp:	
Length of chela:	11.6
Length of femur:	6.0
Length of tibia:	6.5
Length of hand:	3.8
No. 4 abdominal plate length:	5.8
No. 7 tergite length:	6.6
No. 8 tergite length:	4.8
No. 9 tergite length:	5.7
No. 10 tergite length:	5.7
No. 11 tergite length:	5.7
Stinger length:	8.7
Aculeus length:	5.5

Specimen III.—Paratype of *Eoscorpius granulosus* Petrunkevitch, 1913 (YPM 130), shown in Text-figure 57.

This specimen comprises only the mold of the dorsal side of a scorpion larger than the two previously described. It is preserved in an ironstone concretion, showing parts of the prosomal appendages, most of the prosoma and nearly all of the mesosoma. It adds but little to the description of the species, but the carapace and pedipalp are rather well preserved.

The carapace is subquadrate, with base nearly straight and lateral edges tapering slightly anteriorly. The anterior is mainly straight with a glossate process in front, which likely was bent downward in life. Two small, rounded, median eyes are present on a crushed mound directly behind the anterior process. A Y-shaped sulcus continues posteriorly from the ocellar mound. No lateral eyes were noted. A narrow doublure occurs at least on the base and lateral margins. The carapace is covered with small tubercules.

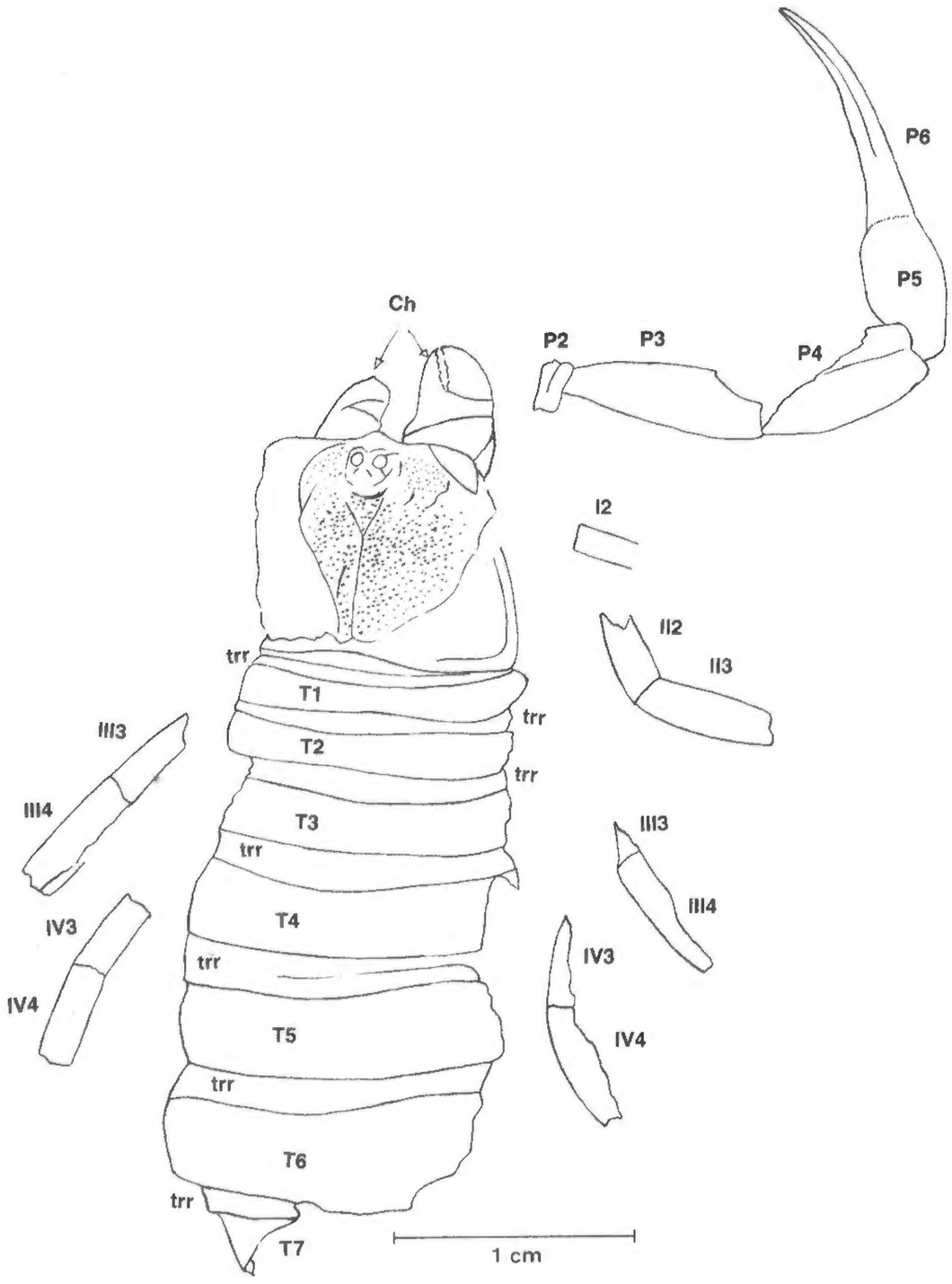
The appendages of the prosoma are preserved only in fragments, except for the right pedipalp, which is almost complete. The femur is about as long as the tibia, both of which are strongly developed. The hand and free finger are almost complete and reveal a strong chela with subquadrate hand and curved free finger. A

narrow crest or groove occurs along part of the length of the finger, which very likely represents an infolding of the chitin as this crest or groove does not extend to the hand as was noted in the previous specimen. No denticles were discerned on the edge of the finger.

The almost complete mesosoma is preserved from the dorsal side. It shows that each tergite increases in size posteriorly, and that each is bounded anteriorly by a massive anterior ridge. The last (seventh) tergite of the preabdomen is preserved only as a fragment and, other than showing the typical anterior ridge, little else is preserved. The mesosoma is wide and suggests that this specimen was a female.

Measurements (in mm) of Specimen III, YPM 130.—

Overall length:	90.0 (estimated)
Carapace length:	8.0
Pedipalp:	
Length of femur:	6.7
Length of tibia:	6.4
Length of chela:	13.2
Length of free finger:	8.5
No. 1 tergite length:	1.7
No. 2 tergite length:	2.2
No. 3 tergite length:	2.6
No. 4 tergite length:	3.0
No. 5 tergite length:	4.0
No. 6 tergite length:	4.4



Specimen IV.—The holotype of *Mazoniscorpio mazonensis* Wills, 1960 (BU 721A,B,C).

The excellently preserved specimen which Wills developed and minutely described (1960, pp. 290–300, pls. 49, 50 and 51, figs. 4–6; text-figs. 10–31) was described as a new genus and species, as at that time only highly erroneous figures and interpretations of the other Mazon Creek scorpions were available in the existing literature. A restudy of the holotype of *Palaeobuthus distinctus* Petrunkevitch (see above), has revealed the carapace, true sternum, type of abdominal plates, and the details of the coxosternal region. The details of the morphology of this specimen, coupled with additional new information from the specimens YPM 127 and 130, unfortunately reveal that the superbly described *Mazoniscorpio mazonensis* Wills, 1960, is a junior synonym of *Palaeobuthus distinctus* Petrunkevitch, 1913.

My reasons for considering *Mazoniscorpio mazonensis* Wills as a junior synonym of *Palaeobuthus distinctus* Petrunkevitch are as follows (it should be noted that they are from the same horizon and locality):

1. The two carapaces are identical. Both show the same surface contours and the same anterior, lateral and basal margins. The small, rounded median eyes, located on a small, anteriorly-placed mound, and the lack of lateral eyes, are identical in both. The peculiar coarse pustulation of the carapace also is similar.

2. Both lack ornamentation on the mesosomatic tergites.

3. The very coarse tubercles surmounting the two crests on the dorsal side of the last preabdominal tergite are identical.

4. The coxosternal arrangements of the two are the same.

5. The shape and relative size of the sternum are identical in both.

6. Both are meristosternous scorpions.

7. The appendages are the same in both.

The only difference that I have been able to see is that the specimen described by Wills is more slender, having a mesosoma that is considerably narrower, at least on the abdominal plates ("sternites"), than YPM 127, which shows these plates well. This is only a sex difference and would indicate that the holotype of *M. mazonensis* is a male, whereas YPM 127 is the female. I consider YPM 130 and the holotype also to be females.

Text-figure 57.—*Palaeobuthus distinctus* Petrunkevitch. Specimen III, YPM 130. (Paratype of *Alloscorpius granulosus* Petrunkevitch.) Female. Upper Carboniferous (Pennsylvanian), Carbondale Formation, lower Francis Creek Shale, Mazon Creek, Grundy Co., IL. See foldout inside front cover for explanation of abbreviations.

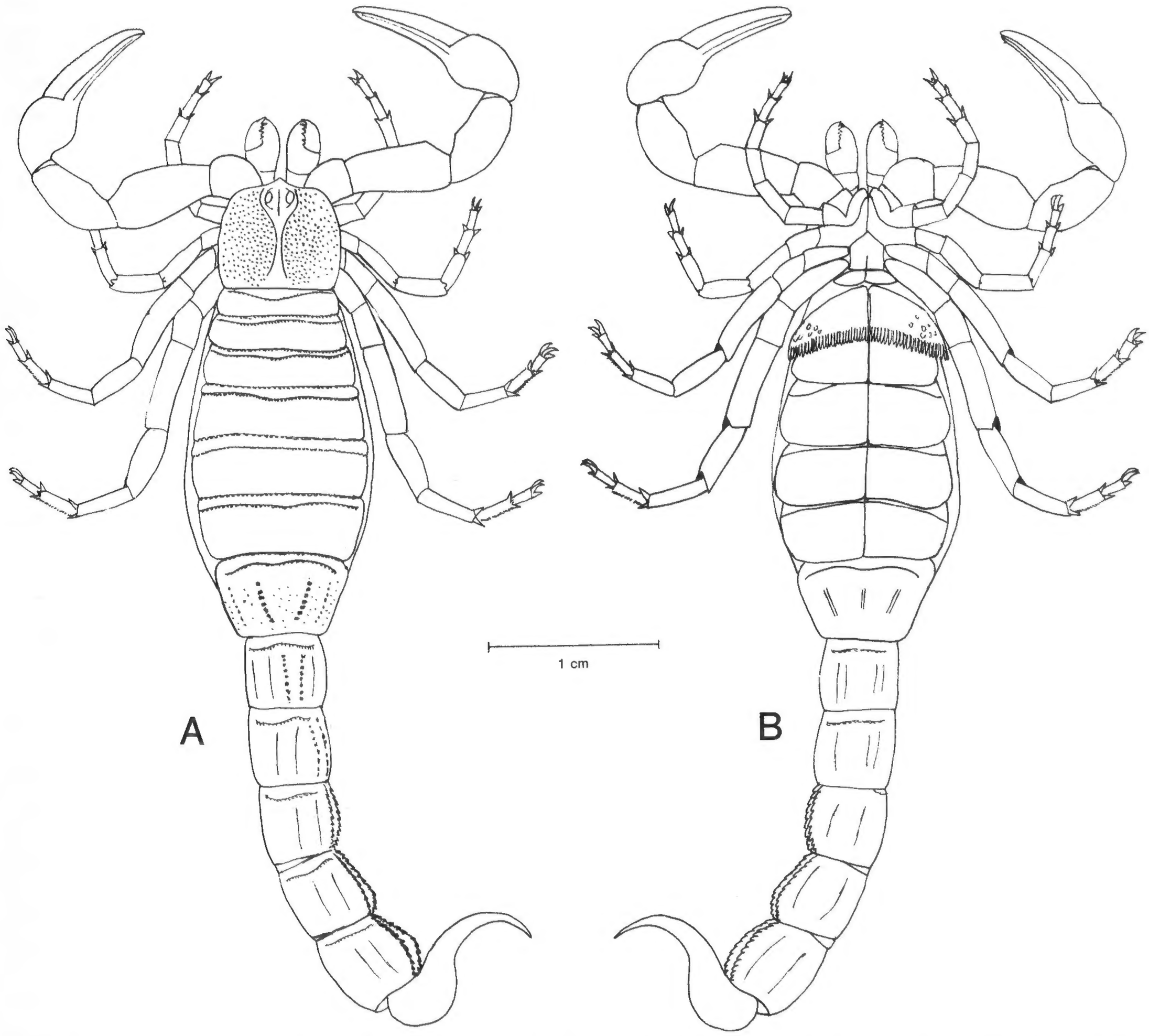
The presence of denticles on the "cutting edges" of the fingers of the pedipalps was not noted in the YPM specimens, but was described by Wills in his specimen (which had been dissolved out of the ironstone matrix). The difference is easily explained because the two YPM specimens were preserved as internal molds of the inside of the pedipalps, and, because the denticles are external structures, they would not be preserved internally. In Wills' preparation, only the original cuticle was used in the description of the minute denticles.

Type information.—The holotype (YPM 133), YPM 127, YPM 130, and the holotype of *Mazoniscorpio mazonensis* Wills (BU 721A,B,C) are from the Pennsylvanian Carbondale Formation, lower part of the Francis Creek Shale at Mazon Creek, Grundy County, IL.

Remarks.—It is possible to make a restoration of this species as all morphological parts are known (see Text-fig. 58).

Infraorder **LOBOSTERNINA** Pocock, 1911
(*nom. transl.* Kjellesvig-Waering herein, *ex* Lobosterni Pocock, 1911)

Branchioscorpionina with five gently to deeply bilobate abdominal plates with well-developed gill chambers and doublures; gill openings or slits between



Text-figure 58.—*Palaeobuthus distinctus* Petrunkevitch. From the Pennsylvanian (Mazon Creek) of Illinois. Reconstruction of a female, based mainly on YPM 133 and YPM 127, shown in Text-figures 55 and 56, and BU 721, shown in Wills (1960).
A. Dorsal side. **B.** Ventral side.

the doublure and the abdominal plate.

Remarks.—The Lobosternina, the second largest group in the fossil scorpions, was successful from the Silurian through the Triassic. The earliest form, *Palaeophonus nuncius* Thorell and Lindström, 1884, seems to have barely evolved from the Holosternina, with its gently-lobed protolobosternous abdominal plates. Before extinction, the infraorder expanded into at least 37 species, arranged in six superfamilies, 15 families, and 22 genera, and developed abdominal plates so deeply bilobed in *Waterstonia airdriensis,* n. gen., n. sp., from the Lower Coal Measures, as to almost resemble the Bilobosternina.

Superfamily **PALAEOPHONOIDEA**
Thorell and Lindström, 1885
(new definition)

Lobosternina with protolobosternous abdominal plates; legs very thick, short, eurypterid-like, with posttarsus greatly developed as a single spine, and with very short tarsal spurs (ungues).

Type family.—Palaeophonidae Thorell and Lindström, 1885.

Remarks.—As explained above, this scorpion has been considered to be very primitive. This was due to its presence in Silurian beds (Wenlock) and, in particular, to its eurypteroid legs. Whether or not this is a "primitive" scorpion or a highly specialized one is a moot question. The presence of protolobosternous abdominal plates does not support the "primitive" nature of this scorpion. For example, the presence of this scorpion in marine waters in an area with nearby common reef development may indicate a specialization for a reefal existence. The holosternous *Allopalaeophonus caledonicus* (Hunter) of Scotland, however, has rather similar legs and leg terminations, but occurs in marine, dark-green to black shales. Both occur with common eurypterids. It is a difficult matter, if not impossible, to determine scorpion habitats from the type of legs and leg termination. A glance at the leg terminations of some living crabs and their lack of correlation with their habitats, is sufficient to further illustrate the dilemma.

Family **PALAEOPHONIDAE**
Thorell and Lindström, 1885
(new definition)

Palaeophonoidea with large facetted lateral eyes and short subtriangular cup-shaped coxae.

Type genus.—*Palaeophonus* Thorell and Lindström, 1884.

Genus **PALAEOPHONUS**
Thorell and Lindström, 1884
(new definition)

Palaeophonidae with quadrate carapace, median eye node anteriorly-located with sulcus dividing carapace into two large inflated lateral cheeks. Fingers of pedipalps with cultrate inner edges and small denticles developed only on extreme ends, both inner and distal.

Type species.—*Palaeophonus nuncius* Thorell and Lindström, 1884.

Geological range.—Silurian (Lower Wenlock).

Distribution.—Gotland, Sweden.

Remarks.—*Allopalaeophonus caledonicus* (Hunter) was previously included in this genus, but the two are not closely related. *Allopalaeophonus caledonicus* is a holostern rather than a protolobostern and has no lateral facetted eyes. These are, of course, major differences, although the two do have rather similar legs and general dorsal aspect of the body.

Palaeophonus nuncius Thorell and Lindström, 1884
(new description)
Plate 9; Text-figures 59–62

1884a. *Palaeophoneus*[21] *nuncius* Thorell and Lindström, p. 984.
1884b. *Palaeophonus nuncius* Thorell and Lindström. Thorell and Lindström, in the Glasgow Herald, Dec. 19, 1884.
1885. *Palaeophonus nuncius* Thorell and Lindström. Thorell and Lindström, pp. 1–33, pl. 1.
1901. *Palaeophonus nuncius* Thorell and Lindström. Pocock, p. 296, fig. 1.
1904. *Palaeophonus nuncius* Thorell and Lindström. Frič, p. 63, text-fig. 78.
1913. *Palaeophonus nuncius* Thorell and Lindström. Petrunkevitch, p. 13.
1949. *Palaeophonus nuncius* Thorell and Lindström. Petrunkevitch, pp. 127–128, fig. 170.
1953. *Palaeophonus nuncius* Thorell and Lindström. Petrunkevitch, pp. 5–8, figs. 1–5, 115.
1955. *Palaeophonus nuncius* Thorell and Lindström. Petrunkevitch, p. 69, fig. 1, a–c.
1962. *Palaeophonus nuncius* Thorell and Lindström. Dubinin, p. 425, figs. 1221a, b, 1223.

This famous specimen was described in great detail by Thorell and Lindström in 1885, when optical instruments were not well developed, particularly for incident light. As a consequence, many important morphological structures that are present on the specimen were not described. In 1953, Petrunkevitch restudied the holotype, but equally as many structures were again omitted. The holotype, because of its geological age and unique morphology, attracted world-wide attention. This fame mainly depended on the fact that it was unquestionably accepted as the first known air-

[21] Footnote in Thorell and Lindström, 1885, p. 9: "The name of the genus should be written, as it is here, *Palaeophonus,* not *Palaeophoneus.*" A.S.C.

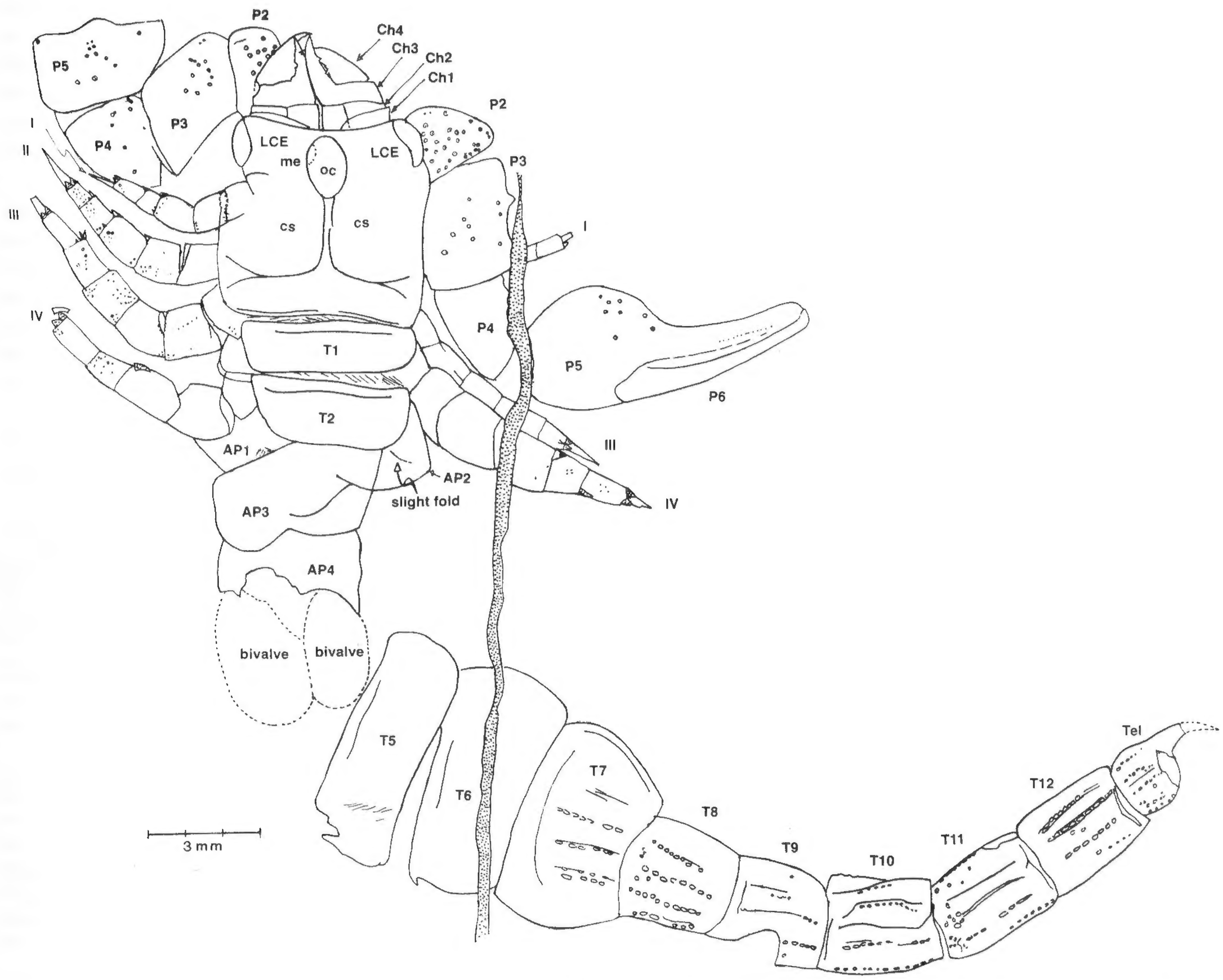
breathing, land-dwelling animal in the geological record. It is a rare Historical Geology text-book that does not still consider this scorpion in the same light and, because of this, it has possibly been figured in more text-books than almost any other fossil. This is curious and incongruous, as the premise that it was an air-breather was without basis, and that it was a land-dweller was equally without solid morphological foundation.

The parts, or morphological organs, all of great value for diagnostic, taxonomic and morphological purposes, that have been totally unreported previously are as follows:

1. The presence of large facetted lateral eyes.
2. Protolobosternous rather than holosternous abdominal plates.
3. The four-jointed chelicerae.
4. The presence of two tarsal spurs—these are developed in other scorpions into the ungues (claws).
5. The presence of two basitarsal spurs and very likely two tibial spurs on each leg.

Other than the holotype (SRM Ar. 32235), which is the most important specimen, there are in the Riksmuséet in Stockholm, Sweden, several small fragments that add to our knowledge of this scorpion.These include two fingers of the pedipalp, a complete protolobosternous abdominal plate, and three disjointed caudal segments. In view of the above major and hitherto undescribed morphologic structures, as well as the undescribed specimens, it is necessary to redescribe the species completely, as well as to emend the genus and family. The taxonomic part has been done above and the new description of the species follows:

Carapace subquadrate, rounded at the anterolateral



Text-figure 59.—*Palaeophonus nuncius* Thorell and Lindström. Holotype (SRM Ar. 32235). From the Middle Silurian, lower Wenlock, Visby, Gotland, Sweden. One of the most famous fossil scorpions. See foldout inside front cover for explanation of abbreviations.

angles, gently but noticeably emarginate along the frontal margin, and straight at the base with a narrow posterior marginal rim. The cephalic area is divided by a narrow sulcus into two elevated or inflated pouchlike areas, and the basal part is again elevated in a wide, bowlike area that Petrunkevitch (1953, p. 7) mistakenly assumed represented the covered or "hidden" first tergite, and that resulted in further "evidence" of his ill-fated theory concerning an eight-tergite preabdomen (see Kjellesvig-Waering, 1969, pp. 171–176). At the rounded anterolateral angles are two large facetted lateral eyes surrounded by a narrow rim. These eyes are protuberant, and of the type that are present in the family Eurypteridae of the Eurypterida, namely, facetted with very small ommatidia. The small facets seem to be preserved on both eyes, but this is not entirely certain, as in *Eurypterus* and *Baltoeurypterus,* these facets are rarely large enough to be seen unless the skin is taken off and mounted on a slide and viewed with reflected light. However, the large lateral, bulbous, facetted eyes are definitely present and the very narrow rim enclosing them is clearly outlined. It follows that ommatidia have to occur. These eyes may be seen in the photograph (see Pl. 9) and in the drawings (see Text-figs. 59, 60A).

The surface of the carapace is devoid of ornamentation, but most of the skin has been peeled away. It is known that the ornamentation could not have been composed of pustules of the type present on the chelicerae, or any kind of pustules, as these would have been preserved in the internal mold. The skin covering the carapace, however, could have had some fine setal openings around the ocellar node, which retains some skin, but no such setae or setal sites are present.

Midway in the front of the carapace is a large ocellar node, oval in shape and well elevated. Eyes are not preserved sufficiently well to be certain of their presence, but this is suggested by a rounded, small area on the left anterior part of the node. I do not doubt that this scorpion has well-developed median eyes. Previously, it was thought to be blind, but now we know that large lateral, bulbous, facetted eyes do occur. It would be incongruous to have these large facetted lateral eyes and have a well-developed, elevated, ocellar node without median eyes. I consider it unreasonable to suspect such a condition, if not an impossibility. All scorpions with lateral eyes, simple or facetted, have median eyes. Scorpions without any type of lateral eyes always have well-developed median eyes. An exception, however, is the modern troglobite scorpion, *Typhlochactas* of Mexico, which has neither lateral nor median eyes. But the morphology and habitat of *Palaeophonus* are quite different and not to be compared to the former, as it is anything but blind, having great facetted lateral eyes, and certainly is not a troglobite.

The prosomal appendages are very well preserved. The chelicerae were described well by Thorell and Lindström, except that only three joints were noted. Actually there are four joints, as commonly found in Paleozoic scorpions.

The first joint of the chelicera is short, probably cup-shaped as in other scorpions, although the base was covered in the holotype. The second joint is also short, with a well-developed longitudinal suture or flange on the dorsal side, as in some modern scorpions (see *Heterometrus*). The hands of the chela also are short and this is followed by a nearly straight fixed dactyl.

This dactyl has small teeth along the edge; in particular, a larger, subterminal one that serves as a socket for the opposing free dactyl. The latter is very wide, curving and pointed at the end. When closed against the fixed dactyl, it overlaps at the end. Several large teeth are present on the edge, but their arrangement, except as shown in the drawing (see Text-fig. 60D), is not possible to know, since the entire chelicera occurs in a flattened state; thus it is not possible to discern the number of teeth on each side of the chela, ventral or dorsal. All parts of the chelicera are covered with small pustules, no doubt setaceous.

The pedipalp is known in its entirety; it is a very stout, strong structure. The base of the pedipalp or coxa is completely covered, but the first joint, or trochanter, is beautifully preserved. This is largely triangular with a remarkable number of unusual, large, rounded papillae (see Text-figs. 60A–C, G). These papillae are scattered about the dorsal surface (venter not seen) in no apparent arrangement.

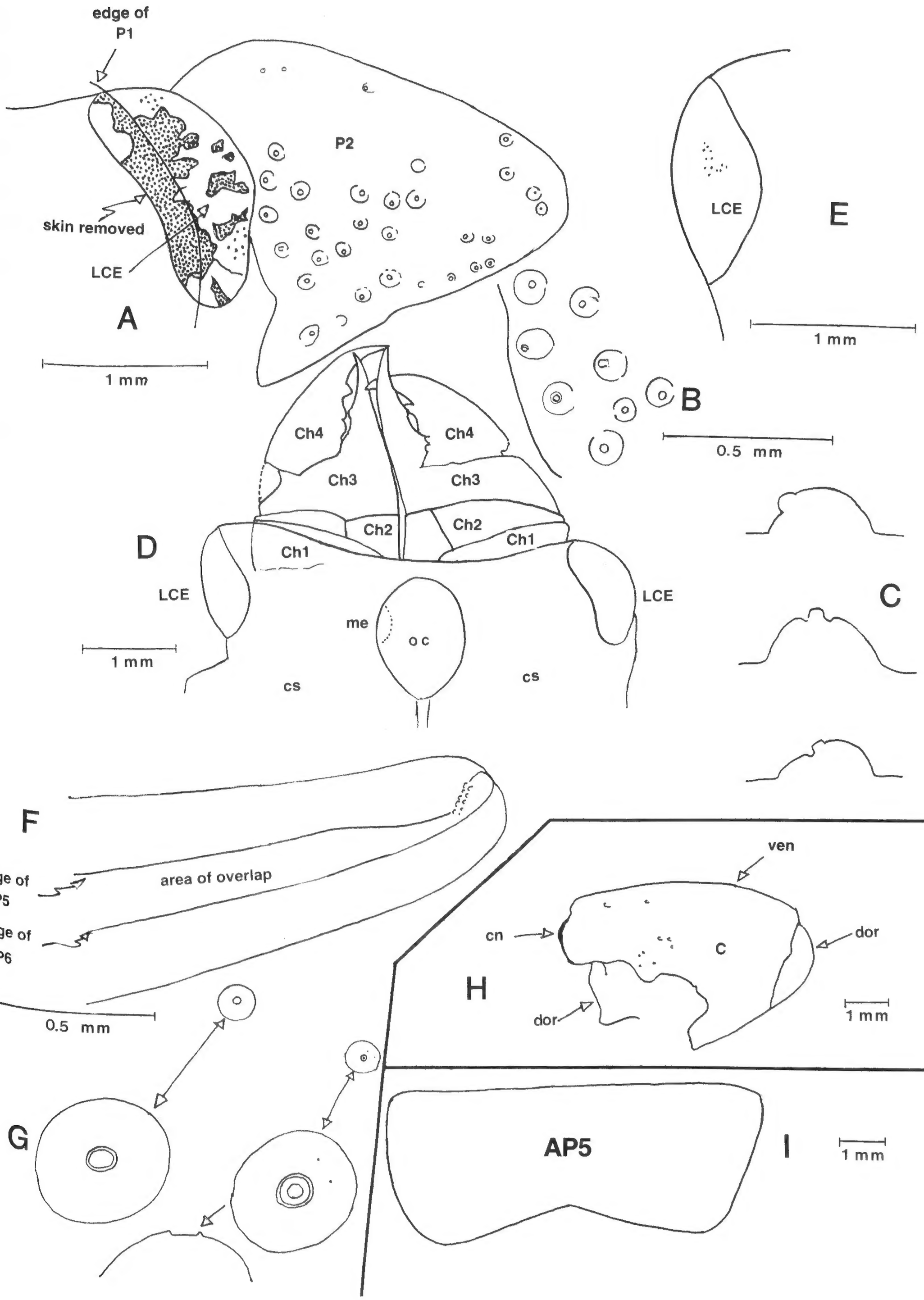
The papillae are also rounded in cross-section, but each has a stumplike protrusion and it is reasonable to assume that these are the bases of very coarse setae. These setae, in turn, occur in a rounded depression that is bordered by a very narrow rim, as in present-day trichobothria of scorpions. The trochanters, therefore, must have been particularly hirsute (see Text-figs. 60B–C, G).

Text-figure 60.—*Palaeophonus nuncius* Thorell and Lindström. Holotype (SRM Ar. 32235). From the Middle Silurian (lower Wenlock), Visby, Gotland, Sweden. See foldout inside front cover for explanation of abbreviations.

A. Right lateral compound eye. In stippled areas the cuticle is lost. **B.** Enlargement of a part of the pustulous area of the trochanter of the right pedipalp (**P2**). **C.** Cross-sections through pustules shown in figure B. No cuticle remains on the specimen. **D.** Details of the anterior carapace and chelicerae. **E.** Left eye. All the cuticle is peeled away, but evidence of some facets is left. **F.** Right pedipalp of holotype showing the scissorlike overlapping of the free and fixed dactyls. **G.** Pustules on left brachium (**P5**) of holotype pedipalp. Cuticle intact. Pustules are slight holes with slight lip.

H. A coxa from a topotype (SRM Ar. 32243).

I. Protolobate abdominal plate, 8.4 mm wide, from topotype (SRM Ar. 32242).


edge of P1
skin removed
LCE
A
1 mm
P2
B
0.5 mm
LCE
E
1 mm
Ch4
Ch4
Ch3
Ch3
Ch2
Ch2
Ch1
Ch1
D
LCE
1 mm
me
oc
cs
cs
LCE
C
F
edge of P5
edge of P6
area of overlap
0.5 mm
ven
cn
dor
C
H
dor
1 mm
G
AP5
I
1 mm

The femur of the pedipalp is short and stout and covered with setal sites in the form of coarse rounded papillae as described above for the trochanter, except that they are far less common.

The tibia also is short and stout and covered with sparse papillae.

As expected from the heavily-constructed femur and tibia, the chela of the pedipalp is large and stout also. The hand is large, rounded anteriorly and rather gently rounded posteriorly, but devoid of the coarse papillae except for small setal openings (see Text-fig. 59). The fixed finger is curved backward, the edge is cultrate and the end round. Small setal openings in the form of small round holes occur on the middle of the dorsal side. The free finger is incurving, to fit the recurving fixed one. The two dactyls in the holotype, however, are seen to have a scissorlike action, and overlap along the edge for a considerable depth (see Text-fig. 60F). At least two short rows of denticles occur at the distal end of the free finger (see Text-fig. 60F).

A free ramus (SRM Ar. 31818), or finger of the pedipalp was found on a small slab next to the telson of *Baltoeurypterus serratus* (Jones and Woodward). This finger measures 7.5 mm in total length, thus about the same size as the holotype (see Text-fig. 61K). It is curved inwardly; the inner edge is cultrate except at the posterior end, near the junction with the articulation with the fixed finger where a small area of small denticles occurs. There are no other denticles present on the entire edge (except as noted for the holotype) and, inasmuch as preservation was perfect, there should be no question of further denticles.

The midsection of the ramus, presumably the outer (anterior) part, has a row of small perforations, no doubt the sites for setae, and a very narrow ridgelike fold is present on the middle of the ramus, which likely was an inconspicuous carina.

The free finger (SRM Ar. 31818) shows interesting ornamentation in the form of a wide row of setal sites composed of small rounded openings. These setal sites are in no particular arrangement, except that they are in a wide row, about four to five perforations across. The holotype has these also on the fixed finger. In the holotype, the fixed finger has covered the free dactyl, thus masking the row of setal sites on the anterior side of the free finger (see Text-fig. 59).

The walking legs are spectacular in the sense that they were purported to represent very primitive legs, much like those found in some eurypterids. The comparison to the eurypterids is, however, superficial and in reality these are specialized legs, very likely for movement or attachment over hard surfaces such as rocks or reefs. Previous to this study the legs had been described as being tubular, or cylindrical, and this is correct. They are terete, ending in a sharp long spine, which is the posttarsus. Thorell and Lindström (1885) recognized that the coxae of the legs were covered by the carapace, but Petrunkevitch (1953) stated that the coxae were visible under alcohol, and therefore the entire leg was present. This resulted, according to Petrunkevitch, in a leg with five joints and the coxa. This would indeed be a great departure from all scorpions. But furthermore, the so-called coxae were arranged in a linear series at the edge of the carapace and this would have resulted in a sternum of colossal proportions. I do not doubt that the sternum of *Palaeophonus nuncius* was large, perhaps as large as that of the Scottish *Allopalaeophonus,* or even the German *Waeringoscorpio,* but these enormous sterni would be mere trifles compared to what was indicated by Petrunkevitch for *Palaeophonus.* In reality, there are no coxae exposed, either seen under alcohol or in the dry state. The first leg of the left side reveals only seven joints—the coxa being covered. The "coxa" shown by Petrunkevitch (1953, fig. 1) is the third joint (**I3**). In the other legs, the so-called coxae noted by Petrunkevitch are the second (**II2**) joint in the second leg, the first (**III1**) joint in the third leg, and the first (**IV1**) joint of the fourth leg (see Text-figs. 61A–D respectively). All legs therefore, have seven joints plus the coxa, and thus the implied gigantic sternum shrinks to a size comparable to those of early Paleozoic scorpions.

The terete legs increase in thickness progressively posteriorly, so that the last or fourth leg is considerably thicker than the previous. An entire coxa is shown from specimen SRM Ar. 32243, and this shows it formed half an ellipse (see Text-fig. 60H). If all the coxae were like this one, then they would radiate outward from the sternum as in *Proscorpius* and *Waeringoscorpio.* All legs have short joints, but the curious factor in these legs is that the tarsus is relatively long, longer than that of *Allopalaeophonus caledonicus* and certainly much longer than that of Recent forms.

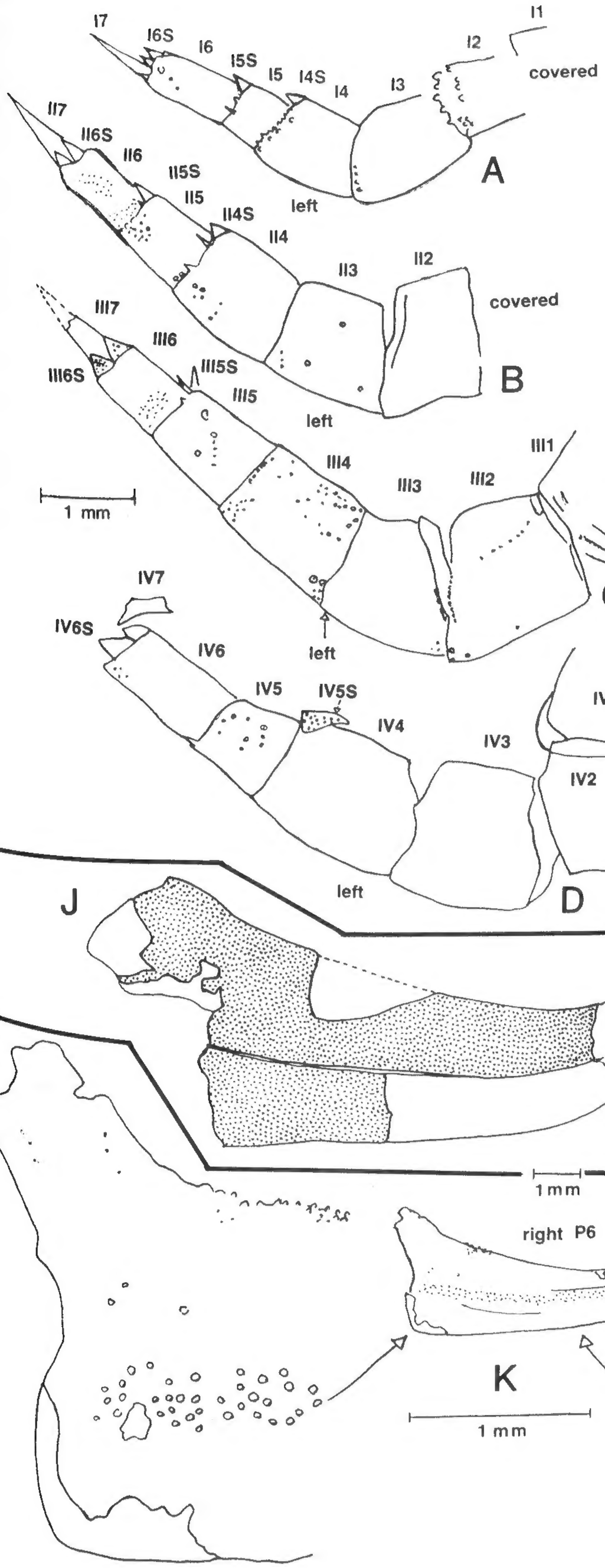
Although both Thorell and Lindström (1885) and Petrunkevitch (1953) showed one leg to have a single spur, all legs contain these movable spurs and are here described and figured in detail. The legs of *Palaeo-*

Text-figure 61.—*Palaeophonus nuncius* Thorell and Lindström. Holotype (SRM Ar. 32235). From the Middle Silurian (lower Wenlock), Visby, Gotland, Sweden. See foldout inside front cover for explanation of abbreviations.

A. First left leg (**I**). (See Text-fig. 61E.) **B.** Second left leg (**II**). (See Text-fig. 61F.) **C.** Third left leg (**III**). (See Text-fig. 61H.) **D.** Fourth left leg (**IV**). **E.** Terminus of first left leg (**I**). **F.** Terminus of second left leg (**II**). **G.** Terminus of third right leg (**III**). **H.** Terminus of third left leg (**III**). **I.** Terminus of fourth right leg (**IV**).

J. Fingers of the pedipalp; stippled area preserves original cuticle. From topotype (SRM Ar. 31591).

K. Free finger of the pedipalp, with enlargements of indicated areas for pustular detail. From topotype (SRM Ar. 31818).


I7
I6S
I6
I5S
I5
I4S
I4
I3
I2
I1
covered
A
left
II7
II6S
II6
II5S
II5
II4S
II4
II3
II2
covered
B
left
III7
III6
III6S
III5S
III5
III4
III3
III2
III1
covered
C
left
1 mm
IV7
IV6S
IV6
IV5
IV5S
IV4
IV3
IV2
IV1
left
D
J
1 mm
I7
I6S
I6
I4S
I5
E
left
II7
II6S
II6
II5S
II5
F
left
IIII7
IV5
IIII6S
sup
sp
IV4S
IIII6
G
right
III7
III6S
III6
III5S
III5
H
left
IV7
IV6S
IV6
IV5S
IV5
I
right
right P6
K
1 mm

phonus have the same basic plan as all scorpions have, namely, a long posttarsus with two well-developed tarsal spurs underneath, two basitarsal spurs, and two tibial spurs. All spurs of the tibia have not been seen on all legs, but it seems safe to assume that each had double spurs. The tarsal spurs may have a short supplementary spur. These tarsal spurs are short, stout, covered with setal openings, and the anterior one is larger than the posterior, as in many other Paleozoic scorpions. The large posttarsal spine is straight and tapering, but no spines, such as occur in *Allopaleophonus* on the ventral side, are present.

On the third leg of the right side, Petrunkevitch (1953, fig. 4) shows a peculiar terete object that he considers to be a new organ. This is merely the dorsal projection of the distal end of the tarsus, directly above the terminal spine. There are no triple, rounded objects at the end of this projection, and they are here dismissed as fictitious.

The four legs have very little ornamentation; most of it consists of very fine pustules or setal openings concentrated on certain local areas, which are shown on Text-figures 61A–I.

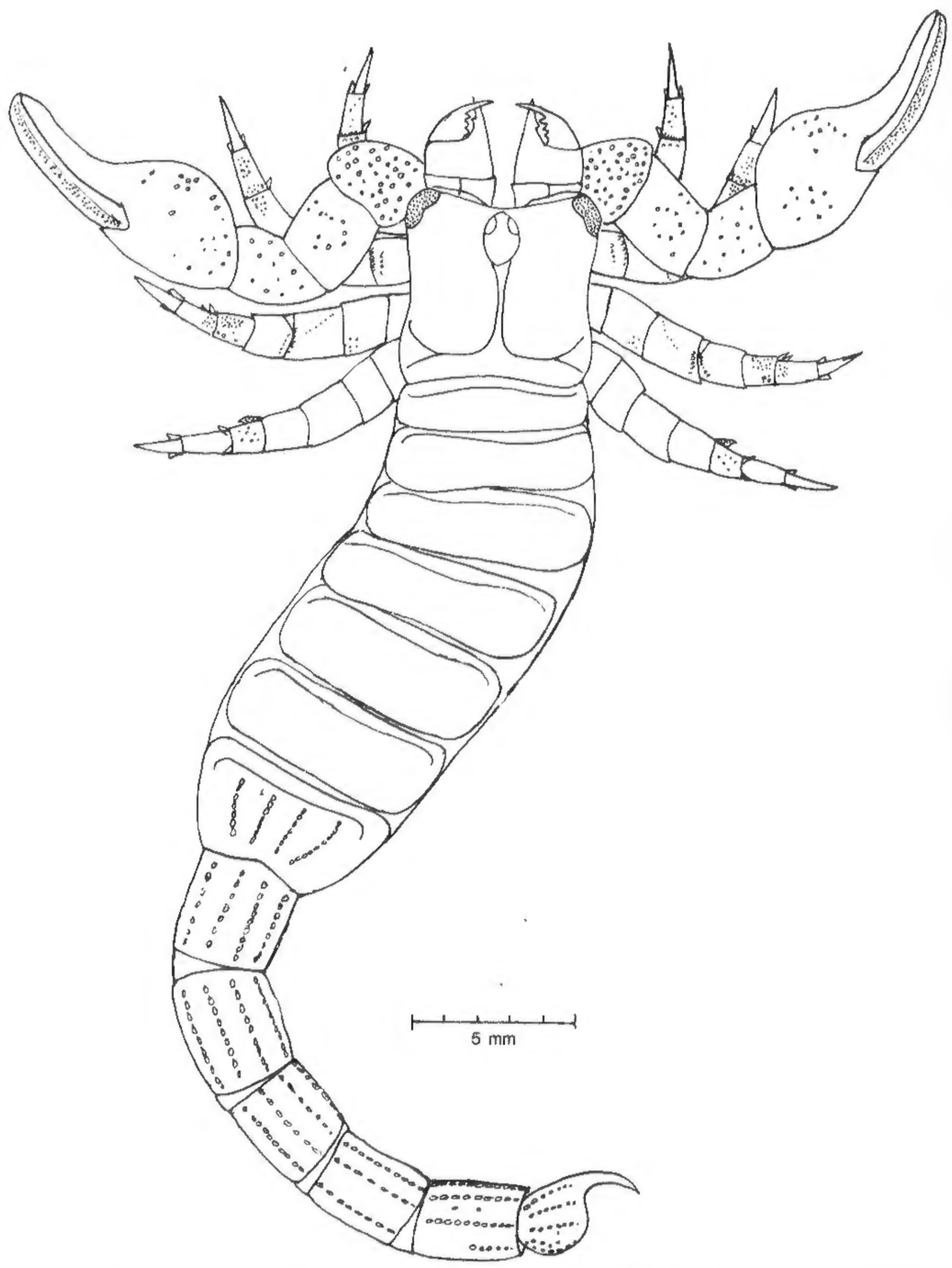
The sternum, opercular plates, and pectines were either covered or otherwise not preserved. Petrunkevitch (1953, fig. 1) reveals a small, double, scutiform object at the posterior part of one of the middle body segments, which he states may be the operculum. This is a large ostracode, with both valves open, which lies under the body segment. This condition, of ostracodes being found under and inside cast-off arthropod skins, is a very common occurrence in eurypterid specimens.

The first two tergites are mainly smooth, but with the usual narrow transverse ridge. The first is shorter than the second, indicating, as will be seen by the other tergites, that they progressively become longer posteriorly. A very large bivalve occurs midway between the two parts of the scorpion, where it has broken apart prior to burial. I am unable to determine whether the bivalve is a pelecypod or one of the large ostracodes that are common at the Vattenfallet locality. This bivalve has been indicated in the drawing (Text-fig. 59) and may be seen in the photograph (Pl. 9).

The fifth and sixth tergites are also mainly bald or without ornamentation, but with the transverse anterior ridge developed. They show the progressive lengthening mentioned above. The seventh tergite is triangular, with a large opening in the mid-area where the thick caudal segment fits. The anterior has a strong transverse ridge and is bordered by a narrow, flat area. There are definitely four carinae, each of which is surmounted by coarse, elongated pustules.

Of greatest interest, however, is the underside of the abdomen, which has been mistaken as to type, form, and consequently, function. The second, third and fourth abdominal plates are preserved; this shows definitely that the abdominal plates are protolobosternous (see Text-fig. 59). The plates are straight along the anterior, without any transverse ridge, and without appreciable doublures. The posterior is deeply incurving, in an inverted subtriangular form. *There are no stigmata and of course none should have been expected.* A single detached plate, perfectly preserved and previously undescribed (SRM Ar. 32242) verifies the above protolobosternous nature of the abdominal plates (see Text-fig. 60I). This is apparently the fifth abdominal plate, as it tapers posteriorly.

Thorell and Lindström (1885, p. 14, fig. 13) described what they considered to be a slitlike stigma. Petrunkevitch agreed, in 1949 (p. 86) and 1953 (p. 5). Pocock (1911) on the other hand, stated that there were no stigmata present, but this was based on his study of "*Palaeophonus*" (=*Allopaleophonus*) *caledonicus* (Hunter) from Scotland. There is a small, narrow indentation on one side of the third abdominal plate. However, this is only an indentation, possibly made



Text-figure 62.—*Palaeophonus nuncius* Thorell and Lindström. Reconstructed dorsal aspect, based on the holotype (SRM Ar. 32235) and SRM Ar. 31818. From the Middle Silurian (lower Wenlock), Visby, Gotland, Sweden.

by the edge of one side of a crinoid stem joint on the right side, and has no opening of any kind. As no protolobosternous or lobosternous plates have stigmata, it is superfluous to discuss the matter further. The reason it is mentioned here is the insistence of many that the possibility of stigmata existed, thus convenient evidence of the first land dweller.

The cauda is preserved in its entirety, and the description given by Thorell and Lindström (1885) is correct and not to be improved upon. I merely add that it appears as if the crests present are double superior, double laterals, and double inferior crests. The lateral crests on the last tergite become fainter but not obsolete. The stinger or telson also has well-developed pustulose carinae.

A fragment of the pedipalp of another specimen (SRM Ar. 31591), showing only the distal part, is recorded here because it reveals that *Palaeophonus nuncius* could be much larger than the holotype specimen indicated. The pedipalp (SRM Ar. 31591) is approximately twice as large as the holotype specimen, thus indicating that *P. nuncius* reached at least 125 mm in length (see Text-fig. 61J).

Type information.—The holotype and other specimens reported here are from the famous Vattenfallet section: Middle Silurian, Lower Wenlock, top of Högklintslager beds, at the Vattenfallet, Visby, Gotland, Sweden, associated with many eurypterids, and a typical marine fauna consisting of brachiopods, bryozoa, crinoids, ostracodes, etc. The eurypterids present belong in the deepest water or most marine eurypterid assemblage (No. 1 of Kjellesvig-Waering, 1961, pp. 793–794), which is known as the Mixopteroidea-Pterygotina Assemblage.

Remarks.—The holotype specimen has not suffered any appreciable deterioration, such as was reported by Petrunkevitch (1953, p. 5), at least not in areas where the internal molds cannot be used, as in each case, the imprint of the original cuticle is retained. As in the case with the famous Saaremaa eurypterids, the cuticle has a tendency to flake off, and all these specimens should be covered with a *thin* spray of a plastic fixative that will not obliterate any details, but will keep the original cuticle from being destroyed.[22]

There are three caudal segments in the collections of the Riksmuséet (SRM Ar. 32236, Ar. 32244, and Ar. 32067), all of which are excellently preserved, but do not add to the description above. One other fragment of integument is present (SRM Ar. 32270), but this does not add anything to the above description.

[22] Like nearly all paleontologists, I have an aversion to covering fossils with shellac, etc., but in the case of specimens retaining original cuticle, it is absolutely necessary, and a single pass with an aerosol spray to cover the fossil fully, but with a thin layer of fixative, will preserve the fossil indefinitely. This is the method used with irreplaceable oil paintings, some as fragile as any chitinous fossil. The holotype has now been preserved, but should it be necessary to remove the fixative, this can easily be done by using the particular solvent recommended; in this case enamel thinner. E. N. K.-W.

Palaeophonus (?) **lightbodyi** Kjellesvig-Waering, 1954

1859. *Eurypterus* ? possibly *pygmaea* Salter, p. 235, pl. 10, fig. 20.
1954. *Paleophonus lightbodyi* Kjellesvig-Waering, p. 485, fig. 1.

A single pedipalp chela from the Downtonian beds at Ludford Lane, Ludlow, Shropshire, registered under No. 89424 in the Geological Survey Museum, London, England. Its precise taxonomic position is uncertain.

Superfamily **ANTHRACOCHAERILOIDEA**, new superfamily

Lobosternina, but with very primitive abdominal plates that have barely advanced to the bilobate stage (protolobosternous); first two pairs of coxae in front of sternum, but only the second pair meets at midline; first pair has been squeezed away from the midline; last two pairs of coxae abut the sternum.

Type family.—Anthracochaerilidae, new family.

Remarks.—This superfamily is remarkable for the presence of a coxosternal arrangement which is very like that in living scorpions, associated with a very primitive group of legs that are distinctly tubiform, much like the legs of the Silurian genera *Proscorpius* and *Archaeophonus,* and the Devonian *Waeringoscorpio,* etc. The abdominal plates are also remarkable in being barely lobosternous, indicating the development of the lobosternous from the holosternous type (see Text-fig. 4F). The superfamily is therefore an interesting intermediate form, but still distinctly a Lobosternina. The superfamily Pseudobuthiscorpioidea has the same basic coxosternal arrangement, but with fully-developed lobosternous abdominal plates.

Family **ANTHRACOCHAERILIDAE**, new family

Anthracochaeriloidea with first pair of coxae spatulate and projecting beyond the maxillary lobes of the second pair. Sternum pentagonal. Pectines without fulcra, and with approximately 150 teeth on each comb.

Type genus.—*Anthracochaerilus,* n. gen.

Genus **ANTHRACOCHAERILUS**, new genus

Anthracochaerilidae with long, cylindrical walking legs.

Derivatio nominis.—*anthraco* (Gr.) = coal + *Chaerilus,* a living scorpion genus with greatly-inflated first pair of maxillary lobes.

Type species.—*Anthracochaerilus palustris,* n. gen., n. sp.

Geological range.—Lower Carboniferous.

Remarks.—As stated above for the superfamily, it is remarkable that so many advanced structures are found together with primitive tubiform legs reminiscent of much older scorpions.

Anthracochaerilus palustris, new species
Text-figures 63, 112L

1949. *Anthracoscorpio juvenis* Kušta (*partim*). Petrunkevitch, p. 144, figs. 137, 175.
1953. *Anthracoscorpio juvenis* Kušta. Petrunkevitch (*partim*), p. 30.

The holotype comprises a well-preserved scorpion of less than 18 mm in total length. A great part of the original cuticle is preserved, and where not present (indicated by stippled areas in Text-fig. 63A) the impressions of the edges of the structures are clearly discernible. Some original brown coloring has been preserved and in other parts the cuticle has been partly carbonized. Details of the structures are best seen under different angles and intensities of light, but, in particular, either under alcohol, wet with glycerine, or dry. The holotype specimen is a ventral impression with only small patches of the dorsal side of the mesosoma showing through windows. It is preserved in grayish-black shale.

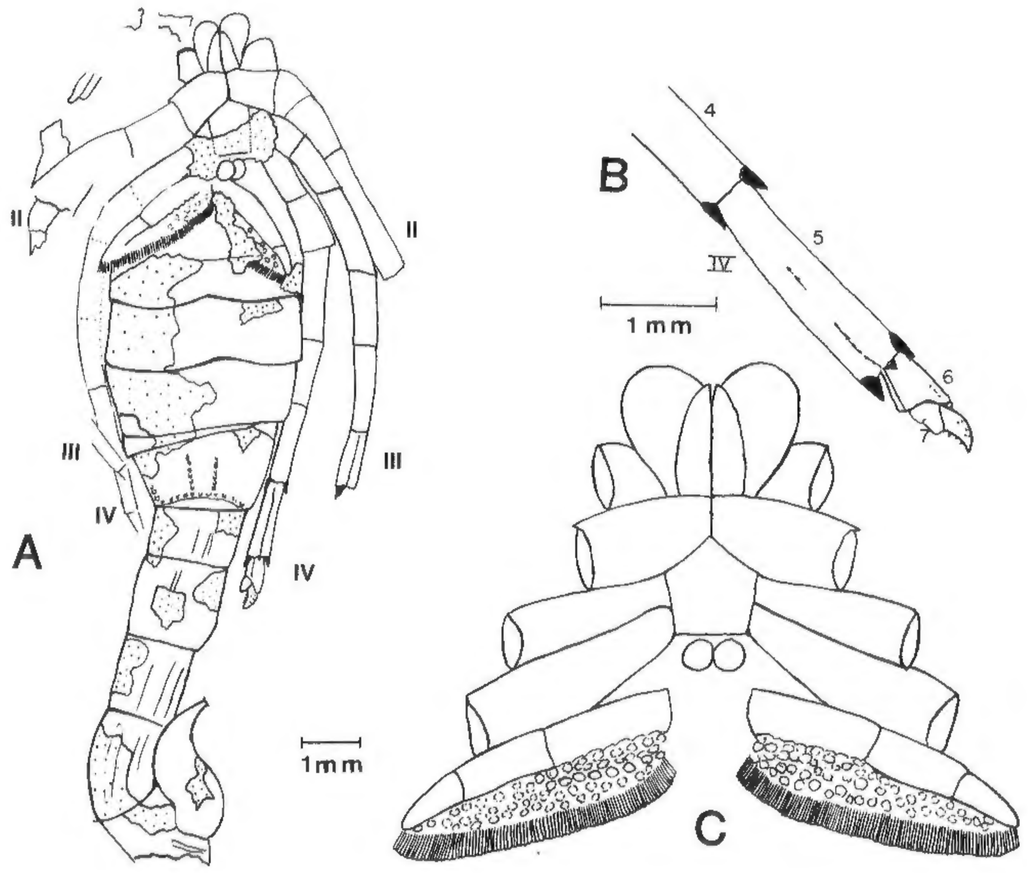
Only the anterior half of the sternum has been preserved, but there is an edge marked by cuticular material that indicates the base of the sternum, which is shown by a line on Text-figure 63A. A reconstruction of the sternum is therefore an easy matter. The sternum is long and pentagonal. The second pair of coxae meets at midsection, directly in front of the sternum, and has squeezed the first pair away from the midline. Maxillary lobes are well developed and extend to the anterior. The first pair extends partly above the second pair anteriorly and is enlarged or spatulate, in a manner that characterizes the living Chaerilidae and many fossil forms such as *Eoscorpius, Kronoscorpio,* etc. The third and fourth pairs of coxae abut the sternum (see Text-fig. 63C).

The legs are not entirely preserved, but at least the third and fourth walking legs are sufficiently well-preserved to reveal several details of taxonomic importance. The right fourth leg is preserved almost in its entirety, and is notable for being the type of cylindrical leg found in some of the Silurian scorpions such as *Proscorpius osborni* (Whitfield). The segments are therefore cylindrical and, for the most part, of the same length. Eight segments constitute the entire leg. The tarsus, unlike that in the Silurian scorpions, has been shortened and is less than half as long as the basitarsus. Well-developed tarsal and basitarsal spurs are present on each side of the corresponding segments. The claws are short, curved, and covered with small pits, very likely setaceous. The posttarsus is rounded and subtriangular, and acts as a heel (see Text-figs. 63A and B).

The opercular plates are relatively small and nearly round.

The pectines are of unusual interest and have more teeth than hitherto known in any scorpion. They are elongate structures which, in life, would project well beyond the limits of the body. The basal lamella is probably composed of three elongate joints. The intermediate lamella consists of small rounded sclerites, a surface that is described as perliform in scorpions such as *Brachistosternus* of the family Bothriuridae. Only a few of the rounded sclerites were seen, but it was noted that the first or basal segment of the basal lamella was scalloped on the inner edge in order to accommodate these sclerites. Fulcra are not present. The teeth are remarkable in being very regular in size, but extremely narrow and unusually numerous. Although the pectinal teeth were not complete, at least 135 were actually counted, and it is estimated that more than 150 were originally present. This is by far a greater count than present in any other scorpion. The teeth are so slender that they appear as hairlike striations at the posterior edge of the pectine. Fulcra, of course, could not be present, as it is doubtful that the sclerites could be broken into such small segments as to fit in between the bases of the teeth.

The abdominal plates are very well preserved, and



Text-figure 63.—*Anthracochaerilus palustris,* n. gen., n. sp. Holotype, BM(NH) In.39764. From the Lower Carboniferous (Lower Viséan), Calciferous Sandstone of the Glencartholm Volcanic Beds, River Esk, Glencartholm, Dumfriesshire, Scotland. See foldout inside front cover for explanation of abbreviations.

A. Ventral view. Cuticle missing in the stippled areas, but impression present. **B.** Fourth left leg, dorsal view. **C.** Restoration of the coxosternal area, also showing the pectinal combs. The pectinal plate has not been seen.

are of the protolobosternous type with a slight emargination at the center. Large rounded pouches, indicating large gill chambers, are noticeable on the abdominal plates, but these were insufficiently well-preserved for description. They are of the same type as noted in other Carboniferous scorpions.

The basal segment of the preabdomen (No. 7) is preserved from the ventral surface and shows a well-developed anterior transverse ridge and two crests on the middle of the plate, both of which are surmounted by large tubercles. Large tubercles are also present on the edges and along the base (see Text-fig. 63A).

The cauda, preserved in its entirety, is thick and has an unusually massive stinger. The first tergite is considerably shorter than the rest and all are marked with longitudinal ridges. It has not been possible to determine the number of crests or ridges present on the cauda.

The telson, or stinger, comprises a large vesicle with a strong stout aculeus. No ornamentation has been noted on the stinger.

Measurements (in mm) of the holotype (BM(NH) In.39764).—

	length	width
Comb:	2.1 (maximum)	0.8 (maximum)
Abdominal plate:		
3	1.0±	3.1 at middle
4	1.0	3.5
5	1.0	3.1
Tergite:		
7	1.4	2.3 at middle
8	0.8	1.5
9	1.2	1.4
10	1.2	1.1
11	1.5	1.1
12	?	?
Telson:	2.3 (incomplete)	1.0 (maximum)

Type information.—Lower Carboniferous, Calciferous Sandstone Series (lower Viséan), Upper Border Group, Glencartholm Volcanic Beds at River Esk, Glencartholm, Langholm, Dumfriesshire, Scotland. The holotype is registered as BM(NH) In.39764 in the British Museum (Natural History).

Derivatio nominis.—*palustris* (L.) = marshy.

Remarks.—Petrunkevitch (1949, p. 144) referred this specimen to the Bohemian *Anthracoscorpio juvenis* Kušta, an identification which is difficult to understand, inasmuch as the Bohemian specimen was thought to be preserved dorsally only, and the Scottish scorpion is a ventral impression. Equally difficult to understand is the description of the ventral side in the text when Petrunkevitch (fig. 137) illustrates only the dorsal surface and the pectines. It is not possible, as Petrunkevitch later stated (1953, p. 30), to compare either the presence of eyes in *Anthracoscorpio* or the lack of eyes in the Scottish specimen, as the carapace is fully covered by the opaque cuticle of the underside. Nothing is known of the dorsal side of this scorpion.

The same is true of *Anthracoscorpio juvenis* Kušta, an altogether different scorpion, belonging to a different infraorder, namely the Holosternina. Actually, only the ventral side of this species is known too (see Text-fig. 43A).

Superfamily **ISOBUTHOIDEA** Petrunkevitch, 1913 (emend.)

(*nom. transl.* Petrunkevitch, 1955, *ex* Isobuthidae Petrunkevitch, 1913)

Lobosternina; coxae of first and second pairs of legs meet in front of the sternum; both meet at the midline; the third pair of coxae abuts the sternum and the fourth pair abuts the genital opercula.

Type family.—Isobuthidae Petrunkevitch, 1913.

Remarks.—Frič (1904) established the genus *Isobuthus,* using *Cyclophthalmus kralupenis* Thorell and Lindström as type, and described the position of the coxae and sternum, although he did not use the coxosternal arrangement as a taxobasis in his classification. He also described the genus *Eobuthus* with *E. rakovnicensis* Frič as type species, and the genus *Feistmantelia* with *F. ornata* Frič as type species. These three genera were referred to Thorell and Lindström's "Series I"—Anthracoscorpii, 1885, which was considered a family, and included the genera *Cyclophthalmus* Corda, 1835, *Microlabis* Corda, 1839, *Eoscorpius* Meek and Worthen, 1868, *Mazonia* Meek and Worthen, 1868, and *Anthracoscorpio* Kušta, 1885.

Pocock (1911), using the "sternites" as a taxobasis, divided the known scorpions into two suborders, Lobosterni and Orthosterni. The genera *Isobuthus, Eobuthus* and *Feistmantelia* were referred to the Lobosterni, whereas *Eoscorpius* Meek and Worthen and *Mazonia* Meek and Worthen could not be classified as their ventral sides were then unknown.

Petrunkevitch (1913) established the family Isobuthidae on the basis of the fourth pair of coxae abutting the opercula, but ignored the structure of the "sternites". Thus the family Isobuthidae consisted of *Isobuthus* (a lobostern), *Palaeobuthus* (a meristostern) and *Eobuthus* (a lobostern). *Feistmantelia* was assigned questionably to the family Eoscorpiidae Scudder, 1884. The other genera (*Cyclophthalmus, Anthracoscorpio, Mazonia,* and *Microlabis*) were referred to other families or were undesignated as to family.

The 1913 treatment of the family Isobuthidae remained the same in Petrunkevitch's monograph of

1949. In 1953, however, Petrunkevitch (pp. 18–19) decided that the genus *Isobuthus* included the genera *Eobuthus* and *Feistmantelia,* having come to the conclusion that the shape of the sternum was not a reliable taxobasis (p. 19) as "I prefer to disregard completely the shape of the sternum in view of its relative unimportance and unreliability in the case of fossils". It is sufficient to dismiss that reasoning merely on the basis that preservation is not a taxobasis but a condition and has nothing to do with taxonomy. In the *Treatise on Invertebrate Paleontology* (1955), Petrunkevitch essentially followed this reasoning, but established the superfamily Isobuthoidea to include the family Isobuthidae Petrunkevitch, 1913, which included the genera *Isobuthus* Frič, 1904, *Microlabis* Corda, 1839, and *Palaeobuthus* Petrunkevitch, 1913. The main contribution was the establishment of the coxosternal arrangement as a superfamily taxobasis; the importance of the coxosternal arrangement had been recognized by Frič (1904) and Pocock (1911) in fossils.

This taxonomic scheme suffered because the coxosternal relationships of many genera were unknown, but it also suffered from the abandonment of the use of other important taxonomic structures as taxobases, and, as shown above, by the misinterpretation of the morphologies preserved. The superfamily Isobuthoidea Petrunkevitch, 1913, however, was correctly described and established, namely: two pairs of coxae in front of the sternum, the third pair abutting against the sternum and the fourth pair against the genital opercula, but totally disregarded the structure of the "sternites". At that time, the underside of *Eoscorpius* Meek and Worthen, 1868, was completely unknown. We now have firm knowledge of the coxosternal arrangement in *Eoscorpius.*

The coxosternal arrangement of *Eoscorpius* is of the same type as that which was defined for the superfamily Isobuthoidea, namely that the two pairs of coxae meet above the sternum, with the third pair against the sternum and the fourth pair abutting against the genital operculum. Actually, the coxosternal arrangement of *Isobuthus* (with *I. kralupensis* as type species), the type genus of the family Isobuthoidea, was somewhat incorrectly understood. I have studied the holotype of *Isobuthus* in Prague, and I find that I am able to add to what Frič had described in 1904. In that publication, Frič described the sternum as rhombic. Petrunkevitch interpreted it as being truncato-oval, considering the holotype of *Eobuthus rakovnicensis* Frič to be an *Isobuthus,* but the sternum has now been verified as being pentagonal. The first and second pairs of coxae occur anterior to the sternum; the third pair abuts the sternum and the fourth pair abuts the genital operculum. The first pair has narrow maxillary lobes, whereas the second pair of maxillary lobes was developed to about half the length of the first pair of lobes (see Text-fig. 64A). This in itself would considerably change the meaning of the family, but not that of the superfamily Isobuthoidea. Because the coxosternal region of the Eoscorpiidae Scudder, 1884, is now known, the family Eoscorpiidae should be emended. This results in the Eoscorpiidae not belonging to the superfamily Scorpionoidea Leach, 1815, but to the superfamily Isobuthoidea Petrunkevitch, 1913. The families Isobuthidae Petrunkevitch, 1913 and Eoscorpiidae Scudder, 1884, are therefore emended; the family Eobuthidae is described as new and the superfamily Isobuthoidea Petrunkevitch, 1913, remains practically the same, but it is restricted to lobosternous scorpions having a coxosternal arrangement as Petrunkevitch had defined it, but with the second maxillary lobes barely produced forward, or only to the middle of the first pair of coxae, which also meets at the midline.

Family **ISOBUTHIDAE** Petrunkevitch, 1913 (emend.)

Isobuthoidea with the first pair of maxillary lobes narrow, meeting anteriorly, and with the second pair of maxillary lobes extending only slightly beyond the middle of the first pair of maxillary lobes; sternum pentagonal, longer than wide.

Type genus.—*Isobuthus* Frič, 1904.

Remarks.—Petrunkevitch (1953, pp. 18, 19) considered the genus *Isobuthus* to be equivalent to *Eobuthus* and *Feistmantelia* and accordingly considered the latter two genera as junior synonyms. I cannot agree that this is the case. It is obvious that the genus *Eobuthus* has certain features that are present in *Isobuthus,* but these are only on the superfamily level. The shape of the first pair of maxillary lobes, which are spatulate, and the lacrimiform sternum of *Eobuthus* would not only require a different genus but a different family from that of *Isobuthus.* In this paper, therefore, the genus *Eobuthus* is considered to be a genus in good standing, and is designated the type genus of the family Eobuthidae, new family.

Regarding *Feistmantelia,* little is preserved of diagnostic value and, although the genus may be separated from *Eobuthus* and *Isobuthus* on the basis of the comb, it can only be referred to the Isobuthidae with considerable doubt. The great number of teeth on the very narrow type of pectines may be sufficient to consider this a good genus, although it might have been preferable to have referred the species questionably to one of the known genera in the first instance. Unfortunately it was not, but nothing is gained by further

guesswork in assigning it to the synonymy of any particular genus.

The family Eoscorpiidae Scudder, 1884, differs from all other families of the superfamily Isobuthoidea in the combination of a very short pentagonal sternum with greatly expanded maxillary lobes of the first pair of coxae and with the developed maxillary lobes of the second coxae extending slightly less than half the length of the lobes of the first pair of coxae (see Text-figs. 75A, B). The coxosternal arrangement of the new family Eobuthidae is similar except that the maxillary lobes of the second coxae are a little longer, and the sternum is suboval in shape.

The genus *Palaeobuthus* is placed in the new family Palaeobuthidae of the infraorder Meristosternina, not the Lobosternina, because the abdominal plates are meristosternous. In this new classification the genus *Isobuthus* may now be described as having a pentagonal sternum and a coxosternal arrangement that is fully known and thus the family Isobuthidae Petrunkevitch, 1913, is on a firm basis. As it is, because the maxillary lobes of the first and second pairs of coxae are known, it is possible to fit this well-known genus into a more properly described family. This ends the dilemma that was recognized by Pocock in 1911 when he used the genus *Eobuthus* extensively rather than *Isobuthus*. At the time, Pocock recognized that the coxosternal arrangement of *Isobuthus* was not well known and that of *Eobuthus* had already been rather well described by Frič. Petrunkevitch followed his own erroneous definition and interpretation of *Palaeobuthus* made in 1913, and continued to do so through his monographs of 1949, 1953 and 1955.

I agree with Petrunkevitch that no stigmata such as Frič shows for the Bohemian scorpions are present. As a matter of fact, important structures of the lobosternous "sternites" (abdominal plates), which were not noticed before, are the well-developed doublures. These are shown very well in *Eobuthus rakovnicensis* and *Isobuthus kralupensis*. On the other hand, the purported "lung slit" on *Cyclophthalmus senior,* which Petrunkevitch shows in text-figure 26 of his 1953 monograph, is the open end of the left coxa of the fourth leg. There are no stigmata on any of the Bohemian scorpions because all were lobosternous, meristosternous or holosternous, having abdominal plates, not sternites, and therefore did not have lungs.

Genus **ISOBUTHUS** Frič, 1904

Isobuthidae with long pectines armed with 30 teeth on a side; coxae of pedipalps small, not forming oral tube walls or extending beyond coxal maxillary lobes.

Type species.—*Cyclophthalmus kralupensis* Thorell and Lindström, 1885.

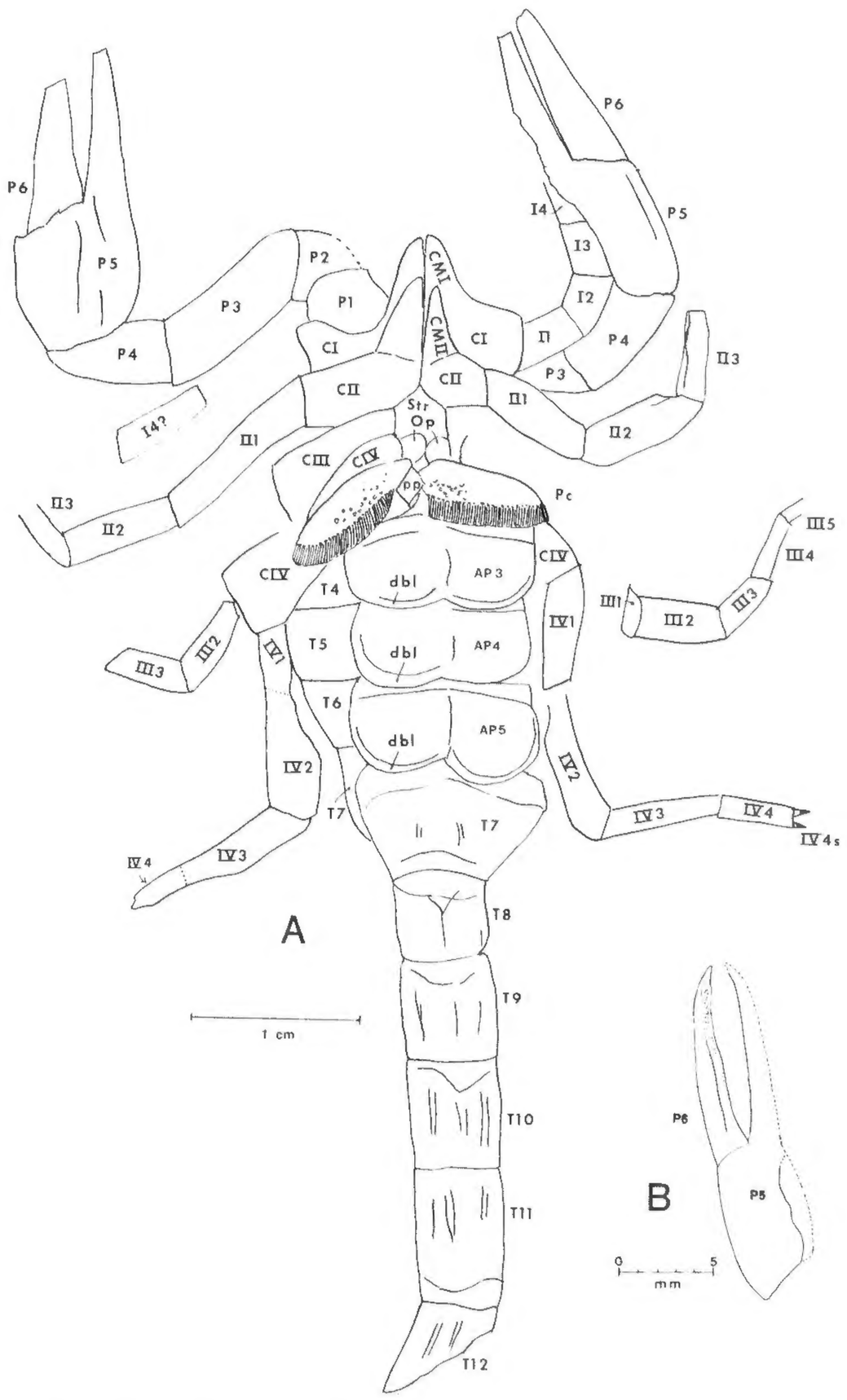
Geological range.—Carboniferous.

Remarks.[23]

Isobuthus kralupensis (Thorell and Lindström), 1885
Text-figures 64, 112D, 113C3

1873. *Cyclophthalmus senior* Corda. Frič (*partim*), p. 9, pl. 1, fig. 1, F.
1885. *Cyclophthalmus kralupensis* Thorell and Lindström, p. 17.
1904. *Isobuthus kralupensis* (Thorell and Lindström). Frič (*partim*), pp. 70–72, text-fig. 88A.

[23] The description of the genus was missing completely in Kjellesvig-Waering's manuscript, and there were only a few fragmentary notes on *I. kralupensis*. The drawings were found. A.S.C.



Text-figure 64.—*Isobuthus kralupensis* (Thorell and Lindström). Holotype (NMP Inv. 837). From the Upper Carboniferous (Westphalian B-C), Radnice Member of the "Lower Gray" Formation, Červená Hůrka hill in Kralupy, Czechoslovakia. See foldout inside front cover for explanation of abbreviations.

A. Ventral side, taken from a rubber cast. This is the equivalent of Frič, 1904, figure 88A. **B.** Obverse of holotype, showing terminus of pedipalp.

1911. *Isobuthus kralupensis* (Thorell and Lindström). Pocock, p. 16.
1913. *Isobuthus kralupensis* (Thorell and Lindström). Petrunkevitch, p. 33.
1944. *Isobuthus kralupensis* (Thorell and Lindström). Lehmann, p. 178.
1949. *Isobuthus kralupensis* (Thorell and Lindström). Petrunkevitch, pp. 136–137.
1953. *Isobuthus kralupensis* (Thorell and Lindström). Petrunkevitch, pp. 19–20, fig. 124.
1955. *Isobuthus kralupensis* (Thorell and Lindström). Petrunkevitch, p. 78, fig. 44(5).
1959. *Isobuthus kralupensis* (Thorell and Lindström). Wills, p. 266.
1962. *Isobuthus kralupensis* (Thorell and Lindström). Dubinin, p. 428, figs. 1228, 1243.

Type information.—Holotype, Steinberg collection 575, NMP Inv. 837A and B in the National Museum, Prague. The specimen, in shaly sandstone with plants, is preserved from the ventral side only, and was collected by Jos. Stiaska in 1868 from the Upper Carboniferous (Westphalian B-C) Radnice Member of the "Lower Gray" Formation at Červaná Hůrka hill in the city of Kralup, Czechoslovakia.

Frič's (1873, pl. 1, fig. F) illustration is quite correct, but his later line drawing (1904, text-fig. 88A), which was mainly taken from it, is not. Text-figure 64A is my interpretation of what is actually visible on the specimen. The lobosternous abdominal plates show a wide doublure on the margins but, of course, no sign of the stigmata which Frič so prominently showed.

The chela of the pedipalp is redrawn from the reverse of the holotype, as it is nearly perfect (see Text-fig. 64B).

A reconstruction of the coxosternal region is shown on Text-figure 112D.

Genus **BOREOSCORPIO**, new genus

Isobuthidae having chelicerae developed with only small, even-sized denticles on the edge; very long basitarsal spines on fourth legs; posttarsus short, small and subconical. Carapace with median groove, Y-shaped sulcus with cordated median eye node anteriorly located. Lateral eyes unknown.

Derivatio nominis.—*boreas* (L.) = northern + scorpion.

Type species.—*Boreoscorpio copelandi,* n. gen., n. sp.

Geological range.—Upper Carboniferous.

Remarks.—Differs from *Eoscorpius* Meek and Worthen in the lack of large teeth on the chelicerae, the different type of cutting edges on the chelicerae, consisting of the convex edge of the immovable finger and the concave movable finger, and in the presence of a very long basitarsal spine on the fourth leg. The carapace of *Boreoscorpio* has a median groove as in *Palaeobuthus* and not the elevated cephalic shield of *Eoscorpius.* The differences from *Paleobuthus* are readily apparent because the two genera belong to different superfamilies.

Boreoscorpio copelandi, new species
Text-figure 65

1957. *Eoscorpius* sp. Copeland, p. 51, pl. 15, figs. 4–5.

Holotype.—GSC 12778, part and counterpart, in the collection of the Geological Survey of Canada.

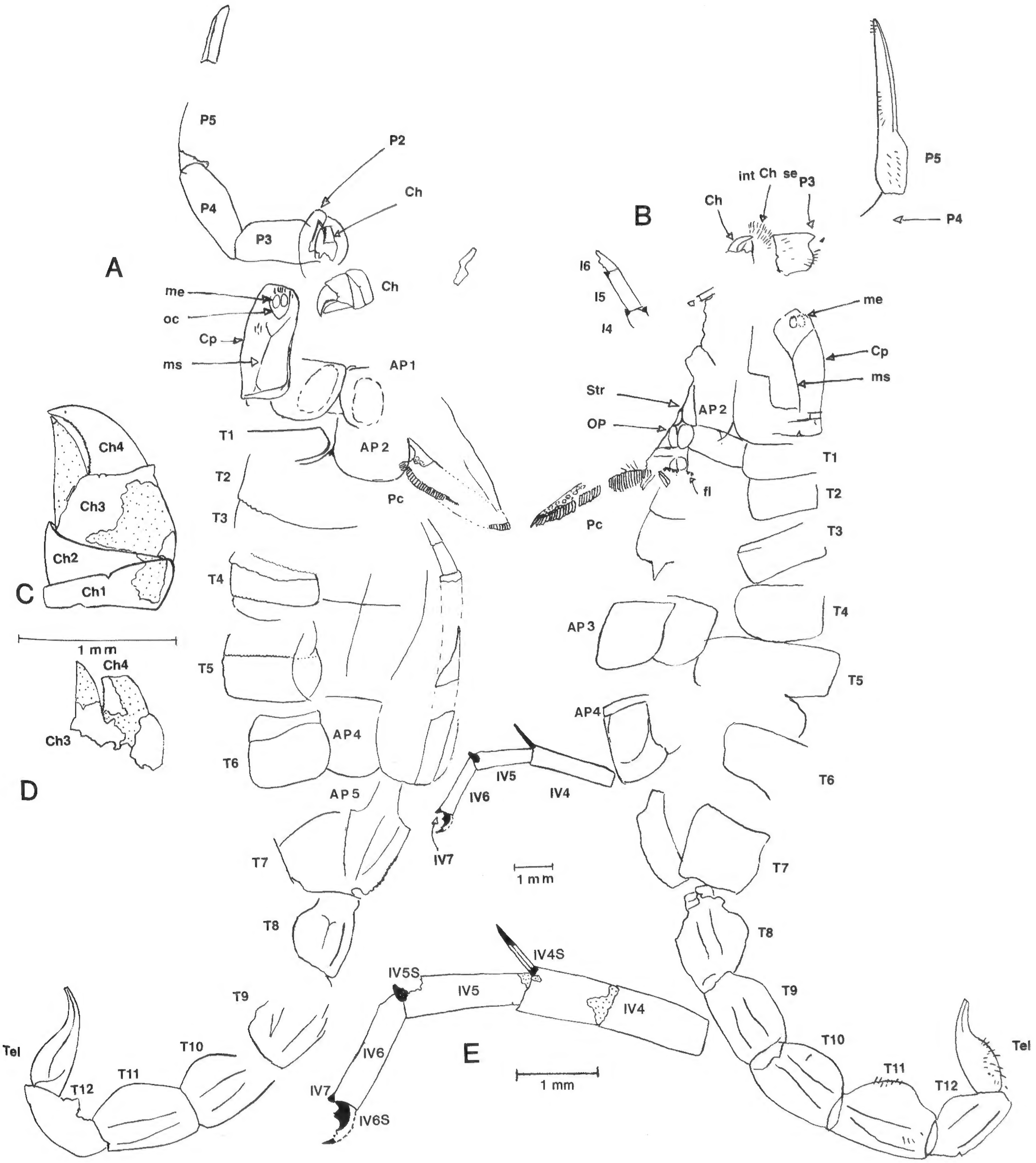
Preserved in hard, greenish-grey shale in two parts, both of which retain parts of the original cuticle as well as imprints of the cuticular exoskeleton. The scorpion is nearly complete, but is preserved on its side. Preservation of the cuticle that is left is good, but much has been lost and interpretation of all parts is not possible. Nevertheless, a considerable part of this scorpion is known and description is possible for much of the anatomy. In fact, most of the diagnostic parts are present.

The carapace is very poorly preserved as it has been squeezed from the lateral margins, but shows a longitudinal median groove that separates anteriorly into a Y-shaped sulcus. In the open end of the Y is a cordate eye node with large elliptical median eyes that likely were round in an uncompressed state. A marginal rim surrounds the basal margin and the posterior lateral margins. No other eyes were noted but it is highly doubtful that preservation was sufficiently good for any to be present.

Fragments of the appendages reveal several interesting details. The chelicerae (see Text-figs. 65C, D) were preserved entirely to reveal that, as in many other Paleozoic scorpions, they were composed of four joints. The first joint is bandlike, has a socket on the dorsal and ventral sides for the articulation of a condyle that occurs in the second joint, which also is bandlike. This gives considerable lateral movement to the chelicerae and is unlike that of present-day scorpions.

The third joint of the chelicera comprises the hand and immovable finger. The hand is nearly square, wider than long. The immovable finger is straight on the outer edge and curved convex along the cutting edge. Small denticles, all of even size, occur along the edge. A socket occurs for the articulation of the free finger. The latter is stout, hooklike, larger than the immovable finger and armed with numerous, small, even-sized teeth along the concave cutting edge. There is a complete absence of large teeth. The concave cutting edge of the movable finger fits exactly into the convex edge of the immovable finger.

The pedipalp of the right side is preserved nearly whole. The trochanter is poorly preserved, and only the edges on the anterior side are noted and these seem to be rounded. The femur is stout, about twice as long



Text-figure 65.—*Boreoscorpio copelandi,* n. gen., n. sp. Holotype (GSC 12778), part and counterpart. From the Upper Carboniferous, Pictou Group, presumably from the Stellarton Coalfield, Nova Scotia, Canada. See foldout inside front cover for explanation of abbreviations.

A, B. Part and counterpart. **C.** Right chelicera from the ventral side. Stippled areas lack cuticle, but the impressions remain. **D.** Left chelicera from the dorsal side; very fragmentary, but shows fixed ramus. **E.** Fourth leg.

as wide, and approximately as long as the tibia, which is also stout.The hand is elongated, rather rectangular in shape, and the immovable finger seems to be straight, very long and with a convex inner edge. No teeth are present on the cutting edge. The entire pedipalp is covered with numerous setae.

A fragment of what may be the first walking leg is preserved. This shows two basitarsal spurs and one tarsal spur, although very likely two tarsal spurs were originally present.

A leg, which has been interpreted as the fourth (see Text-figs. 65B, E), reveals a very long basitarsal spur and a wide, slightly serrated, triangular tarsal spur. It is assumed that single spurs would occur on the other side, giving two basitarsal and two tarsal spurs. The claws and posttarsal joint are well preserved. These show that the posttarsus is very small, short and conical. The two claws are hooklike and of uneven size. The shorter, which is preserved entirely, has two large, wide spines or serrations on the inner part of the ventral arc of the claw.

Little can be described of the coxosternal arrangement or the opercula. However, fragments present give some clues, even though the preservation is very poor. The sternum appears to be notched at the posterior edge and to have straight sides. This fragment would indicate that the sternum was pentagonal in shape, such as found in the Anthracochaerilidae. The opercula are oval, with the long axis aligned with the length of the scorpion. What appears to be the fourth coxa abuts against the opercula, thus restricting this scorpion to the Isobuthidae.

The combs are also fragmentary, but enough are present to note that they are very long, have numerous small, rounded areoles or sclerites, and well-developed triangular fulcra. Larger, rounded sclerites occur toward the inner part of the median lamella, recalling the inflated basal segment of some of the living scorpions (*e.g., Tityus melanostictus* Pocock), which denote the female. It is likely that this specimen is a female as the overall aspect of the opisthosoma is rather wide and stout. At least 50 teeth occur on each comb. The individual teeth are long, slender and rather tubular.

The tergites of the preabdomen are poorly preserved, but at least show the presence of a well-developed transverse anterior ridge on each one, and a progressive lengthening of each tergite from the anterior to the posterior. The seventh tergite apparently has two median crests and is bordered laterally by coarse serrations.

The abdominal plates are definitely of the lobosternous type, but very poorly preserved. They show the usual large, rounded pouches.

The cauda is very strongly constructed and apparently surmounted by two crests or carinae, at least on the first two tergites. The last three tergites seem to have two crests laterally, and the dorsal crests are highly arched. The telson or sting consists of a slightly curved aculeus with a rather elongate vesicle. No crests are present, but there are numerous setae on the ventral part. Setae are also present on the distal joints of the tergites. Apparently this scorpion was quite hirsute.

Measurements (in mm) of the holotype (GSC 12778).—

Estimated overall length:	30.0
Length of carapace:	3.3
Length of preabdomen:	12.8 (estimated)
Length of cauda:	13.8
Length of telson:	2.8

Type information.—Upper Carboniferous, Pictou Group. No label with specimen but assumed to have been collected from the Stellarton Coalfield, Nova Scotia, Canada, by W. A. Bell in the interval between 1912 and 1914 (Copeland, pers. commun., 1966).

Derivatio nominis.—The species has been named in honor of Dr. Murray Copeland.

Genus **FEISTMANTELIA** Frič, 1904 (emend.)

Isobuthidae (?) with long pectines, middle lamella with small, regular-sized areoles, well-developed fulcra and long teeth.

Type species.—*Feistmantelia ornata* Frič, 1904.

Geological range.—Permian.

Remarks.—See description of *F. ornata* Frič.

Feistmantelia ornata Frič, 1904
Text-figure 66

1904. *Feistmantelia ornata* Frič, p. 75, pl. 11, figs. 1–5.
1913. (?) *Eoscorpius ornatus* (Frič). Petrunkevitch, p. 35.
1953. *Isobuthus ornatus* (Frič). Petrunkevitch, pp. 21–22, fig. 13.

The figures given by Frič (1904, pl. 11, figs. 1–5) are essentially correct; those given by Petrunkevitch (1953, fig. 13) are incorrect as they show neither the correct shape nor the anterior transverse ridge. The tarsus and basitarsus are not divided as shown in Frič's original figure. The only two abdominal plates, both lobosternous, are shown in Text-figure 66. The smaller of the two is 14.8 mm wide, indicating a scorpion of about 90 mm in length. The genus probably should not have been described, but certainly there is little that could lead anyone to state that it is a junior synonym of *Isobuthus,* as was done by Petrunkevitch (1953, p. 19). It could just as well be referred in present-day classification to *Eoscorpius, Paraisobuthus, Waterstonia, Eobuthus* and others. All that can be stated is that it

definitely is a Lobosternina. Provisionally, it seems preferable to assign this species to the Isobuthidae.

The Frič drawing of the comb is correct, and this seems to be the only part that is diagnostic other than the two lobosternous abdominal plates.

Type information.—Preserved in dark gray shale from the Permian Kounov Member (=Kounov Beds) of the Upper Gray Formation (Stephanian B in age) from Studnoves, in the neighborhood of Slany, about 30 km northwest of Prague, Czechoslovakia. Collected by Karl Feistmantel and deposited in the National Museum at Prague where it is registered as NMP Inv. 828 (CGH 1981, CGH 1984).

Genus **BROMSGROVISCORPIO**, new genus

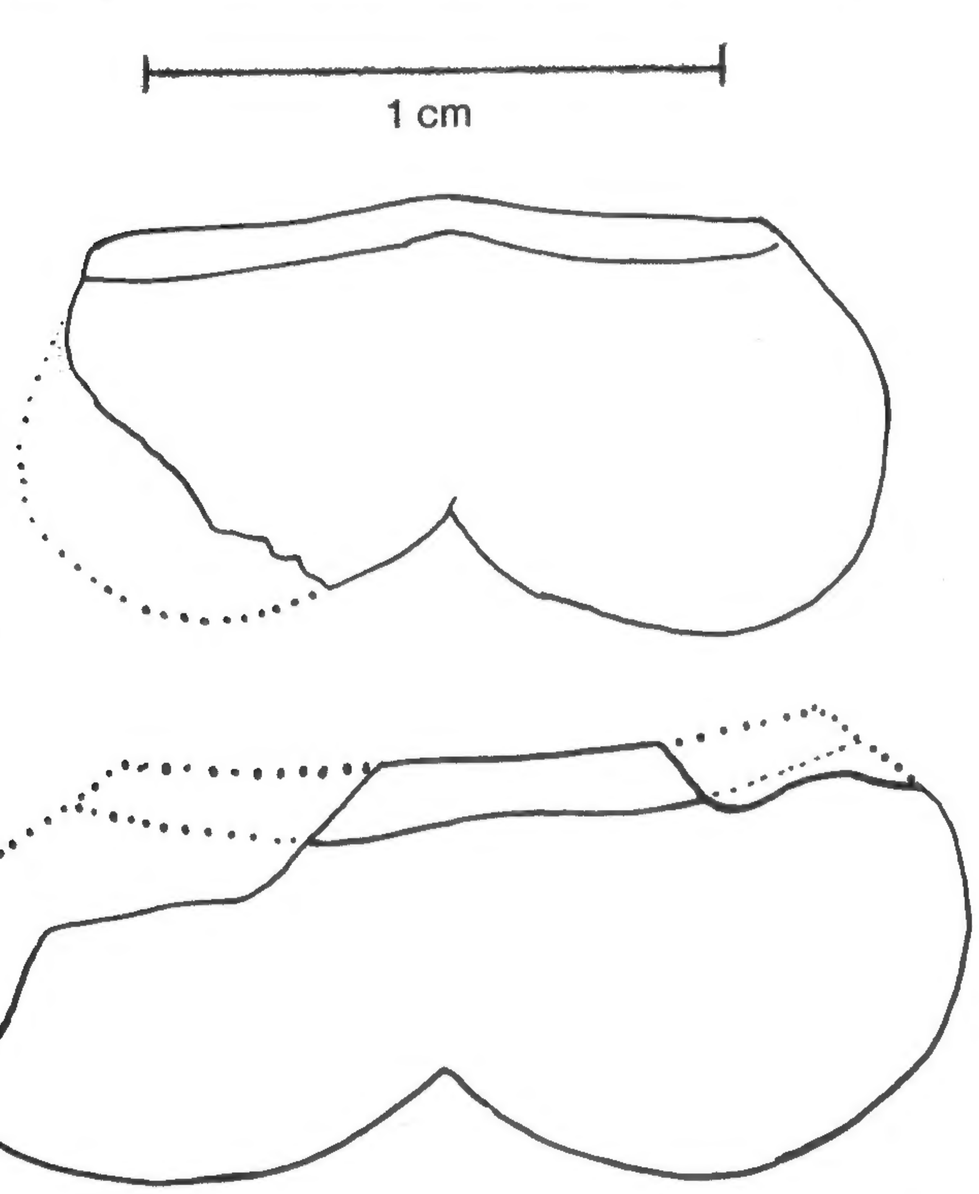
Isobuthidae (?) with large gill-chamber opening located at the junction of the abdominal plate and the doublure, and bordered by thick triangular denticles, inwardly directed. Gill lamellae without spinelets.

Derivatio nominis.—From the Bromsgrove Quarry near Birmingham, England.

Type species.—*Bromsgroviscorpio willsi,* n. gen., n. sp.

Geological range.—Triassic.

Remarks.—It is not at present possible to determine the family of the Lobosternina to which this genus should be assigned, and it is referred questionably to the Isobuthidae until more material is known. No abdominal plate of known Paleozoic species of the Lobosternina has thick spines like those that occur on the gill-chamber opening of this Triassic genus. The specimen is unique among the other Triassic scorpions, both in the gross morphology and the ornamentation. This abdominal plate cannot be referred to any Triassic scorpion and, although it represents only the left half of the first abdominal plate, it cannot be compared to the so-called lobation of the first plate in Wills' specimen 094 (1947, p. 33, text-fig. 13), which is much too poorly preserved. Furthermore, in my review I was unable to verify said lobation. There are no scorpions known in the fossil record in which a bilobate first plate is followed by holosternous abdominal plates.



Text-figure 66.—*Feistmantelia ornata* Frič. Holotype (NMP Inv. 828) (CGH 1981, CGH 1984). Two lobosternous abdominal plates. From the Permian (Stephanian B) Kounov Member of the Upper Gray Formation, from Studnoves, about 30 km northwest of Prague, Czechoslovakia.

Bromsgroviscorpio willsi, new species

1947. *Mesophonus bromsgroviensis* ? Wills, pp. 35, 39, 110, pl. VI, fig. 9; text-fig. 14.

The holotype (Wills, 1947, specimen No. 0163) comprises almost the entire left half of the first abdominal plate. I would not usually describe a new species on the basis of an abdominal plate, but in this case it is necessary because of the unique importance of the specimen. It is not only the only evidence of a lobosternous scorpion in the British Triassic, but at the same time it is the last known straggler of a major division of the Scorpionida, namely the infraorder Lobosternina, which was one of the dominant scorpionid groups in the Paleozoic.

The specimen has been figured by Wills (1947, pl. VI, fig. 9, and text-fig. 14) and will not need to be figured again, as his text-figure 14 is completely accurate and the photograph adequate. The specimen reveals a wide gill slit at the central part of the lobe between the edge of the abdominal plate and the doublure. The gill slit occupies fully half of the posterior margin of the lobe and is bordered by very large triangular denticles. The gill appears to be composed of a single, very wide lamina. There are no spines developed on the gill. For description of the ornamentation see Wills (1947, p. 39, text-fig. 14).

Type information.—A single specimen from the Triassic Lower Keuper Rocks at the Quarry in Bromsgrove, Birmingham area, England. Wills No. 0163 is designated as the holotype and is deposited in the Sedgwick Museum, Cambridge University.

Derivatio nominis.—This species is named because of the perfect preservation, making it easily recognizable again and therefore requiring a name, which has been given in honor of Dr. Wills' great work.

Remarks.—Although the holotype is compared to

Willsiscorpio bromsgroviensis (Wills, 1947, p. 39), the differences are much too great, apart from the lobation. The coarse ornamentation along the anterior ridge is a feature that differs not only from *W. bromsgroviensis* but from all other known Triassic scorpions.

Family **EOBUTHIDAE**, new family

Isobuthoidea with pyriform sternum, and with greatly anteriorly-expanded or spatulate maxillary lobes of the first pair of coxae. Opercular plates not separated, remain as a very small lobostern plate. Facetted lateral eyes present.

Type genus.—*Eobuthus* Frič, 1904.

Remarks.—As stated in the discussion of the superfamily Isobuthoidea, the genus *Eobuthus* was extensively used by various authors until it was erroneously suppressed by Petrunkevitch in 1953, who referred it to the synonymy of *Isobuthus*. The shape of the sternum and the different maxillary lobes of the first pair of coxae are in each case sufficient to form not only a separate genus but also a family. It differs from the Eoscorpiidae in the shape of the sternum.

The presence of a bilobed, but not separated, opercular plate (plates) is of particular interest as it is almost an exact copy of succeeding lobostern abdominal plates.

The differences between the Isobuthidae, Eobuthidae and Eoscorpionidae are tabulated as follows:

Isobuthidae	Eobuthidae	Eoscorpiidae
sternum longer than wide	sternum pyriform	sternum wider than long
second maxillary lobes extend anteriorly to more than half the length of the first coxae	second maxillary lobes extend anteriorly to half the length of the first coxae	second maxillary lobes extend anteriorly to less than half the length of the first coxae
first pair of maxillary lobes long and narrow	first pair of maxillary lobes spatulate	first pair of maxillary lobes spatulate
coxae of pedipalp small, do not form oral tube walls and do not extend beyond maxillary lobes	coxae of pedipalp large, form walls of oral tube and extend beyond coxal maxillary lobes	coxae of pedipalp large, hooklike, form walls of large chamber in front of the mouth and extend past the coxal maxillary lobes

Genus **EOBUTHUS** Frič, 1904

The characters of the genus have been discussed under the family Eobuthidae.

Type species.—*Eobuthus rakovnicensis* Frič, 1904.

Geological range.—Upper Carboniferous.

Eobuthus rakovnicensis Frič, 1904
(new description)
Text-figures 67, 112C

1904. *Eobuthus rakovnicensis* Frič (*partim*), pp. 72–75, pl. 8, figs. 1–2; text-figs. 90, 92.
1911. *Eobuthus rakovnicensis* Frič. Pocock, p. 13.
1923. *Eobuthus rakovnicensis* Frič. Moore, p. 132, pl. 1, figs. 1, 2.
1949. *Eobuthus rakovnicensis* Frič. Petrunkevitch, p. 137.
1953. *Isobuthus rakovnicensis* (Frič). Petrunkevitch (*partim*), pp. 18, 20–21, figs. 18, 134.

Not Eobuthus rakovnicensis Frič (*partim*), 1904, p. 74, fig. 91; Petrunkevitch, 1953, p. 21, figs. 19, 123; Petrunkevitch, 1955, p. 78, fig. 46 (all refer to BM(NH) I.2950 = *Paraisobuthus prantli*, n. gen., n. sp.).

Specimen.—The holotype, Inv. 822 in the National Museum, Prague, consists of one specimen preserved from the ventral side in white, hard, kaolinitic volcanic tuff which contains quartz of magmatic origin, and associated with plants.

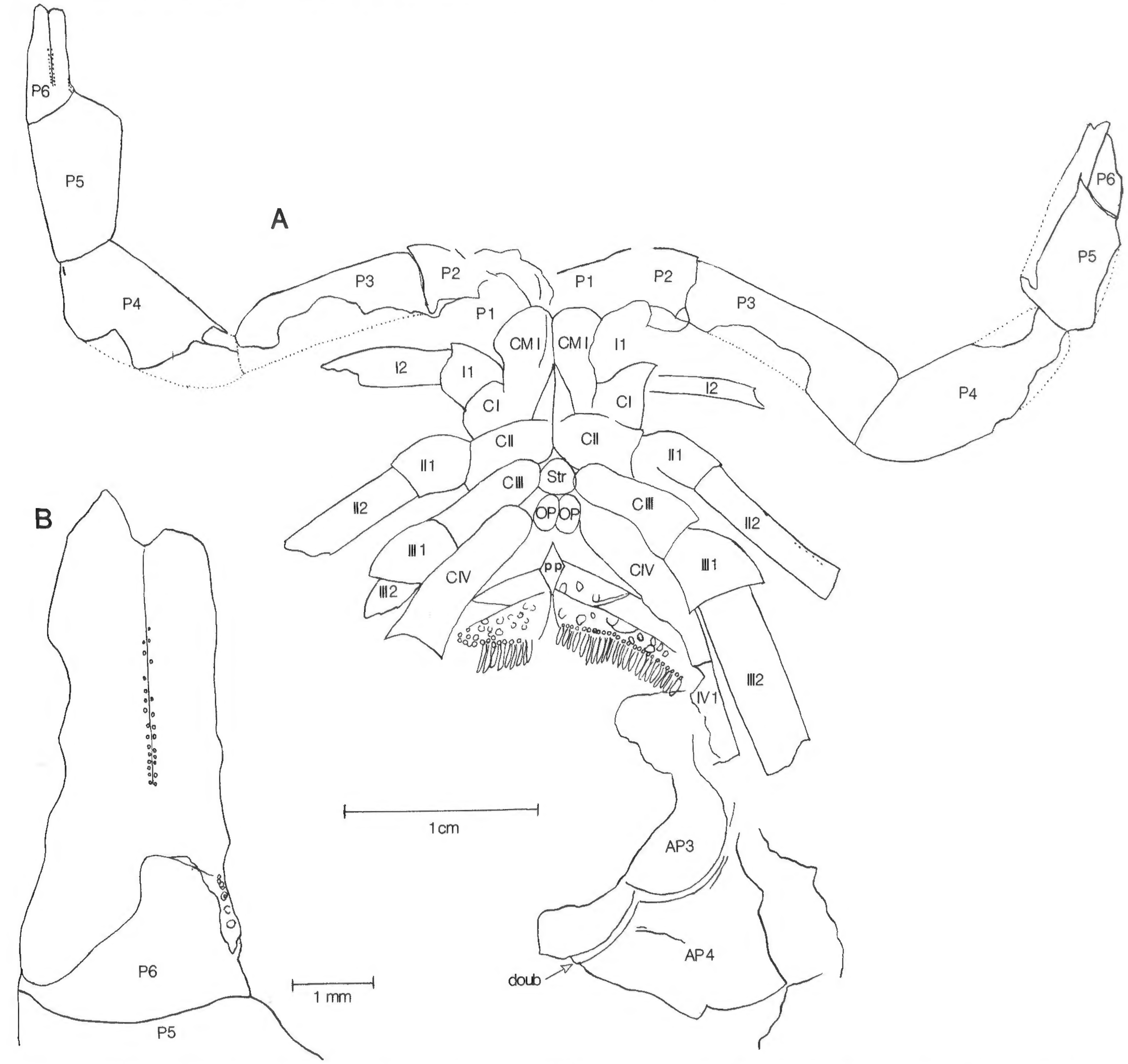
The coxosternal region is perfectly revealed. The sternum is suboval, small, rounded anteriorly and rather truncated, but still rounded at the posterior where it meets two elongate, elliptical, genital opercular plates. The first pair of coxae is large, with well-developed, spatulate maxillary lobes that meet at midsection on the anterior half. Petrunkevitch (1953, pl. 7, fig. 18) apparently mistook these large spatulate lobes for the base of the pedipalps, but this is erroneous as can be shown by many other fossil scorpions (*Eoscorpius, Waterstonia, Anthracochaerilus*) and even in Recent scorpions (*Chaerilus*). He shows these coxae as narrow prolongations. There is a line, marking a fold, on the left side, which undoubtedly led to the wrong conclusion. It is not present on the right side. The second pair of coxae also has maxillary lobes and, although these meet at midsection, they only extend half the length of the first pair of maxillary lobes. The third pair of coxae abuts the ovoid sternum and the fourth abuts the opercular plates. The coxosternal arrangement is therefore typical of the superfamily Isobuthoidea.

Posterior to the opercular plates is a diamond-shaped organ that separates the two large combs. This is apparently the pectinal plate seen in *Branchioscorpio, Gigantoscorpio* and others, but preservation does not permit further description. The combs are large and have small, rounded areoles developed on the rachis, but I was not able to make out the exact divisions of the anterior lamella. Obviously the entire structure is elongated. Fulcra are developed and the teeth are large and elongate. At least 25 teeth occur and it is estimated that no more than 30 occur.

The normal lobosternous abdominal plates are poorly preserved; possibly the third and fourth are present.

A distinct doublure is noted, bordering the posterior part of each abdominal plate.

The appendages are preserved in fragments and other than to indicate the presence of the trochanters and stubs of the femurs, little may be said. The pedipalps are large, stout structures and, although poorly preserved, it was noticed that a ridge occurs at least on the ventral side of the free finger, which has a double row of small granules, alternating, but not in a very uniform pattern, such as noted in *Eoscorpius carbonarius* Meek and Worthen, where a somewhat similar row of setal openings occurs. No setal openings were noted in *Eobuthus rakovnicensis,* only granules. The edge of the free finger shows denticles at the base, but it is not known if these continue on the cultrate edge. The trochanters in particular are devoid of any granules or setal openings and this seems to be the case with the rest of the pedipalps.



Text-figure 67.—*Eobuthus rakovnicensis* Frič. Holotype (NMP Inv. 822). From the Upper Carboniferous (Westphalian B-C), Radnice Member, Radnice Group, in a hard kaolinic volcanic tuff containing plants, Rakovnik, Czechoslovakia. See foldout inside front cover for explanation of abbreviations.

A. Ventral aspect. **B.** Detail of the right pedipalp free finger.

Type information.—Holotype is from the Upper Carboniferous (Westphalian B-C) Radnice Member, Radnice Group, in a hard kaolinitic volcanic tuff containing plants, Rakovnik, Czechoslovakia. Holotype, NMP Inv. 822.

Eobuthus cordai, new species
Text-figure 68

1873. *Cyclophthalmus senior* Corda. Frič (*partim*), pl. 1, fig. 1.
1904. *Isobuthus kralupensis* (Thorell and Lindström). Frič (*partim*), pl. 10, figs. 1, 2, 7, 10, 11; text-fig. 88B.
1953. *Isobuthus kralupensis* (Thorell and Lindström). Petrunkevitch (*partim*), p. 20, fig. 20.

I have great difficulty in identifying some of the figures in Frič's 1904 paper with the specimens. However, this species is adequately founded on several specimens, which I studied in Prague. The holotype (Text-fig. 68A), registered as NMP Inv. 838, comprises a carapace, pectine, seventh tergite, abdominal plate, leg joint and cauda. Another specimen also referred to this species is NMP Inv. 834, considered a paratype, which comprises a well-preserved chelicera and two nearly complete legs (see Text-figs. 68B–E). The longitudinal ribbing of the leg joint in NMP Inv. 838 fortunately furnished the identification for specimen NMP Inv. 834. This species is the only Czechoslovakian fossil scorpion so far known with longitudinal ribs on the legs.

The holotype (NMP Inv. 838) reveals an almost complete carapace, which is squarish, slightly compressed at the midlateral margins, and bowed in front into a short, glossate, median process (see Text-fig. 68A). The facetted lateral eyes are well preserved; indeed, these facets led Frič to assume that this specimen had three lateral eyes (1904, pl. 10, fig. 1 and text-fig. 88B), which error was perpetuated by Petrunkevitch (1953, fig. 20) whose drawing of the carapace was mistakenly truncated at a point slightly behind midsection.

The facetted lateral eye is preserved so as to show clearly the outline or marginal line of the anterior of the eye, enclosing several well-defined facets. Although less than half of the eye is preserved, an estimated 25 facets may not be far from the number present. Therefore, these are coarse facets, not greatly unlike those of *Eoscorpius carbonarius* Meek and Worthen.

The median eyes are large, round, with well-developed orbital ridges, located on a lacrimiform eye node that lies in the middle of the anterior half of the carapace.

A semicircular ridge of coarse tubercles is present in the middle of the carapace on each side of the posterior end of the eye node. The basal margin of the carapace is mainly straight.

The pedipalp chela is preserved lying next to the carapace. The hand is narrow with two cultrate, falcate fingers, and with a ridge or carina running throughout the length of each finger. Both carinae are surmounted with coarse pustules. The bending inward or falcation of the fingers is of particular diagnostic value.

Parts of the pectinal plate are preserved, enough to show that fulcra are present and the teeth are very numerous and of the long slender type. Thirty-six teeth are preserved, but this number is not complete as all were not preserved. Therefore, as in several other Czechoslovakian forms, such as *Cyclophthalmus,* each comb probably had about 50 teeth.

A lobosternous plate, medially deeply-cleft, with very wide doublures is present, lying on top of the seventh tergite. The seventh tergite is important for diagnostic, generic and specific determination; it is tapering and probably preserved from the ventral side, where it reveals four prominent rows of tubercles.

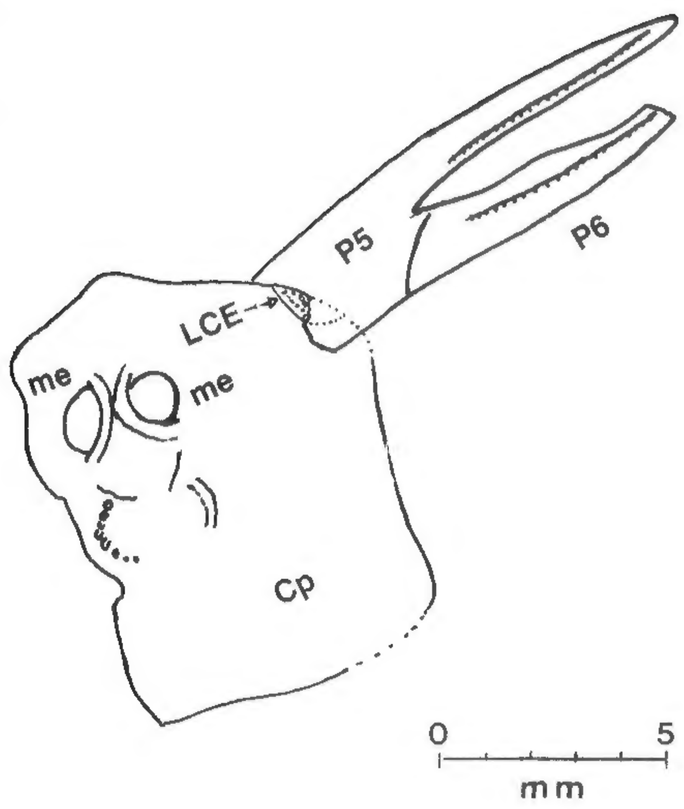
The cauda is preserved on the lateral side, including the segments from the eighth tergite to the telson. The entire cauda is thick, has at least a lateral keel (preserved on the eleventh tergite), and the telson has a very large vesicle, rounded, and the aculeus seems to be only slightly curved, if at all. This specimen is very likely a female.

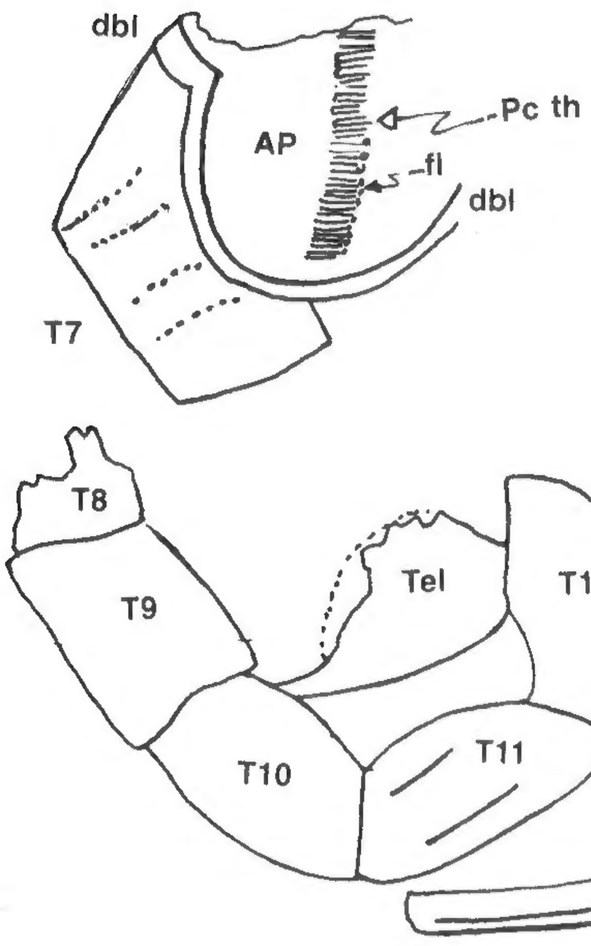
Specimen NMP Inv. 834, a paratype, adds to our knowledge as it shows the chelicera and parts of two legs, identified as the third and fourth (see Text-figs. 68B–E).

The chelicera shows all four joints. The first joint is seen only as fragments with a dorsal flange. This chelicera, therefore, is from the left side. The bandlike second joint is nearly complete. The third joint has a relatively narrow hand with a fixed ramus showing several large denticles; the terminal is falcate and fits between the two terminal teeth of the free finger. The free finger is also armed with denticles, but the characteristics can be shown to better advantage by reference to Text-figure 68B.

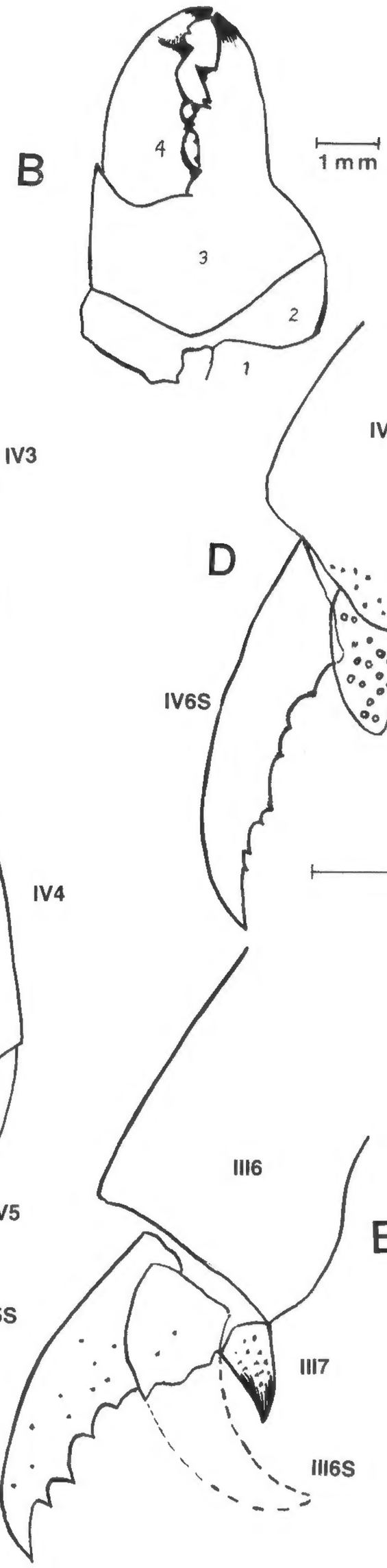
The third and fourth legs are noteworthy for their good preservation. The third leg is preserved from the tibia to the distal end, showing that each joint was long and was reinforced by a narrow keel, at least the tibia was. The tibia has one spur, but very likely two were developed. The basitarsal joint has a flat, obtuse spine in the posterior, and one short spine in front. The wide flat spine was setaceous. The ungues or tarsal spurs are large, falcate, and with traction spines on the underside (see Text-figs. 68C, E). The posttarsus is very short, setaceous and triangular in shape, but inwardly curved.

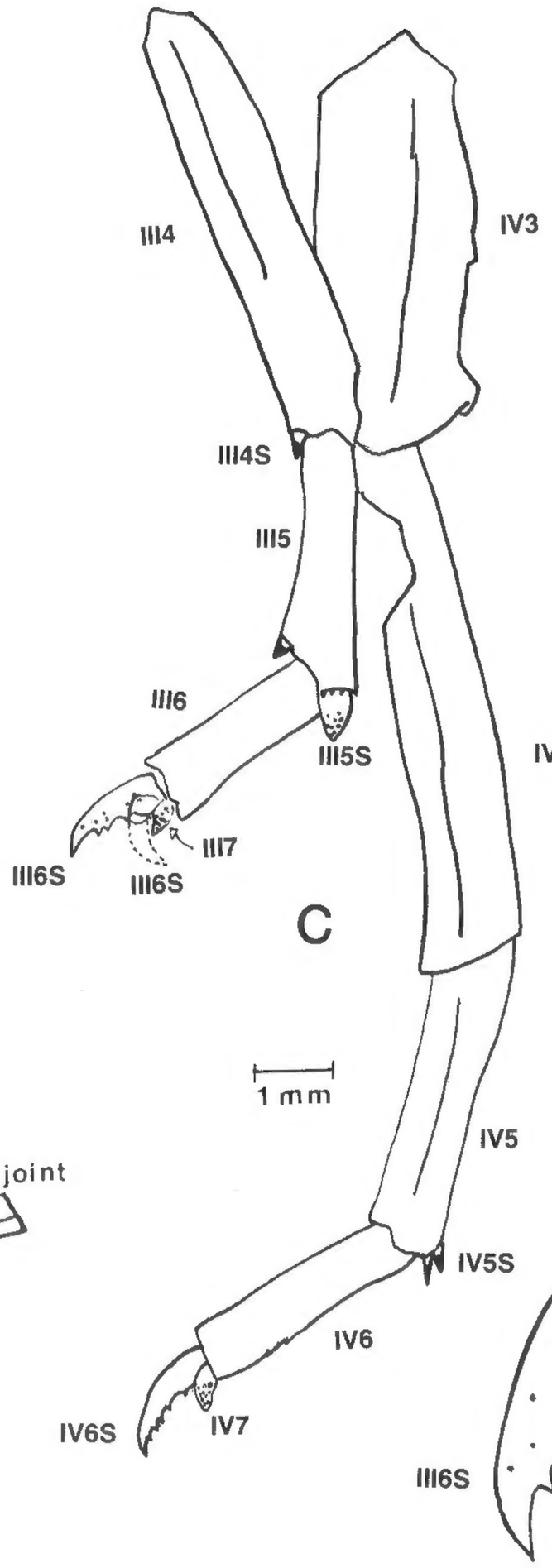
The fourth leg also has longitudinal keels on the femur, tibia, and basitarsus. The tibia does not reveal any spurs or spines, but this may be due to preservation

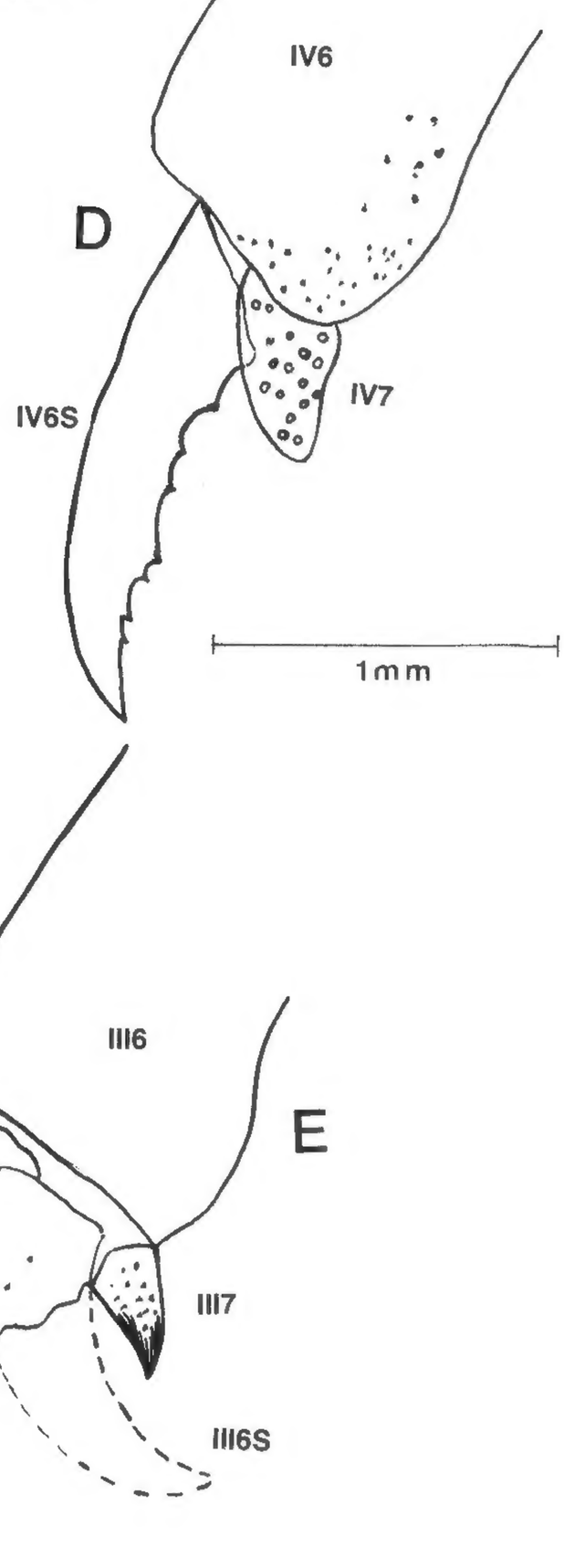




A







Text-figure 68.—*Eobuthus cordai,* n. sp. Holotype (NMP Inv. 838); paratype (NMP Inv. 834). From the Upper Carboniferous (Westphalian B-C), Radnice Member of the Lower Gray Formation, Kralupy Hill, Červená Hůrka, Czechoslovakia. See foldout inside front cover for explanation of abbreviations.

A. Holotype. The specimen is a slab with the dissociated fragments of one animal. Above, prosomal shield with enormous pedipalp claw. Middle, seventh tergite (±) and part of the anteriorly adjacent segment revealing the abdominal plate (**AP**) and part of a pectine. Bottom, distal postabdomen and dissociated prosomal leg joint. **B.** Paratype. Chelicera, showing the prominent serration of the dactyls. **C.** Paratype. Third and fourth legs. **D.** Paratype. Tarsus, posttarsus and unguis of the fourth leg. **E.** Paratype. Third leg tarsus, posttarsus and ungues.

(see Text-fig. 68C). The basitarsus has small spurs at the posterior distal end in the form of short, pointed spines. The tarsus is long with slight serrations on the posterior edge, and has large ungues with ventral traction spines. The posttarsus is quite large, and undoubtedly was heavily setaceous, as numerous setal openings occur (see Text-fig. 68D).

Type information.—Both specimens preserved in shaly sandstone along with numerous plant fragments. Both were in a flattened condition and come from the Upper Carboniferous, Radnice Member of the so-called Lower Gray Formation, Westphalian B-C at Kralupy Hill, Červená Hůrka, Czechoslovakia (Ivo Chlupac, pers. commun., Dec. 3, 1970). The holotype (NMP Inv. 838) and paratype (NMP Inv. 834) are in the collections of the National Museum, Prague, Czechoslovakia.

Derivatio nominis.—Named in honor of A. J. C. Corda, the great Czechoslovakian paleontologist who described the first known fossil scorpions from the Chomle locality in 1839.

Eobuthus holti Pocock, 1911

1911. *Eobuthus holti* Pocock, pp. 14–16, pl. II, fig. 2; text-fig. 1.
1913. *Eobuthus holti* Pocock. Petrunkevitch, p. 33.
1923. *Eobuthus holti* Pocock. Moore, p. 132, pl. 1, figs. 4, 5.
1949. *Eobuthus holti* Pocock. Petrunkevitch, p. 137.
1953. *Isobuthus holti* (Pocock). Petrunkevitch, p. 22.
1962. *Isobuthus holti* (Pocock). Dubinin, p. 428, fig. 1244.

A single specimen from the Coal Measures of Sparth, near Rochdale, England, in the collection of F. Holt. Unfortunately, as of 1953, the specimen has been lost.[24]

Eobuthus (?) species Wills, 1934

1934. *Eobuthus* (?) sp. Wills, pp. 101–103, 1 pl.
1949. *Eobuthus rakovnicensis* Frič. Petrunkevitch (*partim*), p. 137.
1953. *Isobuthus rakovnicensis* (Frič). Petrunkevitch (*partim*), p. 21.

Specimen No. 1422 from 15 m above Seam B and 318 m below the surface, Oranje Nassau Mijn No. III, Heerlerheide, Netherlands. Type specimen lost as of 1979 inquiry.[25]

Family **EOSCORPIIDAE** Scudder, 1884 (new definition)

Isobuthoidea with pentagonal sternum wider than long, parallel sides, with greatly expanded or spatulate first pair of coxae; facetted lateral eyes present.

Type genus.—*Eoscorpius* Meek and Worthen, 1868.

Remarks.—The determination of the coxosternal arrangement, lobosternous abdominal plates and facetted lateral eyes in *Eoscorpius carbonarius* Meek and Worthen means that the family Eoscorpiidae Scudder, 1884, as hitherto described by Petrunkevitch, 1955, is erroneously diagnosed and can no longer be retained in the superfamily Scorpionoidea Leach. The description of the family Eoscorpiidae Scudder, as emended by Petrunkevitch, is based on the coxosternal region of *Eoscorpius typicus* Petrunkevitch, which was, furthermore, incorrectly diagnosed by Petrunkevitch in 1913. From a restudy of the holotype of *E. typicus,* it was determined that the fourth pair of coxae definitely abuts the genital opercula and not the sternum. In the *Treatise on Invertebrate Paleontology,* Petrunkevitch (1955, p. 13, fig. 40(1)) used the coxosternal region of a British Pseudobuthiscorpiidae (BM(NH) I.1555) for that of *Eoscorpius.* Consequently it is necessary to emend the family Eoscorpiidae Scudder in view of the new morphological characters described here. The family Eoscorpiidae is therefore referable to the emended superfamily Isobuthoidea Petrunkevitch, 1913 (for comparison on the family level with Isobuthidae and Eobuthidae, see "Remarks" under family Eobuthidae).

Genus **EOSCORPIUS** Meek and Worthen, 1868 (new definition)

Eoscorpiidae with carapace subquadrate; median eyes placed on conspicuous elevated lacrimiform eye node near exterior margin. Two large raised cephalic ridges differentiate the elevated cephalic from the thoracic area of the carapace.

Type species.—*Eoscorpius carbonarius* Meek and Worthen, 1868.

Geological range.—Upper Carboniferous.

Remarks.—In the *Treatise on Invertebrate Paleontology* (1955), Petrunkevitch referred the following genera to the family Eoscorpiidae Scudder, 1884:

Eoscorpius Meek and Worthen, 1868
Alloscorpius Petrunkevitch, 1949
Trigonoscorpio Petrunkevitch, 1913
Buthiscorpius Petrunkevitch, 1953
Anthracoscorpio Kušta, 1885
Lichnophthalmus Petrunkevitch, 1949
Typhlopisthacanthus Petrunkevitch, 1949
Palaeopisthacanthus Petrunkevitch, 1913
Compsoscorpius Petrunkevitch, 1949
Typhloscorpius Petrunkevitch, 1949
Europhthalmus Petrunkevitch, 1949
Garnettius Petrunkevitch, 1949

[24] This is another species for which Kjellesvig-Waering left only a "do not forget" memo. From the shape of the sternum, it belongs to *Eobuthus* rather than *Isobuthus.* A.S.C.

[25] Kjellesvig-Waering left no further notes. The only thing certain about the specimen, as Wills noted, is that it is a lobostern, from the Upper Carboniferous. A.S.C.

Of these 12 genera, now that the lateral compound eyes and the true coxosternal arrangement of *Eoscorpius carbonarius* Meek and Worthen are known, only the genus *Eoscorpius* Meek and Worthen, 1868, remains in the family Eoscorpiidae Scudder. *Alloscorpius* Petrunkevitch was incorrectly described on the basis of illusionary characters in the type species *A. granulosus* (Petrunkevitch) and it is merely a male of *Eoscorpius carbonarius* Meek and Worthen (see below). *Trigonoscorpio* Petrunkevitch, based on the species *T. americanus* Petrunkevitch, 1913, is based on a single specimen which has been lost,[26] but from a cast in the Peabody Museum at Yale it is possible to determine that the original was a lobosternous scorpion and, without a doubt, a male of *Eoscorpius carbonarius* Meek and Worthen. It would not have been possible for a scorpion to have such a narrow triangular carapace, as the carapace could not possibly uphold, much less fit, the massive appendages, chelicerae, pedipalps and four pairs of legs, under it. *Trigonoscorpio* Petrunkevitch is here referred to the synonymy of *Eoscorpius* Scudder. *Buthiscorpius* Petrunkevitch, 1953, is a Pseudobuthiscorpiidae, being a lobostern with a coxosternal arrangement completely different from Eoscorpiidae. *Anthracoscorpio* Kušta is a holostern and belongs to the Eoctonoidea. *Lichnophthalmus* Petrunkevitch is also congeneric with *Eoscorpius*. *Typhlopisthacanthus* Petrunkevitch is a junior synonym of *Eoscorpius*, a female, as proven by a study of the respective holotypes (see below). *Palaeopisthacanthus* Petrunkevitch has been shown by Vogel and Durden (1966) to possess stigmata and, therefore, is an Orthosternina and cannot remain in the Eoscorpiidae. *Compsoscorpius* Petrunkevitch is also an Orthosternina. *Typhloscorpius* Petrunkevitch turns out to be a junior synonym of *Eoscorpius*. *Europhthalmus* Petrunkevitch is known only from the dorsal side, was incorrectly described, and restudy of the holotype shows that this also is a junior synonym of *Eoscorpius* and identical to *E. pulcher* (Petrunkevitch). *Garnettius* Petrunkevitch has been referred correctly to the family Garnettiidae by Dubinin (1962, p. 432) and a study of the holotype (see above) shows that this is a Holosternina, not a Lobosternina.

Thus the family Eoscorpiidae Scudder, 1884, as emended here, retains only one genus, *Eoscorpius* Scudder, but this genus is very well known morphologically and its geographical range includes central North America and England.

[26] Mr. B. S. Beall (written commun., 1984) reported that he had located the holotype of *Trigonoscorpio americanus* Petrunkevitch in the Museum of Paleontology at the University of Michigan, Ann Arbor, MI. It consists of part and counterpart of a siderite nodule listed as being from "Mazon Creek, Illinois", and is catalogued as UMMP 7224. A.S.C.

Eoscorpius carbonarius Meek and Worthen, 1868
(new definition)
Plates 10–12; Plate 13, figures 5, 6;
Text-figures 69–75, 112B, 113C2

1868a. *Buthus*? (*Scorpio*? *Eoscorpius*?) *carbonarius* Meek and Worthen, pp. 22–24.
1868b. *Eoscorpius carbonarius* Meek and Worthen, pp. 560–562, with fig. [*sic*].
1883. *Eoscorpius carbonarius* Meek and Worthen. Peach, p. 407, pl. 23, figs. 23, 23a, b.
1904. *Eoscorpius carbonarius* Meek and Worthen. Frič, p. 76, fig. 95.
1913. *Eoscorpius carbonarius* Meek and Worthen. Petrunkevitch, p. 37, pl. II, fig. 6.
1913. *Eoscorpius typicus* Petrunkevitch (*partim*), pp. 39–43, pl. I, figs. 2–4; text-figs. 5–7.
1913. *Eoscorpius granulosus* Petrunkevitch (*partim*), pp. 45–46, pl. II, fig. 10; text-fig. 9.
1913. *Trigonoscorpio americanus* Petrunkevitch, p. 47, pl. IV, figs. 17, 18; text-fig. 10.
1913. *Palaeopisthacanthus mazonensis* Petrunkevitch, pp. 49–50, pl. II, fig. 1; text-figs. 13–14.
1949. *Typhlopisthacanthus mazonensis* (Petrunkevitch). Petrunkevitch, pp. 144–145.
1949. *Eoscorpius carbonarius* Meek and Worthen. Petrunkevitch, p. 152.
1949. *Eoscorpius typicus* Petrunkevitch. Petrunkevitch, p. 152.
1949. *Alloscorpius granulosus* (Petrunkevitch). Petrunkevitch, p. 153.
1953. *Eoscorpius carbonarius* Meek and Worthen. Petrunkevitch, p. 27.
1953. *Eoscorpius typicus* Petrunkevitch. Petrunkevitch, p. 27.
1953. *Alloscorpius granulosus* (Petrunkevitch). Petrunkevitch, p. 29.
1953. *Trigonoscorpio americanus* Petrunkevitch. Petrunkevitch, p. 31.
1953. *Typhlopisthacanthus mazonensis* (Petrunkevitch). Petrunkevitch, p. 34.
1955. *Eoscorpius carbonarius* Meek and Worthen, Petrunkevitch, p. 73, fig. 42.
1955. *Alloscorpius granulosus* (Petrunkevitch). Petrunkevitch, p. 73, fig. 43(1).
1955. *Trigonoscorpio americanus* Petrunkevitch. Petrunkevitch, p. 74, fig. 43(2).
1955. *Typhlopisthacanthus mazonensis* (Petrunkevitch). Petrunkevitch, p. 74, fig. 43(5).
1962. *Eoscorpius carbonarius* Meek and Worthen. Dubinin, p. 429.
1962. *Alloscorpius granulosus* (Petrunkevitch). Dubinin, p. 429, fig. 1248.
1962. *Typhlopisthacanthus mazonensis* (Petrunkevitch). Dubinin, p. 431, fig. 1256A, B.
1962. *Trigonoscorpio americanus* Petrunkevitch. Dubinin, p. 431, figs. 1232, 1251.

Specimen I.—The holotype of *Eoscorpius carbonarius* Meek and Worthen, 1868, FMNH (UC) 8949; counterpart in the University of Illinois Geological Museum.[27]

The holotype (Pl. 10; Text-figs. 69, 70) comprises part and counterpart of a well-preserved specimen in a typical ironstone concretion. FMNH (UC) 8949 retains more of the specimen than the obverse, which

[27] Lost as of April, 1985. A.S.C.

unfortunately has been covered with a protective film, probably varnish, which with the years has hardened to a point that it is now almost impossible to remove. The description given here is based on both specimens and all figures are a composite of both halves of the nodule.

The carapace is known in its entirety (see Text-fig. 69). It is subquadrate, rounded at the anterolateral and genal angles. The anterior is produced into a short triangular point, and directly posterior to this median process is a conspicuous, elevated, broadly lacrimiform ocellar node. On the anterior of the eye node are two large, elliptical median eyes. These eyes are capable of forward, lateral and vertical sight, but probably not backward sight. The cuticle covering the eyes is transparent, but is light brown in color, clear and not covered by finely reticulated patterns such as are found in other parts of the cuticle. At the anterolateral corner of the carapace is a relatively small reniform facetted eye. The compound eye is present only on the left side, as the right eye has been buckled under the crushed right side. The ommatidia are relatively coarse, rounded and probably number less than 30.

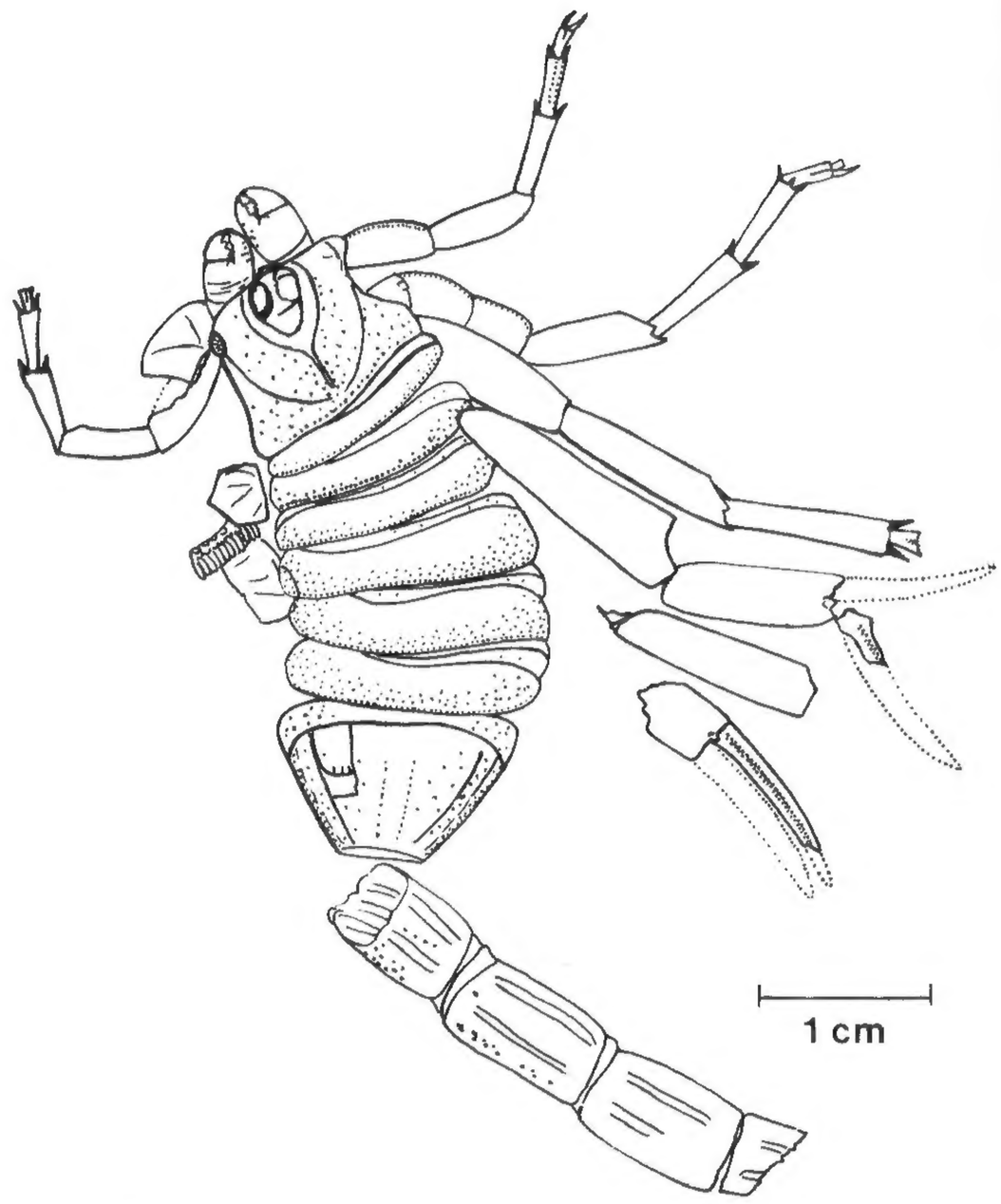
Behind the median ocellar node is a Y-shaped sulcus that extends posteriorly to bisect the two large cephalic ridges. The ridges are very prominent on the carapace and roughly divide it into an elevated cephalic area and a less-pronounced thoracic area. The rear of the carapace is bordered by a raised transverse ridge which articulates with the first tergite (see Text-fig. 69).

The ornamentation of *Eoscorpius carbonarius* is distinctive and consists of coarse pustules, probably setaceous, concentrated along the anterior of the cephalic ridges in the area adjoining the median sulcus. The pustules are also more common in the posterior thoracic area. A single prominent row of pustules, probably setaceous, borders the posterior margin.

Measurements (in mm) of the carapace of FMNH (UC) 8949.—

Length at midsection:	10.2
Length (not including anterior process):	9.6
Width at base:	12.2
Width at midsection:	11.8
Width at base of lateral eyes:	9.6
Length of median ocellar node:	4.1
Width of median ocellar node:	3.3
Length of median ocellus:	1.3
Width of median ocellus:	1.0
Length of facetted lateral eye:	1.4
Width of facetted lateral eye:	0.6

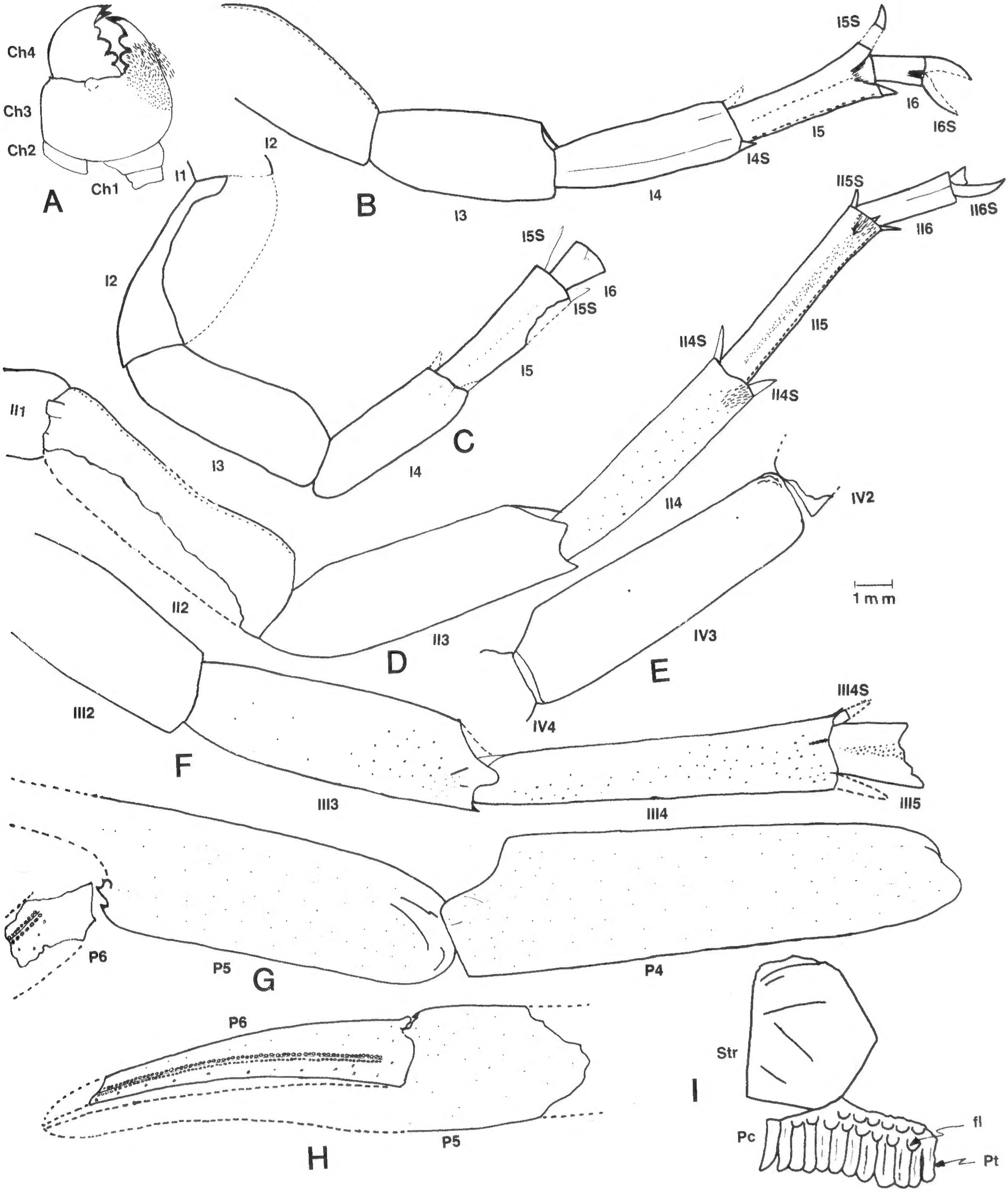
Both chelicerae are well preserved and noteworthy for their robust size. The number of joints cannot be determined with certainty, but it appears that four comprise the complete chelicera—two short, ringlike joints, followed by the pincer of two joints. In the



Text-figure 69.—*Eoscorpius carbonarius* Meek and Worthen. Specimen I, holotype, FMNH (UC) 8949. From the Upper Carboniferous (Pennsylvanian), Carbondale Formation, Lower Francis Creek Shale, Mazon Creek, Grundy Co., IL. This is a composite drawing based on both sides of an ironstone nodule. The carapace is complete.

Text-figure 70.—*Eoscorpius carbonarius* Meek and Worthen. Specimen I, holotype, FMNH (UC) 8949. From the Upper Carboniferous (Pennsylvanian), Carbondale Formation, Lower Francis Creek Shale, Mazon Creek, Grundy Co., IL. See foldout inside front cover for explanation of abbreviations.

A. Right chelicera from the ventral side, somewhat distorted, partly drawn from the left chelicera to make a composite. Small dots are setal bases concentrated on the inner sides of the chelicera, very much as in living scorpions. There are four joints in the chelicera, as shown; this is the same as in eurypterids. **B.** First right walking leg, dorsal view. There is no question of the presence of two terminal claws. Lines on pits on second and fifth joints are probably setaceous. **C.** First left walking leg from the ventral side. **D.** Second right walking leg from the dorsal side. **E.** Central part of fourth (last) right walking leg from the ventral side. **F.** Third right walking leg from the dorsal side. The dots represent pits where presumably tactile setae were attached. **G.** One of the pedipalps, probably the right one. The hand and free finger contain many small openings where presumed tactile hairs were attached; however, they do not appear to be in any particular pattern that would resemble the trichobothria of modern scorpions. **H.** A pedipalp, presumed to be of the left side, which had been turned over to the right side of the holotype. The double row of round lobes is definitely a structure on the outer side of the free finger; if present on the fixed finger of the manus, they are not preserved. The holes were probably attachment sites for very coarse setae. The edges of the fingers are without denticles. **I.** The pentagonal sternum and parts of the pectinal comb, showing small rounded sclerites, fulcra and very long teeth.


Ch4
Ch3
Ch2
Ch1
A
I1
I2
I3
I4
I5
I5S
I6
I6S
B
I5S
I6
I5S
I5
C
I2
I3
I4
II1
II2
II3
D
II4
II4S
II5
II5S
II6
II6S
IV2
IV3
E
1 mm
III2
F
III3
III4
III4S
III5
IV4
P6
P5
G
P4
P6
P5
H
Str
I
Pc
fl
Pt

composite drawing of the two chelicerae (see Text-fig. 70A), the two ringlike joints represent the dorsal side. On the venter, the segment that corresponds to the second joint in the figure increases to double its length. This is in keeping with present-day scorpions, which have the ventral side considerably longer than the dorsal. However, there are four joints in the chelicera of this scorpion, as has been determined here for numerous Silurian, Devonian and Carboniferous scorpions, and which are now known to occur not only in eurypterids such as the Pterygotidae (Kjellesvig-Waering, 1964, p. 334) but in the Eurypteridae (Kjellesvig-Waering, in preparation),[28] therefore, likely in all Eurypterida.

The hand of the chelicera is very wide and, although it is seen in a crushed state, is a massive structure. The immovable ramus is short and stout and is bordered with apparently two large, rounded teeth. On the inner and ventral side is an area with large setae that border the primitive oral tube on each side, as in living scorpions. The free ramus is particularly massive, ends in a double tooth, as also occurs in modern scorpions such as the Buthidae, and is bordered on the masticatory edge by at least three and possibly four rounded teeth. These teeth may have been more pointed in life as they are known from an internal cast of the inner part of the original cuticle. It is also quite possible that these teeth may occur as double rows, or that the masticatory edge on the dorsal side may have other teeth.

The chelicerae protrude beyond the margin of the carapace for at least the equivalent of two-fifths of the carapace length, and it appears likely that the entire last two joints are beyond the anterior edge of the carapace.

Measurements (in mm) of the chelicera of FMNH (UC) 8949.—

Length:	
First joint (incomplete)	0.65
Second joint at midsection (dorsal)	0.5
Second joint at midsection (ventral; incomplete)	1.5
Width of hand	4.2
Length of hand and fixed ramus	4.6
Free finger width	2.2
Free finger length	1.8

In the reconstruction of the chelicera on Text-figure 70A, the hand (probably all that has been crushed) may be wider than it would have been in life. The fingers, however, would not be appreciably expanded by compaction. The entire chelicera would probably still be a very massive organ, not comparable, however, to *Garnettius* of the Kansas Pennsylvanian or *Liassoscorpionides* from the German Jurassic.

[28] Unfortunately, the Eurypterida paper was never completed. A.S.C.

The walking legs have been interpreted as being composed of eight podomeres. The relationship to the sternum is not known as it was displaced to the left of the specimen.

The pedipalps are almost completely known and are described for the first time, as one had previously been mistaken for the fourth walking leg and the other pedipalp had not been exposed on the specimen. The large first joint (trochanter), a curved and unusually-long trapezoidal structure, may be seen on the left side of the holotype. The second joint (femur) is not known in this specimen. The third joint (tibia) is very large, massive, and wider at the distal end (see Text-figs. 70G, H).

The hand is very long, but the fixed finger is unknown. The free finger is nearly complete and is curving, long, narrow and is distinctly devoid of any denticles or other serrations along the inner edge (see Text-fig. 70H). The pedipalp is very well marked by a double row of setal sites on both fingers, appearing as if there were a raised narrow ridge separating each row. This double row runs medially on the side throughout the length of the fingers. Several scattered single setal sites occur throughout the finger and have been noted on the free finger (see Text-fig. 70H). The sites for the rows of setae should not be mistaken for denticles which may have been displaced from the edge, as abundant pieces of the original cuticle were adequately preserved to show that the inner edge of the finger is devoid of any denticles or serrations, and therefore is cultrate. The inner row has coarser setal sites than the outer.

The first and second coxae do not have maxillary lobes exposed, although the first pair seems to be slightly produced anteriorly. Only the edges of both coxae are preserved on the counterpart. These two coxae meet at the midline directly in front of the sternum. The outlines of the last two coxae are also present in this specimen, and the third pair appears larger than the sides of the sternum, therefore it has been interpreted that the third pair abuts against the sternum and the fourth against the genital operculum. This can be proven in other specimens.

The first leg is known almost in its entirety, and is composed of seven joints and the coxa (see Text-figs. 70B, C). The first joint (trochanter) is not preserved. The second joint (femur) is flattened as in living scorpions, wide, massive and with a row of pits along the anterior edge, presumably setaceous. The third joint (patella) is also flattened and wider at the distal end. The fourth joint (tibia) is long and has well-developed tibial spines at the end. The fifth joint (basitarsus), also long and narrow, retains two spurs at the distal end. The posterior part of the joint is lined with a row of small pits, probably setaceous. Pits, smaller in size, are present in a line along midsection. The large double

spines at the end of the joint correspond to the pedal spines of present-day scorpions. The anterior of these spines is much longer than the posterior. This joint, as indicated by the fringe of setaceous pits, is also probably flattened in life. The sixth joint (tarsus) is short, and is distinctly divided by a narrow terminal depression into two tubular ridges that accommodate the double claw. The claws have been seen on the counterpart and only the outer edges are preserved sufficiently to show that they are claws—double, short and curved. However, preservation was not adequate to determine whether these claws may not have been more complicated, as Wills (1959) and Størmer (1963) showed in other Carboniferous scorpions. The post-tarsus or heel was not preserved.

The second walking leg is preserved in its entirety (see Text-fig. 70D). The second pair of coxae meets at the midline in front of the sternum, and has short maxillary lobes (although not seen in this specimen). The first joint (trochanter) is short, whereas the second joint (femur) is long, and both are bordered at the anterior by a single row of pits, probably setaceous. Both joints are flattened in life. The third joint (patella) is long and flattened. A socket for the articulation of the condyle on the next joint occurs at the end of the joint. The fourth and fifth joints (tibia and basitarsus) are very long and narrower than the preceding. The ends are ornamented with two spurs, the anterior being larger than the posterior, corresponding to the tibial and basitarsal (pedal) spurs of present-day scorpions. Scattered setae occur on the fourth joint, and a concentration of these setae occurs at the posterior tibial spur. The evidence for the setae is seen in the small round holes in the cuticle, and also in the presence of the setae that are embedded in the matrix, although in nearly all cases only the cross-section or embedded stump of the seta is seen. The end of the fifth joint has an extra small spine, which likely is all that remains of a fringe of similar spines. The posterior edge of this joint is bordered by a single row of pits, probably setaceous. In the median part of the joint on the dorsal side is a row of numerous pits that represent the bases for single setae. The sixth joint (tarsus) is short, with a narrow median furrow at the end. It is long in comparison to the corresponding joint in living scorpions. The two claws are only partially preserved, but one is complete, showing it to be short and curved (see Text-fig. 70D).

Only the four central joints (femur, patella, tibia and basitarsus) of the third walking leg have been preserved and these show the leg to be constructed like the previous ones, except that it is much larger (see Text-fig. 70F). The socket and condyle of the third and fourth joints are well preserved, and the tibial spurs are present at the end of the fourth joint. The second and third joints are flattened as in the previous leg. Scattered setae, indicated by the setal sites, are present on the third and fourth joints. The fifth joint, although known only from the base, is probably like the previous joint. Numerous setae, concentrated along the median part of the joint, are also present.

The fourth walking leg is represented by a complete joint, which represents the third (patella) beyond the coxa (see Text-fig. 70E). The fourth walking leg that Meek and Worthen (1868, fig. 1) described and figured actually is the pedipalp. It had not previously been exposed or noted by those authors or by Petrunkevitch, who had accepted Meek and Worthen's erroneous determination.

Measurements (in mm) of the appendages of FMNH (UC) 8949.—

Pedipalp:		
Joint No.	maximum length	midsection width
1 (trochanter)	5.9	2.9
2 (femur)	(unknown)	(unknown)
3 (tibia)	14.3	4.0
4 (hand)	9.6	3.6
5 (free finger)	10.0 (estimated)	1.1
Leg No. 1:		
Joint No.		
1 (trochanter)	(unknown)	(unknown)
2 (femur)	6.8	(unknown)
3 (patella)	6.4	2.4
4 (tibia)	4.8	1.7
5 (basitarsus)	4.2	1.5
6 (tarsus)	1.5	0.8
7 (claws)	1.0	—
Leg No. 2:		
Joint No.		
1 (trochanter)	(unknown)	(unknown)
2 (femur)	4.8	(covered)
3 (patella)	4.6	2.3
4 (tibia)	8.0	2.8
5 (basitarsus)	5.6	1.3
6 (tarsus)	2.3	0.8
7 (claws)	1.3	—
Leg No. 3:		
Joint No.		
2 (femur)	(incomplete)	(incomplete)
3 (patella)	8.4	3.1
4 (tibia)	10.0	1.7
5 (basitarsus)	(incomplete)	1.3
Leg No. 4:		
Joint No.		
3 (patella)	9.0	2.8

The tergites are all preserved and reveal that they are strongly constructed with a well-developed anterior, transverse, marginal rim. This marginal rim, a common feature in many living scorpions (*Tityus, Broteochactas, Diplocentrus, Hadogenes, Urodacus,* etc.) and among the eurypterids (*Eurypterus, Buffalopterus,*

Erieopterus, etc.) has repeatedly gone unnoticed in the literature (see redescription of *Mazonia woodiana* Meek and Worthen *in* Kjellesvig-Waering (1969), and *Kronoscorpio danielsi* (Petrunkevitch) here). Meek and Worthen (1868b) and Petrunkevitch (1913, 1949, 1953, 1955) have shown the tergites in these scorpions as long sclerites with rounded ends, and thought the prominent raised anterior ridge was intersegmental tissue. The sclerites are embedded in the skin. Instead, this prominent ridge serves to raise the posterior of the previous tergite in order that greater flexibility is attained. The anterior transverse ridge becomes progressively thinner anteriorly to grade into the flexible intersegmental tissue that connects to the posterior doublure of the previous tergite. This type of articulation is known in countless other arthropods.

Each successive posterior tergite increases in length and is rounded at the posterior genal angles. The anterior marginal rim is one of the distinct and pronounced features of this scorpion, and is wider along the center and the ends than in the pleural areas. The anterior ridge is devoid of any ornamentation as it must slide underneath the previous tergite in any side movement of the opisthosoma. Toward the posterior and the sides of each mesosomatic tergite are concentrated a number of pustules, all of which are probably setaceous, as each is surmounted by a small opening. Along the posterior margin, and at the genal angles and extremities, are single rows of similar setaceous pustules. This is a distinctive character, at least for preliminary determination of this scorpion. The anterior two-thirds of each tergite is mainly devoid of pustules.

The seventh tergite is massively constructed with a well-developed anterior transverse ridge. The entire plate is trapezoidal, and the area that serves for the attachment of the cauda is very wide, in keeping with the wide and powerful tail. At midsection are two rows of granules, probably setaceous. At each side of the tergite is a raised, unornamented, straight crest. At the base and along the sides is the characteristic row of pustules. The extreme sides of the plate are flattened with a few scattered pustules occurring along the highly-impending sides.

The underside of this scorpion is not well known as it is a dorsal impression. However, three structures of great taxonomic importance are known. These are the sternum, combs and parts of the abdominal plates.

The sternum is displaced and lies to the left of the specimen. It is broadly pentagonal, broader than long, with the lateral sides parallel and short. The anterior is triangular and the base is straight. The posterior corners are right angles. The sternum measures 3.0 mm in length and 4.2 mm in width (see Text-fig. 70I).

The combs also have been displaced to the left of the specimen and are poorly preserved and incomplete. Enough is present to show that the teeth are long, with a longitudinal depression running throughout their length. Ten teeth are present, but considerably more must have been present in life. Fulcra are coarse and well developed. At least one row of rounded small sclerites or areoles is present above the fulcra. The rest of the comb is not preserved (see Text-fig. 70I).

The abdominal plates have been revealed on the left side of the specimen where they have been displaced, and can also be seen in place under the anterior part of the seventh tergite where a part is broken away to reveal these important structures. The plates are of rounded, bilobed or lobostern type. The plate that is in place shows a raised rim, much like that present in *Isobuthus kralupensis* Thorell and Lindström, and has a doublure (see Text-fig. 69).

The cauda is known from three well-preserved segments and the anterior part of the fourth. These show that the cauda is very strongly constructed, and each tergite is surmounted by two median carinae. The underside of the first caudal segment reveals that there are three median crests present on the venter; however, it has not been possible to determine whether these are present on the other segments, as all are covered by the dorsal side. Numerous scattered pustules, probably setaceous, are present along the sides of the cauda.

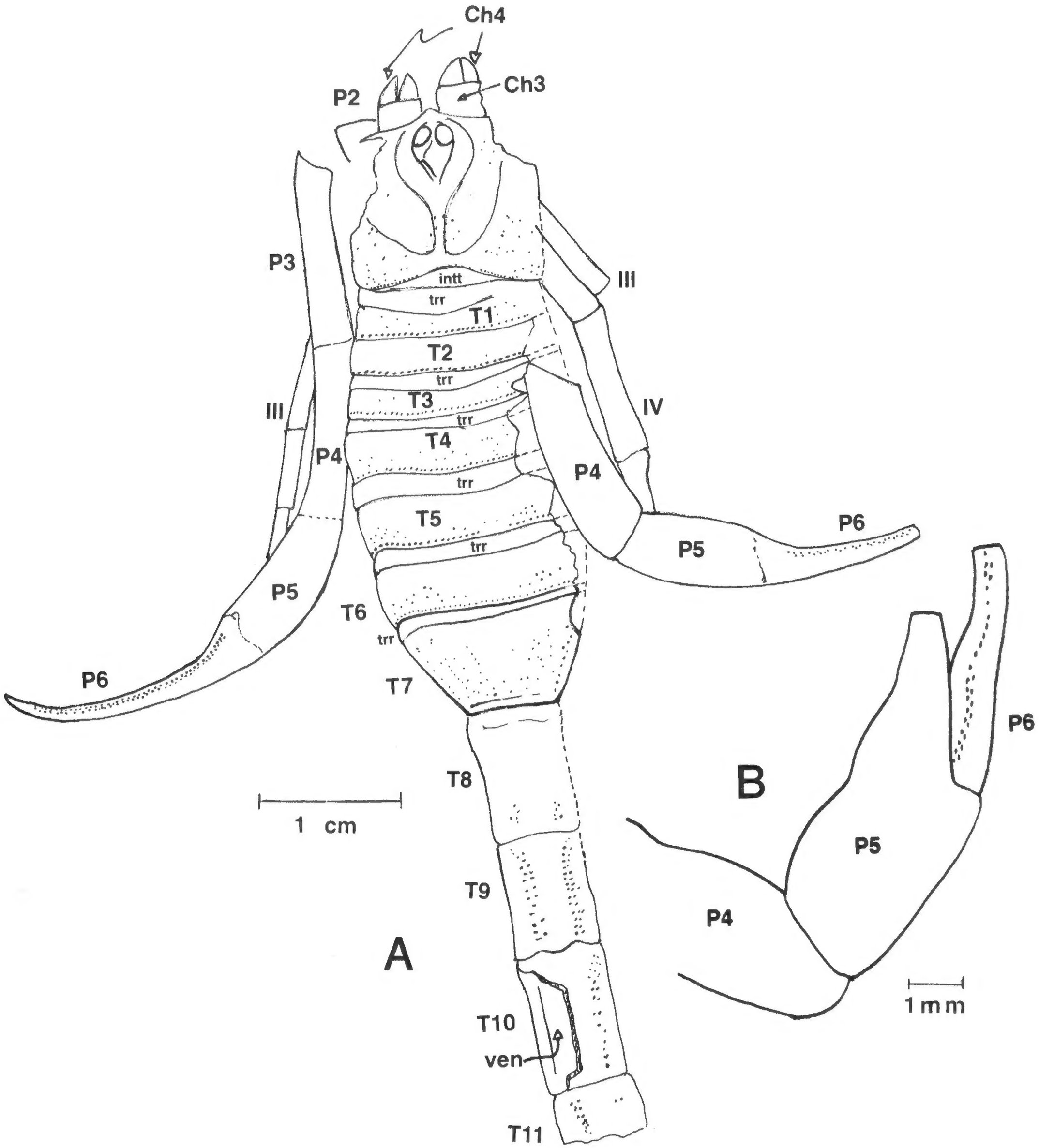
Measurements (in mm) of the opisthosoma of FMNH (UC) 8949.—

Tergite number	length		greatest width
1	1.8		12.6
2	2.8		13.1
3	3.4		14.9
4	3.9		14.9
5	4.2		14.9
6	5.2		15.8
7	9.0	(anterior)	14.0
		(posterior)	7.8
8	8.7		6.5
9	9.4		5.6
10	9.4		5.6

Specimen II.—Holotype of *Alloscorpius granulosus* (Petrunkevitch), 1913, pp. 45–46, fig. 9, pl. II, fig. 10; YPM 128.

This specimen is an estimated 110 mm in overall length (see Text-fig. 71A) and is therefore larger than the holotype of *Eoscorpius carbonarius* Meek and Worthen. Only one-half of the nodule is known, mainly consisting of the dorsal side, preserved from the inside, showing the carapace, mesosoma and parts of the first four tergites of the cauda. Most of the chelicerae, two pedipalps and parts of the legs are preserved and are seen in ventral aspect. The diagnostic ornamentation

of *Eoscorpius carbonarius,* consisting of a single row of pustules along the posterior fringe of the mesosomal tergites, as well as the double row of setal sites in the form of round holes, biserially arranged on the dorsal



Text-figure 71.—*Eoscorpius carbonarius* Meek and Worthen. From the Upper Carboniferous (Pennsylvanian), Carbondale Formation, Lower Francis Creek Shale, Mazon Creek, Grundy Co., IL. See foldout inside front cover for explanation of abbreviations.

A. Specimen II. Holotype of *Alloscorpius granulosus* (Petrunkevitch). YPM 128. **B.** Specimen III. Holotype of *Typhlopisthacanthus mazonensis* (Petrunkevitch). USNM 37977. This is a pedipalp of a female specimen. It shows the characteristic double row of setal sites on the free finger (see Text-fig. 70H).

side of the fingers of the pedipalp, leaves no doubt that *Alloscorpius granulosus* (Petrunkevitch, 1913) is a junior synonym of *Eoscorpius carbonarius* Meek and Worthen, 1868.

Little can be added to the known characteristics of *Eoscorpius carbonarius* Meek and Worthen from this specimen, as preservation is poor and known mainly from the dorsal surface. However, this specimen is larger and shows the median eyes to be proportionately smaller and placed slightly further back from the triangular, glossated anterior margin. The entire fixed finger of the pedipalp was exposed, revealing this structure to be very long and curved. As in the holotype of *E. carbonarius,* the edge of the finger was found devoid of denticles.

The cauda is preserved from the dorsal side, revealing two rows of crests, which are surmounted by coarse pustules; some of these appear elongated in a transverse manner across the crests. The third caudal segment was broken away to expose the ventral surface. A well-developed crest occurs on the side, suggesting, as evidenced in the holotype of *E. carbonarius,* that three crests occur on the ventral side.

Measurements (in mm) of Specimen II, YPM 128.—

Prosoma:	
Greatest width:	10.2±
Length:	10.2
Median eyes:	
Length:	1.4
Width:	0.9
Lateral separation:	0.4
Distance from anterior margin:	0.7
Distance from posterior margin:	7.2
Distance from lateral margin:	3.0
Palpus (chela):	
Length:	25.4±
Pedipalp hand:	
Width:	4.9
Length:	7.0
Free finger length:	18.4
Femur length:	13.5±
Tibia length:	11.0±
Tergites (length):	
1	1.8
2	2.6
3	3.2
4	3.5
5	4.5
6	6.0
7	6.9
8	9.0
9	9.0
10	9.2
Width of seventh tergite:	
Anterior	13.3
Posterior	7.7

Specimen III.—The holotype of *Typhlopisthacanthus mazonensis* (Petrunkevitch), part and counterpart, USNM 37977 (see Petrunkevitch, 1913, pp. 49–50, pl. II, fig. 1; text-figs. 13, 14.

The holotype comprises two parts of an ironstone nodule, showing only the dorsal side. Petrunkevitch's (1913) statement that the underside is preserved is not verified. Both parts of the nodules retain only the dorsal surface. The details of the pedipalp, which is well preserved, show beyond question that it is conspecific with *Eoscorpius carbonarius* Meek and Worthen. This is confirmed by the free finger of the right pedipalp, which shows the characteristic setae in biserial arrangement (see drawing made of this pedipalp, Text-fig. 71B).

The carapace clearly shows the elevated, rounded cephalic shield that characterizes *Eoscorpius carbonarius,* and that Petrunkevitch completely overlooked. The anterior median eyes and node had been broken away and are not present. Details of the lateral eyes are not possible to see without considerable cleaning. Petrunkevitch, in his original figure (1913, p. 50, fig. 13), shows a very long carapace, but this interpretation was only possible because he had mistaken the large chelicerae for maxillary lobes and therefore the carapace was extended to cover the supposed maxillary lobes. The opisthosoma comprises the usual seven segments, but the terminal segment has been partly broken so that it appears to be rounded. This is, however, an illusion, a preservational artifact, and it is exactly the same as in any normal scorpion, with a large opening for a normal caudal segment. All of the segments of the mesosoma have been considerably telescoped forward, making it appear to be a much shorter scorpion. It is, moreover, typical of the female of *Eoscorpius carbonarius.* There are no coxae, sternum or genital opercular plates preserved, as had been shown by Petrunkevitch, whether studied in a dry state or under glycerin, alcohol or water. The small cauda that Petrunkevitch (1913) shows in figure 13, is wholly illusory and represents only the left margin of the last preabdominal segment. Two of the abdominal plates are present toward the posterior end, but these were not sufficiently well-preserved to warrant description.

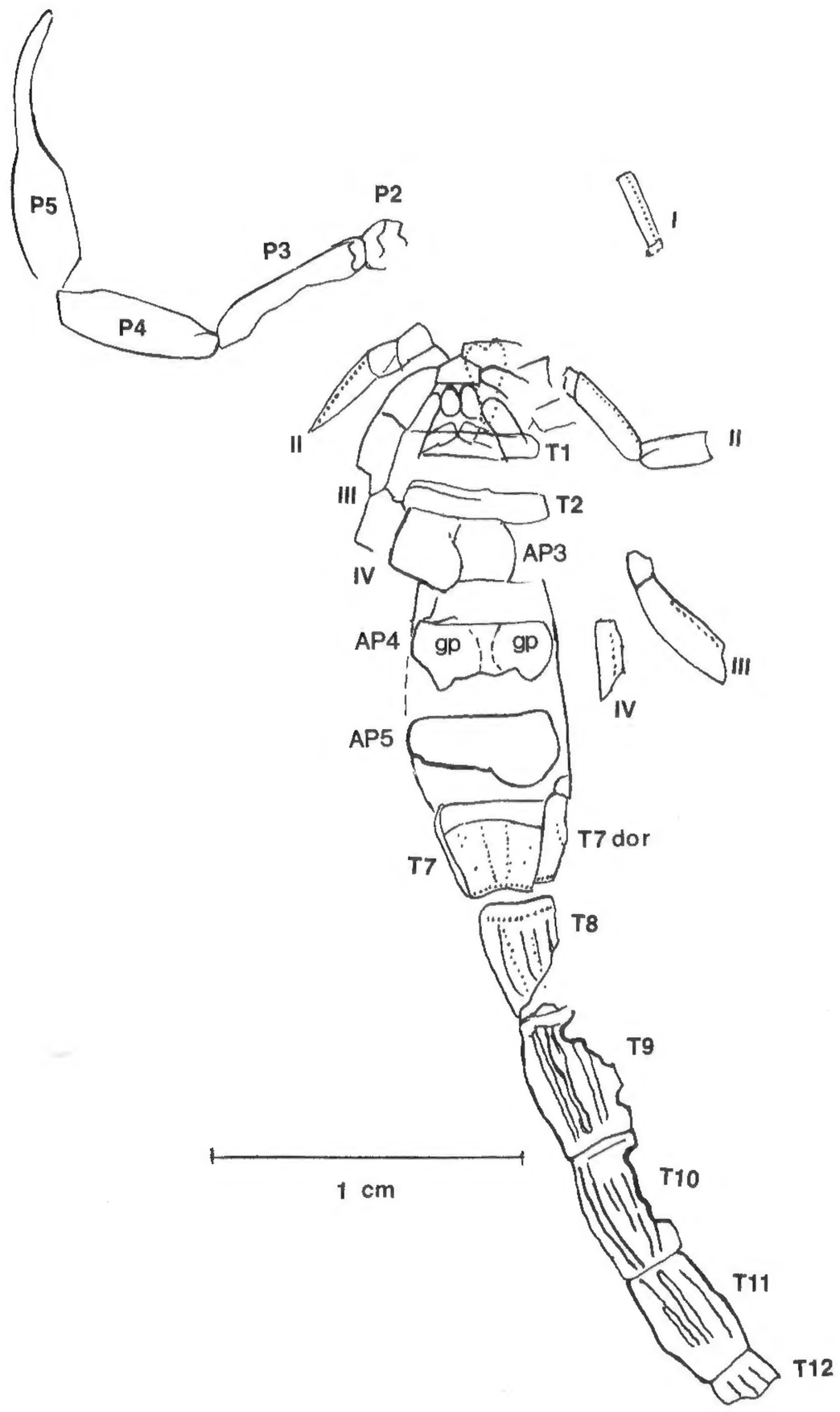
The entire specimen is so poorly preserved that it does not justify further measurements or description, nor further figures other than that given here, in order to prove that it is a junior synonym of *Eoscorpius carbonarius.* The holotype would have to have considerable cleaning to be of much use and even then it is doubtful that anything else could be added to our present knowledge of the species *E. carbonarius* from this specimen. It should be noted that there is no possibility of this scorpion being a gigantic Pseudobuthiscorpiidae, an opinion mentioned to me by some

who have accepted Petrunkevitch's erroneous interpretation of the specimen, but who have not studied the holotype. The presence of the typical double row of setae on the pedipalp precludes any interpretation other than that the holotype of *Typhlopisthacanthus mazonensis* (Petrunkevitch) is a poorly-preserved specimen, probably a female, of *Eoscorpius carbonarius* Meek and Worthen.

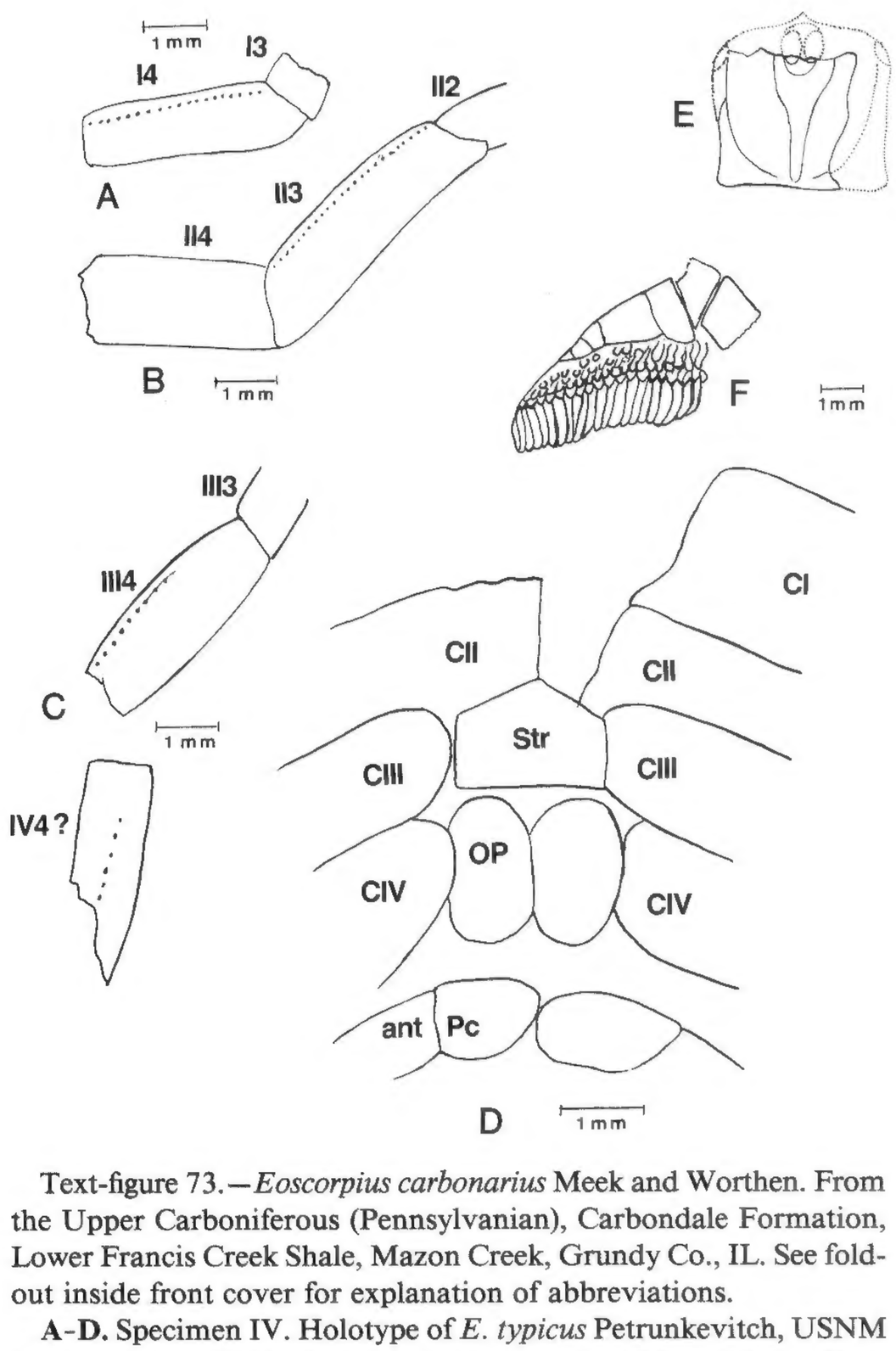
Specimen IV.—USNM 37986, holotype of *Eoscorpius typicus* Petrunkevitch, 1913, p. 39, pl. I, figs. 2, 3; text-figs. 5, 6.

The specimen (Text-figs. 72, 73A–D) comprises half of an ironstone concretion, retaining most of the ventral structures. The obverse, retaining the dorsal side, which was available to Petrunkevitch in 1913, has not been found at the U.S. National Museum where Petrunkevitch (1913, p. 39) states that the two halves were deposited. Fortunately, the more important half, having the impression of the ventral anatomy, was available for this study. Redescription and reinterpretation of the structures present in the holotype reveal that the species *Eoscorpius typicus* is a junior synonym of *Eoscorpius carbonarius* Meek and Worthen and it is probably a male of that species (see Text-fig. 72).

This conclusion is based on several distinct morphological structures, for example: the similar eye node; the fine line of pits along the femur and patella of the



Text-figure 72.—*Eoscorpius carbonarius* Meek and Worthen. Specimen IV. Holotype of *Eoscorpius typicus* Petrunkevitch, USNM 37986. Male specimen. From the Upper Carboniferous (Pennsylvanian), Carbondale Formation, Lower Francis Creek Shale, Mazon Creek, Grundy Co., IL. Figure taken from a rubber mold, therefore reversed. Outline of the impression of the ocellar node indicated by dotted line. See foldout inside front cover for explanation of abbreviations.



Text-figure 73.—*Eoscorpius carbonarius* Meek and Worthen. From the Upper Carboniferous (Pennsylvanian), Carbondale Formation, Lower Francis Creek Shale, Mazon Creek, Grundy Co., IL. See foldout inside front cover for explanation of abbreviations.

A–D. Specimen IV. Holotype of *E. typicus* Petrunkevitch, USNM 37986. Male individual. **A.** Femur and patella of first right leg from the ventral side. **B.** Trochanter, femur and patella of the second left leg from the ventral side. **C.** Part of the femur and patella of the third left leg, and femur or patella of the fourth leg, from the ventral side. **D.** Coxosternal area.

E, F. Specimen V. A paratype of *E. typicus* Petrunkevitch. USNM 37987. **E.** The slightly restored carapace. Only the mound of the median ocellar node was preserved. **F.** A pectine, drawn from the original and rubber casts.

legs (see Text-figs. 73 A–C); the fine, close-set carinae with granules of the seventh tergite (see Text-fig. 72); the presence of three carinae on the ventral caudal segments (see Text-fig. 72); also features such as the lobosternous abdominal plates, similar sterna, opercula and coxosternal arrangements (see Text-fig. 73D). The only differences between the holotypes of *Eoscorpius carbonarius* Meek and Worthen and *E. typicus* Petrunkevitch are that the latter is more slender in mesosomatic girth, and has a longer cauda, and that its ornamentation, although of the same type as *E. carbonarius,* is coarser. All of these characteristics are well-known secondary sexual characters in living scorpions and there seems to be no good reason to consider them to be otherwise in fossil forms. It should also be noted that the paratype, USNM 37987 (see below), shows the presence of the pectines, which are identical to those of *Eoscorpius carbonarius* Meek and Worthen, except that the teeth are finer. The specimen USNM 37987 is also a male, and the presence of finer or more numerous and slenderer denticles in the pectines is a well-known secondary sexual character denoting the male.

Of the four specimens designated by Petrunkevitch as the holotype and three paratypes of *Eoscorpius typicus,* USNM 37986 (the holotype) and USNM 37987 are males of *Eoscorpius carbonarius* Meek and Worthen. YPM 126 is a poorly-preserved specimen of *Anthracoscorpio* (?) sp., whereas YPM 127 has been redescribed as a female of *Palaeobuthus distinctus* Petrunkevitch (see above).

It should be noted that the original descriptions by Petrunkevitch of both *E. typicus* and *Alloscorpius granulosus* are mainly incorrect, and that the original description of the holotype of *Eoscorpius carbonarius* Meek and Worthen is incorrect as well. The carapaces of all three species are identical in length-width relationship, except for normal secondary sexual characteristics. Petrunkevitch's claim (1949, p.153) that the eyes of *Alloscorpius* are much nearer the anterior than in *Eoscorpius,* is based on a comparison that was not possible at that time, because the eyes of *Eoscorpius carbonarius* Meek and Worthen were still covered and unknown. They have not been exposed until this study. The eyes are identical in *Alloscorpius* and *Eoscorpius.* Apart from this, the type species of *Alloscorpius* (*A. granulosus*) has no validity, as it is a large female of *Eoscorpius carbonarius* Meek and Worthen.

The half of the nodule of the holotype of *Eoscorpius typicus* that was available for this study reveals several important morphological structures, which were either overlooked or erroneously described by Petrunkevitch (1913). The carapace is not preserved on the surviving specimen except for an imprint of the outlines of the cephalic shield and the median sulcus, showing the base of the eyes and the eye node. This is shown in dotted outline on Text-figure 72 and in reconstructed outline on Text-figure 73E. This reveals that the carapace comprised an elevated horseshoe-shaped cephalic shield, divided by a deep Y-shaped sulcus, and that the eyes were well forward on the carapace as in *Eoscorpius carbonarius.* Petrunkevitch (1913, fig. 6) shows an altogether different carapace and position of the eyes.

The coxosternal arrangement is clearly preserved. The sternum is pentagonal, broader than wide, but small. The first two pairs of coxae are incompletely preserved and meet in front of the sternum, but it cannot be seen from this specimen whether or not maxillary lobes were present (in the Herdina specimen (FMNH (PE) 32084), it can clearly be seen that maxillary lobes are present). The third pair abuts the entire lateral side of the sternum, a condition that was also apparent in the holotype, since, as stated in the redescription given above, the sternum was too small to have the last two pairs of coxae abutting it. Petrunkevitch shows both pairs abutting the sternum (1913, fig. 6), an impossibility considering the short sides of the sternum. The fourth pair clearly abuts the large pyriform operc̀ula, and this is easily verified in the specimen (see Text-fig. 73D).

The basal segments of the comb are preserved, but these reveal only that both segments are robust. The abdominal plates are very long and definitely of the lobostern type. This can be proven by the last plate, which reveals the characteristic rounded lobes.

The seventh tergite shows the characteristic close-set carinae surmounted by a line of fine granules. The sides are covered with some scattered granules and the base has a characteristic fringe of granules. The dorsal side is incomplete, but does show the characteristic line of granules on one crest and also a fringe along the base of the tergite.

Five caudal segments are preserved ventrally and each reveals three carinae. An anterior row of granules occurs on at least the first tergite. Some granules are present in the depression between the carinae. However, preservation is very poor in the entire cauda.

The appendages of the prosoma show fragments of the legs, which mainly represent the femur and patella (see Text-figs. 73A–C). These are important and show the single row of pits, very likely sites for setae, which occurs on the venter (dorsum also?) of each. The pedipalp is poorly preserved but the outlines reveal a long and strongly-constructed organ with the femur longer and presumably slenderer than the tibia (see Text-fig. 72). Proportionately, and as expected in a secondary sexual character, it is longer than in the female.

Measurements have been given by Petrunkevitch (1913, p. 41).

Specimen V.—Paratype of *Eoscorpius typicus* Petrunkevitch, 1913, p. 40, pl. I, fig. 4; text-fig. 7 (USNM 37987).

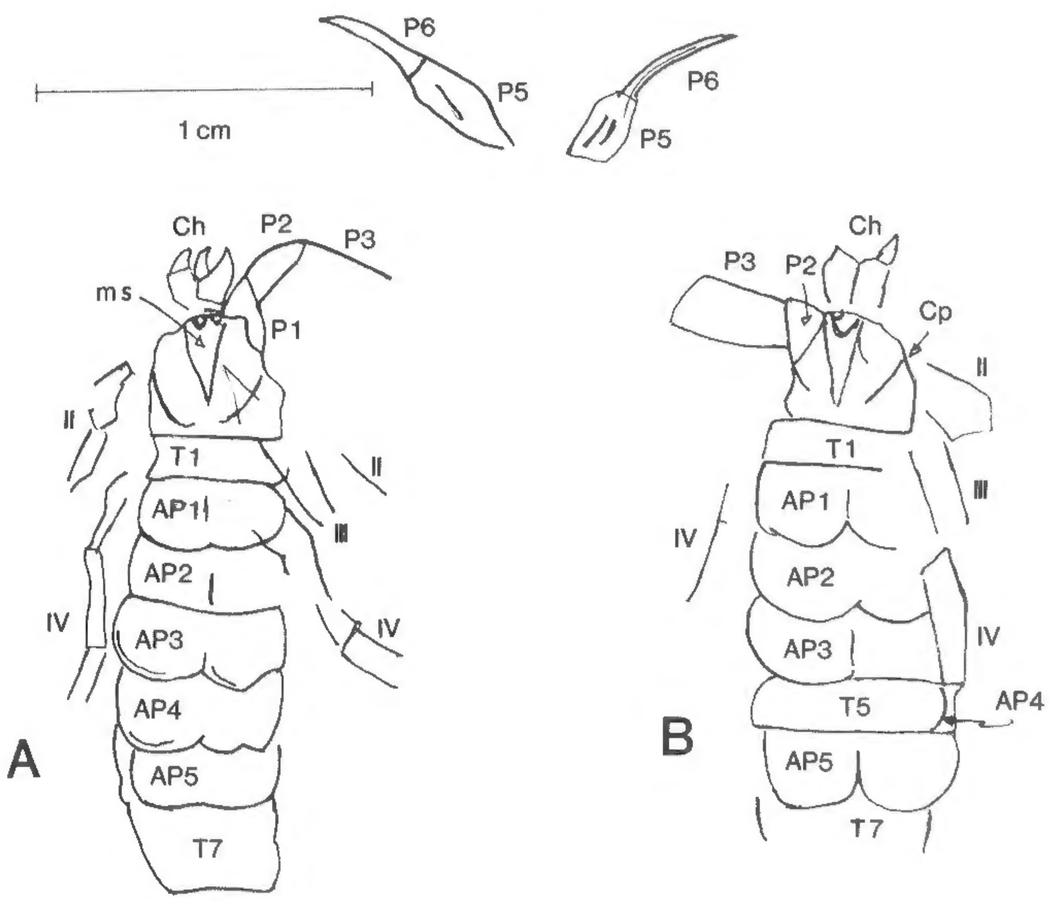
The specimen (Text-figs. 73E, F) is preserved in a typical Mazon Creek concretion, but is in three pieces (two large and one small). It comprises a large, slender scorpion that is considered to be the male. Only the rear part of the carapace (Text-fig. 73E), the mesosoma (turned sideward), the anterior of the mesosoma in ventral impression, part of the last leg and nearly all of a pectine are preserved. Determination is established mainly from the characteristic close-set double row of tubercles on the central part of the venter of the seventh preabdominal tergite, the single row of punctations on the posterior of each preabdominal tergite and the three carinae of the caudal segments. Nothing is added to our knowledge of the species except for details concerning the morphology of the pectine, which was previously known as a fragment in the holotype. Petrunkevitch (1913, fig. 7) had figured the pectine of this specimen but the interpretation given here is considerably different (see Text-fig. 73F). The organ consists of approximately three segments on the anterior lamella, although cracks in the integument make it appear as if five were present. The distal segment cannot be clearly discerned, but is considered likely to be as in the figure. The middle lamella is highly interesting in showing numerous short lacrimiform sclerites (areoles) that become greatly elongated toward the inner part of the pectine. A lower row of the lacrimiform areoles occurs just above the fulcra, which are roughly triangular, well-developed and large. The teeth of the pectines are very large, long, and apparently not more than 25 occur on the male. Petrunkevitch (1913, p. 42) gives 18 teeth, but this is based on the incomplete fragment that formed the basis of his figure 7. A small fragment of the end of a tooth reveals coarse perforations that likely represent sites for the peg organs. A small diamond-shaped sclerite represents the pectinal plate, but it is not known whether this is complete—it may possibly represent the median organ of the pectinal plate.

Specimen VI.—The cast of the holotype of *Trigonoscorpio americanus* Petrunkevitch, 1913, YPM 139. Holotype specimen in the Daniels collection has been lost (see footnote p. 163).

The review given here is based upon plaster casts of the original specimens. These casts were made by Petrunkevitch and are in the Peabody Museum. Photographs of the original were used in part. The plastotypes (see Text-fig. 74) reveal important data, which leave no doubt that the holotype is a juvenile male of *Eoscorpius carbonarius* Meek and Worthen. My interpretation of this scorpion differs greatly from that of Petrunkevitch (1913, p. 47, pl. IV, figs. 17, 18; text-fig. 10).

The scorpion was purported to have a triangular carapace, although how it was possible to accommodate the chelicerae and large pedipalps under this narrow triangle was not easy to understand. It is important to determine how this scorpion is preserved. The carapace obviously is broken and in the obverse, it is preserved as a triangular *fragment*—leading to the misinterpretation of a triangular carapace. The carapace reveals anteriorly-located median eyes, two inflated cheeks, separated by a sulcus and a lacrimiform eye node—all typical of *E. carbonarius*. The carapace and first tergite are preserved in dorsal aspect. The rest of the preabdomen is preserved showing the inside, or dorsal part, of the ventral side. The only dorsal parts of the preabdomen preserved are the first and fifth tergites.

The legs, pedipalp and cauda are too poorly preserved in the plastotype for detailed description, but lack of knowledge of these structures would not meaningfully change the identification. The two pedipalps are present in part, however; the trochanter (**P2**) and the femur of both pedipalps are preserved as dorsal



Text-figure 74.—*Eoscorpius carbonarius* Meek and Worthen. Specimen VI. Holotype of *Trigonoscorpius americanus* Petrunkevitch. Daniels collection, YPM 139, plaster casts of a (lost) original part and counterpart of the ventral surface. From the Upper Carboniferous (Pennsylvanian), Carbondale Formation, Lower Francis Creek Shale, Mazon Creek, Grundy Co., IL.

The drawings were made from the plaster casts, supplemented by photographs of the (lost) originals. This is a juvenile male of *E. carbonarius* Meek and Worthen. Note the broad carapace, rather than the narrow, triangular one postulated by Petrunkevitch. There are five well-developed lobosternous abdominal plates. See foldout inside front cover for explanation of abbreviations.

and ventral impressions, thus appearing on the same side of the nodule.

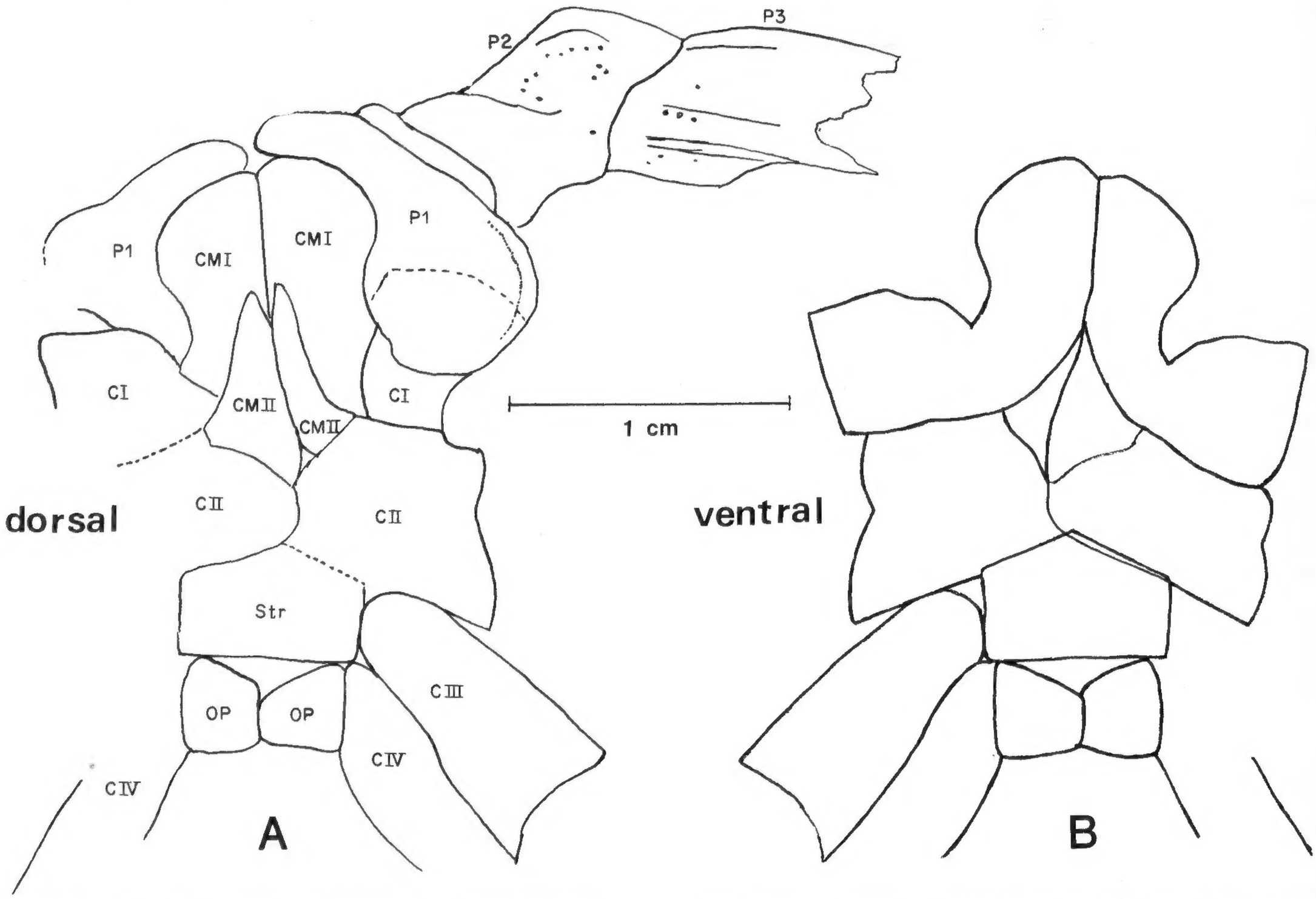
The crucial determination of the abdominal plates as being lobosternous is based on the presence of distinct bilobation and the good development of a wide doublure rimming each lobe. There are five well-developed abdominal plates.

The chelicerae are well preserved and, even in the plastotype, showed that they were composed of four distinct joints.

The overall narrow aspect of the preabdomen indicates that this specimen is a male. I suspect that the overall size of this specimen measured from the anterior of the carapace is about 30 mm, thus a juvenile of the species.

Specimen VII.—Part and counterpart of a nearly complete scorpion measuring about 80 mm long, from the anterior of the carapace to the end of the telson. The specimen (FMNH (PE) 32084) came from the private collection of Jerry Herdina, where it was registered as H-35.

The scorpion (Pl. 11; Text-fig. 75) has been parted so that the coxosternal region and the base of the pedipalps are seen from the dorsal side. It is therefore of great interest to see the attachment of the basal segment of the pedipalps and its relation to the other coxae. This part is rarely seen in fossil scorpions and is of taxonomic and phylogenetic importance. The coxa of the pedipalp is a very wide, rounded segment, with a long anterior process that occurs in front of the maxillary lobes of the first pair of legs. In life these maxillary lobes of the pedipalp coxae would form the sides of the chamber leading to the mouth, whereas the spatulate maxillary lobes of the first pair of walking leg coxae would form the floor or base. Unlike living scorpions, however, the coxae of the pedipalps did not form a narrow tubelike entrance to the mouth, which in Carboniferous time, as well as today, had a central position on the carapace. The anterior entrance was therefore composed of the maxillary lobes of the pedi-



Text-figure 75.—*Eoscorpius carbonarius* Meek and Worthen. Specimen VII. Herdina collection, FMNH (PE) 32084. From the Upper Carboniferous (Pennsylvanian), Carbondale Formation, Lower Francis Creek Shale (Mazon Creek area), Pit 1, Peabody Coal Company, Grundy Co.–Will Co. line, IL. See foldout inside front cover for explanation of abbreviations.

A. Coxosternal area, pedipalp base and opercular plates seen from the dorsal inner side. **B.** Restoration of the ventral side of the coxosternal area, with slight restoration. The anterior of the second maxillary lobe overrides the first.

palps, which formed the sides, followed by a wide chamber with the rest of the coxae of the pedipalps forming the sides, the base (floor) being formed mainly by the maxillary lobes of the first pair of walking leg coxae and the short maxillary lobes of the second pair of walking leg coxae. It has been a matter of conjecture as to the function of the very wide maxillary lobes of the first coxae, but now it is easy to see that this was present because the coxae of the pedipalps formed a very wide chamber, posterior to the anterior opening (see Text-fig. 75).

The second pair of maxillary lobes, also not clearly seen in other specimens, is very well shown in this specimen. They extend only approximately halfway anteriorly to the first pair of maxillary lobes. Both pairs of lobes meet at center. However, of considerable interest is the fact that on the dorsal side, the second maxillary lobes extended further anteriorly, whereas they are partly covered by the spatulate first maxillary lobes on the ventral side, which is nearly always preserved (see Text-fig. 75). Therefore, the ends of the second maxillary lobes (also dorsal) override the first pair of maxillary lobes. The third pair of coxae, as noted elsewhere, abuts the small pentagonal sternum. The fourth pair abuts the genital opercula, which are subtriangular and elongated.

The overall aspect of this scorpion is robust, wide and stout, therefore probably a female. The determination of the species is based on the setal track, composed of a double row of alternating setal openings that parallel the cultrate edge of the fingers of the pedipalp, a character that, among the Mazon Creek scorpions, is only present in *Eoscorpius carbonarius* Meek and Worthen.

This specimen had been sent to me in Norway in February, 1971, by Mr. Jerry Herdina. The drawing of the coxosternal region, described above, was made at that time. Dr. Leif Størmer was shown the specimen and my drawing at the time, because of the exceptional preservation of a part that was not well known. In August, 1977, I borrowed the specimen again, to see if the pregenital plate was preserved. Unfortunately, in the interim, some unauthorized person, obviously lacking knowledge of scorpion morphology, had irresponsibly removed the entire coxosternal region, the base of the pedipalps, the opercula, and other parts of the venter, in order to expose the carapace and the anterior of the dorsal tergites, morphological parts which are well known in this species. The main knowledge that we have of the entire coxosternal area and opercula, as well as the peculiar coxae of the pedipalps is the drawing in Text-figure 75A, which was made with the Wild Drawing Tube, and is therefore correct. Unfortunately, due to the above incident, I find myself in the unenviable position of having to hope that another specimen will be found that will verify my description and drawing.

Specimen VIII.—A very large chela of a pedipalp, FMNH (PE) 32083 (formerly No. H-19 in the Herdina collection).

The specimen consists of the usual ironstone nodule showing part and counterpart of the chela of a very large individual. This chela reveals the great size that this species may attain. The overall aspect of the chela is slender, with the characteristic double row of setal sites along the face of the fingers, which accounts for the identification of *Eoscorpius carbonarius.* The hand is 28.5 mm long at midsection and 18 mm wide at its greatest width. The fixed finger is 6 mm wide at the midsection. The free finger is 5.5 mm wide at the midsection and 34 mm long (see Pl. 12, figs. 1, 2).

A specimen of *Eoscorpius carbonarius* with a pedipalp chela of this size would measure slightly more than 30 cm in length from the anterior of the carapace to the end of the cauda.

Type information.—The holotype of *Eoscorpius carbonarius* Meek and Worthen is from the Pennsylvanian Carbondale Formation, lower Francis Creek Shale at Mazon Creek, Grundy County, Illinois. The holotypes and paratypes (described here) of *Trigonoscorpio americanus* Petrunkevitch, *Eoscorpius typicus* Petrunkevitch, *Alloscorpius granulosus* Petrunkevitch and *Typhlopisthacanthus mazonensis* (Petrunkevitch) are from the same horizon and locality as the holotype of *E. carbonarius.* The Herdina specimen (FMNH (PE) 32084) from Pit 1 of the Peabody Coal Company, on the Will Co.–Grundy Co. line, Illinois, is also from the lower Francis Creek Shale. The Herdina pedipalp specimen (FMNH (PE) 32083) is from approximately the same area (Pits 1–6 undifferentiated) and same horizon.

Remarks.—In 1868, Meek and Worthen described the first American fossil scorpion, a well-preserved specimen from the ironstone concretions of the Francis Creek Shale at Mazon Creek, Grundy County, Illinois. This specimen was described as *Buthus*? (*Scorpio*? *Eoscorpius*?) *carbonarius* in a preliminary note (Meek and Worthen, 1868a) and later changed to *Eoscorpius carbonarius* (Meek and Worthen, 1868b). The description of this fossil was made against a meager background, as the only known fossil scorpions were *Cyclophthalmus senior* Corda and *Microlabis sternbergii* Corda from the Carboniferous rocks of Czechoslovakia.

The holotype of *Eoscorpius carbonarius* Meek and Worthen consisted of two halves of a concretion revealing the obverse and reverse of a scorpion preserved mainly as a dorsal impression. Meek and Worthen gave

an elaborate and careful description which at the time was exceptionally good. Only the dorsal and more obvious parts were described, and no attempt at developing or cleaning the fossil was made. As a consequence, many organs were misidentified, not reported, or not exposed. In 1913, Petrunkevitch borrowed both halves of the concretion and surprisingly reported (1913, p. 37) that Meek and Worthen's inadequate and erroneous description was "quite correct and that nothing of importance could be added to it"! He therefore accepted the description without question, except for changing the measurements from inches to mm. In Petrunkevitch's monographs of 1949, 1953, and finally in the *Treatise on Invertebrate Paleontology* in 1955, no further attempt was made to correct the original error, namely that Meek and Worthen's description was incorrect in many important details. Consequently, scorpion systematics has been seriously handicapped because for a hundred years we have followed an erroneous interpretation of one of the most important fossil scorpions. The importance to scorpion taxonomy of *Eoscorpius carbonarius* is obvious—if for no reasons other than those of priority, and also because Scudder formed the family Eoscorpiidae as early as 1884. The family Eoscorpiidae, having little meaning, quickly became a convenient place to refer any genera whose underside was unknown. For example, because nothing was known of some of the details reported here concerning the holotype, fully 12 genera were placed in the incorrectly-redefined (by Petrunkevitch, not Scudder) family Eoscorpiidae in the *Treatise on Invertebrate Paleontology* (1955), and of these 12 genera it was seen that only one genus, namely *Eoscorpius,* survived within the correct definitions of the family.

It has also been possible to determine some of Wills' genera which were excellently-described morphologically, but, because in a great sense *Eoscorpius* (and *Mazonia*) had not been correctly defined, were not referred to correct genera and families (see Wills, 1959, p. 267).

The review and development of the holotype has resulted in the determination or exposure, for the first time, of: **A**—facetted lateral eyes; **B**—the large median ocelli; **C**—the pedipalps; **D**—presence of lobosternous ventral plates; **E**—the sternum; **F**—presence of anterior transverse ridge of the tergites; **G**—a fragment of the fourth walking leg; **H**—double tibial and basitarsal spurs; **I**—the terminal claws; **J**—the arrangement of the coxae. It is obvious that the lack of knowledge of many of these basic morphological structures has been a decided drawback in the establishment of a workable taxonomy.

Petrunkevitch (1949, p. 153) erected the genus *Alloscorpius* with type species *Eoscorpius granulosus* Petrunkevitch, 1913, for the following reasons:

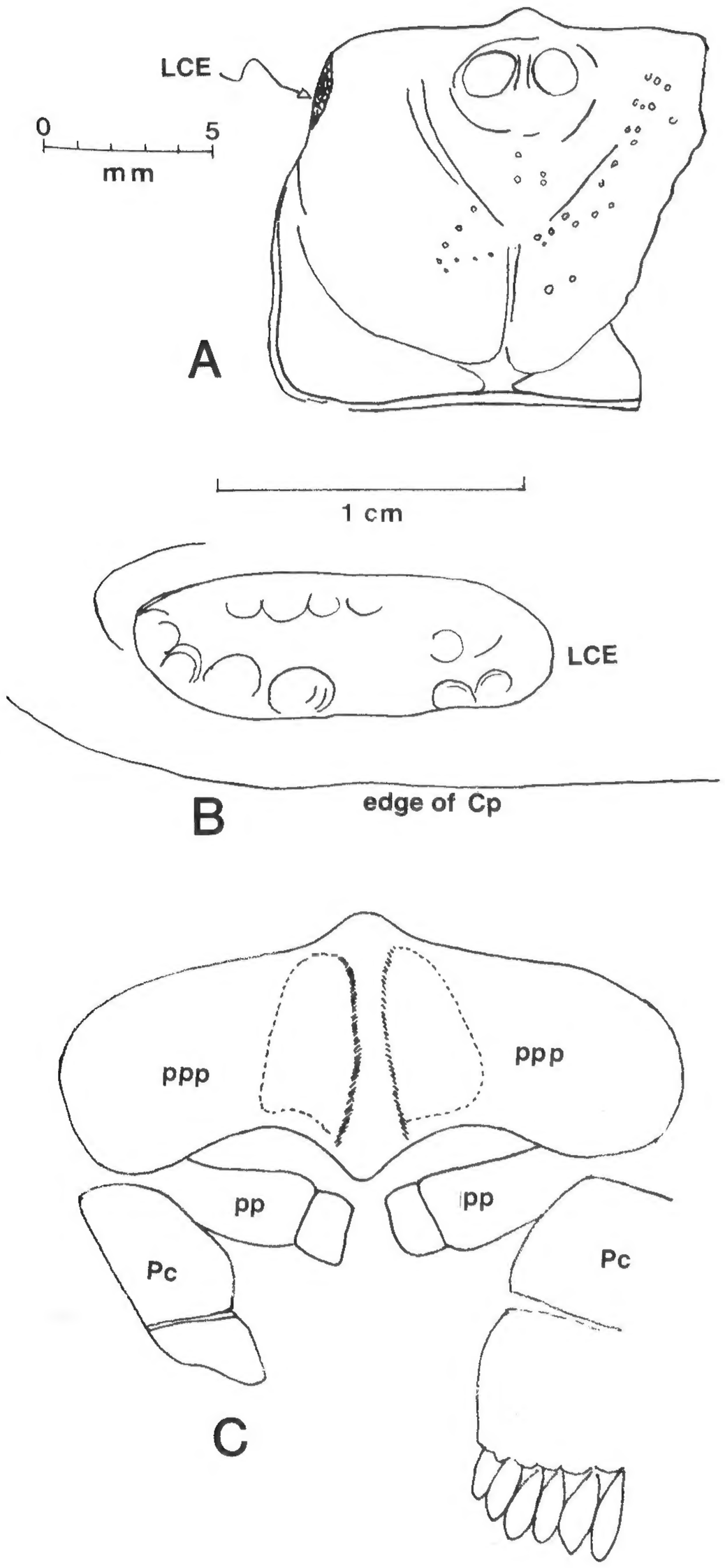
> For whereas in the species to which the genus *Eoscorpius* is restricted here, the carapace is either as long as wide or longer than wide, in both species of *Alloscorpius* it is distinctly wider than long. The position of the eyes is also different. In *Alloscorpius* they are much nearer the anterior edge of the carapace than in *Eoscorpius.*

In the first place, Petrunkevitch could not have restricted *Eoscorpius* to the species *Eoscorpius carbonarius,* as that was done in 1868 by Meek and Worthen. In the second place, Petrunkevitch could not compare the position of the eyes in the holotype, as at that time the holotype, and only specimen known, did not reveal any eyes, as they had not yet been exposed. As a matter of record, the eyes (now exposed) are identical. This leaves as the only difference between *Alloscorpius* and *Eoscorpius* the alleged dissimilarity in the width of the carapaces, a very weak and highly doubtful character for the separation of genera.

Nevertheless, Petrunkevitch is incorrect regarding the measurements of the carapace of *Eoscorpius carbonarius* which, including the anterior process, measures 10.2 mm in length or 9.6 mm in length without the process, and 12.2 mm in width at the base. Therefore, the alleged differences in length and width of the carapaces in the genera are erroneous. The genus *Alloscorpius* Petrunkevitch, 1949, is a junior synonym of *Eoscorpius* Meek and Worthen, 1868. Furthermore, the type species *Alloscorpius granulosus* is identical to *Eoscorpius carbonarius* Meek and Worthen and should be relegated to the synonymy of the latter. All known morphological parts are identical. The ornamentation also is identical, including the characteristic row of pustules along the base of each mesosomatic tergite, as well as the pustules bordering the sides of the last preabdominal tergite. Of greater importance is the characteristic double row of setal openings along the fingers of the pedipalps. This can only indicate an *Eoscorpius.*

The holotype and paratype of *Eoscorpius typicus* Petrunkevitch, the holotype of *Typhlopisthacanthus mazonensis* (Petrunkevitch) and the holotype of *Trigonoscorpio americanus* Petrunkevitch are identical to *Eoscorpius carbonarius.* The other paratypes, YPM 126 and 127 (Petrunkevitch, 1913, p. 39) are referred to *Anthracoscorpio* (?) sp. and *Palaeobuthus distinctus* Petrunkevitch. *Alloscorpius granulosus* and *Typhlopisthacanthus mazonensis* are considered to be females. The holotype and paratype of *Eoscorpius typicus* and the holotype of *Trigonoscorpio americanus* Petrunkevitch are considered to be males. This determination is in keeping with knowledge of secondary sex characters in living scorpions.

Alloscorpius wardingleyi (Woodward) has been referred to *Mazonia* by Kjellesvig-Waering (1969). *Al-*



Text-figure 76.—*Eoscorpius pulcher* (Petrunkevitch). Holotype, BM(NH) In.39772. From the Upper Carboniferous, Crow Coal, Phoenix Brickworks, Crawcrook, near Ryton-on-Tyne, Durham, England. See foldout inside front cover for explanation of abbreviations.

A. The entire holotype, a nearly complete prosomal carapace in original relief. **B.** Detail of the left compound eye. **C.** Reconstruction of the pectinal area. Based on text-figure 4 of Wills (1959) with some revision from the holotype. The structure which Wills called opercula is really the prepectinal plate (**ppp**).

loscorpius danielsi (Petrunkevitch) has been referred to *Kronoscorpio* here, and *Alloscorpius tuberculatus* has been referred to *Benniescorpio* by Wills (1960, p. 322). This completes the list of species that Petrunkevitch had, at one time or another, referred to the illusory genus *Alloscorpius*.

Eoscorpius pulcher (Petrunkevitch, 1949)
Text-figures 76, 77

1949. *Lichnophthalmus pulcher* Petrunkevitch, pp. 147–148, figs. 139, 177.
1949. *Europhthalmus longimanus* Petrunkevitch, pp. 154–155, figs. 140, 141, 174.
1953. *Lichnophthalmus pulcher* Petrunkevitch. Petrunkevitch, p. 33.
1953. *Europhthalmus longimanus* Petrunkevitch. Petrunkevitch, p. 33.
1955. *Lichnophthalmus pulcher* Petrunkevitch. Petrunkevitch, p. 75, fig. 43(7).
1955. *Europhthalmus longimanus* Petrunkevitch. Petrunkevitch, p. 75, fig. 45(1).
1959. *Lichnophthalmus pulcher* Petrunkevitch. Wills, pp. 269–282, pl. 49, figs. 1–9; pl. 50, figs. 1–15; text-figs. 2–8.
1960. *Lichnophthalmus pulcher* Petrunkevitch. Wills, *Addenda* p. 331.
1962. *Europhthalmus longimanus* Petrunkevitch. Dubinin, p. 431, figs. 1236, 1254A, B.
1962. *Lichnophthalmus pulcher* Petrunkevitch. Dubinin, p. 431, fig. 1238.

Wills (1959, text-fig. 4) was able to free what he determined to be the opercula (see *Addenda,* 1960, p. 331). This plate he stated "can be matched closely with the genital opercula of *Mazoniscorpio*" (the latter genus has been shown (above), to be a junior synonym of *Palaeobuthus*). The plate in "*Mazoniscorpio*" is not a single plate, but two normal opercular plates ("**el**" on text-fig. 13 of Wills, 1959) with the prepectinal plate jammed forward and over (under in the text-fig.), an action that may have occurred during ecdysis. This also is intimated by the close proximity of the pectines to the opercular plates (see discussion of the prepectinal plate, above). The part labelled "**il**", which Wills (1959, text-fig. 13) considers the internal lobes of the opercula, is also part of the prepectinal lobe, as the operculum does not have internal lobes, either in fossil or living scorpions. The median organ also is part of the prepectinal plate. The opercular plates of *Palaeobuthus distinctus* can be seen in another specimen (Text-fig. 56B) and will bear out the above. Therefore, the large, undivided, elongated plate of *Lichnophthalmus* is also the prepectinal plate ($\mathbf{p^1}$ and **p** of Wills, 1959, text-fig. 4). The opercular plates of *Lichnophthalmus pulcher* should be long on a perpendicular axis as in other *Eoscorpius*.

The conclusion above (see Text-fig. 76C) means that in *Lichnophthalmus,* instead of having the fourth pair of coxae *forward* of the opercular plates as in Wills (1959, text-fig. 4), the coxae must abut the opercular

plates, which remain unknown in *Lichnophthalmus*. If Wills' interpretation is correct, that the fourth pair of coxae is forward of the opercula, it would necessitate a new family under the Pseudobuthiscorpioidea. However, with the new determinations, it is obvious that the genus *Lichnophthalmus* Petrunkevitch, 1949, having a carapace with well-developed cephalic cheeks, lateral schizochroal eyes, anterior glossate process, and anteriorly-located median eyes on a lacrimiform eye node, is a junior synonym of *Eoscorpius* Meek and Worthen, 1868. The differences are on the species level, such as differences in outline of the carapace, cephalic cheeks, pattern of ornamentation and numerous other details. *Eoscorpius pulcher* (Petrunkevitch) is a well-established species differing from all others in the genus.

The holotype (BM(NH) In.39772), consisting of a single piece showing the carapace in its entirety in original relief, is exceptionally well preserved. Petrunkevitch (1949, p. 147) gives a reconstructed dimension of 11 mm long by 13.7 mm. This does not include the anterior, pointed, glossate process, which would have resulted in a measurement of 12.5 mm as the length.

My conclusions from study of the holotype differ in so many important ways from that of Petrunkevitch (1949, p. 147) that it is superfluous to point out the differences. It is better to redescribe the specimen.

The carapace is quadrate, with a distinct anterior, pointed, glossate prolongation on the midanterior margin, which is bent downward. The median eyes are large and round, located on a prominent elliptical eye node, well forward on the carapace. Petrunkevitch (1949, p. 147) states that the eyes are ellipsoidal, but this is due to compaction, as was shown by Wills (1959) concerning a specimen developed by acid. It should be noted that both eyes are not as shown by Petrunkevitch (1949, fig. 139), where the eyes are placed so that their axes form an angle of 90°. The two eyes are slightly crushed so that neither is as shown in that figure. A small interorbital ridge separates the two eyes.

Of greatest importance is the presence of distinct large, slightly intramarginal, lateral schizochroal eyes that had been completely ignored in the original description, although they are sufficiently well-preserved to be noted in Petrunkevitch's photograph (1949, pl. 55, fig. 177). The excellent photograph even shows the presence of small individual schizochroal eyes. In my drawing (Text-fig. 76B), the eye has been greatly enlarged to show the detail. The ocelli are all rounded and about 30 occur in the elliptical (crushed) area enclosing them.

A median sulcus separates the median eye node from the cephalic area, which is unusually elevated and split at the center line. The thoracic part of the carapace also is inflated, but not to the extent present in the cephalic area. A rounded narrow marginal rim is present on the base and posterior half of the carapace. The cephalic area of the carapace is covered with scattered, sparse tubercles, but not in a linear row as was shown by Petrunkevitch (1949, fig. 139).

It is interesting to note the reasoning used by Petrunkevitch (1949, p. 148) in denying the presence of lateral eyes as:

> distinct ridge visible even in the photograph . . . . However, careful examination failed to show imprints of eyes, and the ridge itself is wanting on the right side.

I am not certain if the absence mentioned by Petrunkevitch meant that preservation was incomplete or that the ridge was not present as should be expected in a bilaterally symmetrical animal. His drawing (139) shows a carapace without the "ridge" (=schizochroal eyes) on either side, and reveals that he thought most, if not all, of the anterior of the carapace was preserved. In the specimen the right side is *not* preserved.

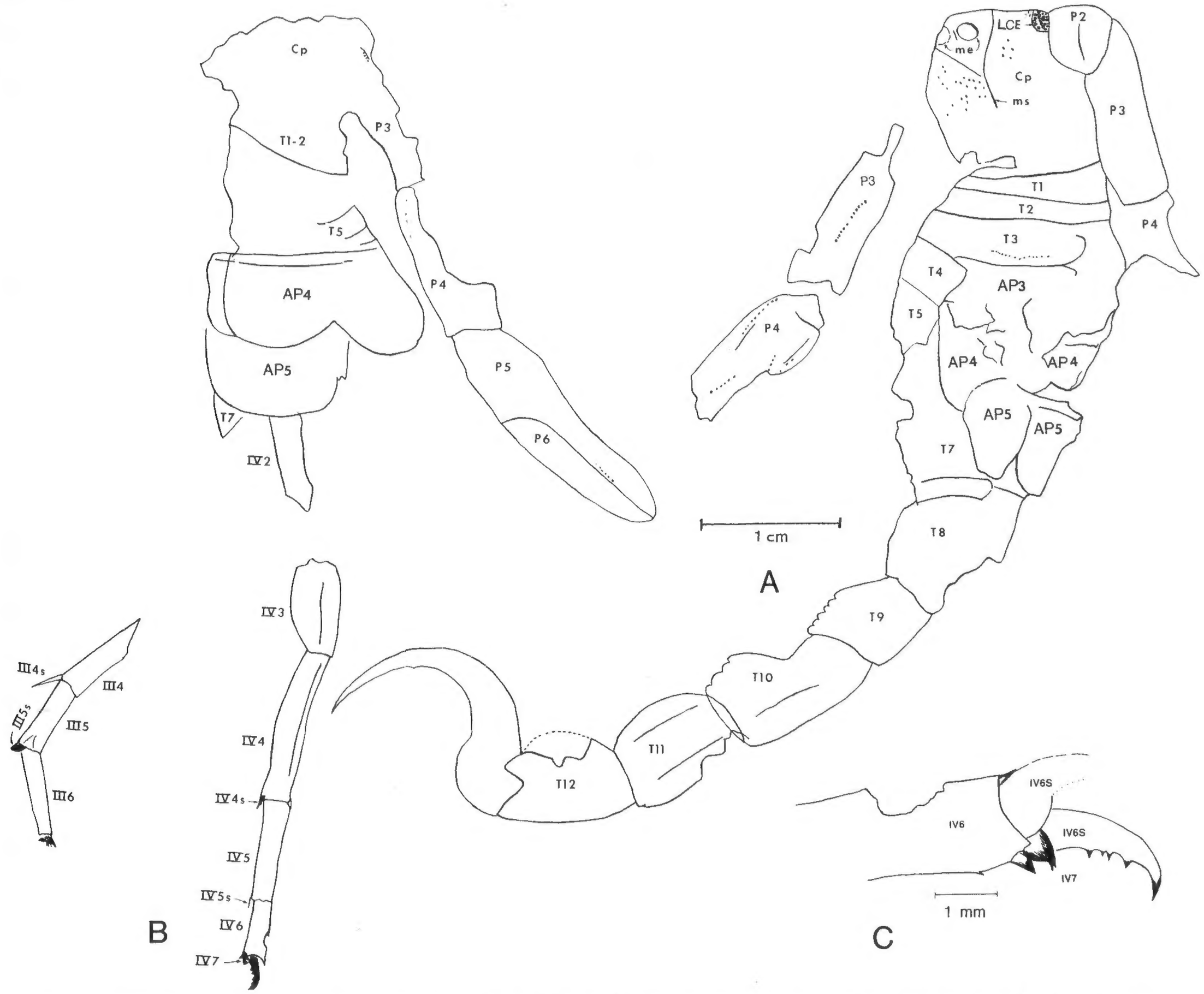
Wills (1959, pp. 269–282, pls. 49–50) successfully extracted most of a topotype specimen, which greatly enlarges our knowledge of this genus and species. I have studied the specimen (BM(NH) In.39770) and my remarks will be restricted to information where differences may occur with Wills' interpretation, as his description is exceptional and can hardly be improved. However, there are some points which I think worth recording. Wills showed that the median eyes are round, and I agree. The lateral schizochroal eyes are too poorly preserved for a good description, but they are present, although not previously recorded. These lateral eyes are seen in Wills' prepared specimen and in a latex cast of the same specimen which I made in 1950.

The anterior transverse ridges, which are prominently developed, were mistaken for intersegmental skin (Wills, text-fig. 2). The basal and postlateral marginal rims of the carapace were not discerned, although they may be seen in his excellent photograph (pl. 49, fig. 2). In his text-figure 6, the basitarsal spurs are mistaken for tarsal spurs.

Europhthalmus longimanus Petrunkevitch was described in 1949 (pp. 154–155, figs. 140, 141, 174), as a new genus and species, which was considered to be the type of the genus *Europhthalmus* Petrunkevitch, 1949. Petrunkevitch had not developed the holotype of *E. longimanus,* as will be shown. Furthermore, he mistakenly thought that two specimens occurred on the same concretion. Scorpions are so rare in the geologic column that it would have been such an improbable condition as to make one question the observation. There is only one specimen, showing mainly the dorsal side.

The holotype of *Europhthalmus longimanus* Petrunkevitch is poorly preserved. The carapace is considerably distorted, leading to the interpretation that Petrunkevitch gave, namely, that it was round on the anterior margin. Obviously this is not the case with this scorpion. Furthermore, it has lateral schizochroal eyes, is a distinct lobostern and the telson is enormously developed. All of these important structures, as well as the third and fourth legs, were entirely missed or otherwise unmentioned, and in the case of the stinger or telson, erroneously reported.

Europhthalmus longimanus Petrunkevitch is a junior synonym of *Eoscorpius pulcher* (Petrunkevitch) because the carapace has identical ornamentation, the median eye node and median sulcus are the same, both are lobosternous, both have lateral schizochroal eyes, and the claws (ungues) of both have spines on the underside. Both occur at the same locality and horizon. The daggerlike posttarsus and long basitarsal spurs found on the first and second legs (Wills, 1959, pp. 277–279) have not been seen on the holotype of *E. longimanus*. However, the legs preserved are not the same, those of the latter being the third and fourth. The part preserved, the ungues of the fourth leg, is identical. I do not think there is much doubt that they are synonymous and, although both were described in



Text-figure 77.—*Eoscorpius pulcher* (Petrunkevitch). BM(NH) In.39766, part and counterpart (the holotype of *Europhthalmus longimanus* Petrunkevitch, 1949). From the Upper Carboniferous, Crow Coal, Phoenix Brickworks, Crawcrook, near Ryton-on-Tyne, Durham, England. See foldout inside front cover for explanation of abbreviations.

A. Dorsal aspect. Note the presence of lateral compound eyes and other details not shown in Petrunkevitch (1949; 1955, fig. 55). **B.** Ventral aspect, showing the long pedipalp; below, legs **III** and **IV** preserved on the same slab. **C.** Termination of leg **IV**. The spur (**IV6s**) is very interesting.

the same publication, *Lichnophthalmus pulcher* Petrunkevitch, 1949 (p. 147), clearly has "page priority" over *Europhthalmus longimanus* Petrunkevitch, 1949 (p. 154), and therefore the latter species name must be suppressed. This has the added advantage that specimens of *E. pulcher* Petrunkevitch have been extracted from the matrix and are therefore far better known than the single specimen of *Europhthalmus longimanus*. At any rate, as *first reviewer,* I hereby select *Lichnophthalmus pulcher* Petrunkevitch, 1949, to be the correct name of the species.

As noted above, the holotype of *Europhthalmus longimanus* Petrunkevitch (see Text-figs. 77A–C) has been inadequately and erroneously described and much information of basic taxonomic value is still to be revealed. Furthermore, the specimen had not been prepared properly, so that the walking legs were unknown (one had been previously revealed, the other exposed by me). The cauda was barely exposed and furthermore, misconstrued in the original interpretation and figure (Petrunkevitch, 1949, fig. 140). The stinger shown on the original figure was merely the fourth caudal segment; the fifth segment as well as the enormous and unusual stinger (telson) were all covered (see latex casts of the original at the British Museum made before exposure). These have now been exposed as well as most of the fourth leg.

It is therefore necessary to redescribe the specimen in order to correct these misconceptions.

The carapace, distorted, was originally quadrate, not rounded anteriorly, as shown by Petrunkevitch (1949, fig. 140). Two large round median eyes occur on a lacrimiform eye node. The surface retains large granules on the sides of the median line. A large compound lateral eye is present at the anterolateral angle. This contains small eyes that are rounded-subhexagonal and each is approximately 0.08 mm in diameter. The entire eye is about 0.8 mm wide, measuring from the margin. The facets, therefore, are relatively large and each lateral eye would contain approximately 30 ocelli—this being a very rough estimate.

The mesosoma is telescoped and highly distorted. There is no such regularity of tergites as shown in the original figure (Petrunkevitch, 1949, text-fig. 140), but of great importance is the presence of deeply-bilobed lobostern abdominal plates. These seem to be the fourth and fifth abdominal plates, and reveal the characteristic deep notch at the posterior middle part.

The cauda was covered in part so that Petrunkevitch's original figure (1949, fig. 174) shows only a part of the base of the cauda up to the fourth caudal segment. Careful exposure revealed all the segments, and this showed that instead of being a scorpion with a very narrow tail, it had a very robust cauda. The cauda is turned sideward and shows that the superior carinae were developed into high, prominent, coarsely-serrated ridges (see Text-figs. 77A, B).

The stinger or telson is of particular interest as this is unusually large and narrow (see Text-fig. 77A). The vesicle is relatively small in size, but this is followed by an enormous scimitarlike aculeus that curves in almost a circular manner. The scimitariform aculeus is extremely long and narrow, gradually tapering in width to end in a point. No tubercle occurs below the aculeus, but midway on the inside of the curve of the stinger is a small protrusion, actually a widening, which likely lent support to the great scimitarlike stinger. No scorpion, to my knowledge, has a stinger that compares with this formidable weapon, although *Palaeobuthus distinctus* Petrunkevitch approaches this one in length.

Measurements (in mm) of the cauda of BM(NH) In.39766.—

Tergite:	length	width from side (height in life)
8	9.0	7.0
9	7.5	7.0
10	9.0	6.3
11	9.6	5.9
12	8.3	6.0 (estimated)
Telson:	13.0	5.4 (at base)

The prosomal appendages are not preserved except for fragments of two legs and the pedipalp. The latter has been described. I have not been able to see well-preserved granules on the edge of the finger, but they are present, although insufficiently well-preserved for detailed description. The entire pedipalp is in keeping with the rest of the scorpion—it is very stout, although the hand of the chela is long. The tibia and finger are thick and are surmounted with carinae that have coarse pustules in rectilinear series.

A fragment of one of the legs is present, but it is not possible to state definitely what leg this was (possibly the third). This is noteworthy for the very long spine present at the end of the tibia. This is an unusually long tibial spine.

The fourth leg (see Text-fig. 77B) is present from the femur to the posttarsus. The segments are all long and narrow, in particular the tarsus and basitarsus. The posttarsus is a small (see Text-fig. 77C) short triangular stub, whereas the only claw that was preserved of the two original ones is long, curved at the tip and armed with small denticles on the underside.

The overall length of this scorpion from the anterior of the carapace to the end of the cauda is estimated at 100 mm.

Type information.—All specimens of *Eoscorpius pulcher* come from the Upper Carboniferous, Crow

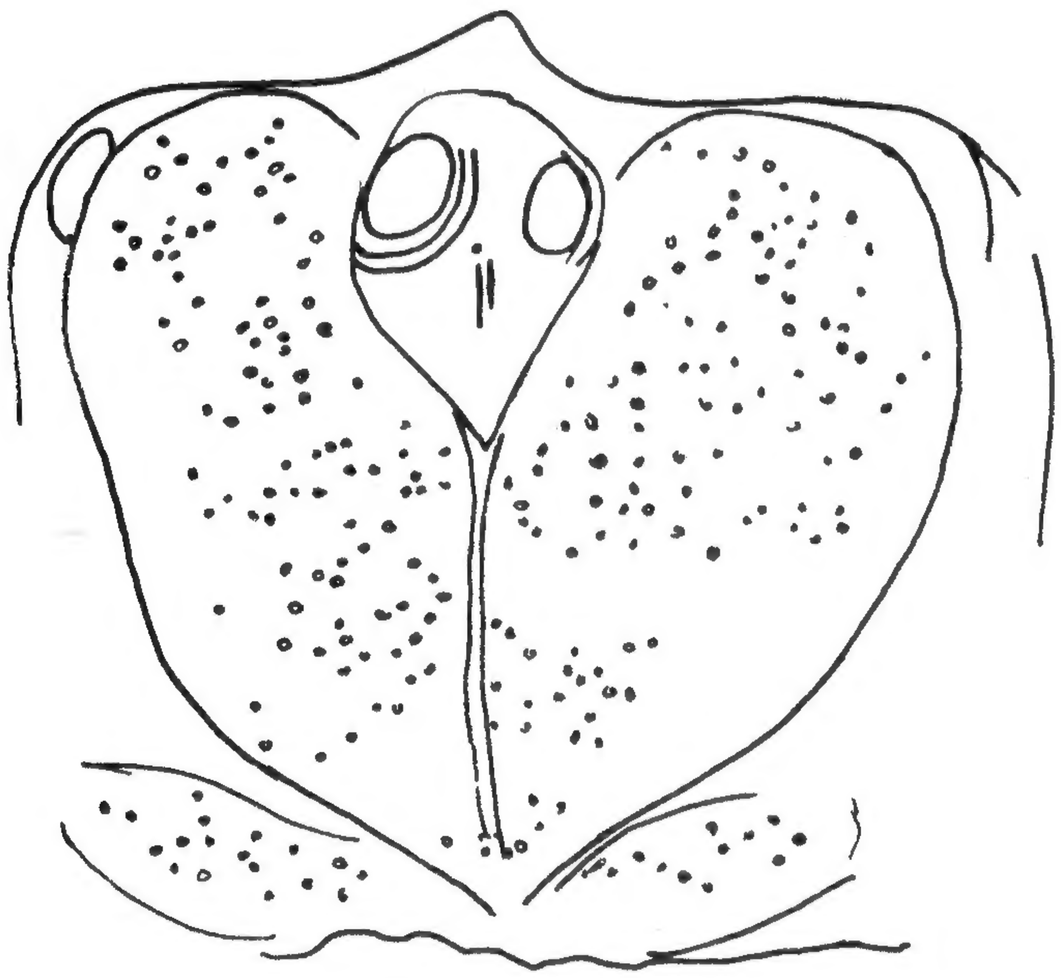
Coal, at the Phoenix Brickworks at Crawcrook, near Ryton-on-Tyne, Durham, England, including the holotype (BM(NH) In.39772), the holotype of *Europhthalmus longimanus* (BM(NH) In.39766), and the specimen used by Wills (1959, pp. 269–282) (BM(NH) In.39770).

Eoscorpius mucronatus, new species
Text-figure 78

1959. *Lichnophthalmus pulcher* Petrunkevitch. Wills, *not* Petrunkevitch (*partim*), pp. 269, 272, pl. 49, fig. 10.

The holotype is represented by a carapace, nearly whole, and in good condition. It is preserved in greenish-gray, soft shale with numerous plants. Previously, Petrunkevitch had considered the specimen as *Lichnophthalmus* ? (unpublished), and it was identified as *L. pulcher* Petrunkevitch by Wills (1959, p. 269). The differences are much too great to warrant placing both in the same species and it is herein described as new. It comes from the same zone (which has considerable thickness), although from a different horizon and locality.

The carapace is preserved in two parts: the specimen proper, and a Marco-cast (see Wills, 1959, pp. 263–265; Wills, 1960, pp. 331–333; Wills, 1965, p. 97) made of the same. Thus both specimens should be studied together, and in fact, the figure (Text-fig. 78) is a composite of the two. Actually, most of the skin adhered to the Marco-cast when prepared by Wills, and hardly improved the specimen. Non-calcareous specimens should not be subjected to the "Wills technique". Nevertheless, both specimens reveal sufficient information to add to our knowledge of the British scorpions.



Text-figure 78.—*Eoscorpius mucronatus,* n. sp. Holotype, GSM PF 1392–1393 (formerly Wills' No. Za.2842). A nearly complete carapace. From the Upper Carboniferous, Coal Measures (*Anthraconaia modiolaris* Zone), Parkgate Coal, Dodworth, near Barnsley, Yorkshire, England.

Carapace typically squarish, rounded at the anterior angles, with the middle of the anterior consisting of a prominent, triangular linguiform process. Median eyes anteriorly, but intramarginally, located. A median eye node, lacrimiform and with well-developed orbital ridges, contains the median eyes, which are round, although slightly distorted. Lateral schizochroal eyes, relatively small, but definitely present in the Marco-cast. These eyes are slightly reniform and are present at the anterior angles of the carapace, but not touching the margin. The carapace is divided by a median sulcus that separates two large, inflated, cephalic cheeks. The base is not present, but the smaller basal cheeks are prominent and inflated. Both the cephalic and the basal cheeks are covered by numerous prominent pustules.

Estimated width at anterior of carapace: 9 mm. Estimated overall length of scorpion about 80 mm.

Type information.—Carboniferous, Coal Measures, *Anthraconaia modiolaris* Zone, Parkgate Coal, Dodworth, near Barnsley, Yorkshire, England; L. Moysey, collector, ca. 1910; GSM PF 1392-1393 (formerly Wills' No. Za.2842).

Derivatio nominis.—*mucronatus* (L.) = pointed.

Remarks.—The differences between this species and *Eoscorpius pulcher* (Petrunkevitch) are readily apparent from the presence of very dense pustulation on the carapace of the new species. However, this difference could well be sexual, since it is a well-known secondary sexual character in the male to have considerably more granulation on the carapace and other areas than the female. There are more important differences: the lateral eyes are placed further back on the carapace in *E. mucronatus*; the anterior linguiform process is longer on *E. mucronatus*; the eye node is lacrimiform, rather than subrounded as in *E. pulcher*; and the lateral cephalic cheeks are larger and more pronounced anteriorly in *E. mucronatus*.

Eoscorpius distinctus (Petrunkevitch, 1949)
(new description)
Plate 13, figures 1–4; Text-figures 79A–B, 80

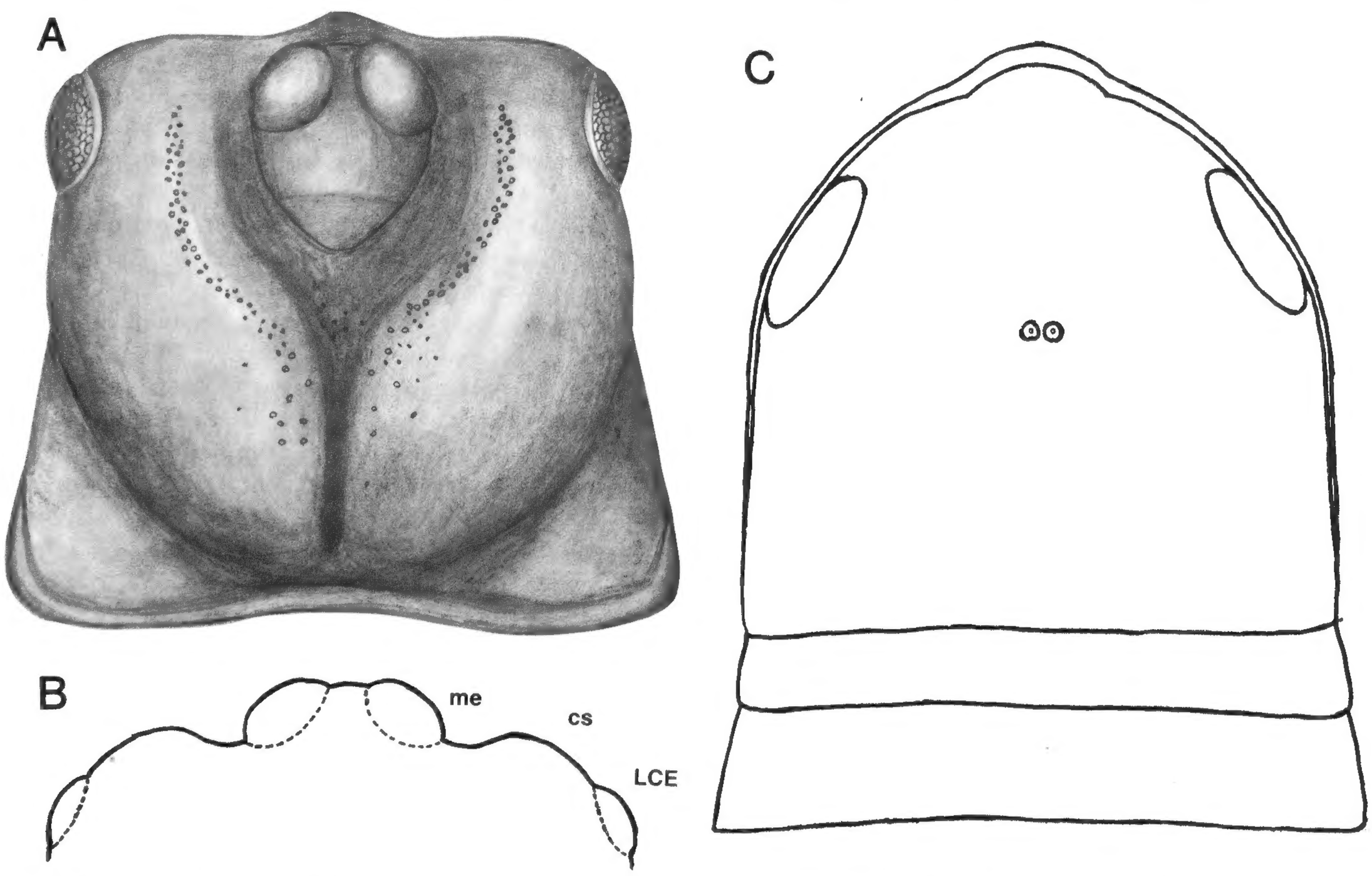
1949. *Typhloscorpius distinctus* Petrunkevitch, pp. 146–147; figs. 146, 178.
1953. *Typhloscorpius distinctus* Petrunkevitch. Petrunkevitch, p. 33.
1955. *Typhloscorpius distinctus* Petrunkevitch. Petrunkevitch, p. 75, fig. 44(2).
1962. *Typhloscorpius distinctus* Petrunkevitch. Dubinin, p. 431, fig. 1237.

Specimen I.—The holotype, BM(NH) In.13990.

Typhloscorpius distinctus Petrunkevitch, from the Upper Coal Measures of Coseley, Staffordshire, England, should be referred to the genus *Eoscorpius,* as will be shown by new evidence. The original description (Petrunkevitch, 1949, p. 146) is erroneous, and it is necessary to redescribe the holotype. A rubber cast of the holotype, obverse and reverse, sent to me by Dr. H. W. Ball of the British Museum (Natural History), reveals a scorpion with features of *Eoscorpius.* Petrunkevitch (1949, p. 146) stated that one of the features that made the scorpion distinct was that "it has no eyes". However, no scorpion known has more eyes than *T. distinctus*! Distinct, large, facetted lateral eyes occur at the anterolateral angles. These facetted eyes are protuberant and were *partly* embedded in the matrix, but fully half of each eye was visible before mechanical development. Later the entire eyes were exposed (see Text-figs. 79A, B). A narrow, raised palpebral rim surrounds the eyes, which have retained fine ommatidia. The ommatidia are much finer in size than those present in the eyes of *Eoscorpius* and *Kronoscorpio.* I estimate that about 75 ommatidia compose the eye, approximately twice as many as in the latter genera. I do not consider the number of ommatidia as of more than trivial importance. The facetted lateral eyes measure 1.2 mm in length. The median eyes, which Petrunkevitch thought were also absent, but are now exposed (see Pl. 13, fig. 4, and Text-figs. 79A, B), are as large as those in *Eoscorpius* and *Kronoscorpio,* and are placed anteriorly on a raised, lacrimiform eye node. The anterior margin is straight, with a triangular protuberance at the center. The eye is elliptical and measures 1.3 mm in length and 0.9 mm in width.

A Y-shaped sulcus, with the median eye node straddling the open end, divides the carapace. Two large, wide cephalic ridges continue on both sides of the sulcus almost to the base of the carapace. Scattered large pustules surmount the ridges and follow the contours of the Y-shaped sulcus. The thoracic part of the carapace rises diagonally from the cephalic ridges to end in a raised, round, basal marginal rim.

It should be noted that the central protuberance at



Text-figure 79.—*Eoscorpius distinctus* (Petrunkevitch). Specimen I, holotype, BM(NH) In.13909. From the Upper Carboniferous, Middle Coal Measures, Coseley, South Staffordshire Coalfield, England. See foldout inside front cover for explanation of abbreviations.

A. Reconstruction of the holotype. All parts shown here have been seen on the obverse or the reverse of the concretion. **B.** Cross-section through the anterior portion of the carapace to show the position of the eyes and the elevation of the eye node. **C.** *Hughmilleria banksi* Salter, introduced for comparison in text.

the anterior margin is curved downward and resembles the glossated front of some of the eurypterids, such as *Eocarcinosoma, Mixopterus, Rhinocarcinosoma,* certain hughmilleriids such as *Hughmilleria banksii* (Salter) and others. This feature is well known in many other scorpions, such as *Proscorpius, Kronoscorpio,* etc. *Eoscorpius* probably was not a scorpion that lived underground, whether in water or not, as the pedipalps are much too long for a burrowing scorpion. However, the bent "plow-nose" or glossate anterior is, in a water medium, an admirable tool for pushing soft sediments over the carapace for concealment. This would correlate with the anteriorly-located and highly-elevated median eyes, as this part would remain exposed, in wait for unwary prey.

The median eye node is bounded on the posterior end by a flattened area. The two large ocelli are separated by a wide sulcus. The median eye node and ocelli were uncovered by Dr. H. W. Ball and Mr. R. Rixon at my request, as it was obvious from the photograph of Petrunkevitch (1949, fig. 178) that the median eyes were present in the counterpart, but had not been exposed by Petrunkevitch in his original study. He had not noted the presence of either the median eyes or the prominent facetted lateral eyes and consequently, believing that the scorpion was blind, erected the genus *Typhloscorpius.*

I consider the genus *Typhloscorpius* Petrunkevitch to be a junior synonym of *Eoscorpius,* on the basis that the holotype specimen does not show any characters that distinguish it from the latter genus. The pedipalp described below further strengthens that determination, although my study of the cast was made in 1965.

Specimen II.—I refer to this species a single pedipalp (BM(NH) I.3172), on the basis that both the holotype and the pedipalp are clearly parts of an *Eoscorpius.* The fact that both are from the same horizon and general locality strengthens that determination. The double row of setal sites on the pedipalp fingers is indicative of the genus *Eoscorpius.*

The pedipalp is from the left side, has most of the trochanter to the free finger preserved, all in excellent condition. The trochanter, however, is too poorly preserved for description.

The femur is very long, narrow and wider at the end than elsewhere. Setal sites are concentrated on the anterior, dorsal side (see Text-figs. 80A, B).

The tibia is preserved so that the posterior half represents the dorsal side, whereas the anterior represents the ventral. The tibia is long, subquadrangular in shape and retains a concentration of setal openings on the ventral side.

The hand is narrow, rounded on the inner side and nearly straight on the outer edge. The hand seems to be devoid of setal openings, a condition that may be due to lack of preservation (see Text-figs. 80A, B).

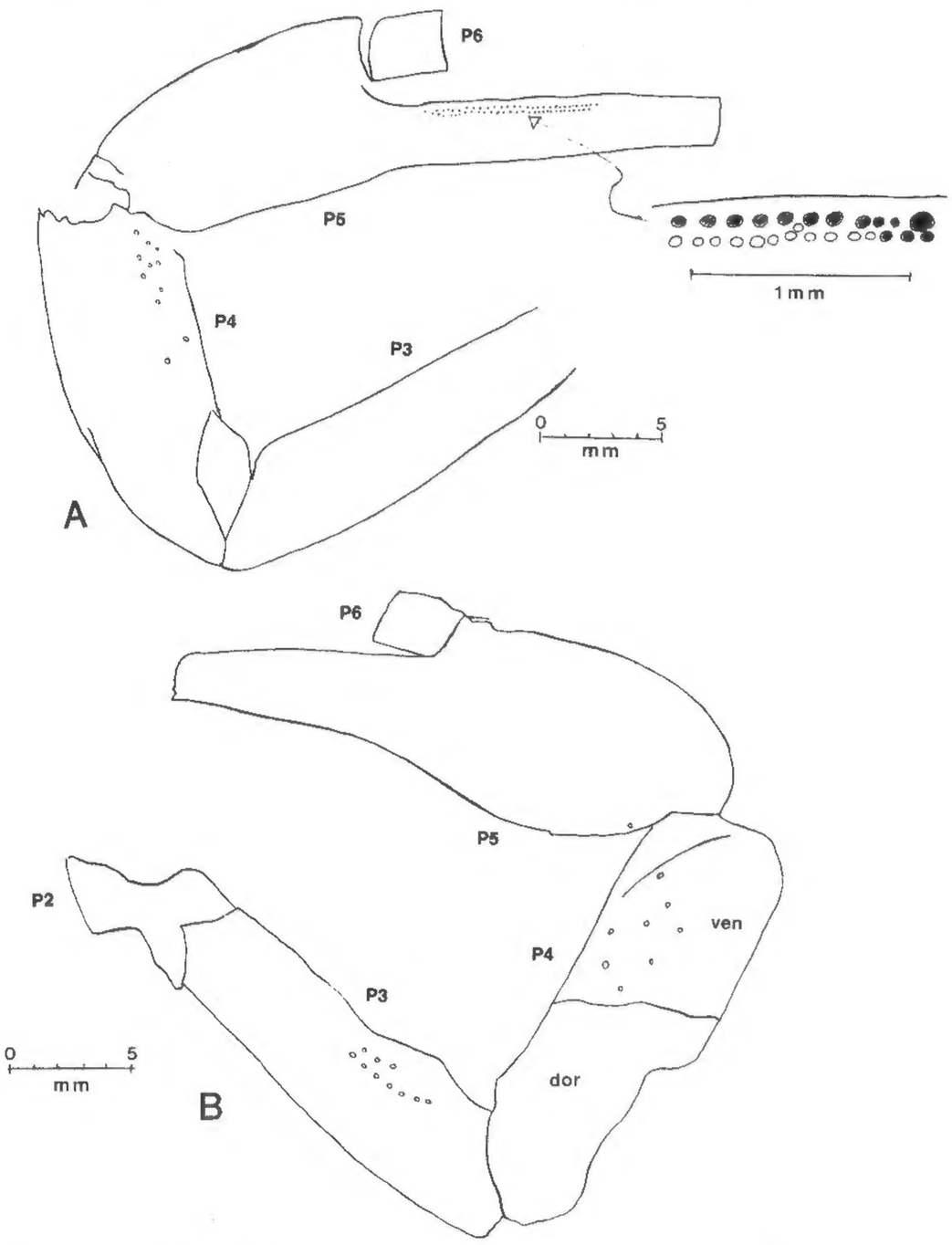
The fixed finger is preserved nearly whole. It is very slender, cultrate, slightly recurving and with a distinct double row of setal sites on the outer (dorsal) face of the finger. The inner row is composed of coarse setal sites which, in many parts of both rows, are filled with a dark material that seems to represent the broken stubs of the setae. The anterior or outer row contains much thicker setal openings than the inner row.

Measurements (in mm) of pedipalp (BM(NH) I.3172).—

	length	width
Femur:	18.9	5.0
Tibia:	17.5	6.0
Hand:	11.5	7.8

Type information.—The holotype is from the Upper Carboniferous, Middle Coal Measures, from Coseley, South Staffordshire Coalfield, England.

The pedipalp (BM(NH) I.3172) described above is also from the Upper Carboniferous, Middle Coal Mea-



Text-figure 80.—*Eoscorpius distinctus* (Petrunkevitch). Specimen II. BM(NH) I.3172. From the Upper Carboniferous, Middle Coal Measures, South Staffordshire Coalfield, Dudley, England. See fold-out inside front cover for explanation of abbreviations.

A. Enlargement of setal rows on the pedipalp finger. **B.** The same pedipalp from the counterpart of the nodule.

sures, South Staffordshire Coalfield, but from Dudley, England.

Both the holotype (BM(NH) In.13909) and the pedipalp (BM(NH) I.3172) are in the collections of the British Museum (Natural History).

Eoscorpius sparthensis Baldwin and Sutcliffe, 1904
(new description)
Text-figure 81

1904. *Eoscorpius sparthensis* Baldwin and Sutcliffe, p. 395, figs. 2–3.
1911. *Anthracoscorpio sparthensis* (Baldwin and Sutcliffe). Pocock, pp. 20–21.
1913. *Eoscorpius sparthensis* Baldwin and Sutcliffe. Petrunkevitch, p. 34.
1923. *Anthracoscorpio sparthensis* (Baldwin and Sutcliffe). Moore, p. 132, pl. 1, fig. 6.
1949. *Eoscorpius sparthensis* Baldwin and Sutcliffe. Petrunkevitch, pp. 152–153.
1953. *Eoscorpius sparthensis* Baldwin and Sutcliffe. Petrunkevitch (*partim*), pp. 27–28, fig. 120; *not* spec. L 8182 in the Manchester Museum.

Specimen.—The holotype of *Eoscorpius sparthensis,* UMM L 6271A, B.

The holotype consists of two parts of a large nodule composed of hard, shaly ironstone. Most of the carapace, opisthosoma and the left pedipalp are preserved. Preservation is good in some respects but requires the use of oblique lighting and investigation under alcohol and in a dry state. Each of these methods will reveal some structures that other methods do not show. The specimen is fully preserved; however, along the carapace, which has been crushed and compressed laterally, the outlines and structures are by no means clear. Nevertheless, on the counterpart, by use of rubber casts as well as the methods described above, considerable detail has been discerned. The carapace is elongate with a glossate process along the central part. Behind this is a large eye node, teardrop-shaped, with two large median ocelli. At the anterolateral corners, seen particularly on the counterpart, is a small, reniform lateral eye that shows small, rounded facets, which probably represent only the impression of the lenses (see Text-fig. 81C). A large, deep sulcus separates the eye node from the elevated area of the carapace, which occurs as inflated cheeks toward the genal angles. Apparently an elevated ridge occurs along the base of the carapace. Large pustules are present along the elevated areas and also on the teardrop-shaped ocellar node, all of which are probably setaceous. What appears to be an ocular ridge, in the form of an inverted "V", occurs at the base and between both median eyes (see Text-figs. 81A, B).

The seven tergites of the preabdomen, each of which increases in length posteriorly, are revealed in dorsal aspect. It appears that their greatest width occurs around the fifth or sixth tergite. Two strong ridges are developed on the seventh tergite. Each tergite is bounded anteriorly by a strong transverse marginal ridge and remnants of small punctations are present on all of the tergites. The venter is not preserved, although on the sixth tergite, part of the tergite has been removed and reveals a round area that undoubtedly is a reflection of a lobostern plate. Also impressed through the third tergite are two rounded areas that represent part of a lobostern abdominal plate.

The cauda is preserved on its side and shows that it has highly elevated, rounded dorsal ridges. On the lateral part of each tergite are two prominent ridges. Each tergite seems to be approximately the same size, although only the eighth to the eleventh are preserved. Only a fragment of the twelfth tergite is present and the telson is unknown.

The entire pedipalp is preserved, and is a slender structure overall. The trochanter is unusually long, with a femur and tibia of approximately the same size. Punctations in linear series are found in two lines across the femur. These undoubtedly occurred on ridges. On the tibia are at least three ridges. The hand is narrow, elongated, and probably retained three ridges in life. Only the free finger is preserved and this is long and curving, but shows a structure that is of considerable importance in the identification of this scorpion as *Eoscorpius.* There is an impression running along the inner part, but not at the edge, of the free finger, which has small setal perforations arranged on either side of the line in which a double row occurs on the inner side, whereas only a single row of these punctations is present on the outer side. This is also found in *Eoscorpius carbonarius,* but there only a single row of setal openings occurs on the inner side of the narrow linear groove (see Text-fig. 81D).

Measurements (in mm) of holotype (UMM L 6271A,B).—

Length of carapace through middle:	11.4
Greatest length of pedipalp trochanter:	5.2
Length of pedipalp femur:	8.4
Length of pedipalp tibia:	9.2
Length of hand (midsection):	7.2
Width of hand (greatest):	4.2
Length of free finger (inner edge):	9.6

Text-figure 81.—*Eoscorpius sparthensis* Baldwin and Sutcliffe. Holotype (UMM L 6271, A,B), part and counterpart. From the Upper Carboniferous, Middle Coal Measures, Sparth Bottoms, Rochdale, Lancashire, England. See foldout inside front cover for explanation of abbreviations.

A. Counterpart. **B.** Part. **C.** Details of the right lateral facetted eye. The marginal rim (**mr**) is indicated. **D.** The right pedipalp and enlargement of the basal part of the free finger to show details of setal arrangement.

A

1 cm

B

C

mr

1mm

P6

P2

P3

P4

P5

1 cm

D

1 mm

Measurements of UMM L6271A, B (cont'd).

Length of tergites:	
1	2.3
2	3.1
3	3.8
4	4.2
5	4.2
6	4.8
7	7.0
8	6.5
9	6.5
10	6.1
11	5.9

Type information.—Middle Coal Measures, Sparth Bottoms, Rochdale, Lancashire, England.

Remarks.—This specimen was first described as *Eoscorpius* by Baldwin and Sutcliffe. Later Pocock (1911) referred the species to *Anthracoscorpio.* Petrunkevitch (1953) states, "but the shape of the portions of the carapace and the general appearance speak strongly in favor of its being an *Eoscorpius*". *Eoscorpius carbonarius* was incorrectly known at that time as such important structures as the facetted lateral eyes, the median eyes, the anterior protuberance of the carapace, the type of the abdominal plates, termination of the legs, and the presence of the spurs on the legs were totally unknown. It became, therefore, rather common to refer any specimen that looked like a scorpion to the genus *Eoscorpius.* No one could with certainty refer a living scorpion to any particular genus on the basis of "shape and proportions of the carapace and the general appearance". And, much less, should this be a criterion with fossil forms. I agree with Petrunkevitch that the species *sparthensis* should be assigned to *Eoscorpius,* but for altogether different reasons. For example, I place this specimen in the genus *Eoscorpius* because it agrees in the presence of the anterior linguiform process, it has median eyes, placed on an eye node exactly as in *Eoscorpius,* and facetted lateral eyes that are also the same as in that genus. The median sulcus of the carapace is identical. It is also important that both are lobosternous scorpions. Again, another factor that shows the species to belong to *Eoscorpius* is the presence of the peculiar and distinct ornamentation, consisting of rows of setae on the free finger of the pedipalp. This is almost exactly as found only in the genus *Eoscorpius.*

Baldwin and Sutcliffe (1904, p. 396) mention that on one side of the specimen is a discoloration of the rock that probably represents the intersegmental tissue between the abdominal plates and the tergites. This discoloration is also present on the left side and I agree with Baldwin and Sutcliffe that this likely represents the intersegmental tissue. Pocock (1911) referred *Eobuthus rakovnicensis* to the synonymy of *Eoscorpius sparthensis,* which he considered to belong to *Anthracoscorpio.* This is incorrect, as *Eobuthus rakovnicensis* is the type species of the genus *Eobuthus.*

The figure which was used in the original description by Baldwin and Sutcliffe (1904, fig. 2) was a rough sketch, which Pocock made for the authors (1911, p. 21). This sketch showed only the side containing the relief. In the figures shown here both part and counterpart are reproduced for the first time, as previously only photographs had been available of this interesting specimen. It is not possible to see many clear details from photographs of scorpions. In this particular case, the counterpart is the specimen which shows by far the greater detail.

Eoscorpius species

1963. *Lichnophthalmus* sp. Laurentiaux-Vieíra and Laurentiaux, pp. 23–25, pl. 3, fig. 1; text-fig. 1.

Under the name *Lichnophthalmus* sp., Laurentiaux-Vieíra and Laurentiaux (1963, p. 23) describe and figure the anterior part of a cephalothorax of a scorpion from the Upper Carboniferous (Lower Autunian) of the Aumance Basin in France. This specimen exhibits two large areas in the shape of half-moons in the anterolateral angles. The writers refer to these areas as "alveolate areás", as Petrunkevitch (1913, p. 43) had done in reference to *Kronoscorpio danielsi.* These lunate areas are undoubtedly the lateral compound eyes, and the "alveolate areas" are the imprints of the ommatidia.

The Aumance specimen is properly referred to *Eoscorpius,* and likely is a form having affinities with, but distinct from *Eoscorpius distinctus* (Petrunkevitch).

The repository of the specimen is not indicated. It may be either in the École Nationale Supérieure des Mines de Paris or in the Geology Department of the Faculté des Sciences de Reims.

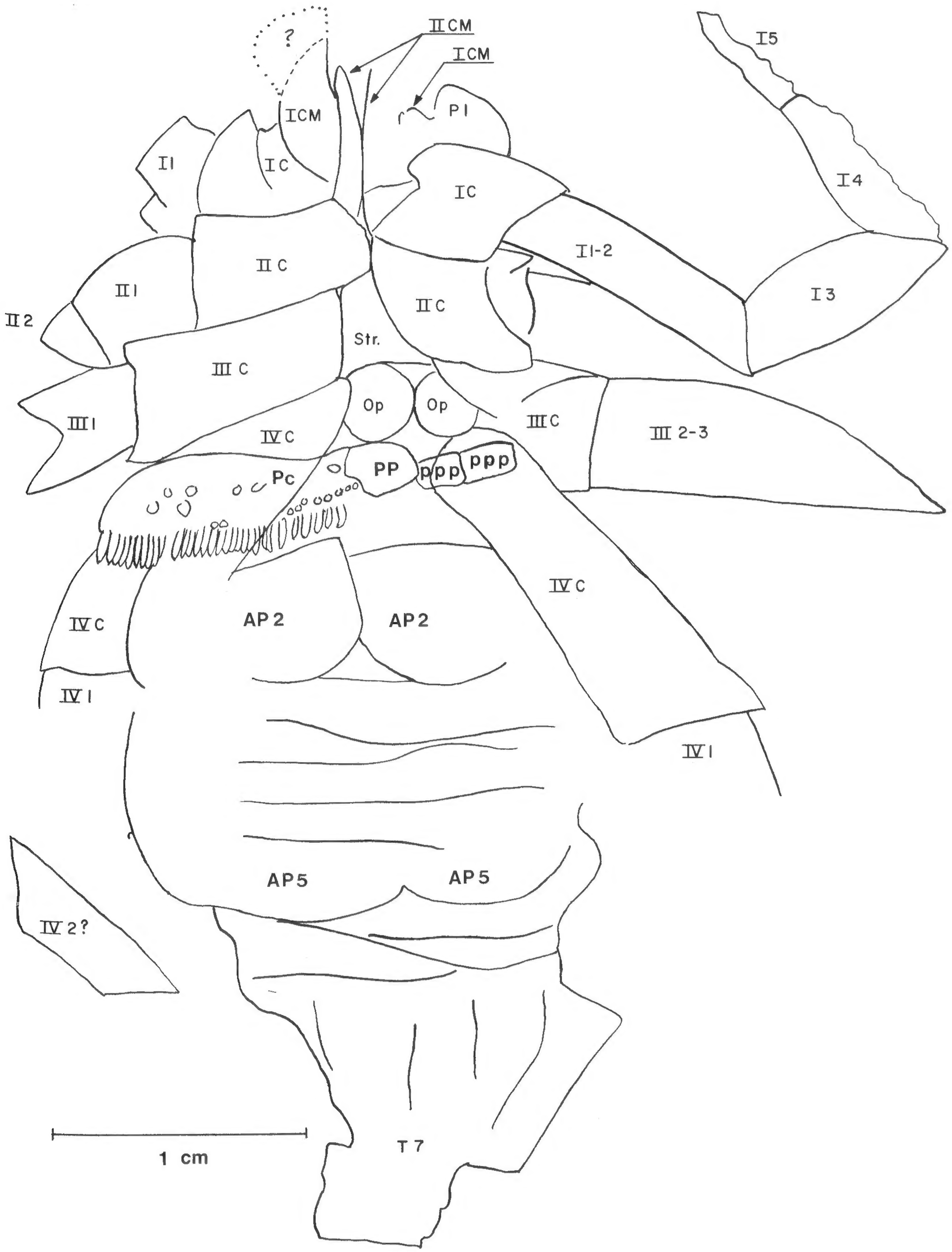
Eoscorpius casei, new species
Text-figure 82

1972. *Eoscorpius* sp. Carroll *et al.,* p. 64.

Ventral surface of a scorpion (PU 87266) comprising the coxosternal region, the mesosoma through the seventh tergite, one side of the pectines, and portions of the walking legs.[29]

[29] Kjellesvig-Waering named the specimen and made a detailed drawing of it, thus indicating his interpretation of what is present, but never got around to writing up the description. A.S.C.

Text-figure 82.—*Eoscorpius casei,* n. sp. Holotype, PU 87266. From the Carboniferous, Lower Pennsylvanian (Westphalian A), from a cliff exposure at West Bay, southwest of Parrsboro, Cumberland County, Nova Scotia, Canada. See foldout inside front cover for explanation of abbreviations.


?
IICM
ICM
ICM
PI
II
IC
IC
I5
I4
I1-2
I3
IIC
IIC
II1
II2
Str.
III C
III1
Op
Op
IIIC
III 2-3
IVC
PP
ppp
ppp
Pc
IVC
AP2
AP2
IVC
IV1
IV1
AP5
AP5
IV2?
T7
1 cm

The dimensions are taken from the drawing, by the compilers, and are approximate at best. The length of the specimen from the anterior end of the maxillary lobe of the first coxa to the posterior end of the seventh tergite is 48 mm. The seventh tergite itself is 10.5 mm long, but is too incomplete in width to measure. The incomplete width of the mesosoma is 19+ mm. The coxa of the fourth leg is complete and is 15.5 mm in length and averages 4.2 mm in width. One of the pectines is well preserved and measures 4 mm in length and 10.9 mm in width. About 30 teeth were preserved, but more were present in life.

Type information.[30]

Derivatio nominis.—The specimen is named after its discoverer, Gerard R. Case.

Genus **TRACHYSCORPIO**, new genus

Eoscorpiidae of large size, carapace with deep, narrow median sulcus, dividing the cephalic area into two narrow, inflated parts; facetted lateral eyes well developed, surrounded by a narrow rim. The pleural area of carapace is very wide; ornamentation comprises large nodular scales. Pectines very large, no areoles, serrated edge; apparently a fossorial adaptation.

Derivatio nominis.—*trachy* (Gr.) = rough (pertaining to the skin).

Type species.—*Trachyscorpio squarrosus,* n. gen., n. sp.

Geological range.—Lower Carboniferous.

Remarks.—The narrow cephalic area and the wide pleural areas of the carapace will distinguish this genus from all others. The lack of fulcra on the large, finlike pectines, devoid of areoles, is an important generic distinction. The fossorial adaptation of the pedipalp is also very important. The maxillary lobes of the second pair of coxae are very short.

Trachyscorpio squarrosus, new species
Text-figures 83A–D

Specimen I.—The holotype is shown on Text-figures 83A, B (BM(NH) In.25985). This specimen reveals about half of the carapace, but includes important structures such as the facetted lateral eye, the cephalic shield, the pleural area of the carapace, rims, both lateral and basal, and the nodular ornamentation. The parts preserved permit a reasonable reconstruction (see Text-fig. 83A).

The facetted lateral eye is reniform, and clearly reveals subrounded facets, is surrounded by a raised rim, and possibly retains as many as 150 ommatidia (see Text-fig. 83B). The carapace is bounded at the base by a raised rim that is thickest at the center and narrows toward the genal angles. The lateral margins of the carapace are bounded by a narrow marginal rim that tapers anteriorly and presumably disappears in the area anterior to the facetted lateral eyes. The pleural area of the carapace is quite strongly elevated, and ornamented with small granules. The cephalic area also is highly raised, rather narrow in comparison with other Lobosternina, and split in the center by a narrow, smooth sulcus. Both lobes of the raised cephalic area are covered with conspicuous large nodules that vary in shape from rounded to irregular-elongated (see Text-fig. 83A). The rest of the pleural area of the carapace is covered with nodular ornamentation. The median eyes are unknown, as they were not preserved. However, they undoubtedly were well developed as all Lobosternina with facetted lateral eyes always have the accompanying median eyes, which are placed on a tear-shaped mound anterior to the median sulcus. The sulcus was preserved.

The facetted lateral eye is 26.5 mm from the base of the carapace, measures 2.4 mm in width and possibly 4.0 mm in reconstructed length. The entire carapace probably measured 44 mm in width at center, and slightly less than that in length. This would indicate

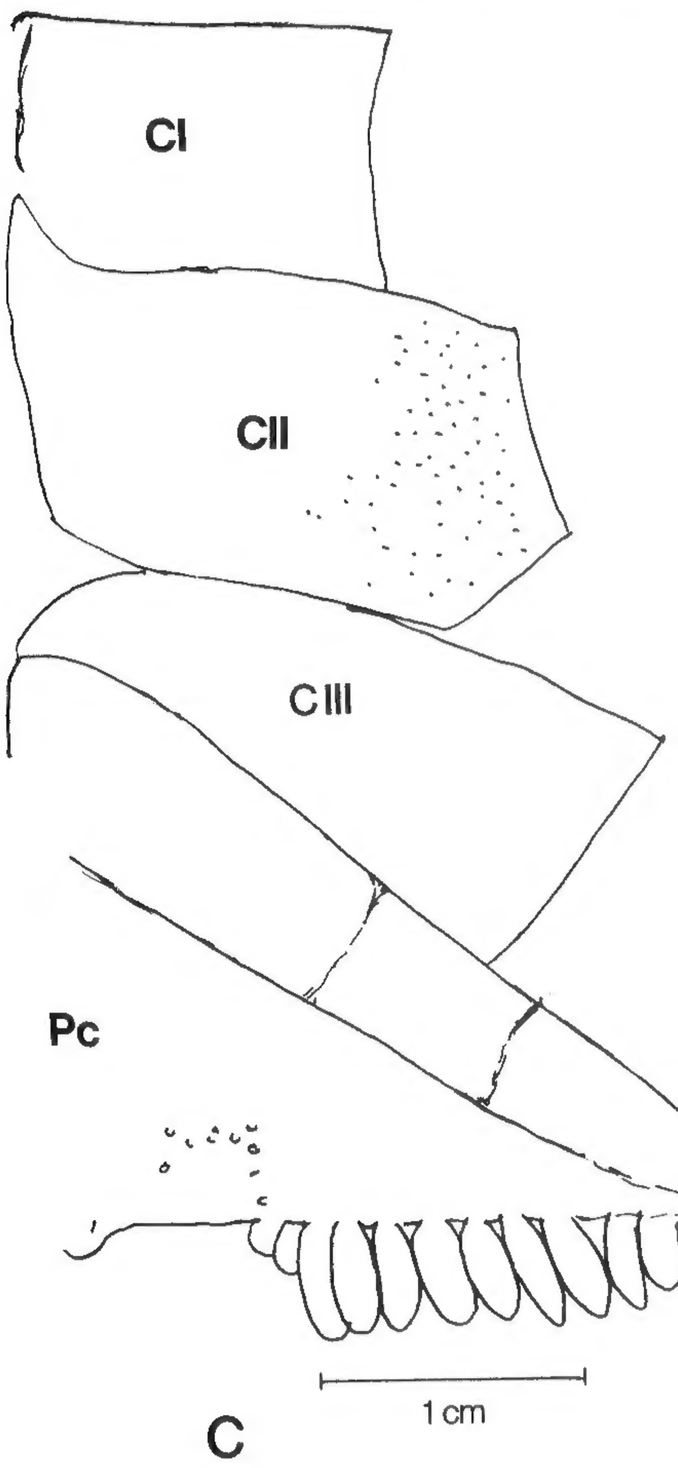
[30] The following information was kindly sent me by Dr. Donald Baird of Princeton University. "The holotype of *Eoscorpius casei* (PU 87266) was discovered by my field assistant, Gerard R. Case, on 21 August 1967. It is preserved on a split section of fine-grained, reddish-brown sandstone cobble containing comminuted plant material. The cobble lay below high-tide level near the western end of the Carboniferous cliff exposure that forms West Bay, southwest of Parrsboro, Cumberland County, Nova Scotia. We were unable to determine the exact source bed, but the cliff between Union Valley and Watering Brook is composed of vertically-standing reddish-brown sandstones and shales belonging to the lower or "red" facies of the Parrsboro Formation of the Mabou Group. This formation has been dated on megafloral and microfloral evidence as Westphalian A, Lower Pennsylvanian. The sedimentology, stratigraphy and paleontology of the locality is discussed by Carroll *et al.* (1972, pp. 58–64), where the *Eoscorpius* specimen is cited on p. 64." A.S.C.

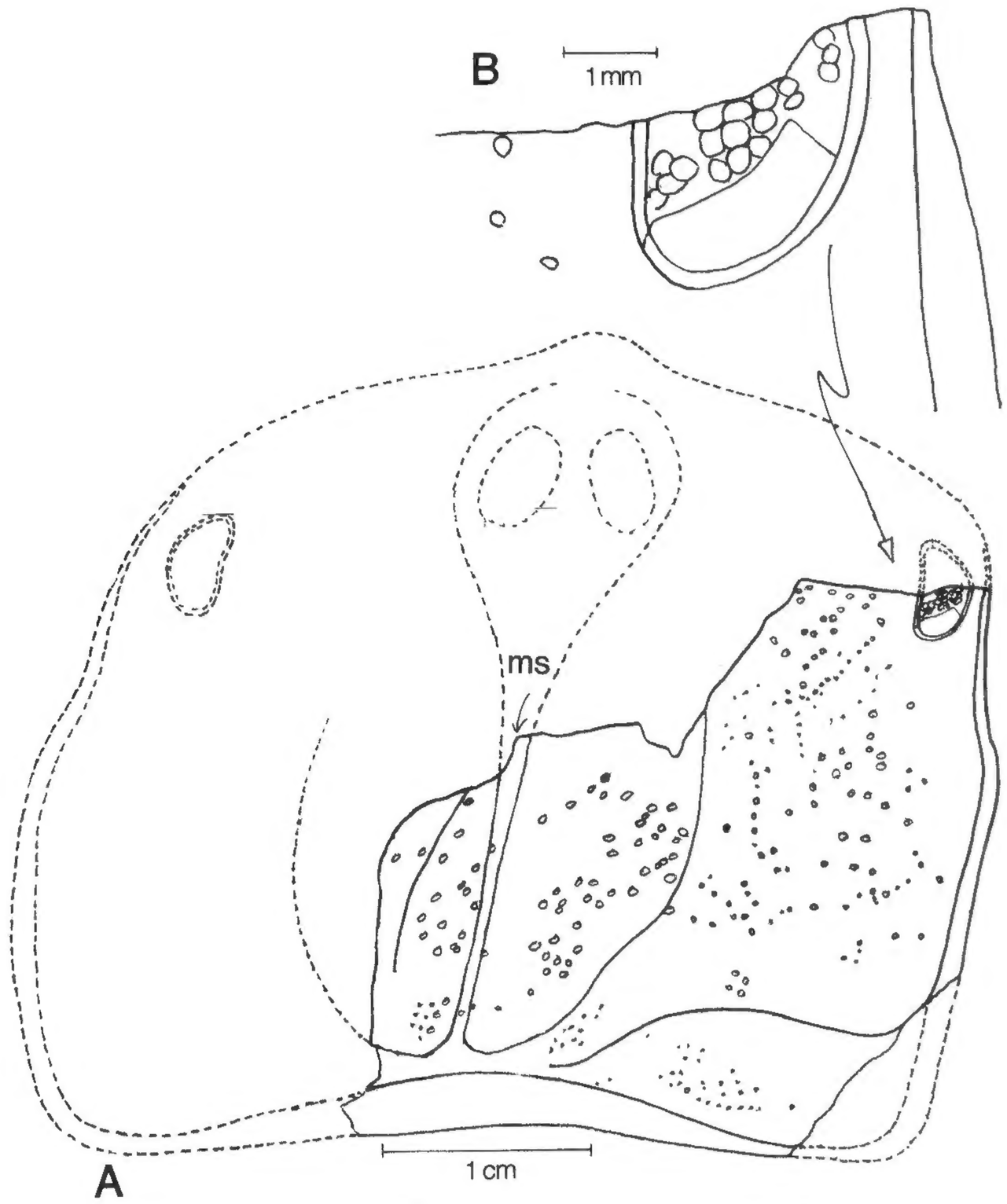
Text-figure 83.—*Trachyscorpio squarrosus,* n. gen., n. sp. From the Lower Carboniferous (Tuedian), Cementstone Group, Calciferous Sandstone Member, near Newton Farm, Foulden, Berwickshire, Scotland. Collected by T. M. Owens, 1924. See foldout inside front cover for explanation of abbreviations.

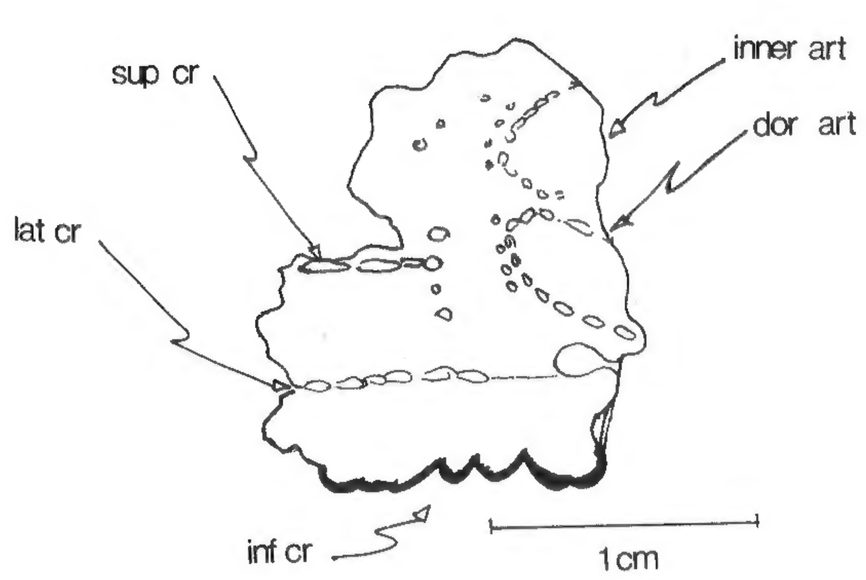
A. Holotype, Specimen I (BM(NH) In.25985). Note the posterior median sulcus of the carapace. **B.** Detail of the partially preserved right lateral compound eye of the holotype (above). **C.** Part of the left coxosternal area and left pectine, nearly complete. Paratype, Specimen III (BM(NH) In.25986). **D.** Distal end of tibia of pedipalp. Paratype, Specimen II (BM(NH) In. 25984). **E, F.** *Trachyscorpio* (?) sp. (BM(NH) In.39765). From the Lower Carboniferous (lowermost Bernician or Viséan S-1), Glencartholm Volcanic Group, Glencartholm, River Esk, Eskdale, Langholm, Dumfriesshire, Scotland. **E.** A lobosternous abdominal plate, presumably a *Trachyscorpio.* **F.** Showing part of the doublure.

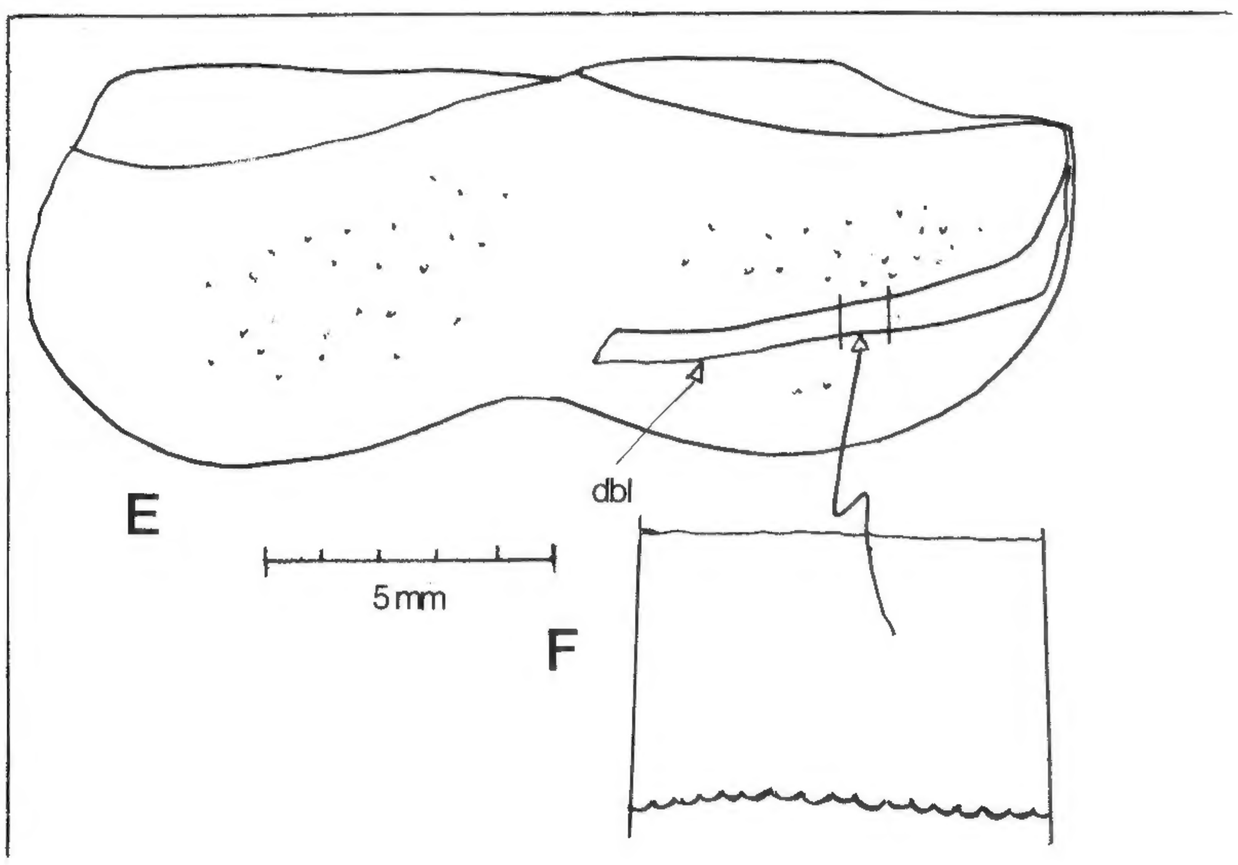
a scorpion of approximately 250 mm in length, a formidable scorpion, but, nevertheless, not comparable to some of the giants among scorpions such as *Gigantoscorpio willsi* Størmer or *Brontoscorpio anglicus* Kjellesvig-Waering.

Specimen II.—A fragment (BM(NH) In.25984), measuring about 18 mm × 20 mm, dark-brown in color, may represent the third joint past the coxa, or tibia, of the pedipalp, and is noteworthy for revealing the large nodular ornamentation as well as the serrated carina or edge, as in the anterior legs of *Garnettius,* showing that this scorpion was an agile digger. Two









rounded areas, marked by large, elongate nodules, reveal the articulating end that adjoins the chela. The rounded area that occurs above the other represents the inner edge, which has been flattened during fossilization. The dorsal and lateral carinae, or crests, are well developed and surmounted with large elongate nodules. These crests indicate that this fragment is part of a pedipalp, and is here considered a paratype.

Specimen III.—BM(NH) In.25986, here designated as a paratype, retains the right pectine along with the right side of the first three coxae. Unfortunately, the opercular plates, sternum and last pair of coxae are not preserved. The second pair of coxae reveals a very short maxillary lobe, indicating that the first pair of coxae would also have very short maxillary lobes, which were not preserved. The third pair of coxae is elongate and cup-shaped. The fourth pair is unknown. The entire coxosternal arrangement, therefore, would be like that in the Eoscorpiidae, except more primitive, as the maxillary lobes of the second pair of coxae are only slightly developed. The second coxa retains ornamentation of small pustules, which probably was present on the other coxae.

The pectine is very large, with elongated, large, rounded teeth. There is no development of areoles in the median lamella, although small semilunar scales do occur and the anterior lamella is divided into approximately three parts. Important on the generic level is the absence of fulcra. The pectine measures 26.0 mm in width, approximately the same in length; the teeth are 4.6 mm in length and approximately 18 were present on each comb.

Type information.—Lower Carboniferous, Tuedian; Calciferous Sandstones, Cementstone Group, near Newton Farm, Foulden, Berwickshire, Scotland. All three specimens were preserved in greenish-gray shale along with fragments of plants on the same bedding plane.

Derivatio nominis.—*squarrosus* (L.) = rough with stiff scales or processes.

Remarks.—The very wide pleural area of the carapace is a feature that is unknown in other scorpions of this family. The distinctive coarse ornamentation likewise is a unique characteristic, as well as the thickened edge of the tibia of the pedipalp, an adaptation for digging, such as in many other arthropods.

The three specimens, all from the same locality, are considered to represent one individual because: 1. The size of the three is compatible with a single individual; 2. The rough, nodular ornamentation is the same on all three specimens; 3. The preservation and characteristics of the bedding plane are the same on all. As stated above, the three pieces indicate a scorpion of approximately 250 mm in length (carapace to telson inclusive).

This scorpion must provisionally be considered an Eoscorpiidae because the coxosternal area is not completely known. Moreover, from what is known of the coxosternal area, it is evident that this scorpion has a more primitive development of this area than *Eoscorpius,* as the maxillary lobes of the second pair of coxae are barely developed.

Trachyscorpio (?) species
Text-figures 83E–F

A single lobostern abdominal plate, unusually well-preserved, gives some light on the breathing apparatus of these early scorpions. The abdominal plate is preserved with the doublure displaced away from the edge. This is not a torn edge, but is a straight edge that was free and not attached to the underlying abdominal plate. Thus the lobostern abdominal plate had a long slit between the edge of the plate and the doublure, as Wills (1947) determined for some of the Triassic scorpions, in particular, a lobostern which he figures on plate VI, figure 9 (see *Bromsgroviscorpio willsi* above). The anterior transverse ridges are well developed. There are no spines on the lip of the doublure or abdominal plate, but there is a single row of small rounded scales. The abdominal plate measures 18.5 mm wide and 5.7 mm long at midsection. Ornamentation consists of very small, sparse, semilunar scales.

Type information.—Glencartholm on the River Esk, Eskdale, Langholm, Dumfriesshire, Scotland. From the Lower Carboniferous, Glencartholm Volcanic Group (=lowermost Bernician or S1 of the Viséan); BM(NH) In.39765.

Genus **ESKISCORPIO**, new genus

Eoscorpiidae (?) with elliptical carapace, large bulbous, anteriorly-located, facetted marginal eyes, mainly in front of the median eyes, which are small and located on a small ocellar mound. Carapace smooth, without development of an elevated cephalic shield.

Derivatio nominis.—The name is taken from the River Esk, Scotland.

Type species.—*Eskiscorpio parvus,* n. gen., n. sp.

Geological range.—Lower Carboniferous.

Remarks.—This genus, although unknown from the ventral side, retains certain characteristics that allow it to be classified with a great degree of certainty as to the generic level. For higher category, it should be acknowledged that the opposite is the case. The shape of the carapace indicates a forerunner of the Buthiscorpiidae. It seems preferable, however, tentatively to refer this genus to the Eoscorpiidae, although this is highly speculative. On the other hand, its being included in the superfamily Isobuthoidea is not so speculative. The species, although firmly established on the generic level, will have to await knowledge of the underside

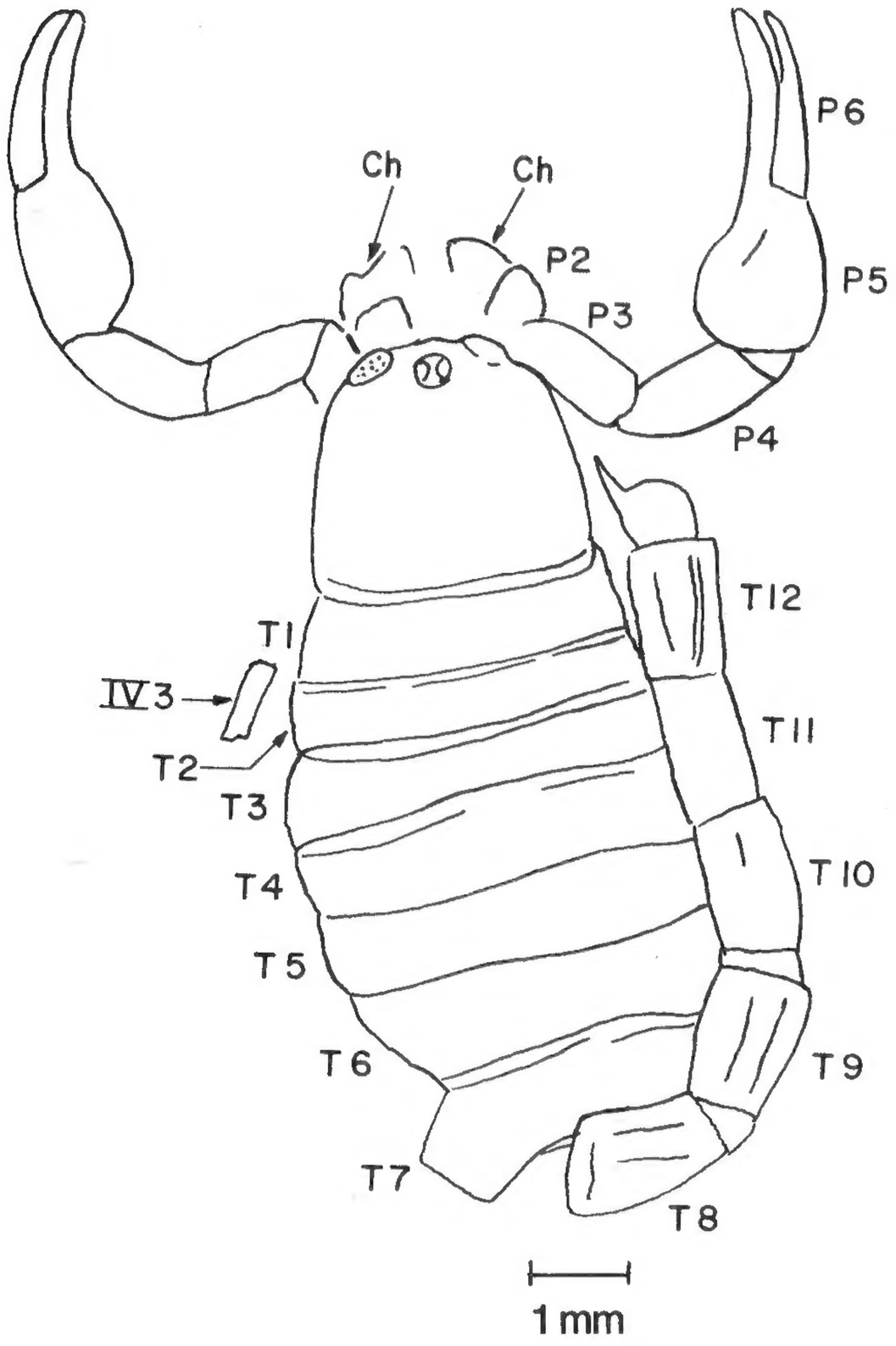
before its true taxonomic position on higher levels is established.

Eskiscorpio parvus, new species
Text-figure 84

The holotype specimen (GSE 2139) is preserved as a dorsal impression of a nearly complete scorpion lacking only the legs and most of the chelicerae. The overall aspect is that of a stout, but small, scorpion, indicating a female. The carapace is rounded along the anterior margin, and long and truncated at the base by a narrow basal rim. No marginal rim, nor ornamentation of any kind is present on the carapace. It is also devoid of a raised cephalic shield. Large, bulbous, marginal compound lateral eyes occur at the anterolateral areas, and facets can be determined on the left eye, which is the better preserved of the two. A round ocellar mound occurs between the lateral eyes and is located very close to the midanterior margin. The median eyes are very small, in keeping with the correlation noted elsewhere in this paper, that large compound eyes are associated with small median eyes, and vice versa.

The chelicerae are too incomplete for description, but they appear to have been rather large. The pedipalps are perfectly preserved and are rather stout with the fingers incurved, that is, the fixed finger is bent backward to accommodate the forwardly-bent free finger. The edges of the fingers are cultrate.

The preabdomen is peculiar in having all of the tergites of approximately the same length. Each is bordered by the usual anterior transverse ridge. Again, like the carapace, none of the seven tergites of the preabdomen shows any ornamentation, including the important (for species determination) seventh tergite. The cauda reveals at least two superior carinae and two more lateral ones that are well developed even on the last tergite. The telson is short, with a rounded short vesicle and a very short, not curved, aculeus. The latter is not a feature commonly encountered and is in great contrast to some of the great scimitar-shaped stingers of other Paleozoic forms.



Text-figure 84.—*Eskiscorpio parvus,* n. gen., n. sp. Holotype, GSE 2139. From the Lower Carboniferous (lowermost Bernician or S1 of the Viséan), Glencartholm Volcanic Group of Calciferous Sandstone Measures, at Glencartholm, 3⅓ miles SSW of Langholm, Dumfriesshire, Scotland. See foldout inside front cover for explanation of abbreviations.

Measurements (in mm) of the holotype (GSE 2139).—

	length	width
Carapace:	2.36	2.81
Pedipalp:		
Humerus:	1.26	
Brachium:	1.0	
Chela:		
Hand	1.03	1.0
Movable finger	1.09	
Tergites:		
1	0.63	
2	0.63	
3	0.8	
4	0.8	
5	0.8	
6	0.82	
7	0.91	
8	1.5	
9	1.5	
10	1.5	
11	1.5	
12	1.5	
Telson:		
Vesicle:	0.61	0.7
Aculeus:	1.1	
Greatest width of preabdomen at fifth tergite:		3.82

Derivatio nominis. —[31]

Type information.—The holotype (GSE 2139) is a

[31] Kjellesvig-Waering did not provide us with a reference to the trivial name of *Eskiscorpio parvus,* n. sp., although it clearly is derived from (L.) *parvus* = little. I suspect Kj.-W. may have been thinking small in terms of the anomalously short telson and aculeus of this species. P.R.H.

single specimen preserved in dark-gray finely-micaceous shale from the Lower Carboniferous Glencartholm Volcanic Group of Calciferous Sandstone Measures (=lowermost Bernician or S1 of the Viséan), at Glencartholm, 3⅓ miles SSW of Langholm, Dumfriesshire, Scotland (Waterston, pers. commun., March 14, 1967). This locality is on the River Esk and is also known as Eskdale.

Remarks.—*Gigantoscorpio willsi* Størmer, *Archaeoctonus glaber* (Peach), *Pseudoarchaeoctonus denticulatus* Kjellesivg-Waering, *Centromachus euglyptus* (Peach), and *Anthracochaerilus palustris* Kjellesvig-Waering occur at the Esk River locality. The first three are fully known from the dorsal side, as a glance at the respective carapaces proves (Størmer, 1963, fig. 23 for *G. willsi,* Text-fig. 21E here for *A. glaber,* and Text-fig. 22 here for *P. denticulatus*). However, *Anthracochaerilus palustris* and *Centromachus euglyptus* (Peach) are known only from the ventral sides, whereas *Eskiscorpio parvus* is known only from the dorsal, thus criticism might be made that *E. parvus* may represent one of those two forms. However, this is not possible. The telson of *A. palustris* is very large with a great vesicle and curved aculeus as against the short bulbous vesicle and short straight aculeus of *E. parvus.* The caudae are different; that of *A. palustris* is very stout, whereas the cauda of *E. parvus* is very slender. Nevertheless, differences might conceivably, but not logically, be considered sex differences. In this respect the sex differences would be of the opposite of what is commonly considered, as the wide preabdomen of *E. parvus* clearly denotes a female, whereas that of the more slender *A. palustris* is almost certainly a male.

However, there are greater and more obvious differences. Although the seventh tergite of *E. parvus* is known only from the dorsal side, it is devoid of carinae and is very short, whereas that of *A. palustris* has well-developed carinae and is much longer. If a scorpion has carinae developed on the venter of the seventh tergite, it follows that these carinae are developed much better on the dorsum. This is a feature that is present in all fossil and even living scorpions. Furthermore, no scorpion would have prominent development of scales on the underside of the preabdomen as in *A. palustris* and be smooth on the dorsal as in *E. parvus.* It would be a complete departure, if not impossibility, for a primitive scorpion like *E. parvus* with marginal, compound lateral eyes to have an advanced coxosternal arrangement such as is present in *A. palustris.*

With regard to *Centromachus euglyptus* (Peach), it is sufficient to state that Størmer's restudy of the holotype showed that it is a holosternous scorpion (Størmer, 1963, p. 80, text-fig. 32), whereas *Eskiscorpio parvus* with its lateral, marginal compound eyes surely is a lobostern.

Family **PAREOBUTHIDAE**, new family

Isobuthoidea with elongate hexagonal sternum; pectine with unjointed or undivided rachis and basal lamella.

Type genus.—*Pareobuthus* Wills, 1959.

Remarks.—Clearly this scorpion, although known only from fragments, is a lobosternous form, with coxal arrangement typical of the superfamily Isobuthoidea, namely, having the third pair of coxae abutting the sternum, whereas the last pair abuts against the genital operculum. Wills (1959, p. 267) proposed the genus *Pareobuthus* for the specimen, which he had previously (1925) described as *Eobuthus* sp. and which he rightly wanted to separate from the genus *Isobuthus.* He stated that the coxosternal arrangement and shape of the abdominal plates closely resembled *Isobuthus.* I agree that among numerous important differences, the above two are significant, but they are of greater than generic value. The coxosternal arrangement of *Pareobuthus* agrees with that of Isobuthidae, but differs in the shape of the sternum, which in the latter family is pentagonal, whereas in *Pareobuthus* it is elongate-hexagonal. Regardless of whether maxillary lobes may or may not be present in the first and second pairs of coxae, at present unknown, the genus *Pareobuthus* necessitates the erection of a family separate from the Isobuthidae.

Perhaps as great a difference is found in the type of combs of *Pareobuthus* and *Isobuthus.* In *Pareobuthus,* they comprise an unjointed base or rachis, well-developed fulcra and numerous teeth, the exact number of which is only important on the generic or, better, species level. In *Isobuthus,* as shown by *I. kralupensis,* the rachis is composed of a basal, jointed lamella followed by an area containing many sclerites, well-developed fulcra, and teeth that are very elongated and numerous.

The peculiar unjointed character of the pectines is known only in some of the Lower Devonian scorpions (see *Branchioscorpio,* Text-fig. 101A).

Genus **PAREOBUTHUS** Wills, 1959

Characters as described for the family and, furthermore, lobosternous abdominal plates that are deeply bilobed and without trace of doublures.

Type species.—*Pareobuthus salopiensis* Wills, 1959.

Geological range.—Carboniferous.

Remarks.—Although the first two pairs of coxae are unknown, the genus can easily be distinguished from other genera by the hexagonal sternum and peculiar unjointed pectines.

Pareobuthus salopiensis Wills, 1959
Text-figure 112K

1925. *Eobuthus* sp. Wills, pp. 87–97, pl. 3; text-fig. 3.
1949. *Eobuthus holti* Pocock. Petrunkevitch (*partim*), p. 137.
1959. *Pareobuthus salopiensis* Wills, pp. 267–269, text-fig. 1.

The species has been fully described and figured by Wills (1925, 1959) and there is no necessity for duplication here.

Type information.—Coal Measures, Upper *Anthraconaia modiolaris* Zone, probably near the Maid Coal of North Wales Coalfield, Preesgweene Colliery, Weston Rhyn, Shropshire, England; GSM 87231.

Remarks.—This is a highly important specimen for phylogenetic purposes. The lobosternous plates are deeply cleft in the middle and completely devoid of doublures. This genus and species therefore seems to be intermediate between the Lobosternina and the Bilobosternina, although definitely of the Lobosternina stock.

Family **KRONOSCORPIONIDAE**, new family

Isobuthoidea with first pair of maxillary lobes spatulate and greatly elongated; lacrimiform sternum, the anterior of which is very narrow and functions as a maxillary lobe, forming part of the base of the pre-oral chamber; tarsal spurs (ungues) and posttarsus greatly elongated; carapace with facetted lateral eyes.

Type genus.—*Kronoscorpio* n. gen.

Remarks.—The strange elongation of the sternum into what may be considered a "maxillary lobe", actually forming part of the ventral part of the pre-oral chamber, is sufficient for considering this family unique and comparison is therefore superfluous. It is clearly an Isobuthoidea having the fourth pair of coxae abutting the genital opercula.

Genus **KRONOSCORPIO**, new genus

Kronoscorpionidae with subquadrate cephalothorax, anteriorly-located median eye node, relatively small, forwardly-directed, rounded median eyes and large, compound lateral eyes at the anterolateral angles of the carapace.

Derivatio nominis.—*kronos* (Gr.) = sea god.

Type species.—*Eoscorpius danielsi* Petrunkevitch, 1913.

Geological range.—Pennsylvanian of Illinois.

Kronoscorpio danielsi (Petrunkevitch, 1913)
Plates 14–15; Text-figures 85, 112H

1913. *Eoscorpius danielsi* Petrunkevitch, p. 43, pl. 4, fig. 16; text-fig. 8.
1949. *Alloscorpius danielsi* (Petrunkevitch). Petrunkevitch, p. 153.
1953. *Alloscorpius danielsi* (Petrunkevitch). Petrunkevitch, p. 29.

Specimen I.—The holotype (UMMP 7216) is well preserved, retaining the carapace, parts of the prosomal appendages and the entire preabdomen, in a typical Mazon Creek ironstone concretion, and is mainly in an undistorted and uncrushed condition.

The carapace is elongate, wider than long, but with a decidedly square aspect. The genal angles are rounded; the lateral margins converge slightly anteriorly and the anterolateral angles are rounded. The anterior margin is nearly straight or slightly emarginate. The base is recurved.

The most prominent feature on the carapace is the ocellar mound, which is centrally located at the anteriormost part. This contains two relatively small, round median eyes, which are anteriorly-located on the ocellar mound and directed forward. The median eyes are located 0.7 mm from the anterior margin, 9.5 mm from the posterior margin, 3.7 mm from the lateral margins, and are 0.8 mm in diameter. A small depression separates the median eyes. Embracing the scutelliform eye node is a deep Y-shaped sulcus whose stem extends posteriorly almost to the base of the carapace. Ridges adjacent to the sulcus are prominently raised. From these ridges, the carapace slopes away to the margins, except at the basal margin, which is bordered by a pair of narrow curved cephalic ridges that raise this basal part of the carapace considerably. The carapace measures 14.3 mm in width along the base, 11.9 mm in width at midsection, 10.8 mm in width at the center of lateral eyes, and 11.0 mm in length. Two bulbous, elongate, reniform facetted eyes, with distinct ommatidia, occur at the anterolateral angles of the carapace (see Pl. 14). Each facetted eye is composed of about 25 ommatidia. The compound lateral eyes are relatively large, and bulge over the edges of the carapace, both vertically and laterally, at a level much lower than the wide cephalic ridges of the carapace. A narrow palpebral lobe may exist, and is faintly shown in the enlargement of the photograph on Plate 14. This would result in an eye much like that present in many eurypterids. The facetted eyes measure 1.6 mm in length and 0.75 mm in width and protrude above the carapace about 0.2 mm (probably more in the original). These eyes are located 7.5 mm from the base of the carapace, and slightly behind the anterolateral margins. The median eyes are in line with the anterior end of the bulbous lateral eyes.

Ornamentation of the carapace consists of scattered granules in no discernable pattern. There is no ornamentation such as was noted on the inner part of the cephalic ridges by Petrunkevitch (see Pl. 15).

The prosomal appendages are well preserved, although not all are present. A part of a stout chelicera is present at the anterior of the carapace, but because of its poor preservation does not merit further description. The left pedipalp is present, although parts of the

hand and fingers are not. The pedipalp is a very elongated organ, and the part of the hand preserved indicates a narrow chela. The width of the hand is 2.7 mm. The tibia is strongly constructed and considerably longer than the femur.

The femur of the pedipalp is concave along the anterior margin and convex on the posterior margin, resulting in a slightly curved joint. The trochanter is unusually long, in keeping with the obviously long femur and tibia.

Only one of the walking legs is preserved on the left side, and parts of two on the right. Probably the leg that is almost completely preserved is one of the anterior ones, possibly a first leg, with fragments of a second leg beside it. The leg on the left side is possibly a fourth leg. This opinion is based on the fact that the leg on the left side has much longer joints than those of the most nearly complete leg on the right side, and also on the short coxa, which does not retain a maxillary lobe. Of considerable morphological importance is the presence of some flattened joints, and paired basitarsal and tibial spurs or spines, and the termination of the legs in three spines, the mesial one being the largest, and considered to be the transtarsus.

The nearly-complete walking leg reveals seven joints past the coxa. The coxa is definitely present and is short, nearly oblong, and without maxillary lobes.

The first joint past the coxa of the first (?) walking leg is short; the second joint is long and wide at the center, and was apparently flattened in life. The third joint is also flattened and not so long as the first, followed by two joints nearly equal in length. The fourth joint shows a constriction at the distal end, where two sockets occur, each of which carried a spur. Petrunkevitch (1913, fig. 8) shows one of these spurs, but no sign appears in the cast. These are the tibial spurs. This joint is also shown with the spurs in place on the corresponding joint on the leg of the left side, which is followed by the fifth joint with two spurs (basitarsal), one on each side. The sixth joint is very short and terminates in three very long spines; the mesial is considered to be the posttarsus. The spines are very narrow, long and straight. This tridactyl termination is quite unlike anything known in other scorpions, either fossil or Recent.

The leg preserved on the left side, which has been interpreted as a fourth walking leg, is similarly constructed except that the joints are longer and much slenderer. The spurs are more prominently developed, but the terminal spines seem to be shorter. This may be due to their not being entirely exposed and therefore appearing to be shorter, in the plaster cast.

The preabdominal tergites are all present. The first four are preserved in one part and the remaining three, as well as parts of two abdominal plates, in another segment. The tergites increase in length posteriorly. The anterior tergites are rounded at the corners. The last three are too poorly-preserved and incomplete to merit description. Some of these tergites are bordered anteriorly by a transverse ridge. No other ornamentation is apparent on the dorsal side of the tergites. A prominent transverse ridge, however, is lacking on the seventh tergite, indicating that the seventh tergite is preserved as a ventral impression of the dorsal tergite. This tergite is pentagonal in outline, comparatively short, and without crests. The base indicates that the cauda is wide and strongly-constructed.

To the right of and anterior to the seventh tergite are remnants of the last two abdominal plates, which are lobosternous, and rounded on each half. A prominent raised marginal rim, denoting a doublure, borders the plates. No openings are revealed, although these would not be expected, and possibly not preserved in the plaster cast.

Specimen II.—FMNH (PE) 32085, collected from the Francis Creek Shale in Pit 11, on the Kankakee Co.–Will Co. line, Illinois (formerly in the private collection of Jerry Herdina, No. H563a,b).

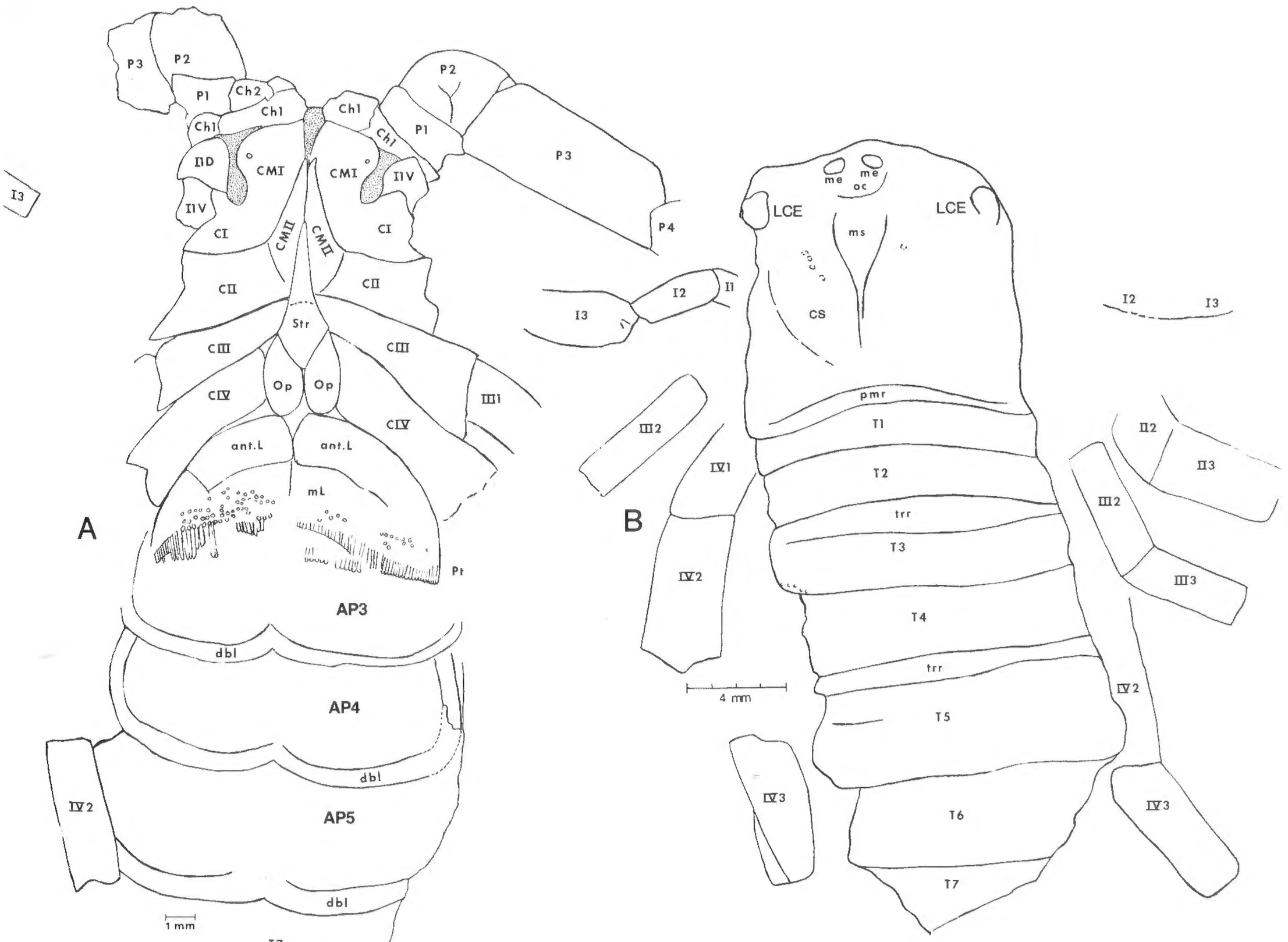
Part and counterpart of a scorpion, including dorsal and ventral sides, preserved from the inside and consisting of the prosoma and basal parts of the appendages as well as the entire preabdomen. The tail and distal parts of the appendages are missing, although most of the basal joints of the legs are preserved, but poorly. The dorsal side is not well preserved, but the ventral side reveals the entire coxosternal area, pectines, genital opercula and all abdominal plates, including the seventh tergite of the preabdomen. Judging from the wide girth of the abdominal plates, this specimen is apparently a female.

The dorsal side is sufficiently well-preserved to assure identification with *Kronoscorpio danielsi* (Petrunkevitch), as the carapace shows the characteristic raised cephalic shield and, in particular, the large facetted lateral eyes and relatively small median eyes, placed very far anteriorly and pointing forward, which are typical of the species (see Text-fig. 85B). The seven tergites show nothing that has not been described for the holotype, and the small section of the appendages remaining do not show anything of interest, as preservation is much too poor for description. However, the great doublures of the abdominal plates are preserved and, coupled with the total lack of ornamentation on the tergites, assure determination with *Kronoscorpio danielsi* (Petrunkevitch).

The ventral side is well preserved, however, and is of great interest, since this rare and unusual scorpion was previously known only from the dorsal side. The

important coxosternal area is well preserved, showing a sternum that is uniquely different from any other scorpion in being greatly elongated anteriorly so that the sternum may be said to have developed an anterior "maxillary lobe". This anterior prolongation actually occupies a position similar to the maxillary lobes, in this case, separating the two maxillary lobes of the second pair of coxae; moreover, it forms part of the base of the "tube" leading to the mouth. Otherwise, the sternum is lacrimiform, pointed at the posterior where it fits against the two opercular plates. The first pair of coxae meets at midsection; the maxillary lobes are greatly expanded into a spatulate area. The second pair of coxae abuts against the aforementioned "maxillary lobe" of the sternum, and further forward meets at midsection. The two lobes extend to less than one-half the length of the maxillary lobes of the first pair. However, a great part of the first pair of coxae has already been squeezed away from the midline. The third pair of coxae abuts the main body of the sternum as in many scorpions, whereas the fourth pair abuts the genital opercular plates, as is characteristic of the superfamily Isobuthoidea. The genital opercular plates are large, elongate, lacrimiform, with the anterior triangular, where the sternum fits between them, and the posterior rounded.

The enormous maxillary lobes of the first pair of coxae are armed with a single large spine or tubercle on the anterolateral angle of each lobe. This is seen, from the inside or dorsal side of the maxillary lobe, as a deep hole that presumably would be the inside of a spine or very large tubercle. This has not been seen on



Text-figure 85.—*Kronoscorpio danielsi* (Petrunkevitch). Specimen II, FMNH (PE) 32085 (formerly Jerry Herdina Coll. H563a,b). From the Upper Carboniferous (Pennsylvanian), Carbondale Formation, Lower Francis Creek Shale, Pit 11, Peabody Coal Company, Will Co.–Kankakee Co. line, IL. See foldout inside front cover for explanation of abbreviations.

A. Showing superbly the organization of the ventral surface of prosoma and mesosoma. The organization is unique among scorpions. The anterior stippled areas are mud-filled depressions in the surface of the anterior lobes of the first coxae. Each lobe bore a single spine, the base of which is a circle. **B.** Dorsal surface.

other scorpions either fossil or living, but this scorpion has other more important unique features, such as the termination of the legs and the type of sternum.

The pectines are poorly preserved, but enough is present for a good reconstruction—at least all essential details are known. The pectines are broad and very long, flipperlike, with a broad anterior lamella that is jointed, presumably as in other Isobuthoidea; the middle lamella is broad and long with small, even-sized, rounded areoles. The fulcra are large and well developed. The denticles are thin, very long and numerous—an estimate is possible since the width of the pectines is known—approximately 48 teeth on each pectine.

The abdominal plates are lobosternous, deeply bilobed with a very large doublure developed. They resemble the abdominal plates of the Czechoslovakian forms, where the doublure is also apparently massively developed.

Measurements (in mm) of FMNH (PE) 32085.—

	length	width
Prosoma:	9.2	10.6
Preabdomen:	23.4 (estimated)	15.0 (estimated)
Overall:	80.0 (estimated)	

This important specimen furnishes and completes much of the knowledge of this peculiar scorpion which was needed, for when this study was begun in 1965, the underside was completely unknown. Therefore it was a pleasure to see the underside, which, as predicted from the unusual dorsal side, was unique and up to the author's expectations.

Type information.—The holotype was in the L. E. Daniels collection and came from the lower Francis Creek Shale of the Middle Pennsylvanian, Carbondale Formation (Westphalian C) overlying Coal 2, at Mazon Creek, Grundy County, Illinois. The plaster cast used here is in the U.S. National Museum. The holotype, thanks to Mr. Bret S. Beall, is now known to be in the University of Michigan Museum of Paleontology, catalogued as UMMP 7216. It is a single nodule half from "Mazon Creek, near Morris, Ill."

The other specimen described is from the lower Francis Creek Shale in Pit 11 of the Peabody Coal Company on the Kankakee Co.–Will Co. line, Illinois, collected by Jerry Herdina, and filed in his collection as No. H563 (now FMNH (PE) 32085).

Remarks.—This scorpion is one of the most unusual and significant fossil scorpions known, although Petrunkevitch failed to recognize and describe certain very important morphological structures. Facetted eyes at the anterolateral angles of the carapace, tridactyl termination of the legs, and rounded lobosternous abdominal plates in this species have important bearing on scorpion taxonomy and phylogeny. Originally described by Petrunkevitch as *Eoscorpius danielsi* in 1913, it was referred in 1949, on the basis of morphological characters of far less importance, to the newly-named genus *Alloscorpius,* with *A. granulosus* (Petrunkevitch) as type species. In his papers of 1953 (p. 29) and 1955, nothing is said of the above-mentioned important morphological characters. As a matter of record, he had illustrated these facetted eyes very well in his text-figure and photograph of 1913, which is reproduced here as Plate 14, and Plate 15, figure 1, with enlargement of the compound eyes to show the distinct ommatidia.

The presence of compound lateral eyes in Chelicerata is well known in the Merostomata. In the Scorpionida, as early as 1885, Whitfield showed the presence of these structures in *Proscorpius osborni* (Whitfield), but for various reasons, unfortunately all fallacious, this discovery was not taken seriously. A review of the holotype of *Proscorpius osborni* by Kjellesvig-Waering (1966) has verified Whitfield's original determination. Wills (1947) also reported well-developed facetted eyes in the Triassic scorpions of England. However, in the *Treatise on Invertebrate Paleontology,* Petrunkevitch (1955, p. 54) stated:

> Compound eyes such as are found in Xiphosura, Eurypterida, Crustacea and Hexapoda are never present in any Arachnida. The organs of scorpions belonging to the Triassic family Mesophonidae and those of the Palaeocharinidae (Devonian members of the order Trigonotarbida) claimed to be compound eyes, are unlike true compound eyes and are probably sense organs of some unknown function.

This statement is clearly erroneous as pertaining to both the scorpions and the Palaeocharinidae.

Concerning the holotype of *K. danielsi,* the facetted lateral eyes are bulbous, protrude considerably above the surrounding surface, and are distinctly composed of about 25 roughly-hexagonal ommatidia. In modern scorpions, the group of lateral eyes, which number from one to five on each side, occur in the same position as the compound eyes of *K. danielsi.* Petrunkevitch had figured these eyes as facets in his 1913 paper (fig. 8), but unfortunately would not accept that the lateral eyes were compound eyes and referred to them as "alveolate areas".

Facetted lateral eyes are not as rare in fossil scorpions as has been thought. In addition to the instances cited above, I have recently found exceptionally well-preserved facetted eyes, which previously had not been reported, in the holotype of *Eoscorpius carbonarius* (Meek and Worthen), *Archaeophonus eurypteroides* Kjellesvig-Waering, *Garnettius hungerfordi* (Elias), *Eoscorpius distinctus* (Petrunkevitch), etc., all of which are redescribed here.

The facetted eyes are much like those found in the

eurypterids. It is probable that the facetted eyes evolved into the present-day series of lateral eyes, inasmuch as they occur approximately at the same spot in living scorpions. The compound eye of the Carboniferous scorpions is reniform or bulbous in shape, and the margins are rounded and clearly delineated, sometimes by a distinct rim (see photographs of *Eoscorpius distinctus*). The individual facets are sharply defined and hexagonal in shape. It also appears (see Wills, 1947, p. 20) that by Triassic time, the individual facets were becoming less sharply defined, and the entire facetted eye lost its reniform or bulbous symmetry. Possibly later some ommatidia became detached from one another, whereas others became obscured or obliterated, and the separate, small, round lateral eyes of living scorpions eventually developed. This could explain why there is variation in some species of living scorpions in the number of individual lateral eyes.

There is no question that many fossil scorpions did not have facetted lateral eyes.[32]

Petrunkevitch failed to note in his description of *Kronoscorpio danielsi* that the two posterior ventral abdominal plates are preserved and that these are of the bilobed type, which designates the scorpion as one of the Lobosternina.

Equally important to the understanding of this fossil is the presence of three long terminal spines in the legs, along with paired spurs on the two penultimate joints. The tridactyl termination has previously gone unrecognized in the scorpions and, although Petrunkevitch showed these structures (1913, fig. 8), he failed to grasp their significance. These trifid claws alone would have been sufficient for the separation of this scorpion from any other known in Petrunkevitch's classification as given in the *Treatise on Invertebrate Paleontology* (1955).

The trifid termination (see Størmer, 1963, p. 86) is probably a very primitive one, and like the presence of facetted lateral eyes, is a character in common with the eurypterids. This scorpion appears to be an anachronism in the Pennsylvanian and in many respects is perhaps more primitive than some of the Silurian forms such as *Proscorpius osborni* (Whitfield), which had developed double claws not greatly unlike most Pennsylvanian and Recent scorpions.

The presence of a tridactyl claw is rare in living Arthropoda. R. F. Lawrence (pers. commun., Oct. 26, 1965) states that these are known in the family Triaenonychidae, the dominant family of Opiliones in South Africa, and in the larvae of some cantharid beetles. It also commonly occurs in living and fossil Acari, including the Devonian *Protocarus crani* Hirst.

Among the primitive trilobitomorphs, the tripartite termination is common in Middle Cambrian genera such as *Marrella* of the marrellomorphs, *Burgessia* of the order Burgessiida and *Naraoia* of the order Nectaspida. In the trilobites the tridactyl claw is common and may be found in such divergent genera as *Olenoides, Triarthrus, Cryptolithus, Asteropyge, Phacops, Ceraurus,* etc.

Although unknown in the living scorpions, the tridactyl claw, in a considerably modified form, is known in the Carboniferous *Eoscorpius pulcher* (Petrunkevitch). Wills (1959, pp. 279–282, pl. 50, figs. 9–10; text-figs. 5–8) shows where the mesial spine or dactyl is turned over to serve as a heel for two curved, rather "normal" scorpionid claws. In this case, the mesial joint, as well as the two claws, is greatly reduced in comparison with the three long, straight spines of the scorpion described here. A further reduction of the posttarsus or heel would result in a termination not greatly unlike that of living scorpions.

I agree with Wills (1959, p. 281) and Størmer (1963, p. 87) that the modified tridactyl claw of *Eoscorpius pulcher* would be useful to an aquatic animal, but not to a land-dweller. The tridactyl claw of *K. danielsi* is even more suited for an aquatic existence.

The posttarsus of modern scorpions therefore represents the mesial spine of the tridactyl claw of scorpions like *K. danielsi,* except that it has been reduced to a small heel or tubercle that rests on the ground. The posttarsus has been turned over so that the dorsal surface now rests on the ground, ventral to the claws. This development is suggested by the morphology of *Eoscorpius pulcher.*

It is therefore highly probable that the posttarsus of *K. danielsi* was turned under and posteriorly, so that two long claws occurred in front and one large "claw" (posttarsus) occurred in back. This would give a "snowshoe" effect and indeed would be excellent for walking over soft bottom muds such as surely occurred in the Mazon Creek environment.

The presence of forwardly-directed median ocelli may be a good indication of the predaceous habits of this scorpion. This characteristic is not known in other scorpions that normally have the median eyes pointing upward and laterally from the carapace.[33]

---

[32] Whenever acids are used to free scorpions from the matrix, it is quite possible that the individual facets may be destroyed from the cuticle that is left as a residue. In this connection, experiments with acids on the eyes of various arthropods show that the ommatidia, occurring below the exocuticle, are mainly or altogether destroyed, leaving little or no trace on the exocuticle. E. N. K.-W.

[33] Waering's search for the holotype of this unusual scorpion (now known to be in the Univ. of Michigan Museum of Paleontology) proved fruitless, and all that was available on which to base a description was the original photograph (see Pl. 4, fig. 16, taken by Petrunkevitch in 1913) and a plaster cast of the original concretion

Superfamily **PARAISOBUTHOIDEA**, new superfamily

Lobosternina with the maxillary lobes of first two pairs of coxae reaching the anterior margin, first pair crowded out of the midline; second pair meets at midline; third pair abuts sternum and fourth pair abuts the genital opercula.

Type family.—Paraisobuthidae, n. fam.

Remarks.—The differences in the coxosternal arrangement between this superfamily and the Isobuthoidea rests in the great elongation of the maxillary lobes of the second pair of coxae; in the latter, the lobes reach only midway the length of the first pair of coxae, as against reaching to the anterior margin. In the Paraisobuthoidea they have squeezed the first pair of coxae away from the midline. This is a fundamental change. Thus, the arrangement of the first three pairs of coxae is much as in modern scorpions. Of course, the similarity to modern terrestrial scorpions rests there, as the fourth pair of coxae abuts the opercula, and the preabdomen retains lobosternous abdominal plates rather than true sternites. This is a well-defined, easily recognizable group, which undoubtedly, from all evidence, developed from the Isobuthoidea.

Family **PARAISOBUTHIDAE**, new family

Paraisobuthoidea with well-developed schizochroal lateral eyes and small pentagonal sternum.

Type genus.—*Paraisobuthus*, n. gen.

Remarks.—This family differs from the Isobuthidae in the development of long maxillary lobes of the first two pairs of coxae, and the squeezing away of the first pair from the midline with the second pair abutting one another. The difference is of superfamily importance.

Genus **PARAISOBUTHUS**, new genus

Paraisobuthidae with well-developed paired cephalic cheeks, pectines with apparent double row of fulcra, and greatly-dilated inner areoles. Pectines very hirsute along the edge. Free finger curving over the recurved immovable finger with both edges meeting throughout the entire cultrate edge.

Derivatio nominis.—*para* (Gr.) = near + *Isobuthus* = a scorpion genus.

Type species.—*Paraisobuthus prantli,* n. gen., n. sp.

Geological range.—Upper Carboniferous.

Remarks.—This represents an unrecognized genus that had previously been included in the Isobuthidae because the fourth pair of coxae abutted the operculum. It is an important genus, which now is accorded its proper taxonomic position.

Paraisobuthus prantli, new species
Text-figures 86–88, 112A, 113C4

1904. *Eobuthus rakovnicensis* Frič (*partim*), p. 74, fig. 91.
1911. *Anthracoscorpio sparthensis* (Baldwin and Sutcliffe). Pocock (*partim*), pp. 13, 20.
1923. *Anthracoscorpio sparthensis* (Baldwin and Sutcliffe). Moore, p. 132, pl. 1, fig. 3.
1953. *Isobuthus rakovnicensis* (Frič) (*partim*). Petrunkevitch, p. 21, figs. 19, 123.
1955. *Isobuthus rakovnicensis* (Frič). Petrunkevitch, p. 78, fig. 46.

The holotype (BM(NH) I.2950), comprises a well-preserved, rather large scorpion preserved so that both dorsal and ventral sides are revealed (see Text-figs. 86A, B). It is preserved in light-greenish-gray shale, appearing to be an underclay.

The part comprises the specimen on the dorsal side with almost the entire surface preserved, with some details of the underside. The counterpart reveals almost the entire underside with the left side of the dorsal surface showing. This has been partly overturned during deposition so that this part of the dorsal area and its relationship to the upper part can be easily noted (see Text-fig. 86A).

Coloration.—A considerable amount of the original cuticle is preserved, which shows that this scorpion was mainly light-brown in color with the tips of the fingers black as in many living scorpions.

The carapace (see Text-figs. 86B, 88E, F) is subquadrate, with two well-developed (elevated in life) cephalic cheeks separated by a deep sulcus. The base is bounded by a wide rim that continues into the lower half of the carapace as a lateral rim. The median eyes appear as elliptical, but undoubtedly were round in an uncrushed state, and they surmount a small ocellar node, which in turn is divided by a narrow sulcus. The ocellar node or mound, is sublacrimiform and located intramarginally on the anterior of the carapace. Two schizochroal lateral eyes are located at the anterior part of the cephalic cheeks; they are relatively small, reniform and consist of about 200 lenses. These are schizochroal in that each is small, rounded, and separated by sclerotic walls (see Text-figs. 88D–F), all of which are contained in a bulbous, reniform structure. The anterior of the carapace is rounded at the anterolateral margin and enough is preserved of the middle to show that a glossate process was present.

The coxosternal arrangement is clearly shown, revealing a small pentagonal sternum that is slightly longer than wide (see Text-figs. 86A, 87G). The first pair

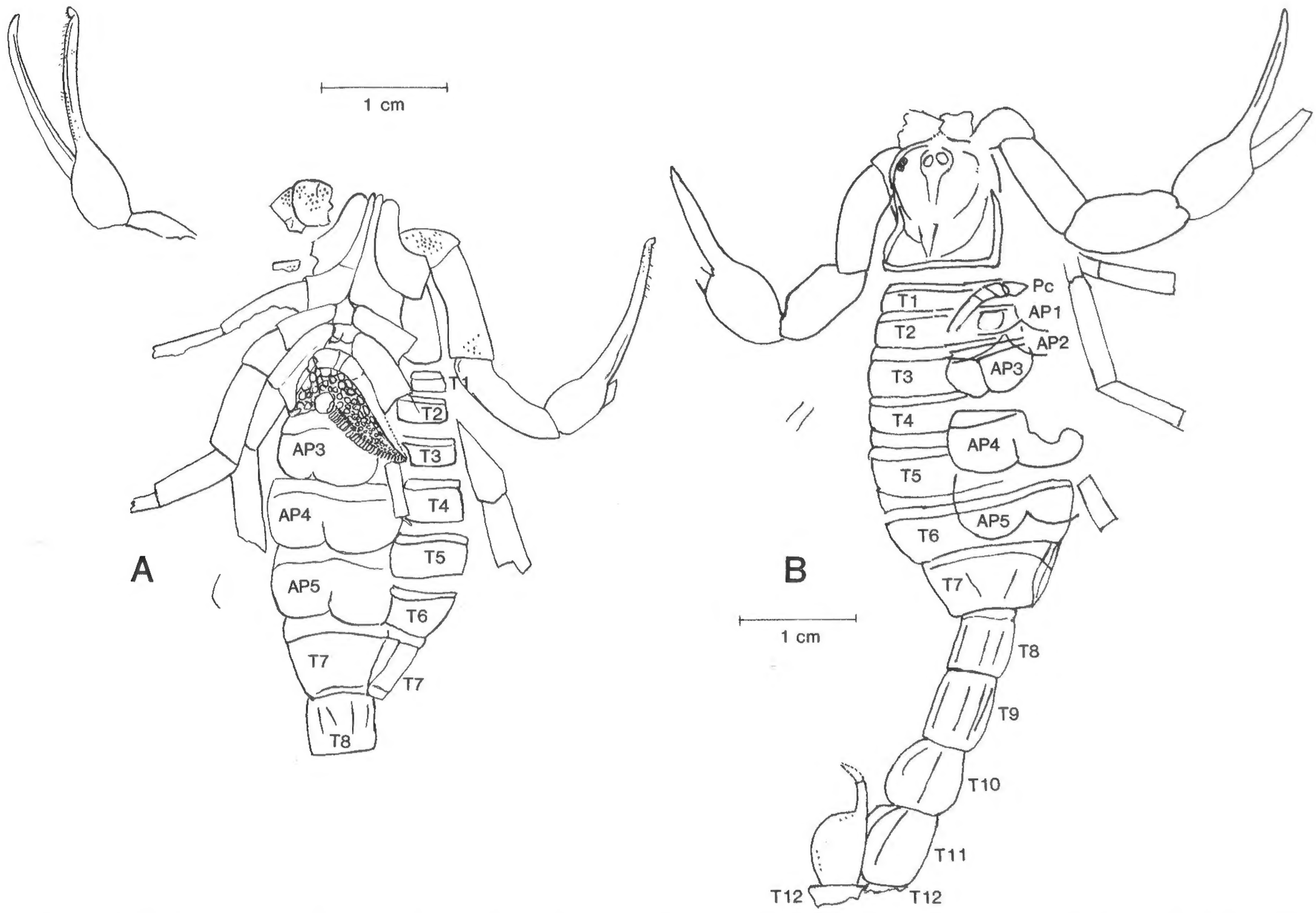
---

made by L. E. Daniels in 1898, now in the U.S. National Museum (USNM 27921). The description given here, in the absence of the holotype specimen, is based on this plaster cast and several enlargements of Petrunkevitch's glass negative, now at Yale University. A.S.C.

of coxae does not meet at the midsection, but meets against the maxillary lobes of the second pair of coxae. The coxae of the first pair have massively-developed maxillary lobes. The second pair of coxae has well-developed narrow maxillary lobes that reach to the anteriormost part of the carapace. The oral chamber of this scorpion, at least on the ventral surface, would be much as in Recent scorpions where the maxillary lobes of the second pair of coxae have crowded out the first pair of maxillary lobes. The third pair of coxae abuts against the sternum, whereas the fourth pair abuts against the genital operculum. The genital operculum appears to be composed of two round parts, although it was not possible to determine whether or not these were two round sclerites that have been coalesced into one.

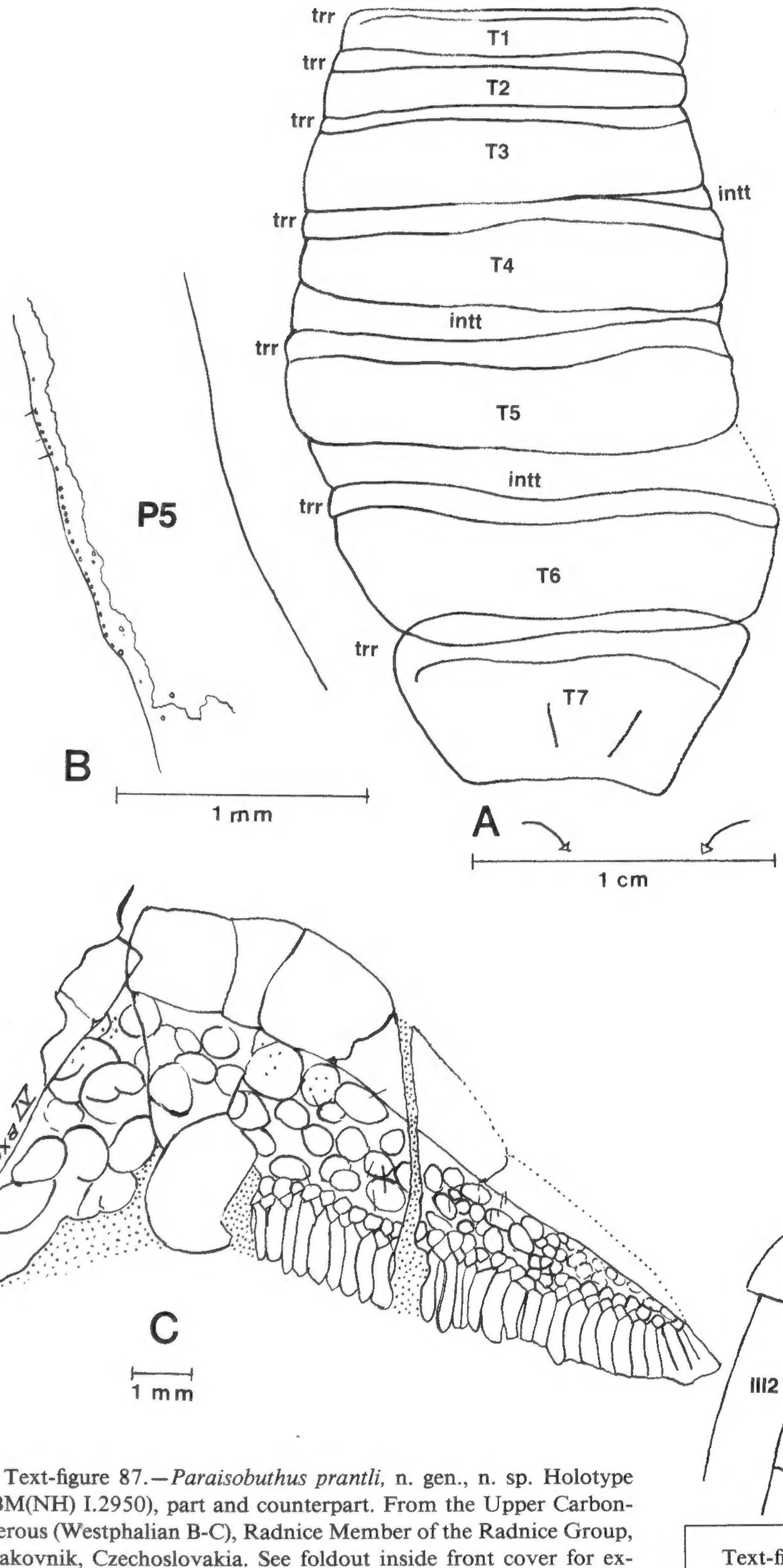
The pectines (see Text-figs. 86A, 87C) are fairly well preserved and show that they are very large with a thickened basal lamella composed of at least five distinct segments followed by the median lamella, which is a very wide area in which many irregular-sized, rounded setaceous sclerites occur. Fulcra are very well developed, with another row of sclerites occurring immediately above the fulcra, which appear as a double row of fulcra. The sclerites of the median lamella become smaller toward the tips of the pectines. A large, rounded, dilated lobe is present on this scorpion, which shows that it is very likely a female. This is common in some living scorpions (for example, *Tityus melanostictus* Pocock), and is known as the basal pectinal lobe. The teeth are very well preserved. They are long and rounded at the ends, and at least 35 are estimated to be present.

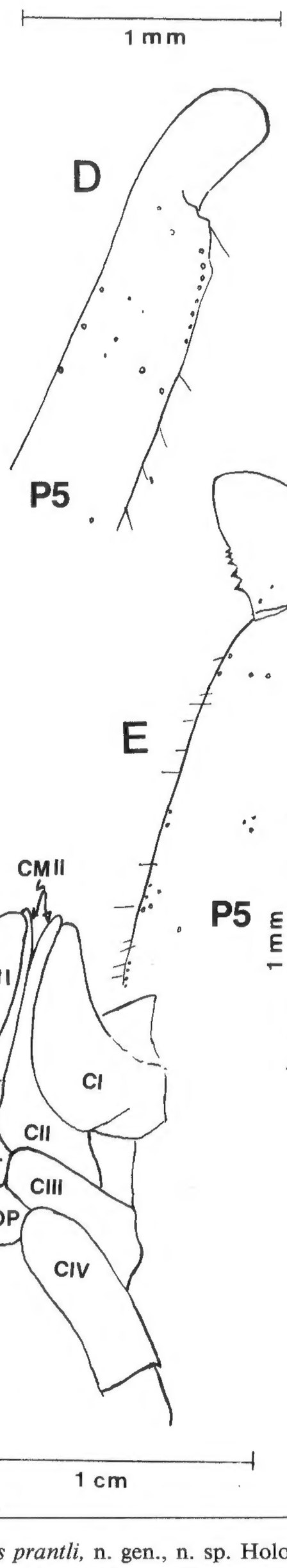
The entire base of the pectines (see Text-fig. 88A) is preserved on the larger specimen. This shows that the pectines are attached to a small trapezoidal sclerite, separated by a small, median, lanceolate, two-jointed organ. The small median organ can be seen best after the removal of the coating of shellac and in a dry state. It is very similar to that found in *Branchioscorpio richardsoni* and *Gigantoscorpio willsi.*



Text-figure 86.—*Paraisobuthus prantli,* n. gen., n. sp. Holotype, BM(NH) I.2950, part and counterpart. From the Upper Carboniferous (Westphalian B-C), Radnice Group, Rakovnik, Czechoslovakia. See foldout inside front cover for explanation of abbreviations.

A. Ventral view of holotype. **B.** Dorsal view of the holotype with some abdominal plate impressions and other ventral features.



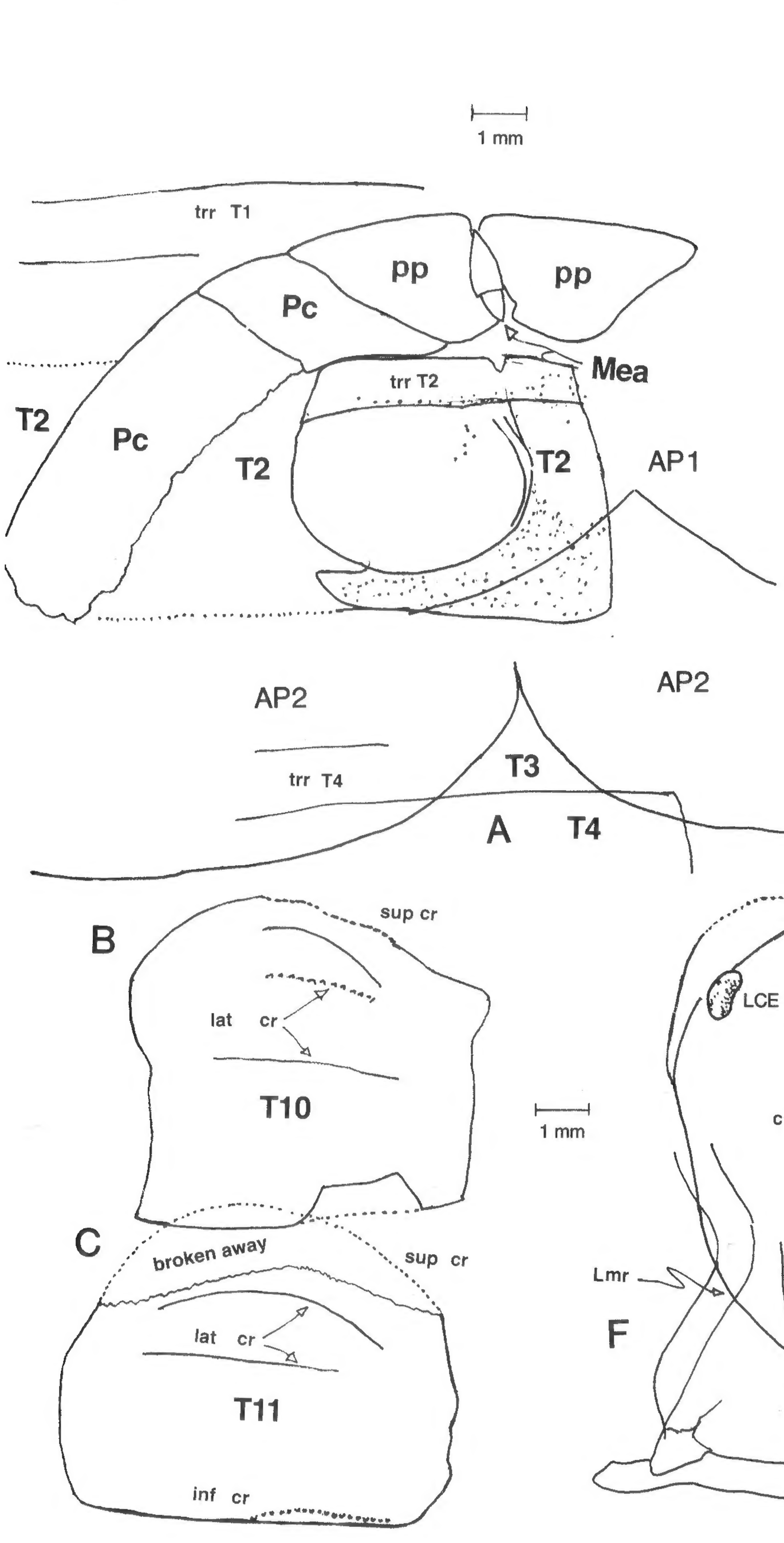


Text-figure 87.—*Paraisobuthus prantli,* n. gen., n. sp. Holotype (BM(NH) I.2950), part and counterpart. From the Upper Carboniferous (Westphalian B-C), Radnice Member of the Radnice Group, Rakovnik, Czechoslovakia. See foldout inside front cover for explanation of abbreviations.

A. The preabdomen; partly restored, but with tergites in place as preserved. **B.** Basal part of fixed finger of right pedipalp. The thin edge, with most of the setal openings, represents the cuticle that is preserved in the impression. **C.** Pectine detail. **D.** Ventral part of the fixed finger of the left pedipalp. **E.** Ventral part of the fixed finger of the right pedipalp. **F.** Telson, drawn from the counterpart. **G.** Coxosternal organization.

Text-figure 88.—*Paraisobuthus prantli,* n. gen., n. sp. Holotype, BM(NH) I.2950. From the Upper Carboniferous (Westphalian B-C). Radnice Group, Rakovnik, Czechoslovakia. See foldout inside front cover for explanation of abbreviations.

A. Ventral details, preserved through the dorsal side of the holotype. **B, C.** Tergites 10 and 11, seen on the ventral holotype slab. **D.** Showing the schizochroal facets of the left lateral eye. **E.** Restoration of the prosomal carapace. **F.** Somewhat distorted prosomal carapace of the holotype.


1 mm
trr T1
pp
pp
Pc
Mea
trr T2
T2
Pc
T2
T2
AP1
AP2
AP2
trr T4
T3
A
T4
1 mm
D
E
B
sup cr
lat
cr
T10
C
broken away
sup cr
lat
cr
T11
inf cr
LCE
me
oc
sul
cc
ms
cc
Lmr
F
Lmr
pmr

The tergites of the preabdomen (see Text-figs. 86A, B; 87A) increase in size gradually posteriorly and each is bounded on the anterior by a strong transverse ridge. The seventh tergite has two faintly-developed carinae dorsally and apparently none ventrally.

The pectines undoubtedly cover the first and second abdominal plates, as shown by the counterpart. These are followed by three others in excellent preservation, each bounded on the anterior margin by a transverse ridge. All are distinctly deeply-bilobed and rounded at the posterior angles. A total of five gill-bearing lobostern abdominal plates are present.

The well-preserved pedipalps are of unusual interest (see Text-figs. 86A, B; 87B, D, E) with the trochanter, femur, tibia and all of the chela present. The tibia and the femur are approximately the same size. The trochanter shows many small setal openings ventrally, and some scattered setal sites are present on the femur and tibia. The fingers of the chela are very long. The movable finger is bent backward and shows a single series of openings along the edge that undoubtedly were occupied by the setae, as some of them are still preserved. The tips of the fixed fingers possibly terminate in a double or bifurcating tip, between which the falcate end of the movable finger would fit. This is the first time that this structure has been noted in the pedipalp of any scorpion. The bifurcating end is known in the chelicerae of scorpions, but only on the movable or free finger. Small pointed denticles very definitely occur on the edge of one of the bifurcations at the tip. No denticles have been noted on any of the rest of the fingers, although preservation is very good and reveals small bristles along the cultrate edge. The free finger curves inward, is pointed or falcate and very long.

This appears to be a very smooth scorpion as neither the ventral nor the dorsal side shows any granules except very sparse and minute ones on the tergites. The walking legs do not merit description since the ends were not preserved. They had been obliterated by careless mechanical development. This seems to have been done long ago by a chisel that broke away the parts where the distal joints of the legs were preserved.

The cauda reveals four well-preserved tergites, but only fragments of the twelfth along with the well-preserved telson or stinger. The cauda is stout with the last three tergites greatly inflated and arched (see Text-fig. 86B). Superior lateral and ventral crests seem to be developed on all the tergites. These are slightly serrate but none noticeably so.

The telson (see Text-figs. 86B, 87F) is rather long, with a bulbous vesicle and a curved aculeus, similar to many living scorpions. The vesicle is 4.7 mm wide (thick) and 5.7 mm in length. The aculeus is 3.0 mm (estimated) in length.

Measurements (in mm) of BM(NH) I.2950.—

	length	width
Chela:	23.8	
Hand	7.3	4.9
Free finger	16.5	
Femur (dorsolateral):	11.0	
Tibia (dorsolateral):	12.2	
Abdominal plate:		
No. 1	(covered)	(covered)
No. 2	6.9	(incomplete)
No. 3	6.9	13.0
No. 4	6.9	12.2
Tergite:[34]		
No. 1	2.3	
No. 2	2.5	
No. 3	2.7	
No. 4	4.0	
No. 5	4.2	
No. 6	5.2	
No. 7	7.7	
No. 8	6.0	

Derivatio nominis.—[35]

Type information.—Holotype (BM(NH) I.2950) consists of two parts, ventral and dorsal of a complete scorpion, preserved in light-green shale from the Upper Carboniferous Radnice Member of the Radnice Group (Westphalian B/C), Rakovnik, Czechoslovakia.

Remarks.—It seems incongruous that after the holotype had been figured repeatedly, first by Frič (1904,

[34] There is considerable intersegmental tissue between the tergites. E. N. K.-W.

[35] Dr. H. W. Ball kindly sent the holotype to me in Trinidad in July, 1968. At the time, I did not question the generic and specific determination previously made (*Eobuthus rakovnicensis* Frič) by Frič and (*Isobuthus rakovnicensis* (Frič)) by Petrunkevitch, both of whom had studied the material.

In November, 1970, I visited the National Museum in Prague where all of the Bohemian fossil scorpions were deposited. By studying the holotype of *Eobuthus rakovnicensis,* I recognized that another species was present in the material from Rakovnik. It was later determined, on my return to Oslo, Norway (Dec. 1970) that the beautiful specimen that had been presented to the British Museum (Natural History) by Frič was different, and it is now named *Paraisobuthus prantli* in honor of the well-known Czech paleontologist, Ferdinand Prantl. It was a pleasant surprise in Mozambique, in January, 1972, when I was restudying the entire "*Isobuthus* problem", to learn that Pocock (1911, p. 13) had noted that the British Museum syntype of *Eobuthus rakovnicenis* represented a different genus and species from the Prague Museum specimen, which Pocock considered the holotype (=lectotype). Unfortunately on page 20 of the same publication, he considered it to be conspecific with *Eoscorpius sparthensis,* although on p. 13 he did consider it as provisional ("for the time being"). It would have saved me considerable trouble had I not waited so long to determine what Pocock previously had thought, but in moving around so much, I have had to work from microfilm, and one knows that this method, although having its advantages, is highly inconvenient for ready reference. Actually, it was not until August, 1977, when Dr. Ball again sent me the original, that most of the figures were made and the "*Isobuthus* problem" was resolved. E. N. K.-W.

fig. 91), and later by Petrunkevitch (1955, fig. 46), that it should emerge as not only an important new genus and species, but also the type genus of a new family and type family of a new superfamily.[35]

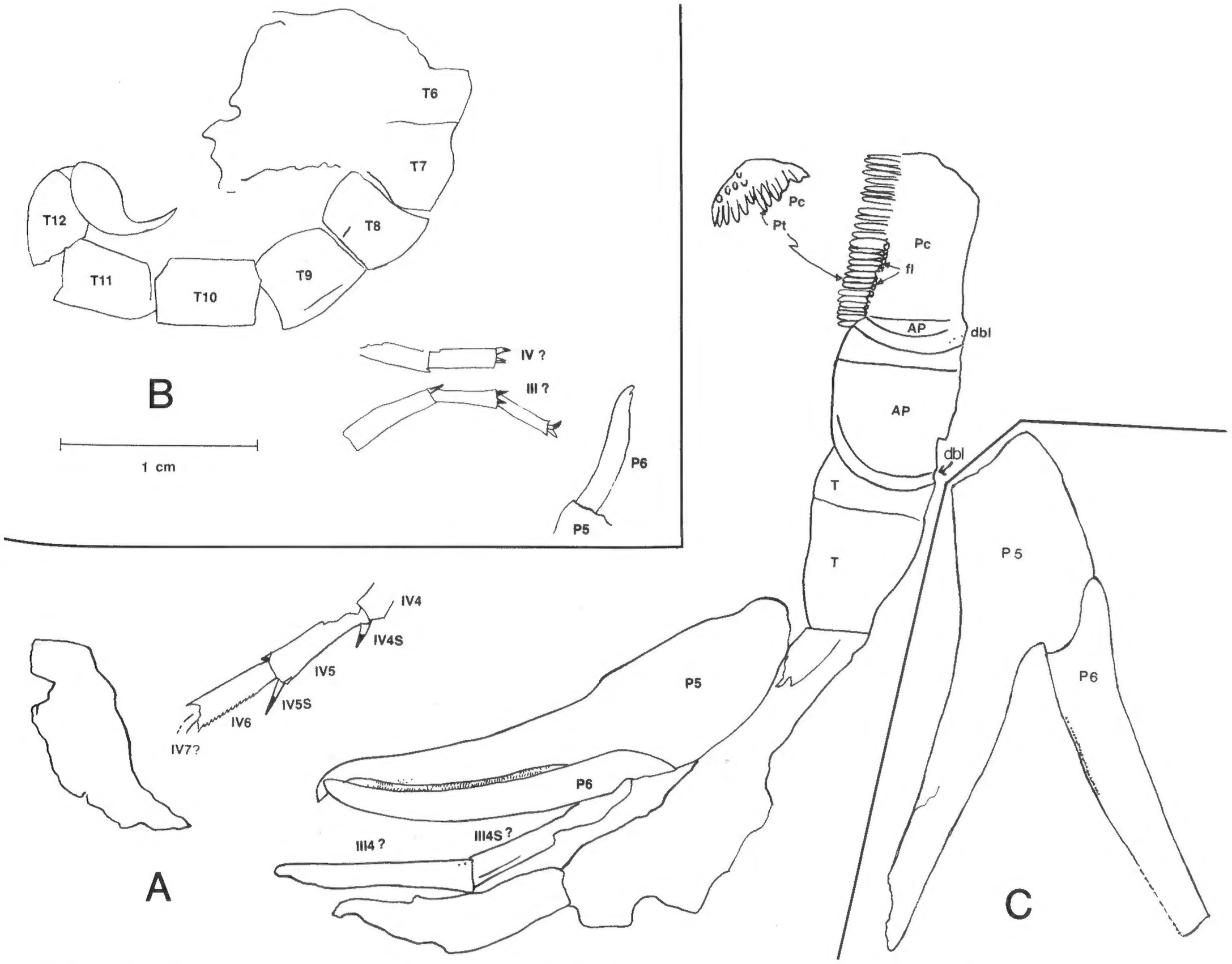
Paraisobuthus frici, new species
Text-figure 89

1873. *Cyclophthalmus senior* Corda (*partim*). Frič, pl. 1, fig. 2.
1904. *Isobuthus kralupensis* Thorell and Lindström (*partim*). Frič, pl. 10, fig. 11.
1953. *Isobuthus kralupensis* Thorell and Lindström (*partim*). Petrunkevitch, p. 20.

The holotype (No. 579; NMP Inv. 827) comprises only fragments, but these are fortunately of considerable diagnostic value. They consist of a complete chela of the pedipalp, parts of combs, fragments of what possibly is the third or fourth leg and small parts of an abdominal plate.

The well-preserved pedipalp comprises a very long hand with an incurved fixed finger that is distinctly falcate at the terminus. The cultrate edge is bounded by small, evenly-spaced, and very short setae. The free finger, equally as slender as the fixed, is curved forward and crosses the anterior falcate terminal part of the opposing finger in a scissorlike manner. The cultrate edge is bordered with the same type of minute setae as the immovable finger. No other ornamentation occurs. Hand width is 5.8 mm, hand length is 12.3 mm and free finger length is 16.4 mm (see Text-figs. 89A, C).

The combs are poorly and incompletely preserved, but they reveal 27 teeth on the large piece and 12 on



Text-figure 89.—*Paraisobuthus frici,* n. sp. Type specimens in the Sternberg collection, National Museum, Prague, Czechoslovakia. From the Upper Carboniferous (Westphalian B-C), Radnice Member, Lower Gray Formation, Kralupy Hill, Červená Hůrka, Czechoslovakia. See foldout inside front cover for explanation of abbreviations.

A. Holotype (NMP Inv. 827). Showing part of the ventral surface, pectine, and the enormous pedipalp. **B.** Paratype (NMP Inv. 826). **C.** Specimen (NMP GH 1973 (73)). Here the free finger of the pedipalp has been distorted and bent backward.

the small. Fulcra are present and raised areoles are found on the rachis. Probably about 50 teeth occurred on each pectine. The teeth are the long type.

The abdominal plates are distinctly lobosternous and have a well-developed doublure.

The leg, which seems to belong to the fourth or last pair, shows tibial spurs, probably double, as well as uneven basitarsal spurs, one of which is greatly elongated (see Text-fig. 89A). The tarsus is long, with a serrated edge on the posterior side and a pointed anterior terminal end. The posttarsus and claws are too poorly preserved for description. A long tibia (?) and femur (?) are also present, possibly of the third pair of legs.

The cauda, fragments of two legs, and the free ramus of the pedipalp occur in a specimen which is registered as Inv. 826 in the collections of the National Museum in Prague, Czechoskovakia. It is from the same locality and horizon as the holotype, and also was previously identified by Frič as *Isobuthus kralupensis* Thorell and Lindström, according to the label on the specimen (see Text-fig. 89B).

The two leg fragments, quite likely parts of the last two pairs of legs, reveal that the basitarsal and tarsal spines were well developed; the ungues and posttarsus were small and developed without supplementary serrations or denticles. The tarsus in each leg is very long.

The cauda is preserved laterally in its entirety, attached to fragments of the sixth and seventh tergites of the mesosoma. It is very thick, with most of the tergites completely smooth. The shortness of the distal tergites indicates a female. The telson is a smooth bulbous vesicle with the usual curved aculeus.

The pedipalp, which was the main factor in determining the identification of this specimen as a species of *Eobuthus,* reveals only the entire fixed finger. It occurs with a crack that was at first mistaken for the junction of the hand with the free finger. However, the recurving of the finger shows that it is the fixed finger or part of the fifth joint. The finger is recurved, cultrate, and with a small notch at the extremity.

Type information.—The holotype and paratype, preserved in shaly sandstone, come from Kralupy Hill, Červená Hůrka, which lies 25 to 30 km north of Prague, Czechoslovakia, from the Upper Carboniferous Radnice Member of the so-called Lower Gray Formation, Westphalian B/C (Ivo Chlupac, pers. commun., Dec. 3, 1970). The holotype is registered in the collection of the National Museum, Prague, as Sternberg Collection No. 579; NMP Inv. 827. The paratype is registered as NMP Inv. 826.

Derivatio nominis.—Named in honor of Dr. Anton Frič (Fritsch), to whom we owe most of our knowledge of Czechoslovakian scorpions.

Remarks.—The differences between *Paraisobuthus frici,* n. sp., and *P. prantli* from Rakovnik, are numerous. The hand of the latter is much shorter, with much longer fingers, and with a groove running the length of the fingers. The denticles at the end of the fingers of *P. prantli* are not present in *P. frici.* The double row of large fulcra in *P. prantli* differs from the small fulcra of *P. frici.* The abdominal plates of *P. prantli* do not have as rounded a configuration as in *P. frici.*

Another specimen, also from Kralupy Hill, and registered in the National Museum collections at Prague, Czechoslovakia, as GH 1973 (73) is also referred to this species. It consists of a nearly complete chela of the pedipalp, but the free finger is not incurving, although it is obvious that this finger has been distorted, as no scorpion could have a chela in which the fingers could not possibly close. The row of setae on the cultrate edge, however, is present and agrees otherwise with the holotype specimen (see Text-fig. 89C).

Paraisobuthus duobicarinatus, new species
Plates 16–18; Text-figure 90

1911. *Eobuthus holti* (?) Pocock, pp. 15–16, pl. II, figs. 2a, b.
1913. *Isobuthus holti* (Pocock). Petrunkevitch (*partim*), p. 22.

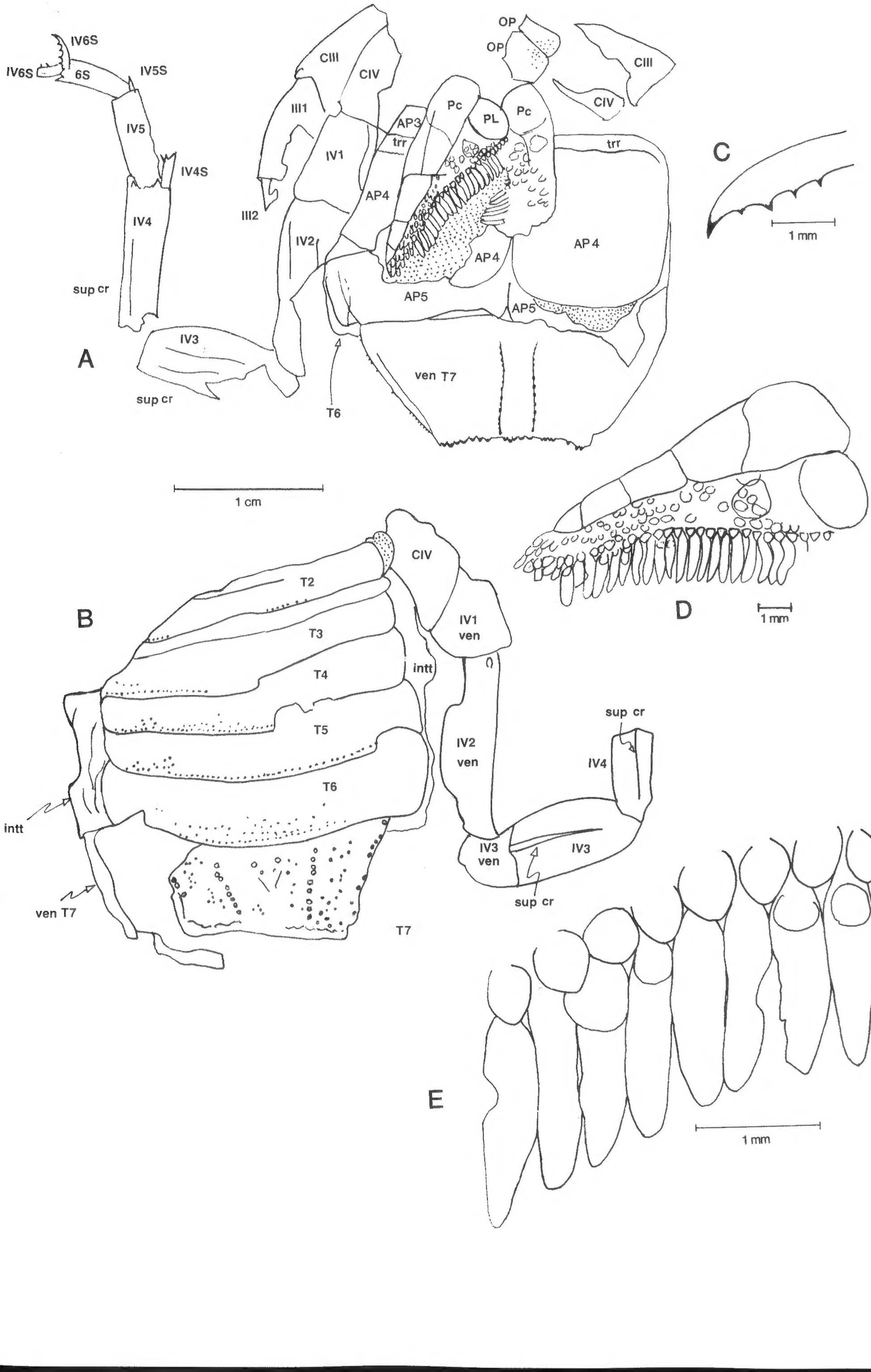
The holotype comprises a single specimen, preserved in an ironstone concretion, that reveals both dorsal and ventral sides of a robust scorpion. Almost the entire preabdomen is present, and, although telescoped, is remarkably preserved. The entire fourth walking leg is also preserved in an uncrushed condition. A part of the fourth abdominal plate was lifted out of the specimen, exposing the entire comb and, more important, part of the details of the gills and gill chamber.

The seventh tergite is preserved apart as an external mold, showing some degree of original inflation and both dorsal and ventral sides. The species is therefore well founded, requires a name, as it can easily be recognized again, and is referred on the basis of the combs to the genus *Paraisobuthus.*

The tergites have been slightly telescoped, and the second to the seventh inclusive are preserved. They

Text-figure 90.—*Paraisobuthus duobicarinatus,* n. sp. Holotype, GSM 30245 (ventral part) and 30246 (dorsal part). From the Upper Carboniferous, Coal Measures (lower *Anthracosia similis–Anthraconaia pulchra* Zone), Shipley (Digby) Clay Pit, Kimberley, Nottinghamshire, England. See foldout inside front cover for explanation of abbreviations.

A. Shows the ventral half of the holotype. The deep lobation of the fourth abdominal plate (**AP4**) is notable; also the excellently-preserved right pectine. **B.** Shows the dorsal half of the holotype. **C.** Right posterior claw of leg **IV** of the holotype. **D.** Right pectine. **E.** Detail of the center of the right pectine, showing the areoles on the pectinal teeth.


IV6S
IV6S
6S
IV5S
IV5
IV4S
IV4
sup cr
IV3
sup cr
A
1 cm
CIII
CIV
III1
III2
IV1
IV2
AP3
AP4
AP5
trr
Pc
PL
Pc
OP
OP
CIII
CIV
trr
AP4
AP5
ven T7
T6
C
1 mm
B
CIV
T2
T3
T4
T5
T6
T7
intt
intt
ven T7
IV1
ven
IV2
ven
IV3
ven
sup cr
IV4
IV3
sup cr
D
1 mm
E
1 mm

reveal a row of pustules on the posterior edge, and scattered pustules in the epimeral parts. Each is anteriorly bounded by a strong transverse ridge (see Text-fig. 90B).

The dorsal side of the seventh tergite (Text-fig. 90B) has two median carinae, each of which is surmounted with very coarse pustules. There is another carina on each side, also surmounted by very coarse pustules. Fine to very coarse pustules cover the center and lateral areas, apparently not in a uniform manner or discernible pattern. The tergite undoubtedly has a strong anterior transverse ridge, and the base also seems to be bounded by a transverse ridge.

The underside (Text-fig. 90A) shows that the abdominal plates are lobosternous, long, and divided by a deep cleft in the posterior median part. All are bounded anteriorly by a strong transverse ridge. The ventral part of the seventh tergite is nearly smooth except for two median carinae, close-set, each surmounted by medium-sized pustules.

Part of the abdominal plates covered most of the pectines, but a crack in the rock permitted the lifting of a small slice of rock containing the right abdominal plate, revealing the entire pectine. It fortunately revealed loose fragments of cuticular matter representing the inside of the abdominal plate and the body wall. These skins were lifted off the specimen and embedded in Canada Balsam. Much to my surprise, the pieces showed shiny dark-brown cuticle (see Pl. 16, fig. 1; Pl. 17) along with white, thick, spongy tissue (see Pl. 16, figs. 2, 3; Pl. 18), which contrasted dramatically with the sclerotized parts. Covering the spongy tissue on one side were abundant cone spines such as characterize the gill tracts of eurypterids (see Wills, 1965; Waterston, 1975, p. 241). This is the first direct evidence of gills in lobostern scorpions, although it has certainly been known that such would be the case.

The white spongy tissue that composes the gill tract shows no discernible structure (see Pl. 18, fig. 3). Cone spines (see Pl. 16, figs. 1–3), however, are dark brown, occur only on one face, the outer face of the body wall, and show some striations. There are some much smaller spines (see Pl. 17, fig. 1), which are also considered to belong to the gill tracts, as the form is much like that of the cone spines, rather than to the gill chamber (see Waterston, 1975, p. 250, fig. 3).

It is considered, therefore, that the lobostern abdominal plate is the same as that which was revealed by Wills (1965) and especially by Waterston (1975). This reveals a large gill chamber with the gill tract being part of the body wall and with the abdominal plate overlapping. Waterston (1975, p. 252) suggests with good reason that the water entered the gill chamber laterally and was expelled through the posterior slit, as happens in *Limulus*. This is probably why the spines present on the posterior slit, bordering the posterior of the abdominal plate and doublure (see Text-figs. 50F, G), point to the posterior. If the spines pointed anteriorly, they would slow the passage of the water. Inasmuch as they point posteriorly, the spines do not impede the passage of the water outward and furthermore serve to keep extraneous material out of the gill chamber.

The pectines (see Text-figs. 90A, D) are beautifully preserved, showing a segmented anterior lamella possibly of three or four joints; the distal one disappears before the actual distal end of the entire comb is reached. The middle lamella is composed of irregularly-sized areoles, rounded, that range in shape from circular to irregular-elliptical. The areoles decrease in size toward the distal end. The inner part of the margin retains a very large, elliptical, basal pectinal lobe. This structure, present also in *Paraisobuthus prantli,* is known in much reduced form in some species of *Tityus,* where it denotes the female. It is probable that this specimen is a female, as the preabdomen is very wide. Fulcra, subtriangular and large, are well developed and separate the teeth of the combs. The latter are long, and approximately 30 occur on each comb. Areoles, although scarce, occur on some of the teeth of the combs (see Text-fig. 90D).

The fourth walking leg is preserved in its entirety except for the posttarsus (see Text-figs. 90A, B). The coxae (III, IV) are long and flaring. The first joint is short, followed by a long second joint. The third joint is robust, greatly expanded and with a strong dorsal carina. The fourth joint is long and dorsally carinated. This joint carries a long, thick spine at the distal end that has secondary spines on at least the inner part. This species possibly has double spines, although only one was noted, but the other is covered, if present. The fifth joint or basitarsus is also long with a pair of rather long spines. The tarsus or sixth joint is long and carries the paired claws or ungues.

The claws are of the long type, falcate at the end, and with a single row of sharp spines on the ventral side. The spines are perpendicular to the shaft of the ungues, thus assuring the greatest traction against the substrate.

Type information.—Holotype is from the L. Moysey Collection (GSM 30245, 30246, 30247 and 30248), from the Upper Carboniferous, Coal Measures (lower *Anthracosia similis–Anthraconaia pulchra* Zone), at Shipley (Digby) Clay Pit, Kimberley, Nottinghamshire, England. The slides of the gills are also filed with the specimen.

Derivatio nominis.—*duo* (L.) = two + *bicarinatus* (L.) = double-keeled.

Remarks.—Pocock (1911, p. 15) "provisionally" referred this scorpion to *Eobuthus holti* Pocock, but the presence of the type of keels on the venter of the seventh tergite is sufficient to refer this scorpion to a separate species. In *E. holti,* the keels are convergent; in the new species described above, they are close-set and parallel.

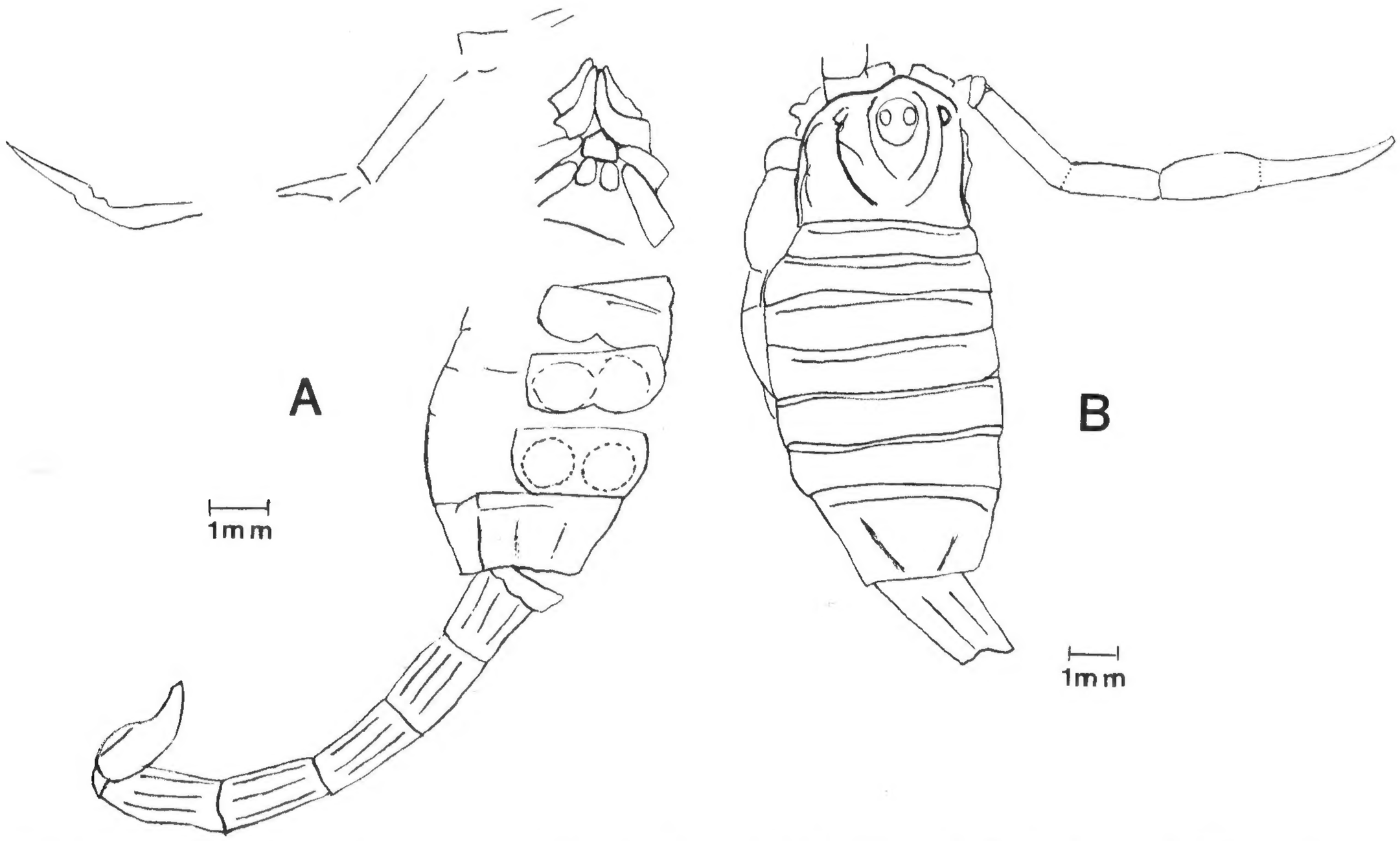
Paraisobuthus duobicarinatus differs from the type species, *P. prantli,* in having very well-developed carinae on the dorsum and venter of the seventh tergite that are lacking in the Bohemian form. This difference, as followed in the modern treatment of living scorpion classification, is sufficient to refer them to separate genera, and this may be the case here when more is known of each. I have referred the species nomen *duobicarinatus* to *Paraisobuthus* because the large rounded sclerite of the pectines is also present in *Paraisobuthus prantli.*

Paraisobuthus virginiae, new species
Text-figure 91

1913. *Eoctonus miniatus* Petrunkevitch (*partim*), pp. 51–52, pl. III, fig. 15.
1953. *Alloscorpius granulosus* (Petrunkevitch). Petrunkevitch, p. 15.

Included as a paratype of *Eoctonus miniatus* Petrunkevitch was a small scorpion whose only similarity to the holotype was the small size. It is, however, a lobostern scorpion, whereas *E. miniatus* is a holostern. In addition to this major difference, the coxosternal arrangement is very different, for example, the third and fourth pairs of coxae abut the sternum in *E. miniatus,* whereas in the new species, the fourth pair abuts the genital opercula. Petrunkevitch (1953, p. 15) apparently arrived at the conclusion that the specimen did not represent *Eoctonus miniatus* Petrunkevitch and the problem was dispensed with by the statement, "The paratype, No. 132, proved to be a distorted specimen of *Alloscorpius granulosus* (Petrunkevitch) and there is no need to consider it further here."

The specimen is preserved in two parts, showing both dorsal and ventral surfaces in nearly complete preservation. As in other Mazon Creek materials, it is preserved in an ironstone concretion (see Text-figs. 91A, B). Apart from the underside, the characteristics of the carapace (*e.g.,* outline, strong cephalic shield, shape of the eye node and eyes, and the presence of three carinae on the ventral side and two on the dorsal



Text-figure 91.—*Paraisobuthus virginiae,* n. sp. Holotype, YPM 132, part and counterpart. (This is a paratype of *Eoctonus miniatus* Petrunkevitch.) From the Upper Carboniferous (Pennsylvanian), Carbondale Formation, Lower Francis Creek Shale, Mazon Creek, Grundy Co., IL.

A. Counterpart, showing lobate abdominal plates and characteristic carinate postabdomen. **B.** Dorsal surface, showing complete carapace and nearly complete slender pedipalp.

side of the cauda), clearly show that this specimen is not referable to *Eoctonus miniatus* Petrunkevitch.

The dorsal side is largely flattened, but the left lateral eye, and in particular, the median eye node with the two eyes, are exceptionally well preserved. The median eye node is scutelliform, with two relatively small round eyes separated by a space slightly larger than the width of the eyes. The anterior glossate area of the carapace is well preserved and occurs in front of the median eyes. The cephalic part of the carapace has been almost completely flattened, but definite traces are present on both sides. The lateral eyes occur on the same level as the median eyes, and are small, elliptical and protruding.

The preabdomen is preserved in its entirety, but some telescoping of the tergites occurs. Compression has obliterated most of the anterior transverse ridges, but they can be discerned in rubber casts. Little ornamentation was noted, as the texture of the rock on this particular nodule is too coarse for good preservation. The tergites increase in length posteriorly to reach greatest length at the seventh tergite. Greatest width of the preabdomen occurs at the anterior of the fourth tergite.

The pedipalp is preserved nearly whole and reveals a strong chela, the complete length of which is probably greater than that of the femur and tibia together. Overall, the pedipalp is quite slender, and in life would reach past the second caudal segment. Both the femur and tibia are narrow, with the femur being considerably longer. The hand is long and slender, and the finger, not complete, is unusually long and bent. It is considered to be the fixed finger; the other finger is not present.

The coxosternal region clearly reveals a Paraisobuthoidea with two pairs of coxae in front of the sternum, both with well-developed maxillary lobes, reaching to the anterior end, the third pair abutting the sternum and the fourth pair abutting the opercular plates. The sternum is not well preserved in outline, but is large and pentagonal. The opercular plates are large, elongate, rounded or ellipso-triangular, considerably longer than wide.

Of particular interest is the presence of the abdominal plates. They are lobosternous, but each shows a very noticeable large, rounded area in the center of each half, occupying most of the inner surface of the plate. The last abdominal plate shows these rounded areas in excellent preservation. These areas are actually depressions in the plates, occurring as shallow pouches and are considered to be the gill chambers.

The last preabdominal tergite appears to have two faint crests on the ventral side. The dorsal side of this tergite has two crests, at a diagonal to each other, that are better seen in the latex casts.

The cauda is preserved in its entirety and is known from both dorsal and ventral sides. Each tergite increases in length slightly to the posterior. The ventral side reveals three prominent crests on each tergite, whereas the dorsal shows only two. The telson or stinger is large, rather elongated, and bent as in other scorpions. It definitely appears to have two crests on the ventral part of the vesicle, a structure common in many living scorpions.

Measurements (in mm) of YPM 132.—

Prosoma:	
Width at base:	3.4
Length:	3.4
Palpus (chela) length:	4.0
Pedipalp:	
Femur length:	2.5
Tibia length:	2.1
Length of tergites:	
1	0.8
2	0.8 (telescoped?)
3	1.0
4	1.2
5	1.2 (telescoped?)
6	1.3
7	2.0
8	1.6
9	1.8
10	2.1
11	2.2
12	2.5
Telson length:	2.5 (incomplete)
Vesicle width:	0.8
Total body length, excluding chelicerae:	26.0 (estimated)
Abdomen length:	8.3
Caudal length:	12.8 (incomplete)

Type information.—Pennsylvanian, lower part of the Francis Creek Shale, at Mazon Creek, Illinois. Holotype is YPM 132, part and counterpart.

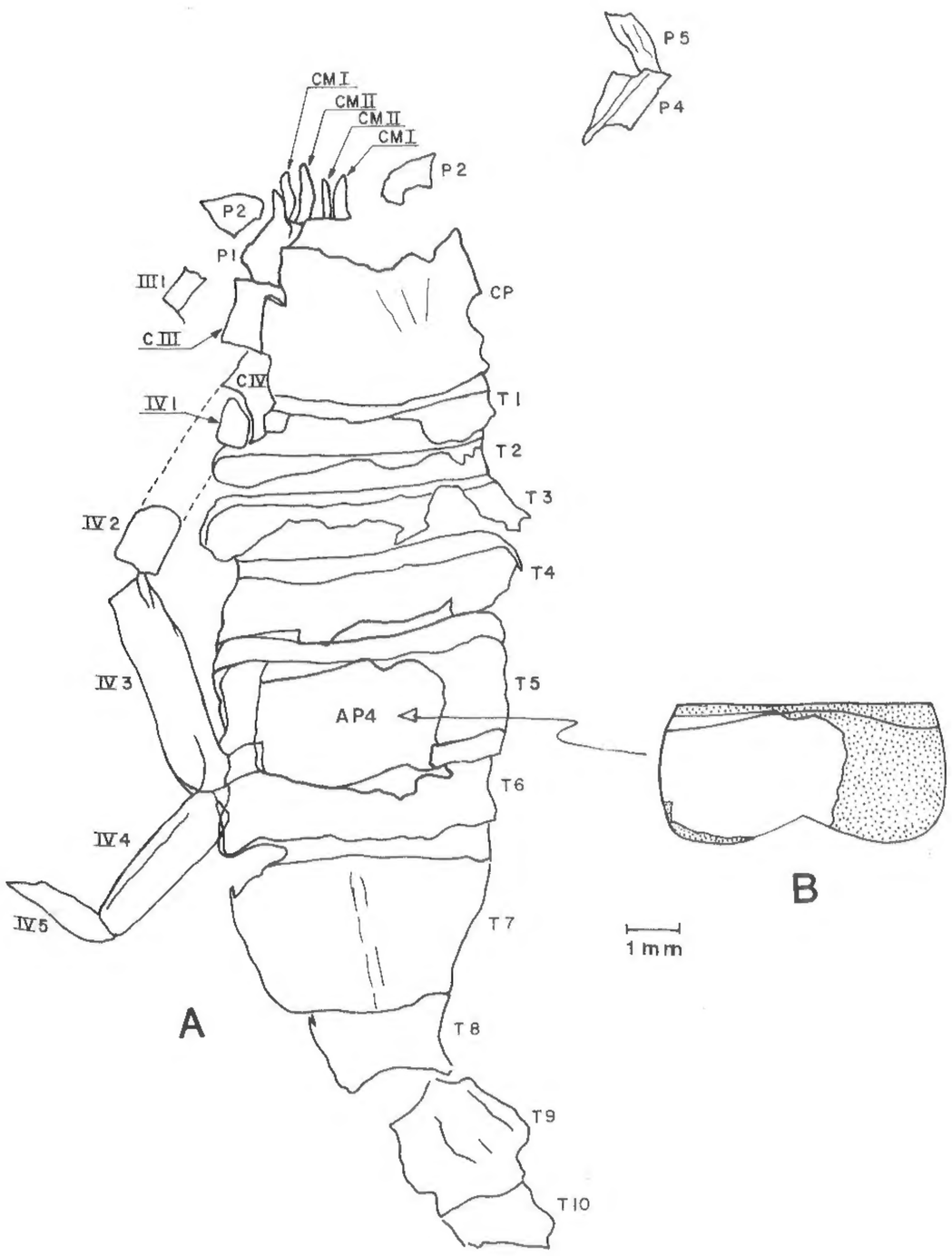
Derivatio nominis.—Named in honor of my wife Virginia, who has contributed much to this monograph, and to whom fell the more onerous tasks of this work.

Remarks.—Petrunkevitch (1913, p. 52) states that the underside was so deformed that "no details of structure can be made out". This is incorrect. Although there are better-preserved scorpions, the preservation is quite good, and many details of major importance can clearly be discerned (see Text-fig. 91A). In comparing the lobosternous scorpions occurring in the Mazon Creek biota, namely *Eoscorpius carbonarius, Kronoscorpio danielsi,* and *Telmatoscorpio brevipectus,* only the first mentioned, *E. carbonarius,* might be confused with this new species. The main difference between *Eoscorpius* and *Paraisobuthus* is in the max-

illary lobes of the first two pairs of coxae, which reach to the anterior end or to the same level in *Paraisobuthus,* in contrast to the maxillary lobes of *Eoscorpius,* in which the second pair only reaches the midsection of the first pair. In *Paraisobuthus,* the second pair has squeezed the first pair away from the midline, and the first pair of lobes is narrow, whereas in *Eoscorpius* the first pair is greatly expanded or spatulate.

The same differences apply to the maxillary lobes in *Kronoscorpio danielsi*; the sterna are also totally unalike. The large pentagonal sternum of *Paraisobuthus* is sufficient to separate it from *Telmatoscorpio* with its small barrel-shaped sternum.

On the species level, if it is necessary to list some differences, details of the seventh tergite, which nearly always is an easy character for quick identification, will separate all three listed lobosternous scorpions in the Mazon Creek biota.



Text-figure 92.—*Leioscorpio pseudobuthiformis,* n. gen., n. sp. Holotype, BM(NH) In.22832 (one of Pocock's subsequent study suite of *Buthiscorpius buthiformis* (Pocock), designated as a paratype by Petrunkevitch, 1953). From the Upper Carboniferous, Upper Coal Measures, Etruria Marl Group, Coseley, South Staffordshire Coalfield, England. See foldout inside front cover for explanation of abbreviations.

A. Complete specimen. **B.** Lobosternous abdominal plate (**AP4**), stippled area restored.

Genus **LEIOSCORPIO**, new genus

Paraisobuthidae with very narrow maxillary lobes of the first and second pairs of coxae; dorsal side smooth without any granulation and with seventh tergite with a single median carina.

Derivatio nominis.—*leios* (Gr.) = smooth, bald.

Type species.—*Leioscorpio pseudobuthiformis,* n. gen., n. sp.

Geological range.—Upper Carboniferous.

Remarks.—No confusion between *Leioscorpio* and *Pseudobuthiscorpius* should exist. Although both occur in the same bed, at the same locality, the former is mainly known from the dorsal side, whereas the latter, at least for the important parts, is known from the ventral, but the maxillary lobes are totally different. In *Leioscorpio,* the maxillary lobes are very narrow, which, along with the lobosternous abdominal plates, relegated it to the Paraisobuthidae, although we have no knowledge of the eyes, median or lateral, since the anterior carapace is unknown. The very wide maxillary lobes of the second pair of coxae in *Pseudobuthiscorpius,* as well as the protolobosternous abdominal plates, indicate that this genus belongs to a different family, the Pseudobuthiscorpiidae.

The complete seventh tergite is preserved in both genera, but the central carina of *Leioscorpio* is not present in the Pseudobuthiscorpiidae. Pocock (1911, pp. 26–27, fig. 8) mistook the maxillary lobes of the first two pairs of coxae for the chelicerae.

Leioscorpio pseudobuthiformis, new species
Text-figure 92

1911. *Anthracoscorpio buthiformis* Pocock (*partim*), pp. 26–27, fig. 8.
1953. *Buthiscorpius buthiformis* (Pocock). Petrunkevitch (*partim*), p. 32.

The specimen comprises part of the dorsum of the carapace with only remnants of the pedipalp and legs, except for the fourth leg of left side, which is fairly completely preserved. The preabdomen is complete, but only the anterior caudal elements are present. Original convexity is preserved. This specimen was one of the four paratypes of *Buthiscorpius buthiformis* (Pocock) and like the others, it has been referred to other genera and species. The designation of paratypes was made by Petrunkevitch (1953, p. 32), not by Pocock (1911, pp. 26–28), who merely referred these specimens to his previously described scorpion:

> In addition to this specimen I have several examples from Dudley which, in the absence of satisfactory proof of their distinctness from each other, and from the type, I provisionally refer to this species.

The "type" referred to was the specimen considered the holotype of *Buthiscorpius buthiformis* (Pocock),

which is from different beds and from Sparth Bottoms, rather than Dudley (Coseley).

One of the important features of this specimen is that the ends of the first and second pairs of coxae are preserved. These are very narrow, of equal thickness, and with the second pair of maxillary lobes reaching the anterior margin to crowd the first pair from the midline. The carapace is preserved only as a fragment, but shows a slight median triangular sulcus. No ornamentation is present.

The postabdomen is robust, with the tergites increasing in size posteriorly; each is stoutly constructed with a heavy, transverse ridge along the anterior edge. No ornamentation is present on these tergites. The seventh tergite is roughly triangular, long, with a noticeable narrow median ridge.

The lower part of the preabdomen is broken away to reveal an underlying fourth abdominal plate. This is of the normal lobostern type, being well notched or bilobed at midsection (see restoration, Text-fig. 92B).

The caudal segments (**T8**, **T9** and **T10**) are stoutly constructed, about as long as wide, and also devoid of ornamentation. All are fragmentary.

The fourth walking leg is partly preserved and is long, stout and extends posteriorly to the end of the preabdomen, as in living scorpions. Measurements are given by Pocock (1911, p. 27) and will not be repeated here.

Type information.—A single specimen, well preserved, but incomplete, preserved in dorsal aspect in an ironstone concretion collected by Dr. Wheelton Hind from the Carboniferous, Upper Coal Measures, Etruria Marl Group, Ten Foot Ironstone bed at Coseley, South Staffordshire Coalfield, England; BM(NH) In.22832.

Derivatio nominis.—*pseudo* = (Gr.) false + *buthiformis*, the species under which this specimen had previously been classified.

Remarks.—The differences between this species and the only other lobostern from the Coseley area with which it might be confused, are discussed under "Remarks" concerning the generic description.

Family **TELMATOSCORPIONIDAE**, new family

Paraisobuthoidea with small barrel-shaped sternum; carapace with small compound lateral eyes, large median eyes anteriorly located.

Type genus.—*Telmatoscorpio,* n. gen.

Genus **TELMATOSCORPIO**, new genus

Telmatoscorpionidae with square carapace, anterior not greatly glossate; genital operculum larger than sternum; pedipalp with deep groove, studded with row of elongate pits (setal sites).

Derivatio nominis.—*telmatos* (Gr.) = swamp + *scorpio.*

Type species.—*Telmatoscorpio brevipectus,* n. gen., n. sp.

Geological range.—Pennsylvanian.

Telmatoscorpio brevipectus, new species
Text-figures 93, 112F

1913. *Eoscorpius granulosus* Petrunkevitch (*partim*), pp. 45–46, pl. III, figs. 11, 12.
1949. *Alloscorpius granulosus* (Petrunkevitch). Petrunkevitch, p. 153.
1953. *Alloscorpius granulosus* (Petrunkevitch). Petrunkevitch, p. 29.
1955. *Alloscorpius granulosus* (Petrunkevitch). Petrunkevitch, p. 73.
1962. *Alloscorpius granulosus* (Petrunkevitch). Dubinin, p. 429.

The holotype (YPM 129) originally was a paratype of *Eoscorpius granulosus* Petrunkevitch, which has been referred to the synonymy of *Eoscorpius carbonarius* Meek and Worthen. The specimen consists of two parts of an ironstone concretion that had never been cleaned of the calcite crystals that covered nearly all of the essential details reported here. The specimen is preserved showing the dorsal side on one half of the concretion and the ventral side on the other. Both sides are preserved from the inside. Preservation, after removal of the calcite, is unusually good. The dorsal side has been greatly flattened.

The carapace is subquadrate with a short anterior glossate process (see Text-fig. 93B). Two subelliptical (probably round in life) median eyes are placed on an elevated, heart-shaped ocellar node, directly behind the glossate process. From the lines present, it appears that an elevated cephalic area was well delineated in the form of a shield. Facetted lateral eyes, insufficiently well-preserved to warrant description, are present, and presumably are small and not unlike those in *Eoscorpius.* A prominent raised posterior marginal rim occurs.

The dorsal side of the preabdomen consists of the usual seven tergites, all of which increase in length posteriorly. All are bounded anteriorly by a prominent transverse ridge, and all are fringed along the posterior by a single row of small tubercles (see Text-fig. 93B). Indeed, the dorsal side of the carapace and preabdomen greatly resembles that of *Eoscorpius carbonarius,* for which it could easily be mistaken if only the dorsal side were preserved. However, the tubercles are far more numerous in the latter than in *T. brevipectus.*

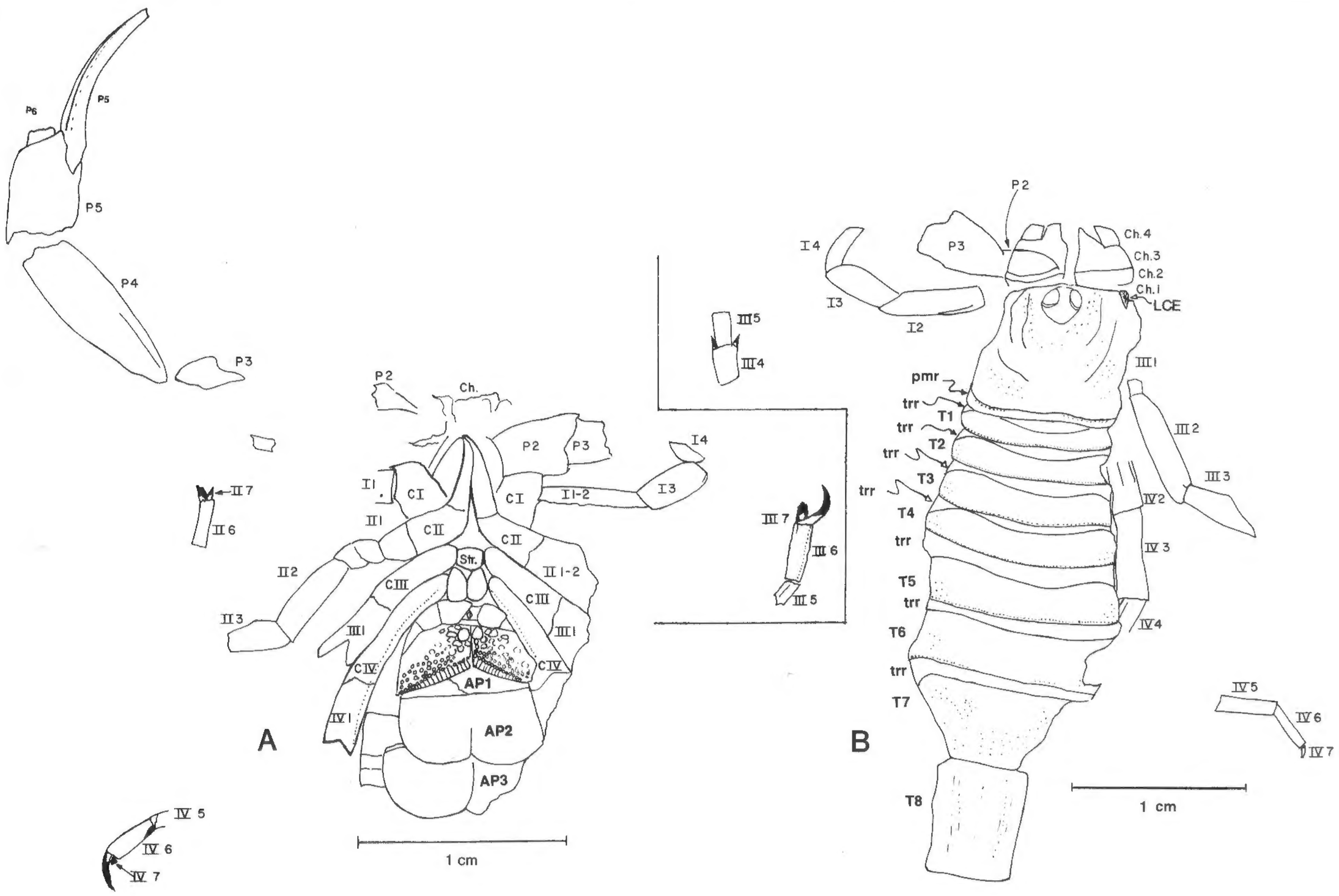
The last tergite of the preabdomen (**T7**) is very different from that of *Eoscorpius carbonarius.* It is bounded anteriorly by a wide, raised transverse ridge, whereas the rest of the tergite is sparsely covered with tubercles, all minute. None appears aligned in rows or crests. *Eoscorpius carbonarius* has two well-defined rows of punctae on the corresponding tergite.

The sternum consists of a barrel-shaped, or roughly rounded, hexagonal plate (see Text-fig. 93A). This is very small and only the third pair of coxae abuts it. The fourth pair abuts against the large opercular plate. The second coxae occur directly in front of the sternum, have well-developed narrow maxillary lobes that extend anteriorly as in living scorpions. The first coxae are not well preserved in the region of the maxillary lobes, but the latter are clearly developed, narrow in shape, and abut the maxillary lobes of the second pair. They are not expanded as in the Eoscorpiidae, but appear to be much as in living scorpions such as the Buthidae, Scorpionidae and Diplocentridae, etc.

The legs are preserved only in fragments, but enough are present to permit certain important interpretations. The chelicerae are badly smashed and, other than indicating their presence, little can be described. The denticles are present, but these are too poorly preserved for description. Three joints were noted, but four joints probably occur.

The pedipalp is preserved from the dorsal side, along with the ventral side of the opisthosoma, but only the tibia, hand and fixed finger remain (see Text-fig. 93A). The entire structure reveals a powerful pedipalp (see "Measurements"). The tibia is stoutly constructed, but too poorly preserved to reveal any ornamentation. The hand is poorly preserved, but enough is present to show that it is wide and not very long. The fixed finger is curved backwards, which indicates that the free finger, of which only the base is present, would be curved forward to fit against the immovable finger. No denticles occur along the inner edge of the finger, therefore, the inner edges are cultrate. A deep narrow groove is present, parallel to the shaft of the free finger and close to the inner edge. Several deep, elongate small pits, probably sites for bristles, occur on the inner edge of the groove.

The walking legs are not well preserved, but show that the tarsus was unusually long, had two very large, curved claws, and a posttarsus, or heel, which was elongated, although preservation of the heel was not complete. It suggests a structure much as Wills found



Text-figure 93.—*Telmatoscorpio brevipectus,* n. gen., n. sp. Holotype, YPM 129. (This is a paratype of *Eoscorpius granulosus* Petrunkevitch.) From the Upper Carboniferous (Pennsylvanian), Carbondale Formation, Lower Francis Creek Shale, Mazon Creek, Grundy Co., IL. See foldout inside front cover for explanation of abbreviations.

A. Ventral aspect. **B.** Dorsal aspect.

in *Eoscorpius pulcher* (Petrunkevitch). Double tarsal spurs are present, at least on the third pair of legs (see Text-figs. 93A, B).

Fine punctae occur as a single row on, at least, the fourth coxa, trochanter and tarsus. This row of punctations is probably present on all the legs, as it has been seen on the two extremes of the leg (*e.g.*, the coxa and tarsus). A small fragment of the matrix, above the tarsus of the second leg, was taken off the specimen and dissolved in acid. This revealed the presence of numerous short brown setae, which undoubtedly occurred in the row of punctae.

The opercular plates are very large, nearly as large as the sternum. They are elongate, and sublacrimiform, with their greatest axis parallel to the body.

The large pectines (see Text-fig. 93A) are preserved in their entirety, except where part of the teeth are covered by the overlying abdominal plate. These remarkable structures appear to have a very wide basal lamella that comprises at least three segments. The distal end is covered by an overlying tergite and may continue underneath. The middle lamellae are composed of a great number of rounded sclerites, which are coarsest or largest toward the anterior middle part and diminish in size toward the posterior and distal parts. Fulcra are well developed. The teeth are numerous, elongated, and at least 16 can be counted before they are covered by the overlying tergite and first abdominal plate. It should be repeated that the scorpion is seen from the inside of the ventral side at this point. The pectinal plate is largely covered by the pectines, but of interest is the presence of a diamond-shaped organ that may be the median organ of the pectinal plate, and that has been noted on other fossil scorpions.

The first abdominal plate is very poorly preserved and only a small part is present. The second and third abdominal plates are very well-preserved and show that they are deeply bilobed, lobosternous, and with a deep cleft in the middle. No ornamentation is present.

Type information.—The holotype (YPM 129) is from the Pennsylvanian, Carbondale Formation, lower Francis Creek Shale at Mazon Creek, Grundy County, Illinois.

Derivatio nominis.—*brevi* (L.) = short + *pectus* (L.) = shield.

Remarks.—The specimen was covered with a thin layer of drusy calcite crystals that obstructed all the details reported here. This layer of crystals was removed with HCl, which revealed the beautifully preserved structures described above.

Measurements (in mm) of the holotype (YPM 129).—

	length	width
Carapace:	6.8	8.2 at base
Median eyes:	0.7	0.55
Tergite:		
1	1.4	
2	1.7	
3	2.0	
4	2.35	
5	3.0	
6	3.2	
7	4.7	
8	5.8	
Pedipalp:		
Femur:	9.0	2.5
Hand:		2.9
Fixed finger (incomplete):	7.4	
Sternum:	1.0	1.2

Family **SCOLOPOSCORPIONIDAE**, new family

Paraisobuthoidea (or Isobuthoidea) with carapace without "compound" lateral eyes.

Type genus.—*Scoloposcorpio,* n. gen.

Remarks.—To all appearances, the large *Eoscorpius*-like cephalic cheeks should have relegated this form to the Eoscorpiidae or Mazoniidae. However, the lack of compound lateral eyes precludes the possibility of this form belonging to the Eoscorpiidae, and the presence of lobosternous abdominal plates disposes of the Mazoniidae. It is referred to the Paraisobuthoidea with considerable misgivings, but with our present knowledge, this is the only superfamily that can accommodate this family even tentatively. This is based on the lobosternous abdominal plates, which are not excessively bilobate.

Genus **SCOLOPOSCORPIO**, new genus

Scoloposcorpionidae with quadrate carapace, median eyes located in the middle of the anterior half of the carapace on a lacrimiform eye node. A deep median sulcus divides the carapace into two well-developed inflated cephalic cheeks.

Derivatio nominis.—*scolopo* (Gr.) = anything pointed + *scorpio.*

Type species.—*Scoloposcorpio cramondensis,* n. gen., n. sp.

Geological range.—Lower Carboniferous.

Remarks.—Although the superfamily designation is still not conclusive, there seems little doubt that this family and genus are necessary as they seem to occupy the same taxonomic position among the Lobosternina as the Mazoniidae does in the Holosternina.

Scoloposcorpio cramondensis, new species
Text-figure 94

1883. *Eoscorpius tuberculatus* Peach (*partim*), pp. 398–400, pl. 23, figs. 8b, c.

The holotype (GSE 2173) consists of two detached parts preserved together on the same bedding plane and not more than 20 mm apart, in black micaceous, slightly arenaceous shale. The parts preserved are the carapace and half of a lobosternous abdominal plate, very likely the second (or first) gill-bearing appendage. Another half of an abdominal plate, in the same collection, is listed as GSE 5862. The holotype carapace was figured by Peach (1883, pl. 23, fig. 8b).

The carapace is much like that in *Eoscorpius* except that the lack of "compound" lateral eyes indicates a different family, either in the Isobuthoidea or the Paraisobuthoidea. When the coxosternal area is known, the matter will be settled (see Text-fig. 94A).

The carapace is subquadrate, straight along the base, with parallel sides, rounded at the anterolateral angles and with a pointed glossate process in the median anterior margin. The basal margin is bounded by a thick, raised rim that occurs on the lateral margins and continues on to the basal fourth of said margins.

Two well-developed, raised, cephalic cheeks surround a deep sulcus, and are separated from one another by a deep sulcus. The raised lacrimiform eye node is located well within the anterior margin, in the middle of the anterior half of the carapace. The median eyes are round, and located on the anterior of the lacrimiform eye node.

There are no lateral compound eyes and enough of the carapace is preserved to assure that they would have been preserved if present. The carapace measures 7.1 mm in length and 8.2 mm in width at the base.

The associated abdominal plate (see Text-fig. 94B) is a typical lobostern, and seems to be, from its shape, the left half of the second or first gill-bearing abdominal plate, which undoubtedly had a median sulcus separating the two lobes, and a wide doublure. The plates are covered with very minute pustules. The plate half measures 6.7 mm in length and 9.3 mm in width.

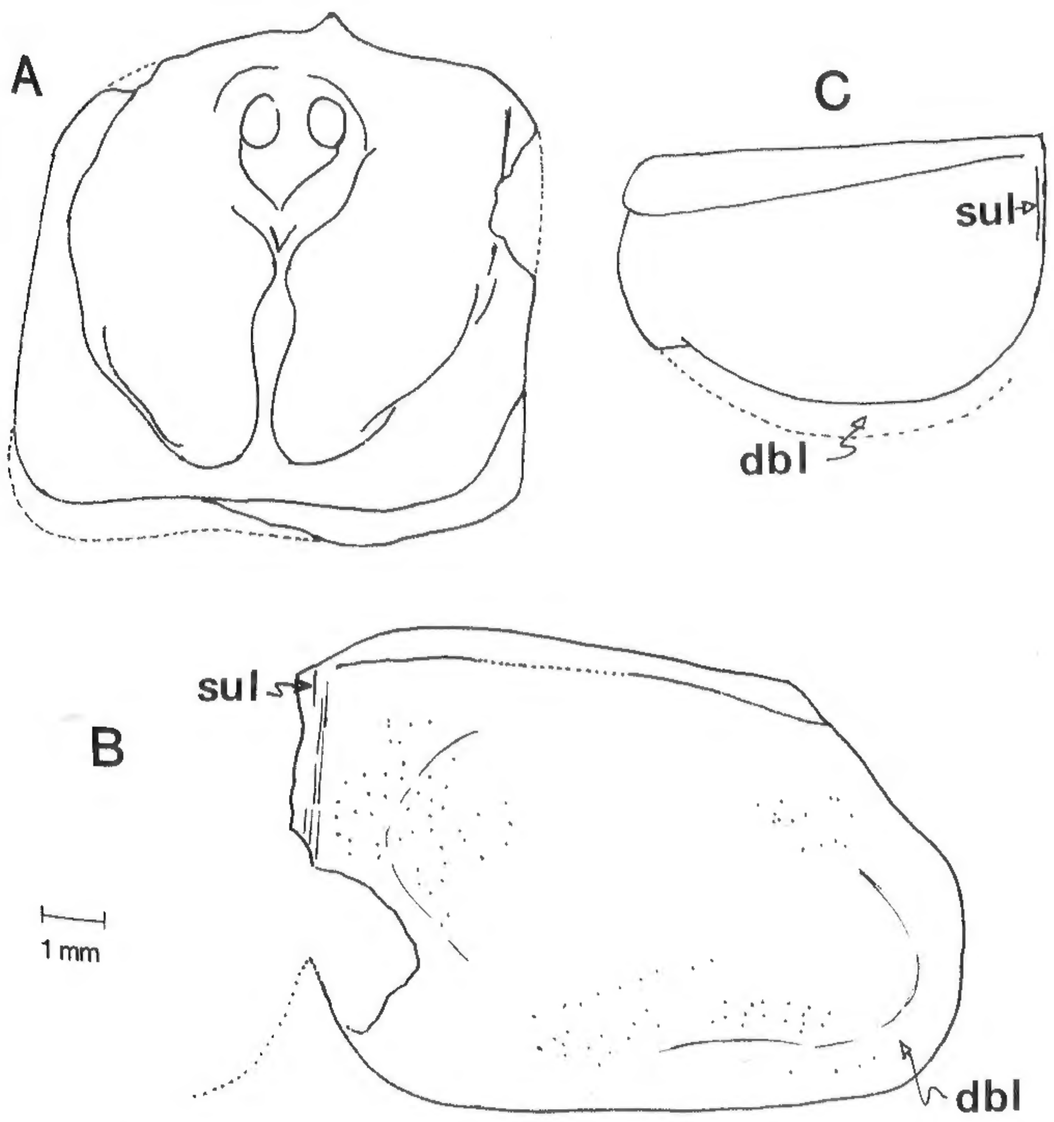
Another abdominal plate (paratype (GSE 5862), see Text-fig. 94C), but of a smaller individual, is also included in this species. The abdominal plate is probably the second or third, and reveals an entire half of a typical lobostern plate, with the deep median groove and thick doublure. It measures 6.0 mm in width.

Type information.—Lower Carboniferous, Calciferous Sandstone Series, Lower Oil Shale Group (lower Viséan), shore, west of Eagle Rock, Cramond, near Edinburgh, Scotland.

Derivatio nominis.—Named after Cramond, near Edinburgh, Scotland, the type locality of the holotype.

Remarks.—Peach (1883, pl. 23, figs. 8b, c), included under the name of *Eoscorpius tuberculatus* two carapaces from Cramond. The subject of 8b is now the holotype of *Scoloposcorpio cramondensis,* whereas the other may also be referred to the same species, although my identification of the latter is based on Peach's figure since the original has not been found.

The holotype of *Eoscorpius tuberculatus* Peach was made the type species of the genus *Benniescorpio* by Wills (1960, p. 322), who also correctly noted the discrepancy in Peach (1883), who included several unrelated specimens in his species. *Benniescorpio tuberculatus* (Peach) is from the Coal Measures at Blair Point, near Dysart, Fife, Scotland, whereas the other specimens were from the Lower Carboniferous Calciferous Sandstone. The species here described, and figured by Peach (1883, figs. 8b, c) represent two of the specimens that had been misidentified. Petrunkevitch (1953, p. 29) accepted Peach's determination as listed in his synonymy of the species, and neither questioned the determination nor noted the great difference in



Text-figure 94.—*Scoloposcorpio cramondensis,* n. gen., n. sp. From the lower Carboniferous (Lower Viséan), Cramond, near Edinburgh, Scotland. See foldout inside front cover for explanation of abbreviations.

A. Holotype (GSE 2173). Prosomal carapace. **B.** Holotype (GSE 2173). Left half of deeply lobate abdominal plate. **C.** Paratype (GSE 5862). Right half of a lobate abdominal plate.

stratigraphic age involved between the specimens.[36]

Genus **BENNIESCORPIO**[37] Wills, 1960

(?) Scoloposcorpionidae with quadrate carapace, large median eyes located on a heart-shaped eye node very near the front of the shield, no compound lateral eyes.

Type species.—*Eoscorpius tuberculatus* Peach.

Geological range.—Carboniferous.

Benniescorpio tuberculatus (Peach, 1883)

1883. *Eoscorpius tuberculatus* Peach, p. 398, pl. 23, figs. 8, 8a, 8d, 8e.
1885. *Centromachus tuberculatus* (Peach). Thorell and Lindström, p. 25.
1911. *Archaeoctonus tuberculatus* (Peach). Pocock, p. 19.
1913. *Archaeoctonus tuberculatus* (Peach). Petrunkevitch, p. 34.
1953. *Alloscorpius tuberculatus* (Peach). Petrunkevitch, p. 29, figs. 27, 28.
1960. *Benniescorpio tuberculatus* (Peach). Wills, pp. 322–327, pl. 56, fig. 5; pl. 57; text-figs. 28, 29.
1962. *Benniescorpio tuberculatus* (Peach). Dubinin, p. 429, fig. 1230.

Holotype.—GSE 9675 (or 456) and GSE 9676 (or 457). The specimen consists of part and counterpart preserved in gray shale with plant remains, collected from the Coal Measures at Blair Point, near Dysart, Fife, Scotland.

For description and discussion see Wills (1960).

Family **OPSIEOBUTHIDAE**, new family

Paraisobuthoidea with short, wide, lacrimiform sternum, with notch at posterior end. The maxillary lobes of the first pair of coxae occur above the maxillary lobes of the second pair and are expanded anteriorly to form flat, spatulate lobes; prepectinal plate greatly developed and with protolobosternous abdominal plates.

Type genus.—*Opsieobuthus,* n. gen.

Remarks.—Although it is much too soon to postulate phylogeny in the fossil scorpions, it is of importance to note that this family seems to have developed directly from the Eobuthidae by the elongation of the second pair of maxillary lobes, and the inflation of the first pair of maxillary lobes, which has been squeezed out of the midline. It differs from the Telmatoscorpionidae in the shape of the sternum, the shape of the first pair of maxillary lobes (spatulate in the Opsieobuthidae and narrow in the Telmatoscorpionidae), the lack of prepectinal plates in the Telmatoscorpionidae and the deeply-bilobate abdominal plates of the Telmatoscorpionidae as compared with the protolobosternous plates of Opsieobuthidae.

Genus **OPSIEOBUTHUS**, new genus

Opsieobuthidae with pectines having well-developed, bandlike pectinal plate.

Derivatio nominis.—*opsi* (Gr.) = late + *Eobuthus* = a genus of Carboniferous scorpion.

Type species.—*Eobuthus pottsvillensis* Moore.

Geological range.—Upper Carboniferous of Indiana.

Opsieobuthus pottsvillensis (Moore, 1923)
Text-figures 31A, 95, 112E

1923. *Eobuthus pottsvillensis* Moore, p. 131, pl. 2, figs. 1–4.
1949. *Eobuthus pottsvillensis* Moore. Petrunkevitch, p. 137.
1953. *Isobuthus pottsvillensis* (Moore). Petrunkevitch, p. 22.

The holotype comprises a nearly complete scorpion, preserved in greenish-gray shale as a ventral impression, and associated with numerous plants. The scorpion measures 40.0 mm overall, with a prosoma and preabdomen 20.5 mm in length, and a cauda (including the stinger) 19.5 mm long. The original colors are preserved, consisting of shiny, bright, brown cuticle throughout, covering the mesosoma and coxal areas, and becoming darker brown along the pedipalps and the extremities of the cauda. Preservation is unusually good and all details are readily discernible (see Text-fig. 95A).

The coxosternal region (see Text-fig. 95B) is preserved in its entirety. The maxillary lobes of the first pair of coxae above those of the second pair are greatly inflated anteriorly, spatulate, rounded at the outer margins, and do not meet at midsection, but are actually behind and above the thin maxillary lobes of the second pair of coxae. The very thin lobes of the second pair of coxae meet at midsection; they are elongated and do not project so far anteriorly as do the maxillary lobes of the first pair. The third and fourth pairs of coxae are triangular and elongate, the third abutting against the sternum and the fourth against the opercula. The sternum is wide, lacrimiform, and retains a small notch at the posterior, has rounded sides, and the anterior is pointed. It measures 2.0 mm in length and 1.7 mm in width. The genital operculum consists of two large ellipsoidal plates that fit the base and part of the sides of the sternum. The pectinal plate is trapezoidal, very large, long, and divided at the median part posteriorly (see Text-fig. 31A). The pectinal plate is

---

[36] It seems highly unlikely that the two parts preserved on the holotype slab (GSE 2173, Text-figs. 94A, B), belong to the same individual, because the complete abdominal plate would have been more than twice as wide as the carapace, which would mean an animal with a preabdomen resembling the eurypterid *Carcinosoma.* A.S.C.

[37] Kjellesvig-Waering never got around to assigning *Benniescorpio tuberculatus* (Peach) to any family. Such notes as were found were written before he had worked out the ventral structures of *Mazonia woodiana,* and no longer apply, since *M. woodiana* is a holostern and *B. tuberculatus* is a lobostern. A.S.C.

composed of two narrow thin plates, each of which is joined by a suture at midsection, where the articulation with the pectines occurs. A narrow transverse ridge borders each plate. Should there ever exist any doubt that the pectinal plate (and pectines) represent a somite, the presence of the transverse ridge along the paired pectinal plates should dispel that notion. The large pectines are attached to the middle section of these plates, and are preserved in excellent condition, showing approximately three or four joints along the anterior lamella. The intermediate lamella is undoubtedly perliform, with numerous small rounded sclerites, and attached to the posterior side of each pectine are approximately 20 long teeth. These teeth, in shape, are the type common in living forms such as the Buthidae. Small fulcra are definitely present.

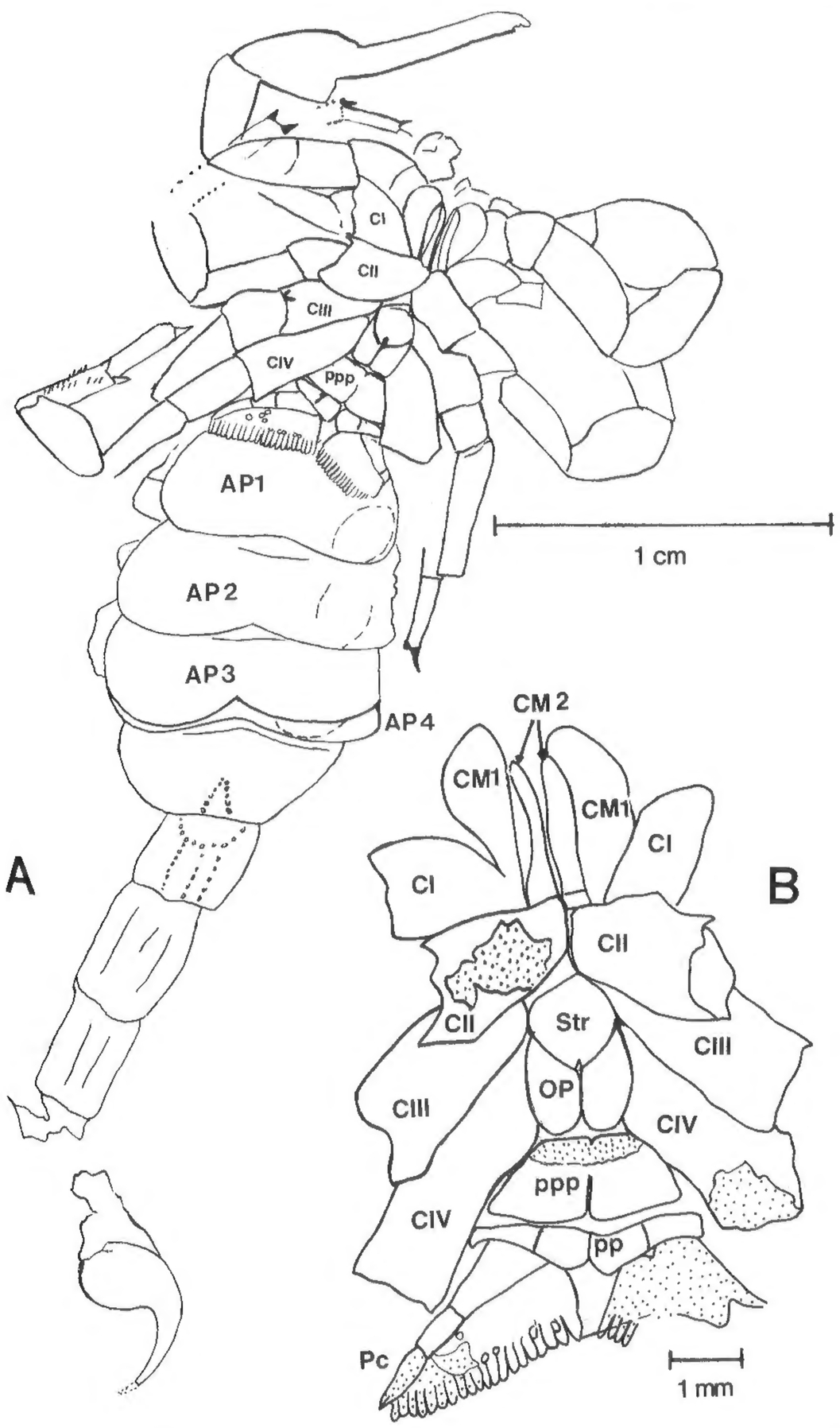
On the preabdomen, all abdominal plates are present, but the fourth has been pushed under the third. The plates are rounded at the genal angles and have a slight emargination at the middle. These lobosternous plates are therefore of the type referred to here as protolobosternous, and are considered to be derived from the holosternous plates. On the right side of the scorpion are large oval impressions, interpreted as gill chambers, that have been covered by the abdominal plates. There is no ornamentation of any kind on the three plates. The last preabdominal segment is broadly triangular and with a triangular area in the posterior center, composed of two converging crests surmounted by coarse tubercles.

The cauda is almost complete, but details of the ventral crests are not very discernible in the last three tergites. The first caudal segment shows a half-moon of tubercles on the anterior side with three crests running the length of the segment. These are surmounted by tubercles. The second caudal segment is not so well preserved, but seems to have three crests also. The third caudal segment is not well preserved, but at least two crests are visible. The fourth and fifth segments are too poorly preserved for description. The telson is well preserved, showing a long aculeus and a bulbous vesicle without the presence of a subaculear tooth. The aculeus is stout, long and curved. The entire telson measures 5.0 mm in greatest length and 2.5 mm in greatest width.

The appendages are not so well preserved, but some structures are discernible. The pedipalps are strongly developed, having a massive chela. The femur is considerably longer than the tibia and the palp shows only the hand and most of the fixed finger. The fixed finger has been broken at the end, but it is long, nearly straight, and at the end it curls into a hook. There are no denticles along the edge. Little can be said about the walking legs except that there seem to be double basitarsal and double tarsal spurs on each. The two claws are long and curved. Of particular interest, however, is the very wide tibia developed on each leg. The basitarsus on one leg has many setae on the ventral surface, and, although part of the setae seem to be in linear series, it is not possible to be sure.

Type information.—Pennsylvanian, Pottsville Series, in strip pit in Clay County, near the Owen County line, east of Clay City, Indiana. Holotype, FMNH (UC) 37984.

Remarks.—Very few specimens are preserved as well as this one. The relationship of the underside of the abdomen is especially well shown in the remarkable



Text-figure 95.—*Opsieobuthus pottsvillensis* (Moore). Holotype, FMNH (UC) 37984. From the Upper Carboniferous (Pennsylvanian), Pottsville Series, Strip Clay pit, near Owen Co. line, east of Clay City, IN. See foldout inside front cover for explanation of abbreviations.

A. Complete specimen. Note the protolobosternous abdominal plates. **B.** Details of the coxosternal and pectinal areas.

preservation. Much has been added to our knowledge of the pectinal plate and the prepectinal plate, which commonly are not well preserved (see Text-fig. 31A).

Moore's description (1923, p. 131) is unusually good, although details of the above-mentioned plates were not noted.

The oral chamber in *Opsieobuthus* is the same as that in modern scorpions, namely, the first two pairs of maxillary lobes form the floor of the oral chamber and the coxae of the pedipalps, the lateral sides of said chamber. This scorpion, as advanced as it appears, is nevertheless a lobostern. Thus it is seen that fundamental structures, which presumably are attributed to terrestrial existence, were developed before the respiratory organs changed from gills to lungs. This idea was first expressed by Laurie (1899, p. 576) in connection with the description of the Silurian species *Dolichophonus loudonensis,* and seems to be borne out by this beautifully-preserved specimen (see also Størmer, 1954). It is, of course, possible and probable that this scorpion lived much like gill-bearing crabs that move from water to air along the roots of trees, in the swamp environments in which both lived. The water, which gave the required moisture, was carried in ample gill chambers or pouches of the scorpions. They were amphibious, and able to eat outside of the water because of the development of the oral chamber.

Superfamily **LOBOARCHAEOCTONOIDEA**, new superfamily

Lobosternina with first pair of coxae without maxillary lobes and meeting in front of the sternum; other three pairs of coxae abutting the sternum. Legs tubiform.

Type family.—Loboarchaeoctonidae, new family.

Remarks.—Loboarchaeoctonoidea is essentially the lobosternous "counterpart" of the holosternous Archaeoctonoidea.

Family **LOBOARCHAEOCTONIDAE**, new family

Loboarchaeoctonoidea with very large, pentagonal, longer than wide sternum. Median eyes placed well forward on the carapace; compound lateral eyes present.

Type genus.—*Loboarchaeoctonus,* n. gen.

Genus **LOBOARCHAEOCTONUS**, new genus

Loboarchaeoctonidae with lanceolate carapace, very short legs and well-defined median carina on the mesosoma.

Derivatio nominis.—*lobos* (Gr.) = a rounded projection, lobed + *Archaeoctonus* = a scorpion genus.

Type species.—*Loboarchaeoctonus squamosus,* n. gen., n. sp.

Geological range.—Lower Carboniferous.

Loboarchaeoctonus squamosus, new species
Text-figures 96, 111J

1949. *Archaeoctonus tuberculatus* (Peach). Petrunkevitch (*partim*), pp. 138–139, figs. 138, 175.
1949. *Centromachus euglyptus* (Peach). Petrunkevitch (*partim*), p. 141, fig. 136.
1962. *Centromachus euglyptus* (Peach). Dubinin, p. 428, fig. 1242.

Specimen I.—The holotype, BM(NH) I.988, consists of a small scorpion, preserved mainly in dorsal aspect, exhibiting the carapace and nearly all of the opisthosoma as well as one well-preserved pedipalp, part of the chelicera and several walking legs. Little can be noted of the ventral side, but some impression of the coxosternal region occurs through the carapace, so that this important area can be discerned in detail. The imprint of a lobosternous abdominal plate is also present. The holotype is preserved in black shale associated on the same bedding plane with what appear to be carbonaceous plant remains. Most of the specimen is composed of the original cuticle although many patches have now peeled off. When restudying this specimen after some ten years, it was found that peeling had continued and the specimen was quite deteriorated. Nevertheless, all details reported here can be seen on the specimen, under alcohol, and in a dry state under a very low-angled light.

The carapace is broadly lanceolate. This type of carapace looks much like that of the eurypterid *Hughmilleria.* The lateral margins are nearly parallel, rounded at the anterolateral angles and the anterior. The base is straight and very likely a ridge occurred at the base. The median ocelli are small and are located anteriorly on the carapace. They appear to be elliptical in shape, probably round in life, and are placed on a broad, lacrimiform ocellar node. The lateral eyes are compound, reniform, and located at the anterolateral angles. They apparently are slightly intramarginal.

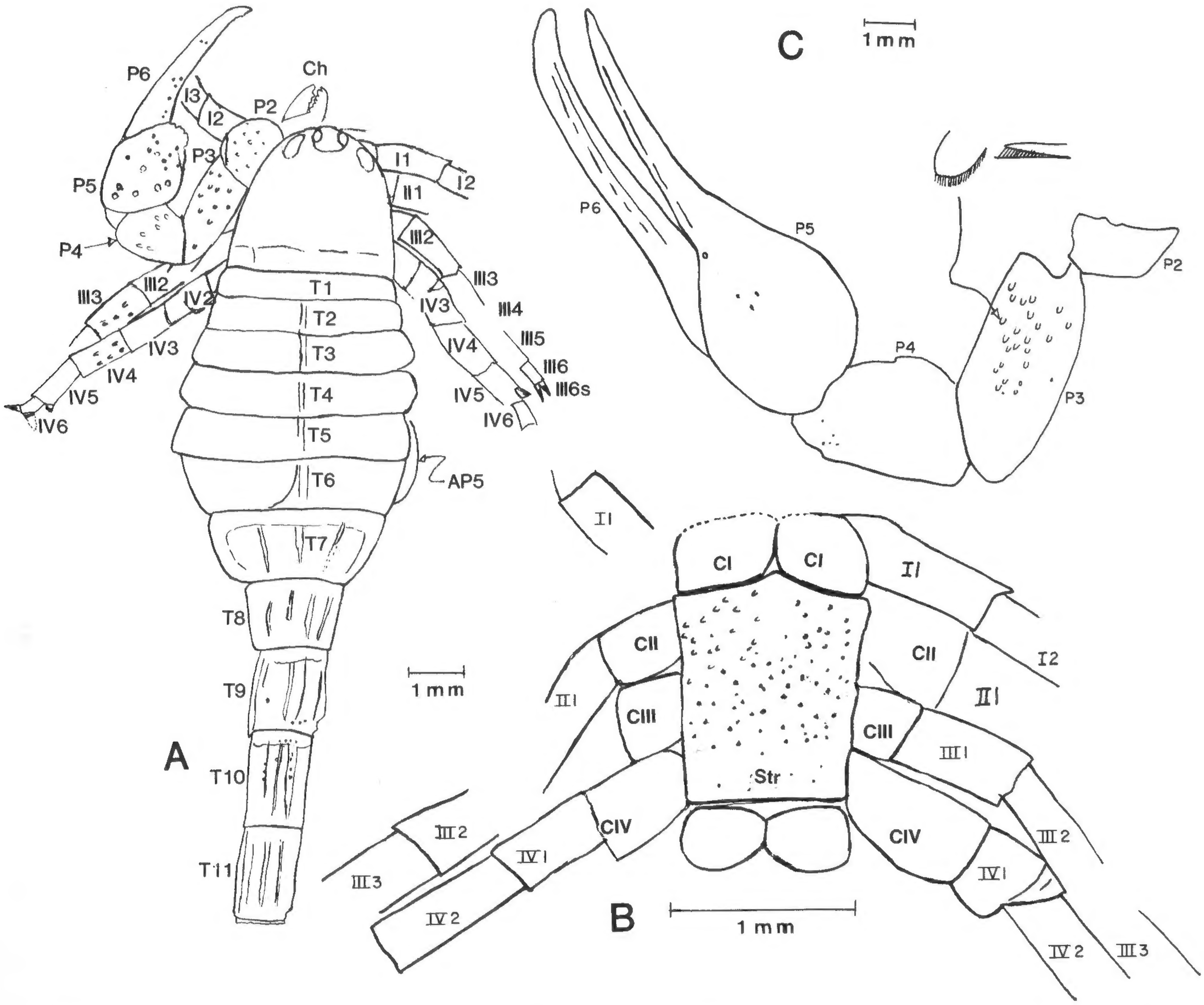
The preabdomen is composed of the usual seven tergites, each of which increases in length posteriorly. A prominent median ridge is present on at least the second to seventh preabdominal tergites. The seventh tergite also has two well-developed carinae on either side of the median ridge.

Only four caudal tergites were preserved. These show a great lengthening in the last two tergites preserved, and probably indicate that the fifth caudal segment, which is not preserved, would be longer. Four definite carinae occur on the first segment and very likely on the second segment. Only three dorsal carinae occur on the last two segments that are preserved. Large setal openings occur on the tergites and some of them occur at the crest of the carinae.

One of the surprising features is the enormous pedipalp and another is the short length of the walking legs. The entire pedipalp is preserved, with the trochanter

developed as a massive segment. The femur is longer than the tibia and both are massively constructed. The hand is quite wide, quadrate, and the free finger, also a massive structure, curves inward. Large squamose raised markings occur on all joints of the pedipalp, and the curved movable finger retains several setal openings. Preservation was not sufficient to determine any particular pattern. The walking legs, of which only the last two are preserved nearly whole, show that all were short and tubular. The longest leg, which is the fourth, barely extends to the middle of the sixth tergite. Squamose markings are also present along the legs. Two massive spurs occur, at least on the last leg, that would correspond to the basitarsal spurs. No tibial spurs seem to be preserved. The termination of each leg consists of two claws that are not curved but seem to be short and straight. Nothing was seen of the posttarsus, although it must be assumed that it was present. The left chelicera is poorly preserved and reveals only that the edges of the chelae had small teeth. The chelae are curving but not hook-like.

The coxosternal arrangement is noted as impressions left on the area of the carapace. The squamose structure covering the coxae and sternum was responsible for the erroneous determination made by Petrunkevitch, who considered the carapace to be highly granular, as shown in his drawing of this specimen (Petrunkevitch, 1949, fig. 138). The first pair of coxae meets at midsection, does not have any development of maxillary lobes, and is covered with squamose ornamentation.



Text-figure 96.—*Loboarchaeoctonus squamosus,* n. gen., n. sp. From the Lower Carboniferous (lower Viséan), Glencartholm Volcanic Beds, Eskdale, near Langholm, Dumfriesshire, Scotland. See foldout inside front cover for explanation of abbreviations.

A. Holotype (BM(NH) I.988: a paratype of *Archaeoctonus tuberculatus* (Peach) of Petrunkevitch, 1949). Complete specimen. **B.** Holotype (BM(NH) I.988). Ventral organization of the coxosternal area as impressed through the carapace. **C.** Paratype (BM(NH) In.12848). A pedipalp.

The last three pairs abut against a large, longer-than-broad, pentagonal sternum. The pentagonal sternum also seems to be ornamented with squamose markings along the frontal part (see Text-fig. 96B). There are two oviform opercular plates. This is best seen under very oblique lighting. Nothing can be noted concerning the rest of the underside except to show that in the region of the fifth and sixth tergites, the gill pouch of the fourth or fifth abdominal plate was partly impressed through the sixth tergite, and also is present on the lateral part at the right hand side of the mesosoma. Although the abdominal plates are not preserved completely, enough is present to state definitely that this scorpion is lobosternous.

Measurements (in mm) of the holotype (BM(NH) I.988).—

	length	width
Carapace:	3.5	3.3 (at base)
Preabdomen:	6.8	4.3 (greatest)
Postabdomen:		
Tergite 8:	1.5	
Tergite 9:	1.7	
Tergite 10:	2.1	
Tergite 11:	2.1	
Pedipalp:		
Femur:	2.2	
Tibia:	1.4	
Hand:	1.6	1.5
Free finger:	3.0	
Estimated overall:	18.0	

Type information.—Glencartholm on the River Esk (Eskdale), 3½ miles SSW of Langholm, Dumfriesshire, Scotland. From the Lower Carboniferous (lower Viséan) Glencartholm Volcanic Beds, Upper Border Group.

Derivatio nominis.—*squamosus* (L.) = scaly.

Remarks.—After studying the holotype specimen (BM(NH) I.988), my results differ almost totally from those of Petrunkevitch (1949, p. 138, fig. 138). The differences are so great that comparison or detailing them would be superfluous. It is best to refer to Petrunkevitch's figure 138 and compare it with Text-figures 96A and B here.

Specimen II.—Also from the same locality and horizon is a single, well-preserved, nearly complete pedipalp (BM(NH) In.12848, In.12849; see Text-fig. 96C). Petrunkevitch (1949, p. 141) identified this specimen as *Centromachus euglyptus* (Peach), because "The shape of the hand and its fingers conforms fairly well with the figure given by Peach for his type." I disagree with the determination, as the ornamentation is entirely different; the shape of the fingers and the hand is different, and *C. euglyptus* has fingers with denticles that have a serrated appearance, as stated by Peach and verified here, whereas the fingers of BM(NH) In.12848 are entirely cultrate. Apart from this, the fixed finger is recurving to fit the curved falcate finger along its entire length. In *C. euglyptus,* the two fingers are opposable-falcate and do not join along their length. This pedipalp is referred to *Loboarchaeoctonus squamosus* because the shape of each joint is identical, the inner edges of the chela are recurving and cultrate, and the ornamentation is the same.

The ornamentation is very interesting because it is identical to that of the "scorpionid type" eurypterids (the Carcinosomidae, Megalograptidae, Mixopteridae and others), in which the opisthosoma had a shape very much like that of the scorpions, and also had a tubiform cauda capable of overhead thrusting like the scorpions. In some of these eurypterids, the telson was developed as a curved, downwardly-bent spine, much like the scorpions, also capable of overhead thrusting.

The ornamentation comprises long, rounded scales, raised at the apex and slanting into the rest of the integument. The raised lateral walls are very finely striated. These scales are always black, contrasting with the dark-brown color of the rest of the integument. They are commonly setaceous. The rounded "bead-like" tubercles, which Petrunkevitch (1949, p. 141, fig. 136) reported, are not tubercles, but are secondary formations and a matter of preservation, as shown by Størmer (1963, pp. 37–38) in his study of *Gigantoscorpio willsi* from the same beds and having the same preservation.

The chela, including the hand and fingers, measures 10.0 mm in length. It represents a much larger scorpion than the holotype.

Superfamily **PSEUDOBUTHISCORPIOIDEA**, new superfamily

Lobosternina with the first pair of coxae abutting the second pair, which in turn meets at the midline; both pairs anterior to the sternum; last two pairs abut against the sternum.

Type family.—Pseudobuthiscorpiidae, new family.

Remarks.—The Pseudobuthiscorpioidea differ from the Isobuthoidea, both of which are Lobosternina, in having the last pair of coxae abut against the sternum, as in living scorpions, and not against the opercular plates. It seems possible that the Pseudobuthiscorpioidea represent a stage in development out of the Anthracochaeriloidea, which differs only in having protolobosternous abdominal plates.

Family **PSEUDOBUTHISCORPIIDAE**, new family

Pseudobuthiscorpioidea with fully-developed maxillary lobes of the first and second pairs of coxae. The maxillary lobes of the second pair of coxae extend forward to be in line with the anterior of the first pair

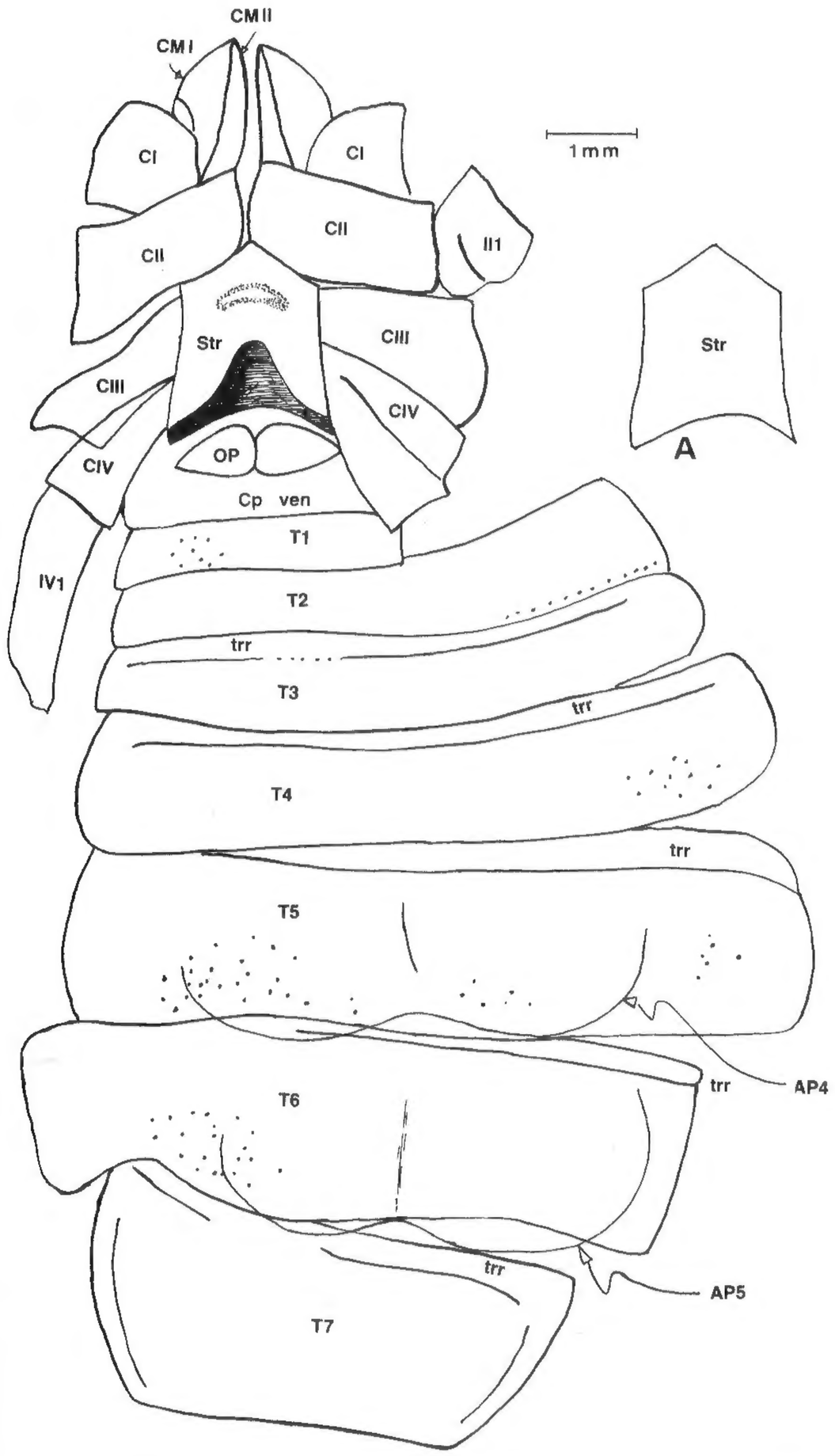
of maxillary lobes. Sternum pentagonal, very large and concave at the posterior margin.

Type genus.—*Pseudobuthiscorpius,* n. gen.

Genus **PSEUDOBUTHISCORPIUS**, new genus

Pseudobuthiscorpiidae with maxillary lobes developed so that both reach the anterior margin, and with the first pair wide but not flaring. All coxae are very short (see Text-fig. 112J).

Derivatio nominis.—*pseudo* (Gr.) = false + *Buthiscorpius* = a genus of fossil scorpions.



Text-figure 97.—*Pseudobuthiscorpius labiosus,* n. gen., n. sp. Holotype, BM(NH) I.1555, part and counterpart. From the Upper Carboniferous, Upper Coal Measures (*Modiolaris similis* and *pulchra* Zones), near Coseley, Staffordshire, England. Some parts of the coxae are taken from both halves of the type and from rubber casts. All tergites are dorsal, but the protolobosternous abdominal plates are preserved beneath them. See foldout inside front cover for explanation of abbreviations.

Type species.—*Pseudobuthiscorpius labiosus,* n. gen., n. sp.

Geological range.—Upper Carboniferous.

Remarks.—There is no other scorpion with the characters of this genus, and although the dorsal surface is unknown, it cannot be mistaken for any other. It apparently is one of the rarer scorpions at the Coseley locality. This specimen (BM(NH) I.1555) was erroneously included in *Anthracoscorpio buthiformis* Pocock (Pocock, 1911); Petrunkevitch (1953) thought it represented the underside of *Buthiscorpius buthiformis* (Pocock) and later, in 1955, having referred the specimen to *Buthiscorpius,* which he included under the family Eoscorpiidae, he used this specimen as the subject of a drawing purportedly showing the coxosternal arrangement of *Eoscorpius* (Petrunkevitch, 1955, p. 73, fig. 40(1)). In reality, the underside of *Eoscorpius* was then unknown; it is known now and it is a very different scorpion.

At the time, the underside of *Buthiscorpius* was unknown, as the holotype of *Buthiscorpius buthiformis* (Pocock) was preserved as a dorsal impression. Now that the Mazon Creek fauna has furnished a remarkably well-preserved specimen of *Buthiscorpius* (*B. lemayi*) it is clear that the well-known specimen BM(NH) I.1555 does not belong with *Buthiscorpius,* as that genus is a Holosternina, whereas *Pseudobuthiscorpius* is a Lobosternina.

Pseudobuthiscorpius labiosus, new species
Text-figures 97, 112J

1911. *Anthracoscorpio buthiformis* Pocock (*partim*), pl. 1, figs. 2 and 2a.
1913. *Eoscorpius buthiformis* (Pocock). Petrunkevitch (*partim*), p. 35.
1949. *Eoscorpius buthiformis* (Pocock). Petrunkevitch (*partim*), p. 153.
1953. *Buthiscorpius buthiformis* (Pocock). Petrunkevitch (*partim*), p. 32, figs. 34 and 45 (labelled *Euscorpius*).

The holotype (BM(NH) I.1555) comprises a small ironstone concretion with a nearly perfect impression of the ventral side of the coxosternal region and the inside of the dorsal side of the mesosoma. The coxosternal region is shown in great detail.

The sternum is very large with an overall pentagonal outline, but deeply invaginated, roughly in a triangular depression in the posterior. This deep inverted triangular area is very noticeable in the posterior part, and a narrow low ridge occurs transversely along the anterior part of it. The posterior margin of the sternum is concave and the lateral margins flare slightly posteriorly.

The coxae of the first two pairs of legs have well-developed maxillary lobes and occur in the same arrangement as that in living scorpions, namely, the sec-

ond pair meets at midsection and squeezes the large maxillary lobes of the first pair to the side. These maxillary lobes are thereby fully developed. The third and fourth pairs of coxae abut the sternum. The opercular plates are tear-shaped, the bulbous parts of which oppose each other, and are considerably wider than long.

The legs were not preserved except for one joint of the fourth walking leg. The dorsal side of the mesosoma shows that the tergites increase in size posteriorly. There are no carinae on any of the tergites, including the seventh tergite. Small scattered granules on the sides of the tergites increase in size toward the posterior of each tergite. A single row of pustules probably is present at the posterior of each tergite.

The large abdominal plates, the fourth and fifth at least, were impressed on the tergites, and can best be described as protolobosternal, that is, the central posterior part is emarginate, but not deeply-notched as in typical lobosternal forms.

Type information.—The holotype (BM(NH) I.1555) consists of two halves of an ironstone concretion collected by W. Egginton from the concretions in the shales 10 ft above the Thick Coal, Upper Coal Measures (*Modiolaris similis* and *pulchra* Zones) near Coseley, in the South Staffordshire Coalfield, England.

Derivatio nominis.—*labiosus* (L.) = large-lipped.

Remarks.—No other scorpion combines all the characters that set this apart from others on the superfamily, family and generic levels: therefore, comparisons are unnecessary. However, some scorpions occurring in the same bed may be confused with this species. It differs from *Coseleyscorpio lanceolatus* Kjellesvig-Waering (see above) in that the coxae of the first pair of legs in *C. lanceolatus* are very narrow in contrast to the "thick-lipped" first pair of coxae of *Pseudobuthiscorpius labiosus. C. lanceolatus,* furthermore, is a holostern instead of a protolobostern. With regard to the lobosternous *Leioscorpio pseudobuthiformis,* the same important differences are apparent in the first pair of maxillary lobes. These are major differences that cannot under any circumstances be explained by either factors of preservation or of variation.

Family **PETALOSCORPIONIDAE**, new family

Pseudobuthiscorpioidea with first two pairs of coxae meeting at the midline, with the second pair extending less than halfway the length of the first pair. Sternum pentagonal.

Type genus.—*Petaloscorpio,* n. gen.

Remarks.—The family differs from the Waterstoniidae in the shape of the sternum, and in having the second pair of coxae not reaching so far forward nor being so well-developed as in the Waterstoniidae. It also differs from the Pseudobuthiscorpiidae in the coxosternal region, for in the Pseudobuthiscorpiidae the second pair of coxae has squeezed the first pair away from the midline and the maxillary lobes no longer abut one another as they do in the Petaloscorpiidae.

Genus **PETALOSCORPIO**, new genus

Petaloscorpionidae with large pectines that lack differentiation of the basal and middle lamellae and have a rachis with numerous rounded sclerites, all of which are unusually homogeneous in size.

Derivatio nominis.—*petalos* (Gr.) = broad, flat + *scorpio.*

Type species.—*Petaloscorpio bureaui,* n. gen., n. sp.

Geological range.—Pennsylvanian.

Remarks.—The unusual perliform comb, with anterior or basal lamellae undifferentiated, may well be a family character rather than generic.

Petaloscorpio bureaui, new species
Text-figures 98, 112I, 113C1

One specimen of a well-preserved scorpion showing mainly the dorsal side of the mesosoma and anterior tergite of the metasoma with impression of the coxosternal region faintly imprinted; preserved in greenish-gray shale with numerous plants on the same horizon.

The specimen is quite well-preserved with small details such as the combs and the ornamentation readily visible, and although there is no doubt concerning its uniqueness on the species level, the type of abdominal plates and the shape of the sternum are not entirely certain. Therefore, on the generic level, there is some doubt.

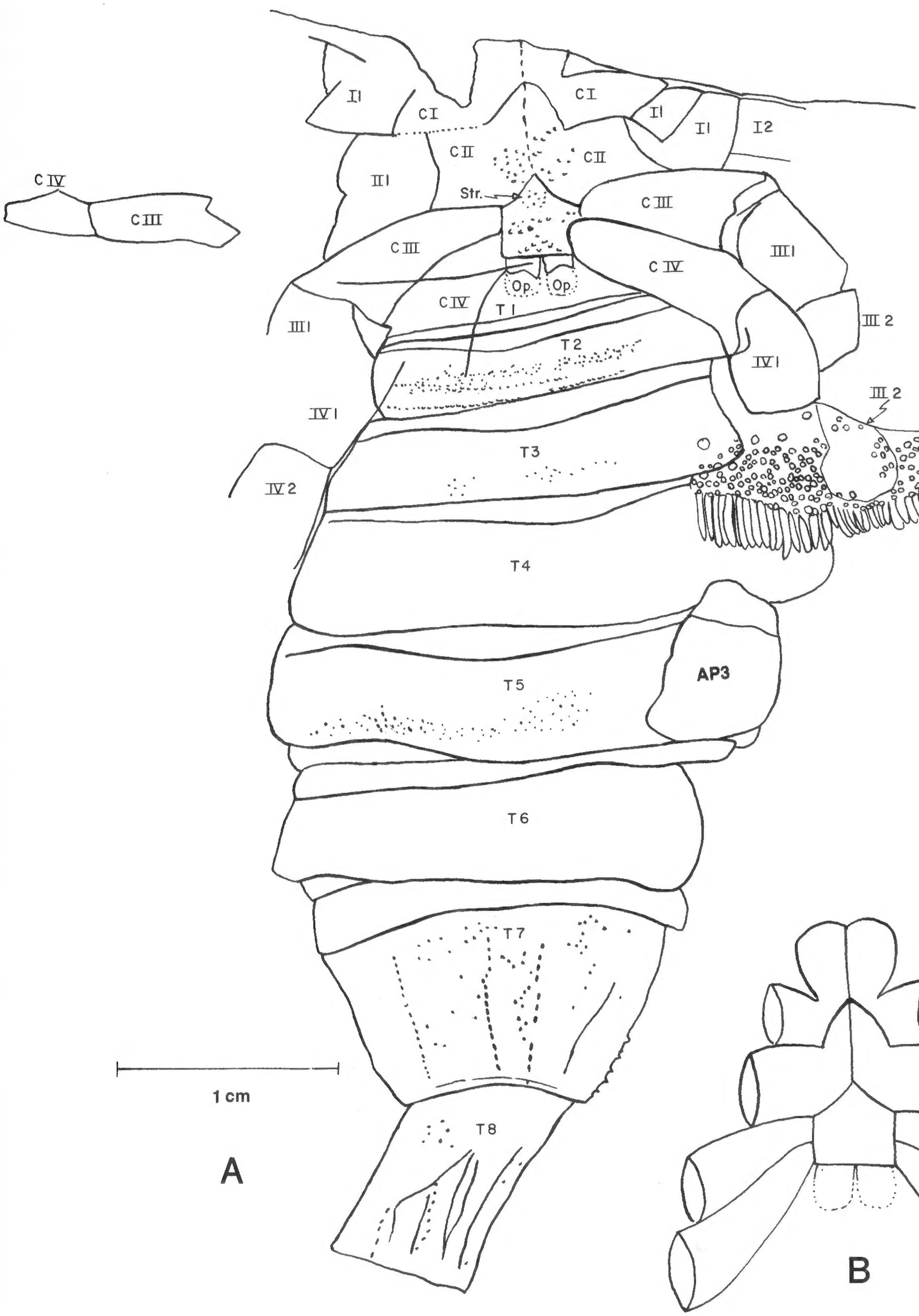
The coxosternal region is only faintly preserved. The sternum is probably pentagonal and the last two pairs of coxae (**CIII** and **CIV**) abut against it. The maxillary lobes of the second pair seem to extend midway up the length of the maxillary lobes of the first pair, and the first pair of maxillary lobes are broadly spatulate, as indicated by the preserved basal part, and meet at the midline.

Rather coarse, scalelike ornamentation covers the sternum and the second pair of coxae (**CII**). The genital opercular plates are very poorly preserved and apparently are longer than broad.

The left comb is preserved in its entirety and all details are revealed. There is no anterior lamella and the overall width of the comb is very great, and flaring anteriorly. The teeth decrease in size to less than one-

Text-figure 98.—*Petaloscorpio bureaui,* n. gen., n. sp. Holotype (UL 1092). From the Upper Carboniferous (Pennsylvanian), Escuminac Formation at Bernard's Lot, Miguasha, Bonaventure Co., Quebec, Canada. See foldout inside front cover for explanation of abbreviations.

A. Complete specimen. **B.** Reconstruction of the coxosternal area.


C IV
C III
II1
C I
C II
Str.
C III
Op.
Op.
C IV
T 1
III1
T2
IV1
T3
IV2
T4
T5
T6
T7
T8
C I
II1
II1
I2
C II
C III
III1
C IV
III 2
IV1
III 2
AP3
1 cm
A
B

half their length from the center to the distal end. There are approximately 50 teeth (48 counted). Fulcra are present but greatly reduced. The rachis is composed of nearly rounded, small areoles, notable for their overall small size as compared with those in all other scorpions.

The tergites increase in size posteriorly, and the greatest width probably was reached at the fifth or sixth tergites. All are ornamented in the posterior part by punctae and by a row of semilunar scales at the base.

The seventh tergite retains two central carinae, each of which is surmounted by elongated or linear pustules. Two similar carinae occur on each side of the central ones. The lateral edge of the seventh tergite is apparently serrated. Numerous pustules occur between the carinae.

Only the first caudal segment was preserved, and this shows the same pustules as the preceding tergite, and carinae, which are too poorly preserved for determination.

Only one small fragment of an abdominal plate, which seems to be the third, was preserved, and is of the lobosternous type.

Measurements (in mm) of the holotype (UL 1092).—

	length	width
Tergites:		
1	2.6	(partly covered)
2	3.6	(partly covered)
3	4.5	(partly covered)
4	5.6	(partly covered)
5	6.3	(partly covered)
6	6.3	18.0
7	9.4	16.3 (anterior) 9.2 (posterior)
8	9.0	6.4
Pectines:	15.0	5.5 at midsection
Overall:	140.0 (estimated)	

Type information.—Collected from Zone 5 of Pennsylvanian Escuminac Formation at Bernard's Lot, Miguasha, Bonaventure County, Quebec, Canada (locality also known in literature as being in Scaumenac or Escuminac Bay) by René Bureau in 1964, and registered as No. 1092 in the collection of the University of Laval, Quebec City, Canada.

Derivatio nominis.—The species is named in honor of the collector, René Bureau.

Remarks.—Comparison with other scorpions is superfluous as the comb is sufficiently different to distinguish it and to warrant description as a new species.

Family **WATERSTONIIDAE**, new family

Pseudobuthiscorpioidea with lacrimiform sternum and well-developed maxillary lobes of the first two pairs of coxae, but with the second pair reaching only to the lower two-thirds of the maxillary lobes of the first pair; third and fourth pairs abutting the sternum. No lateral eyes present.

Type genus.—*Waterstonia,* n. gen.

Remarks.—The family combines rather primitive, deeply-bilobate abdominal plates with highly-advanced coxosternal characters, which, interestingly enough, are almost identical with those of the Lower Devonian species *Branchioscorpio richardsoni.* I suspect that this scorpion is amphibious and could carry water in the gill chambers in order to live on land. The well-formed oral chamber is considered an adaptation for living on land, although not necessarily permanently.

Genus **WATERSTONIA**, new genus

Waterstoniidae with elongated, anteriorly-rounded carapace with two large, anteriorly-located elliptical median eyes, no lateral eyes. Tarsus of first pair of legs greatly elongated.

Derivatio nominis.—Named in honor of Charles D. Waterston whose eurypterid work, particularly on the abdominal plates and gills, is exceptional and has great bearing on our knowledge of scorpions, and who kindly furnished the holotype specimen for description.

Type species.—*Waterstonia airdriensis,* n. gen., n. sp.

Geological range.—Upper Carboniferous.

Waterstonia airdriensis, new species
Text-figures 99, 112G

The holotype comprises part and counterpart of a medium-sized specimen that is fragmentary, but in which all the parts important for taxonomic purposes are well preserved. It occurs in micaceous gray shale, and it was possible to expose part of the structures that were embedded therein. Thus it has been possible to reveal many of the important parts that make this specimen unique.

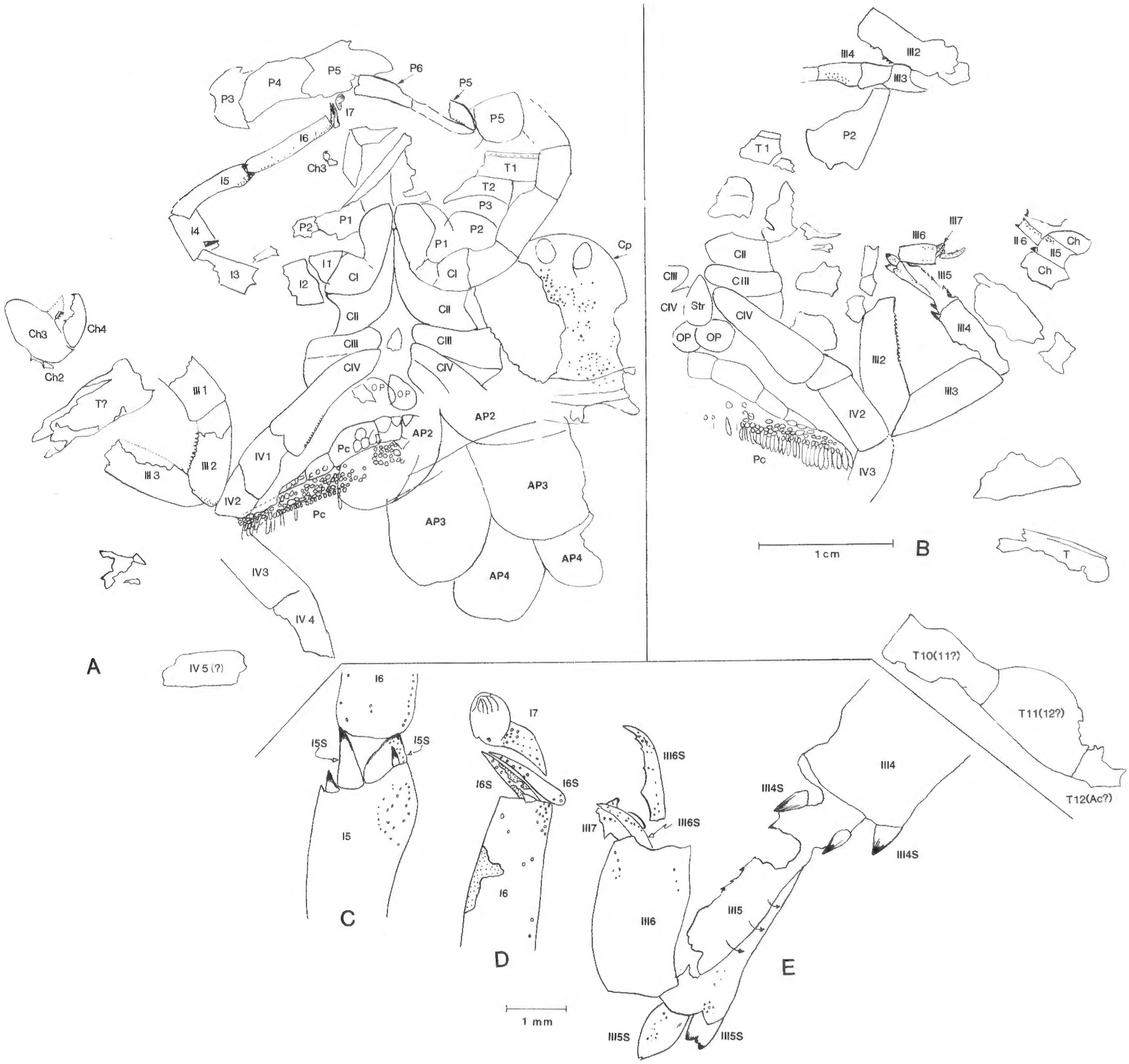
The original cuticle is perfectly preserved, some of which would have peeled off the specimen had it not been coated with a preservative.

Enough of the carapace is preserved to show that it was very long, rounded on the anterolateral corners and along the anterior margin. The base is nearly straight, with an elevated ridge along the basal part. It is covered with coarse pustules, mainly over the central part and posterior parts. Two large elliptical eyes (probably round in life) are located on the anterior part of the carapace. These are the median eyes and there is no trace of compound lateral eyes.

Nearly all parts of the taxonomically-important coxosternal region are known and the arrangement is of particular interest. The sternum is badly crushed, but enough of the outline is left, I believe, to be able

to reconstruct it. It is lacrimiform, rounded on the posterior side and pointed at the anterior end. It is small and would extend into the junction of the second coxae. The third and fourth coxal pairs abut against the sternum.

The first pair of coxae has very large and wide maxillary lobes. They are broadly club-shaped or spatulate and nearly flat along the anterior edge. They abut each other along the anterior third of the maxillary lobe, thus the lower, outer part of the oral chamber was composed only of the maxillary lobes of the first pair of coxae. They are rounded on the outer, lateral part and constricted where they adjoin the rest of the coxae, resulting in a pair of spatulate organs. The second pair of coxae also has well-developed maxillary lobes, but these are pointed and long and occur within the posterior two-thirds of the first maxillary lobes. The third and fourth pairs of coxae are rounded at the inner part



Text-figure 99.—*Waterstonia airdriensis,* n. gen., n. sp. Holotype (RSM 1957.1.4996). From the Lower Carboniferous, Lower Coal Measures (Westphalian A), Whiterigg Colliery, Airdrie, Lanarkshire, Scotland. See foldout inside front cover for explanation of abbreviations.

A. Showing the disposition of prosomal ventral features and proximal preabdomen. **B.** Counterpart. **C.** End of the basitarsus of the first leg (I), showing the two basitarsal spurs and minor spines adjoining the end of the tarsus. **D.** Probably the first leg, showing very large distal spurs of the sixth joint and analogous structure on the seventh joint. **E.** Third leg, distally folded back on itself.

and abut the sternum. The only ornamentation noted was a single row of granules along the posterior edge of the fourth coxae. The opercular plates are also lacrimiform with a flat area where they adjoin each other along the midsection (see Text-figs. 99A, B).

The pectines are of particular interest and show that the anterior or first lamella consists of at least four segments. These are covered with irregularly-shaped, rounded sclerites. The larger sclerites occur toward the inner part of the pectines. The middle lamella is quite wide and broad and is covered with small rounded sclerites. One or two larger sclerites were noted, but most of them are small. The fulcra are well developed and are made up of rounded small sclerites. The denticles of the pectines are long and narrow. Thirty of these teeth have been counted, but, undoubtedly, there is room for 45 to 50 teeth on each pectine (see Text-figs. 99A, B).

The chelicerae are only partially preserved, but they appear to be rather wide, although probably crushed. However, the hand of the chelicera, forming most of the third segment, seems to be unusually wide. The two chela are armed with teeth, but it was not possible to determine their arrangement.

Little can be noted concerning the pedipalps, as only fragments were preserved. However, they appear to have been stout, and it was noted that small denticles occurred along the edge of the free fingers. The ends of the immovable and free fingers seem to be rounded and without falcate terminations.

The first walking leg is preserved almost in its entirety. This is mainly slender with a particularly long tarsus (see Text-figs. 99A, D). Basitarsal spurs occur (see Text-fig. 99C), one of which is a flat short spur, whereas the other is a longer, pointed spur. Another spur occurs in the same intersegmental membrane. The tarsus is particularly long and tubular, and the claws are straight and quite long (see Text-fig. 99A). These are covered with setal openings, revealing that they were rather hirsute. The posttarsus is pointed, with a round, ball-like internal area that shows definite deep and linear muscle scars (see Text-fig. 99D). Setal openings are also present on the tarsus. The tarsus, as well as the basitarsus, is also covered in part with setal openings.

The second leg is largely unknown except for the coxae. The third leg (see Text-figs. 99B, E) is perhaps the most interesting of all, as it shows that the tibia was armed on the inner side with a very serrate edge. The tarsus is greatly reduced from what it is on the first leg. The ungues are rather straight, falcate and with spines on the venter. The fourth walking leg reveals a very long coxa, followed by a short trochanter. Only parts of the femur, tibia and patella are present.

The dorsal side of the mesosoma is practically unknown, but fragments of the tergites do occur, and show that they were bounded on the anterior edge by a prominent transverse ridge with a row of setal openings. The underside, however, is preserved and shows that the scorpion was a typical lobostern with very wide, deeply-bilobate abdominal plates that were bounded at midsection by a suture. The indentation or cleft at the posterior middle of the two lobes is very deep. The cauda is represented only by fragments of three segments and, other than to show that this was a rather thick tail, nothing more can be described.

Measurements (in mm) of the holotype (RSM 1957.1.4996).—

Length of prosoma:	12.8 (estimated)
Width at base:	10.0 (estimated)
Median eye length:	2.0
width:	1.6
Estimated total length:	125.0

Type information.—The holotype (RSM 1957.1.4996) is in the collections of the Royal Scottish Museum, Edinburgh, Scotland, and is from the "Fern Bed", from which many fine plant specimens were described by R. Kidston, and which occurs in Whiterigg Colliery, Airdrie, Lanarkshire, Scotland. The fern bed lies 20 ft above the Upper Drumgray Coal. This horizon is in the *communis* Zone of the Ammanian (Lower Coal Measures or Westphalian A) (Waterston, pers. commun., August 19, 1968).

Derivatio nominis.—Species name is taken from the town of Airdrie, in Lanarkshire, Scotland.

Remarks.—The original coloration was preserved in this specimen and it showed that the entire test was dark-brown in color and that it apparently must have been a rather hirsute animal.

Waterstonia (?) **brachistodactyla**, new species
Text-figure 100

The holotype consists of a single specimen, preserved in black shale in unusually good condition. Although only part of the pedipalp is preserved, enough is present so that its recognition will be easily assured if found again. The skin is totally without ornamentation, presenting a bald appearance, which is unique. Only part of the hand and all of the fixed finger of the pedipalp are preserved. The parts preserved show that this scorpion likely reached a length of approximately 20 cm.

The fixed finger is very slender, unusually short, cultrate, tapering and with a very slight swelling at the base along the cultrate edge; it tapers to a point rather abruptly. It is straight along the outer edge.

Type information.—The holotype label reads "From

a shale a few fathoms above main clay ironstone, Crookhill-Beith". According to personal communication with C. D. Waterston, it comes from "1 to 3 fathoms" above the "Main Clay Ironstone", or the Dalry Clayband Ironstone, near the Johnstone Shell-Bed horizon—that is, the Limestone Coal Group of the Scottish Carboniferous succession, Namurian E_{1a} from Crookhill near Beith, North Ayrshire, Scotland. The specimen is registered as RSM 1978.5.1 in the Royal Scottish Museum [Craig Collection], Edinburgh, Scotland.

Derivatio nominis.—*brachistos* (Gr.) = shortest + *dactylos* (Gr.) = finger.

Remarks.—The new species cannot be compared with *Waterstonia airdriensis* from the same general locality because the pedipalp is not known in the latter. However, because *W.* (?) *brachistodactyla* occurs in a different horizon, and lacks the ornamentation present in *W. airdriensis,* it is considered different.

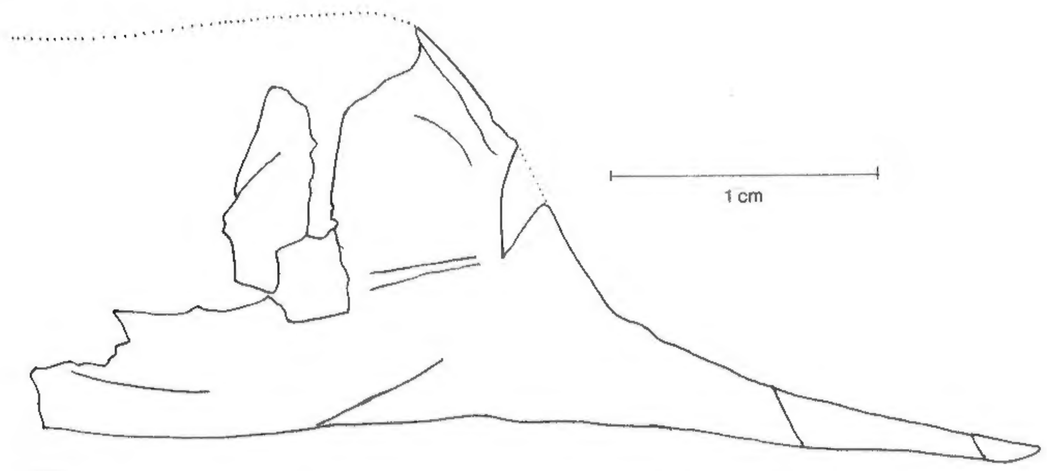
Infraorder **BILOBOSTERNINA**, new infraorder

Branchioscorpionina with five pairs of abdominal plates consisting of two completely-separated, rounded lobes, without doublures, below the body wall, which may have become slightly sclerotized and developed into sternites.

Remarks.—The Bilobosternina seem to reveal the direction of evolution of the early scorpions. The abdominal plates are joined to the body wall only at the inner anterior part, and serve only to cover the gills. These scorpions are intermediate between the lobosterns and the living forms, and the plates are in the process of being reduced completely.

Superfamily **BRANCHIOSCORPIONOIDEA**, new superfamily

Bilobosternina with first two pairs of coxae having well-developed maxillary lobes meeting at the midline in front of the sternum; last two pairs of coxae abutting the sternum.



Text-figure 100.—*Waterstonia* (?) *brachistodactyla,* n. sp. Holotype (RSM 1978.5.1) [in the Craig Collection]. Incomplete hand and finger of the pedipalp. From the Upper Carboniferous, Coal Measures, Crookhill-Beith, North Ayrshire, Scotland.

Type family.—Branchioscorpionidae, n. fam.

Remarks.—The coxosternal area is remarkably advanced for a superfamily known to date only from the Silurian and Devonian.

Family **BRANCHIOSCORPIONIDAE**, new family

Branchioscorpionoidea of small size with a pointed oval-shaped sternum; orthostern sternites with the suggestion of a median line, above the paired abdominal plate lobes.

Type genus.—*Branchioscorpio,* n. gen.

Remarks.—This is an easily recognizable family, differing from all others of its age in the shape of the sternum and arrangement of the coxae, but, oddly enough, almost identical with the Upper Carboniferous genus *Waterstonia* in its coxosternal arrangement. The Silurian family Proscorpiidae Scudder, 1886, as emended by Kjellesvig-Waering (1966), bears some affinities to this new family. It has a sternum that is somewhat similar to the Branchioscorpionidae, though proportionately much larger; however, the arrangement of the coxae is different. In the Proscorpiidae the first pair of coxae lacks maxillary lobes and meets in front of the sternum, but all four pairs of coxae abut the sternum. Apart from this, the abdominal plates of the Branchioscorpionidae are of the bilobostern type, whereas those of the Proscorpiidae are holostern in shape.

Genus **BRANCHIOSCORPIO**, new genus

Branchioscorpionidae with operculum composed of two large subquadrate sclerites immediately posterior to the sternum; pectines large, unjointed, composed of one large plate, and basally bordered by a narrow lamella to which are attached eight rounded teeth; preabdomen covered with large, thickened scales, and each sternite bordered posteriorly by a well-developed transverse ridge; legs much like those of present-day scorpions; large rounded gills (at least in ventral aspect) open to the outside by a large slit located at the anterior outer margin.

Derivatio nominis.—*branchia* (Gr.) = the gills of fishes + *scorpio.*

Type species.—*Branchioscorpio richardsoni,* n. gen., n. sp.

Geological range.—Lower Devonian of Wyoming.

Remarks.—Little is to be gained by a comparison of this genus with any other, as it is unique.[38]

Branchioscorpio richardsoni, new species
Text-figures 101, 111F

The species is based on a single specimen (FMNH (PE) 6176a,b) collected by Eugene S. Richardson, Jr. and Robert H. Denison from the Field Museum of Natural History collecting site in Cottonwood Canyon, Wyoming, in 1962.

The holotype is preserved so that the cuticle retains the original colors which, as in some modern scorpions, consist of an overall light-brown, darkening toward the ends of the pedipalp. The preservation can hardly be surpassed, as the original cuticle is present, however, in a compressed condition. It is a scorpion of about the same size as the medium-sized species of the present day, based on the size of the organs present (the carapace and most of the cauda are missing). Only the ventral side is known.

The coxa (first joint) of the pedipalp, seen in ventral aspect, comprises an elongate, roughly triangular joint (**P1**), about twice as long as wide. It has been displaced, along with the rest of the pedipalp, to the left side of the mouth. It is rounded outward and has a small triangular spine at the inner anterior corner. Length of the coxa is 2.3 mm and 1.1 mm in greatest width. The surface of the joint is covered with crowded, very minute, triangular, thornlike spinules very similar to those that Wills reported for *Mesophonus* (Wills, 1947, p. 84) on coxae **1** and **2**. The spinules are all of the same size and all point toward the inner edge of the joint. They differ from those of *Mesophonus* in being arranged so that they point away from the oral opening rather than being haphazardly distributed. The spinules toward the side of the trochanter, however, are longer and narrower. They are important because they have been considered to be stridulating[39] organs by Wills and others.

The color of the first joint is light-brown, and because of the minute spinules, absorbs light, giving it a duller appearance than the other joints.

One feature of considerable interest about the coxa of the pedipalp is the presence of a row of small triangular teeth, forming a gnathobase, as in eurypterids, along the posterior part of the coxa, and in life, on each side of the passage to the mouth.[40]

The complete trochanter (**P2**) of the pedipalp (see Text-fig. 101A) is preserved, turned so that the dorsal side is placed anteriorly. As such it is a triangular structure, with the dorsal side rounded, but without any ridges such as occur in the trochanters of many Recent scorpions, which almost appear as if two joints had been fused. In *B. richardsoni* the entire structure is smooth, except for two or three very small granules along the dorsal (anterior) part. In color the trochanter is light-brown and shiny. Along the dorsal side it measures 2.3 mm in length.

The femur (**P3**) of the pedipalp, preserved flattened, with ventral side showing as in life (see Text-fig. 101A), is a long, possibly cylindrical, structure, and quite massive in relation to the rest of the pedipalp. This joint is diagonal, and is ornamented with very small granules in no apparent pattern. Some of these could be setal sites or trichobothria, but this was not definitely established under high magnification. The color is light-brown, but becoming slightly darker toward the distal end. The femur measures 4.6 mm in greatest length and 1.7 mm in width at midsection.

The tibia (**P4**) of the pedipalp (see Text-fig. 101A) is much shorter than the femur and, although not entirely preserved, enough is present for a suitable description. It is preserved from the ventral side, and is thicker than the femur and only about half again as long as wide. In color it is shiny light-brown; the ornamentation comprises semilunar mucrones, coarser than those on the femur, but scattered about in no discernible pattern, except that they are mainly concentrated in the posterior part of the podomere. The

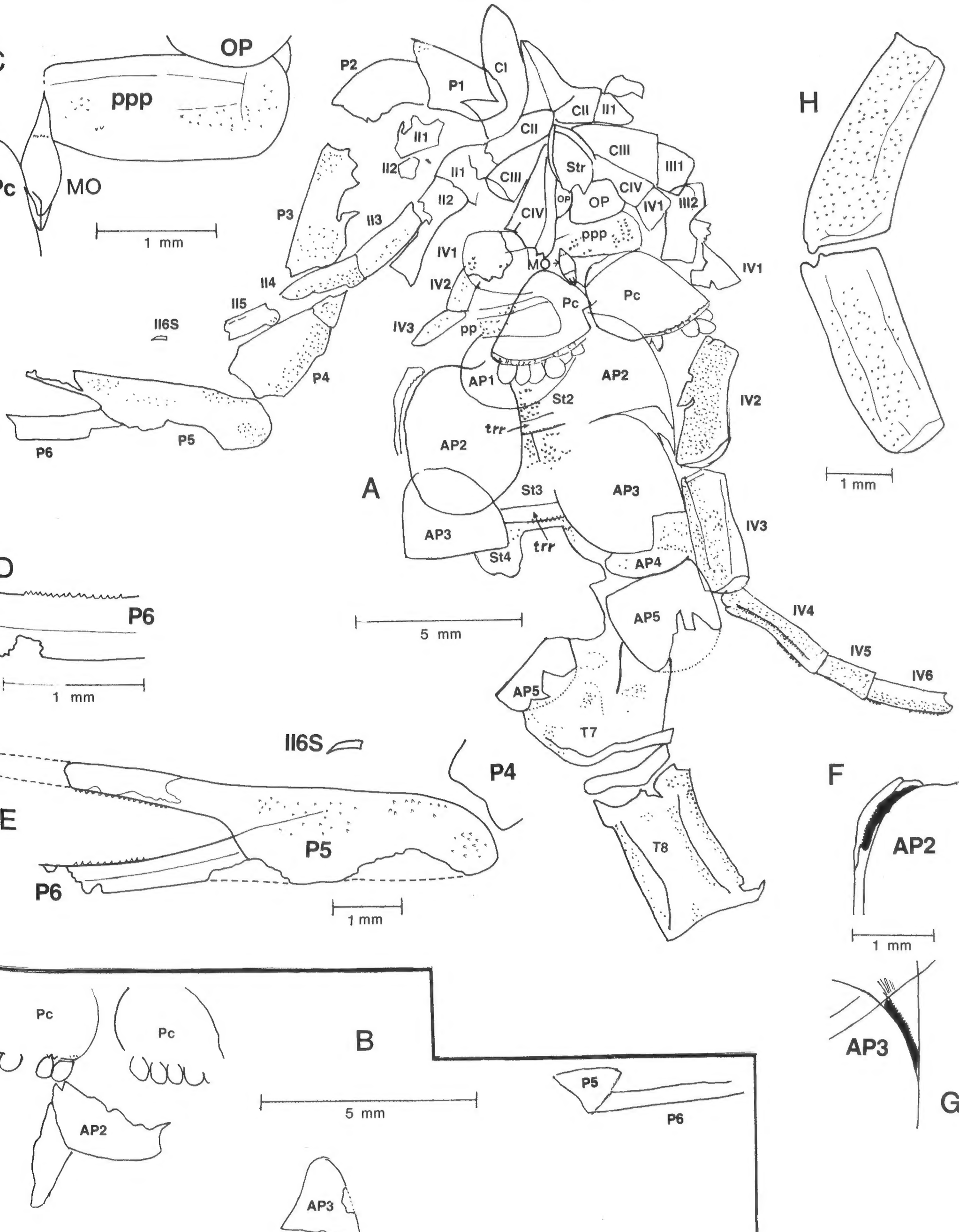
[38] The most difficult part of preparing this manuscript for publication has been the attempt to reconcile the revised illustrations of *Branchioscorpio richardsoni* with the only description of the genus and species available, dating more than 12 years earlier, before Kjellesvig-Waering had completed his world-wide study of the available types and had formulated his theories of fossil scorpion classification. Among his papers was a jubilant note that he had just completed the revision of the figures of *B. richardsoni* in January, 1979, in line with his final ideas, but that he had had to stop short of making a reconstruction of *Branchioscorpio* and writing up the new parts. Shortly thereafter he went to the hospital, and it was too late. Scattered throughout the completed parts of the manuscript were comments and comparisons with *B. richardsoni* to suggest what he thought the species was really like. A.S.C.

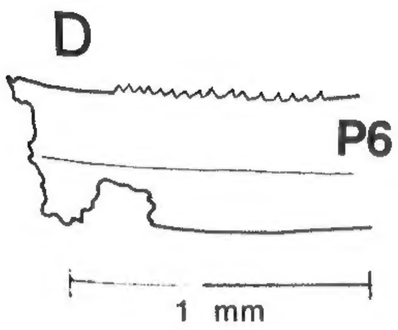
[39] These "organs" were eliminated in the final version of Text-fig. 101A. A.S.C.

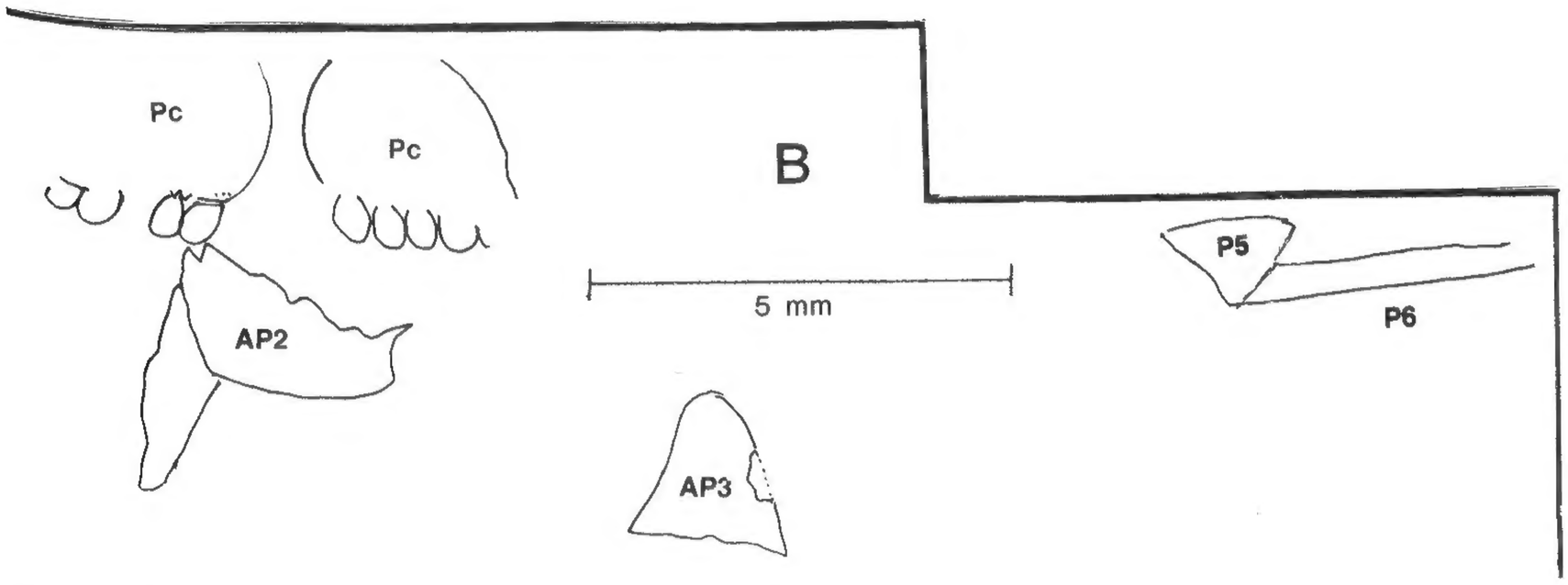
[40] This is another detail omitted in the final figure. A.S.C.

Text-figure 101.—*Branchioscorpio richardsoni,* n. gen., n. sp. Holotype, FMNH (PE) 6175a,b). From the Lower Devonian, Beartooth Butte Formation, of Cottonwood Canyon, Big Horn Mts., WY. See foldout inside front cover for explanation of abbreviations.

A. The ventral surface exposed in the holotype (dorsum unknown). This shows both sternites[41] (body wall features) (**St2-4**) and abdominal plates (**AP1-5**), which cover the gills. **B.** Reverse of holotype slab (fig. 101A): only the few parts identifiable on the surface are drawn. **C.** The prepectinal plate (**ppp**) and its median organ (**MO**). **D.** A portion of the free ramus of the pedipalp. Note fine denticulation (serration) on the cutting edge. **E.** A composite of the part and counterpart of the pedipalp, showing the serrations on both cutting edges of the dactyls. **F.** Showing the slitlike anterior gill opening (in black) of the second abdominal plate (**AP2**), left side. **G.** The slitlike anterior opening of the third gill, right side (**AP3**). **H.** Right leg **IV**, showing condyle and socket.







[41] It might be argued that the structures **St2–4** are internal surfaces of tergites, but Kjellesvig-Waering believed otherwise. His interpretation here is crucial to his concept that abdominal plates and sternites are non-homologous structures, which at full development, to the exclusion of one or the other, performed analogous function. In response to a question from Dr. Rolfe concerning the sternite–tergite problem, Kjellesvig-Waering (written commun., date unknown) replied: "You may wonder how I could detect [sic] the sternites (**St**) from the tergites. Easy—two ways: 1st the ornamentation is pointing (the U) ventrally and 2nd the transverse ridges are bowed ventrally (**trr**)". A.S.C.

tibia measures 2.6 mm in greatest length and 1.9 mm in greatest width, which is at midsection.

Almost the entire chela is preserved except for the distal end of the fingers (see Text-figs. 101A, E). It also is preserved from the ventral side and is unusually long and narrow. The hand, in particular, is very long, measuring 1.7 mm in width and 4.3 mm in length through the midsection, or to the inner junction with the free finger. It is rounded at the posterior end, with the two sides parallel. The entire chela is shiny dark-brown increasing to darker shades at the distal ends. It is covered only in part by small scalelike mucrones, or granules, some of which are rounded and definitely reveal a small opening that, no doubt, represented sites for setae. Smaller round openings can also be noted, although not in any defined pattern. Some of these may represent trichobothria.

The fixed ramus is nearly complete (see Text-figs. 101A, B, E), although parts of the extreme distal end are lacking. It occurs on both part and counterpart, in particular on FMNH (PE) 6175b. The fingers are long, tapering structures with an inner serrated edge that consists of a single row of triangular denticles. Both rami contain the same denticles, and are approximately of the same size. The fixed ramus measures 3.9 mm along the inner edge to the junction with the free ramus. This is an incomplete measurement as the distal end is gone. The fingers are very dark-brown in color and no ornamentation was noted.

Of the four walking legs, only the second and fourth are preserved almost entirely, although the basal podomeres of all are present and reveal the important coxosternal area, which seems to be of great diagnostic value in our classification. The coxae of all the legs are preserved complete, and show that the first two pairs join together at midsection much the same as in present-day scorpions, whereas the last two pairs abut against the sternum described above. This arrangement of the coxae (Text-fig. 111F), surprisingly is much like that present in *Buthiscorpius, Eoscorpius* and *Mazoniscorpio* among the Carboniferous scorpions, and still more surprising, as in modern scorpions. The shape of the sternum, however, is totally different from anything known, except in *Waterstonia* (see Text-fig. 112G).

The second walking leg on the left side (underside) is preserved almost entirely, but parts of it are missing (see Text-fig. 101A). The trochanter (**II1**) is a large triangular, flaring podomere and, although not entirely preserved, enough is present to reveal its unusual size. Junction with the coxa is very clearly seen. In color it is dark-brown, and quite shiny. No ornamentation is present. The following joints (**II2** to **II6**) are rather incomplete, although **II3** and **II5** are nearly complete. The latter are cylindrical and retain a few scattered scales. Joint **II5**, the basitarsus, is noteworthy for having a swelling at the posterior junction with the previous joint. Some scales occur on the swelling, otherwise the joint does not retain any ornamentation. A single claw, undoubtedly the anterior (the posterior claw was lost in excavation), occurs in normal position. It is long and slightly curved, but not as in modern scorpions. It is important to note the complete lack of any spurs in the integumental tissue between the joints. This is also true of the fourth leg.

The last leg (**IV**) on the right side is well preserved except for the trochanter, which is fragmented, and the distal end (see Text-figs. 101A and H).

Measurements (in mm) of the last leg of the holotype (FMNH(PE) 6175a,b).—

	length	width at midsection
IV2:	3.6	1.2
IV3:	3.0	1.0
IV4:	2.8	0.8
IV5:	1.4	0.6
IV6:	2.0	0.4

Each joint appears to be cylindrical but slightly tapering. All are covered with scales, pointing distally, much coarser than any noted elsewhere, and many of these scales have a small perforation, very likely representing the site of a seta. In the distal joints (**IV4** to **IV6**) the posterior part is ornamented with a single row of serrations. Joint **IV4** reveals two rows, probably one on each side of the leg. No spurs are present on any of the joints. Podomere **IV2** reveals a condyle at the distal end, and opposing this is the corresponding socket (see Text-fig. 101H). The color of the leg is light-brown, with the scales being of a darker color.

The sternum is elongated, subovoid, pointed anteriorly and not so pointed on the posterior end. A narrow doublure occurs dorsally, and this is separated at the anterior into two separate bands (see Text-fig. 101A). The sutures of the doublure of the metasoma in the eurypterids have been described (Kjellesvig-Waering, 1961, p. 817), and it is apparent that these sutures are the same or quite similar in the sternum of the scorpions. No ornamentation occurs on the sternum and the color is uniform light-brown, with a darker shade on the doublure. The sternum is 1.8 mm in length and 1.2 mm in width.

The genital operculum comprises two large subquadrate plates, one of which is preserved completely, whereas the other is mainly covered by the coxa of the last leg. The cuticle of the opercula is more dark-brown in color than the other parts of this scorpion, except the pedipalps. The opercula measure 1.1 mm in di-

ameter, and are devoid of any ornamentation.

The pectines are preserved in their entirety and are quite different from those known from any scorpion in the Upper Paleozoic. (The only other scorpion from the earlier Paleozoic that shows the pectines, very poorly-preserved, is *Waeringoscorpio hefteri* Størmer, 1970.) Each is composed of a large unjointed plate, nearly triangular in shape, with the sides rounded. Along the basal edge is a very narrow, also unjointed, lamella to which are attached eight elliptical and very wide teeth. It appears certain that each comb is composed of eight teeth. These teeth show minute perforations along the outer edge that apparently are the peg organs. These can be seen under high magnification on the second tooth of the right comb. It is interesting to note that the neonates of the living species *Megacormus granosus* Gervais of Mexico (Hoffmann, 1931, fig. 14) reveal a basal unjointed rachis that recalls the comb of *Branchioscorpio richardsoni.* Jointing of this part occurs in later stadia. The pectines measure 2.2 mm in length and 2.1 mm in width.

The combs are attached to a narrow base that is the first "sternite" or anchor to the combs (**ppp** in Text-fig. 101A). Point of attachment seems to be at a notch-like lobe at both ends. In the center, however, (see **MO** in Text-figs. 101A, C) is a short clublike organ. It was not possible to note any joints, but the end appears to be divided. This organ resembles in many respects the short female (Type B) organ of the eurypterids, in particular that of *Megalograptus ohioensis* Caster and Kjellesvig-Waering (1964, fig. 19).

The underside of the mesosoma is the most interesting part of the scorpion as the separate, rounded abdominal plates seem to underlie large, rounded or ovoid gills. The abdominal plates are of the split or bilobostern type. The mesosoma appears to have been thrust foward, perhaps due to ecdysis, so that abdominal plates and the corresponding gills overlap one another. The abdominal plates can be seen in the posterior part of the mesosoma. The first pair apparently had been mainly lost before deposition, as only the right posterior abdominal plate is present. Following this, and covering the undisturbed gills (**AP2**), are three long, squarish sternites. On the counterpart (FMNH (PE) 6175b), the relationship of the gill to the outlines of the plates is well shown. This reveals that the abdominal plates are separated by a considerable distance from each other (see Text-fig. 101A).

The gills are almost surely much more complicated than they appear in the specimen. They are large, ovoid, cuticular membranes and are not attached to the abdominal plate, but must be attached to the venter of the scorpion. It has been noted (see Text-figs. 101A, F, G) that at the outer anterior end of the gills is a large opening, bounded on the outer lip by a single series of serrations, which cannot be referred to any known scorpionid structure. By inference, it appears that this must also be part of the gills, perhaps an opening, or outlet of the gills; it occurs in the same place in relation to two different gills and retains the same structure. There is little doubt that other parts of the gills have been flattened out and that all that can be seen now is the ovoid part and the opening (outlet?). This is a problem that must be settled with additional material.

The ovoid part of the gills, which is the ventral part, reveals a dendritic pattern, probably cuticular reinforcement, such as is found in the lungs of some scorpions, rather than vascular markings, and is similar in many respects to the arborescent ridges on the gills of the eurypterids (see Moore, 1941, pp. 64–66).

The sternites are bordered by a well-developed anterior transverse ridge and the ornamentation comprises wide, semilunar, thick scales scattered in no apparent pattern.

The metasoma is known only from the anterior two tergites. The first, which forms the last tergite of the preabdomen, is roughly pentagonal, and is seen from the inside of the dorsal side. It is covered with the same type of thick scales as the rest of the dorsum, and is surrounded by a thick doublure, but no crests are developed.

The first tergite of the cauda is nearly twice as long as wide, but nevertheless is wide enough to suggest a well-developed or strong cauda. It is surmounted on the venter by two crests, each of which is covered with small scales as also are the sides, suggesting lateral crests. This tergite measures 4.1 mm in length and 2.2 mm in width at midsection.

Type information.—The holotype (FMNH (PE) 6175a,b) comes from the Beartooth Butte Formation, light-gray, argillaceous, dolomite (dololutite) of Lower Devonian age, associated with eurypterids, plants, and fishes, from Cottonwood Canyon, Big Horn Mountains, WY, U.S.A.

Derivatio nominis.—The specimen was named in honor of Dr. Eugene S. Richardson, Jr., invertebrate paleontologist at the Field Museum, who first called my attention to the Cottonwood Canyon scorpions.

Family **DOLICHOPHONIDAE**
Petrunkevitch, 1953
(emend.)

Branchioscorpionoidea with carapace having compound lateral eyes and small median eyes placed on a small intramarginal eye node.

Type genus.—*Dolichophonus* Petrunkevitch, 1949.

Remarks.—Discovery of the bilobosternous abdominal plate means that the family can no longer retain

the genus *Proscorpius,* as advanced by Petrunkevitch (1955, p. 70), as the latter is a holostern.

Genus **DOLICHOPHONUS** Petrunkevitch, 1949 (emend.)

Carapace subrectangular, tapering anteriorly, very long and strongly emarginate on the anterior margin; compound lateral eyes at the anterolateral corners, protruding.

Type species.—*Palaeophonus loudonensis* Laurie, 1899.

Geological range.—Middle Silurian.

Remarks.—Generically there is no scorpion that can be mistaken for this one, which is the oldest known. It occurs, as do all Silurian and Lower Devonian scorpions, associated with eurypterids.

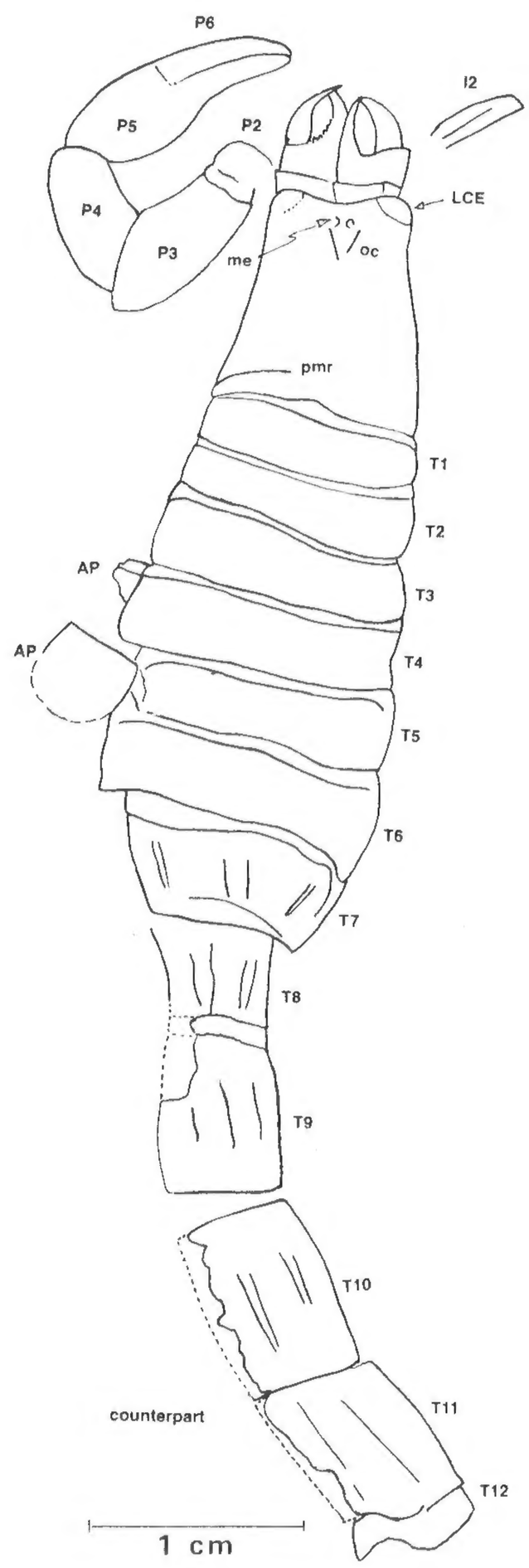
Dolichophonus loudonensis (Laurie, 1899) Text-figure 102

1899. *Palaeophonus loudonensis* Laurie, p. 576, pl. 1, fig. 1.
1904. *Palaeophonus loudonensis* Laurie. Frič, pp. 64–65, text-fig. 80.
1913. *Palaeophonus loudonensis* Laurie. Petrunkevitch, p. 32.
1949. *Dolichophonus loudonensis* (Laurie). Petrunkevitch, p. 132, fig. 171.
1953. *Dolichophonus loudonensis* (Laurie). Petrunkevitch, pp. 11–12, figs. 7–10, 117.
1955. *Dolichophonus loudonensis* (Laurie). Petrunkevitch, p. 70, fig. 38(4).
1962. *Dolichophonus loudonensis* (Laurie). Dubinin, p. 425, fig. 1224.

Type information.—Holotype, Middle Silurian, Wenlock, at Gutterford Burn, Pentland Hills, Scotland, registered as RSM 1897.32.196 [Hardie Collection]. Preserved in yellow-brown, shaly sandstone, the fossil retains considerable convexity or relief.

The holotype consists of only one piece, preserved as a mold (counterpart) of most of the upper surface of a scorpion that barely reached an estimated 80 mm in total length from the anterior of the carapace to the end of the stinger (not present). Most of the twelfth tergite is not preserved, but this was mistaken for the telson (stinger) by Petrunkevitch (1953, fig. 7). The specimen also retains small fragments of abdominal plates that are of great importance for taxonomic purposes. The holotype was studied in Edinburgh, both in a dry state and (particularly) under alcohol, which revealed several important morphological features hitherto unknown. An excellent rubber cast made by Charles D. Waterston of the Royal Scottish Museum revealed further details. The drawing made by the writer on Text-figure 102 reveals all the details that had previously been overlooked. The carapace is very long, rectangular, slightly tapering, but definitely strongly-bowed inward. Two small median eyes, on a low small teardrop-shaped eye node occur on the anterior central part. The eye node can best be seen on the rubber cast. Large, bulbous, compound eyes undoubtedly occur. Under alcohol, the left eye (in life) was easily discernible, although facets were not preserved in the coarse matrix. As noted in other primitive scorpions, small median eyes "always" are accompanied by large, compound lateral eyes, and *vice versa.* It came as a distinct surprise that the small median eyes had not been previously noted as, even in the dry state, they are well shown. This is the oldest scorpion known, and therefore of considerable taxonomic importance.

The appendages are mainly unknown except for the



Text-figure 102.—*Dolichophonus loudonensis* (Laurie). Drawn from the holotype RSM 1897.12.196 [Hardie collection], under alcohol and a rubber cast thereof, made by Charles Waterston. From the Middle Silurian, Wenlock, at Gutterford Burn, Pentland Hills, Scotland. See foldout inside front cover for explanation of abbreviations.

right pedipalp (note that the figure is of the counterpart), which is not notable for any peculiarity and will not be described further as the drawing reveals all that can be said about it. No denticles were noted and the edges apparently are cultrate. A small fragment of the first leg of the left side is preserved.

The chelicerae are well preserved and are falcate; small denticles were noted on the fixed ramus of the right chelicera, but they probably represent only a small part of the teeth on the edges of these chelate appendages. The mesosoma likewise is normal, with strong, anterior transverse ridges not noted by Petrunkevitch (1953, fig. 3). Each tergite increases in length. The overall slenderness of the mesosoma may indicate a male, but not necessarily so, as unimpregnated or younger females are also slender in mesosomal aspect. The last tergite of the preabdomen (first metasomal) definitely shows two rounded ridges on the side, and two ridges rather close together on the midsection.

The cauda, unlike that shown by Petrunkevitch (1953, fig. 7), is incomplete and, instead of being thin, is actually rather thick and wide. Only four caudal tergites and a small piece of the fifth are present. No telson, despite Petrunkevitch, is present.

By far the most important morphological feature found is the presence of a full half of an abdominal plate of the bilobosternous type. This plate resembles those of *Branchioscorpio richardsoni,* n. gen., n. sp. The plate is sufficiently well-preserved to show that it had to hang free and independent of the corresponding half on the other side.

The so-called "hidden first tergite", upon which the suborder Protoscorpiones Petrunkevitch, 1953 (p. 5) was based is, of course, fictitious (as was stated before by Kjellesvig-Waering, 1966, p. 361, in regard to *Proscorpius osborni* (Whitfield)), and merely represents a swelling at the back of the carapace, known also in many other scorpions, fossil and living.

The nature of the rather coarse rock (very sandy) precluded the preservation of such details as setae, ommatidia, etc.

Inasmuch as there are so many differences with respect to the structure of this scorpion from that given here and what Petrunkevitch (1953, pp. 11–12) postulated, it is necessary to give new measurements.

Remarks.—As stated above in the description, important taxobases such as the median eyes, the median eye tubercle, the compound, or aggregated, lateral eyes and, in particular, the small fragment of a bilobosternous abdominal plate were found for the first time, and therefore, because of these characters, it was necessary to emend the family and generic descriptions as given above. My study disagrees almost entirely with that of Petrunkevitch (1953, pp. 11–12), as do the corresponding drawings. The right pedipalp is not present, and the small segment present is likely the second joint of the first leg. Transverse ridges are present, as are well-developed carinae on the seventh to eleventh tergites (twelfth tergite only partially preserved). Petrunkevitch (1953, p. 11) states and shows in his figure 7 that the cauda is supposed to be very narrow. Laurie (1899, p. 576, pl. 1, fig. 1) also shows a very narrow cauda. Both of these authors mistook the median carina for the the edge of the caudal segments. These carinae can be clearly seen in Petrunkevitch's photograph (1953, fig. 117), as well as the actual thick cauda extending beyond the two carinae. The photograph also reveals the impossibility of there being more than the four full segments and a fragment of the fifth (**T12**) instead of the five plus a stinger as shown by Petrunkevitch (1953, fig. 7).

Measurements (in mm) of the holotype (RSM 1897.12.196).—

Carapace length:	10.5 (at midsection)
Width at base:	10.0
Width at anterior:	7.5
Opisthosoma:	length
Tergite No. 1:	2.4
Tergite No. 2:	3.2
Tergite No. 3:	3.4
Tergite No. 4:	3.6
Tergite No. 5:	4.0
Tergite No. 6:	4.0
Tergite No. 7:	5.6
Tergite No. 8:	4.5
Tergite No. 9:	7.0
Tergite No. 10:	7.0
Tergite No. 11:	7.0
Tergite No. 12:	(incomplete)

Suborder **NEOSCORPIONINA** Thorell and Lindström, 1885 (emend.)

(*nom. transl. et correct. ex* Neoscorpii Thorell and Lindström, 1885)

Terrestrial scorpions breathing through book-lungs, sternites perforated by stigmata.

Type family (herein designated).—Scorpionidae Leach, 1815.

Geological range.—Carboniferous to Recent.

Infraorder **ORTHOSTERNINA** Pocock, 1911

(*nom. transl.* and restricted *ex* Orthosterni Pocock, 1911)

Neoscorpionina with undivided, stigma-bearing, rectilinear true sternites, without doublures, that characterize all living scorpions.

Geological range.—Carboniferous to Recent.

Superfamily **SCORPIONOIDEA** Leach, 1815
(*nom. transl.* Petrunkevitch, 1955 *ex* "family" Scorpionides Leach, 1815)

Orthosternina with first coxae meeting at median line or wedged behind second pair; second pair of coxae meeting in front of sternum; third and fourth pairs of coxae abutting sternum. Sternum pentagonal or ranging from very wide to triangular-pentagonal.

Geological range.—Carboniferous to Recent.

Family **PALAEOPISTHACANTHIDAE**, new family

Scorpionoidea with well-developed prepectinal segment (sternite No. 1). Very large sternum, with maxillary lobes of first pair of coxae broadly spatulate. Sternites with small round stigmata.

Type genus.—*Palaeopisthacanthus* Petrunkevitch, 1913.

Geological range.—Upper Carboniferous of North America and England.

Remarks.—There are numerous structures that resemble those of some of the living families. The large sternum is a structure that is more common in older fossil forms. However, the development of spatulate maxillary lobes of the first pair of coxae is quite similar to that in the Chaerilidae and some of the Chactidae. I consider the type of stigma to be of family value, and the round stigma of the new family is found in some living genera, such as the chactid *Broteochactas* and in the Chaerilidae. It is not the purpose of this study to revise the living families, but there is no doubt that, as they stand, there is little meaning to the separation. The presence of the well-developed prepectinal lobes is, of course, a major difference from the other Orthosternina. One genus is recognized: *Palaeopisthacanthus* Petrunkevitch, 1913. Another genus, *Compsoscorpius* Petrunkevitch, 1949, is also referred to this family, although the first maxillary lobes of this genus are not spatulate, but narrow; very likely it should go into a different family. Nevertheless, the coxosternal area of *Compsoscorpius* is mainly unknown and, until specimens revealing the venter are known, it seems preferable to maintain *Compsoscorpius* within the family Palaeopisthacanthidae. The three simple lateral eyes certainly indicate the terrestrial habitat of this genus.

Genus **PALAEOPISTHACANTHUS**
Petrunkevitch, 1913
(new definition)

Palaeopisthacanthidae having carapace with strongly-cuspidate anterior margin.

Type species.—*Palaeopisthacanthus schucherti* Petrunkevitch, 1913.

Geological range.—Pennsylvanian of Illinois.

Palaeopisthacanthus schucherti Petrunkevitch, 1913
Text-figures 103, 104, 111G

1913. *Palaeopisthacanthus schucherti* Petrunkevitch, pp. 48–49, pl. 2, figs. 8–9; text-figs. 11–12.
1949. *Palaeopisthacanthus schucherti* Petrunkevitch. Petrunkevitch, p. 154.
1953. *Palaeopisthacanthus schucherti* Petrunkevitch. Petrunkevitch, p. 33.
1955. *Palaeopisthacanthus schucherti* Petrunkevitch. Petrunkevitch, p. 74, fig. 43(6).
1962. *Palaeopisthacanthus schucherti* Petrunkevitch. Dubinin, p. 431, figs. 1231, 1255a, b.
1966. *Palaeopisthacanthus schucherti* Petrunkevitch. Vogel and Durden, pp. 655–658, pl. 81, figs. 1–3; text-figs. 1–2.

Petrunkevitch, in his original description and in several other reports (see above), did not notice the important stigmata, which are perfectly preserved. These were reported in an outstanding paper by Vogel and Durden (1966, p. 655). To date, the stigmata reported by Vogel and Durden remain the only ones known in a Paleozoic scorpion. Other reports of stigmata by Frič (1904, pp. 69–71) regarding *Microlabis sternbergii* Corda, and in *Palaeophonus nuncius* Thorell and Lindström (1885, p. 14) have been fully checked by me and are entirely erroneous. Petrunkevitch (1953, pp. 20 and 24) also studied the same specimens and agreed that there were no stigmata. It is now possible to go further and state that it would have been impossible for these forms to have had stigmata, as these would have to occur on the face of the abdominal plate and not the sternite, inasmuch as the two scorpions in question are meristosternous and lobosternous respectively.

The holotype and only known specimen is preserved in two parts, showing the interior of the dorsal and ventral sides respectively on each half of the nodule. Preservation is remarkably good, showing fine details such as the lateral eyes and punctations throughout the scorpion. It also revealed that the skin on parts of the pedipalp is finely punctate, with larger, limbated setal openings scattered throughout, which indicate trichobothria. The preservation is so perfect that an attempt is made to detail the position of these trichobothria (see Text-figs. 104C–H) on the pedipalp.

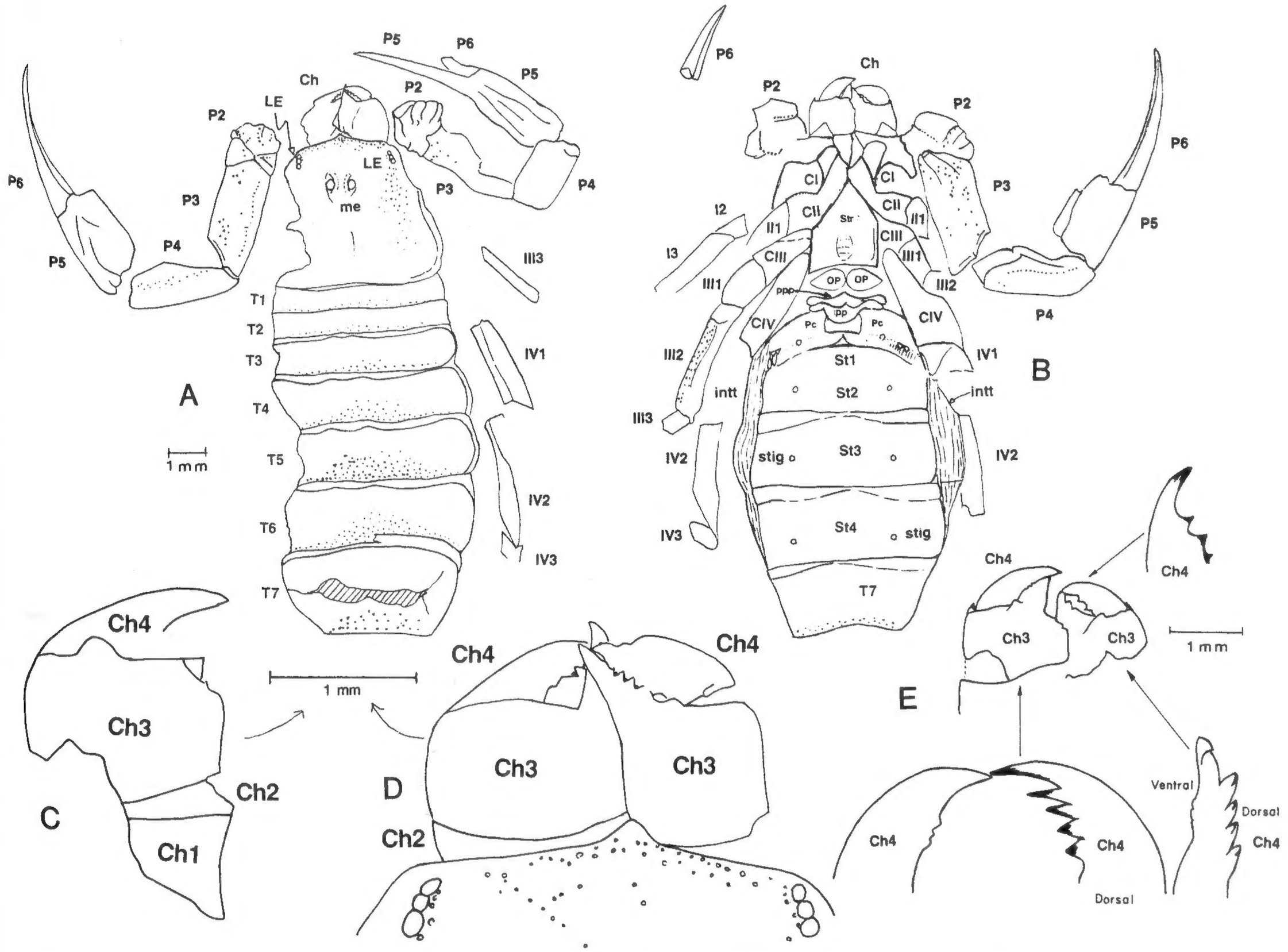
The carapace is trapezoidal, wider than long, with greatest width posteriorly, and the anterior edge glossate at the central part. There are three lateral eyes at the anterior corners, and the median eyes are on an elongate mound approximately in the middle of the anterior half of the carapace. The median eyes are circular, with strong interocular ridges. A raised marginal rim is developed on the lateral edges and posterior part of the carapace. Fine punctations occur along the anterior edge and on the lateral parts of the carapace; otherwise it is smooth. It is very similar to the carapace in some of the living scorpions, although the anterior

is cuspidate. It is not, however, produced forward to the extent that it is in scorpions such as *Mazonia, Gigantoscorpio, Eoscorpius,* etc., which are considered aquatic and in which the glossate anterior was apparently a structure used for digging in the mud.

The dorsal tergites are seen from the inside, each bounded on the anterior by a heavy marginal rim and on the lateral sides by a doublure. Each tergite increases in length posteriorly and is ornamented with numerous punctations that are concentrated on the central and lateral margins.

The chelicerae are robust, showing that the free finger has four inner teeth and approximately three smaller rudimentary teeth or ridges on the inner side. This type of chelicera would seem to correspond more closely to those of the Chaerilidae than any other family. The opposing fixed ramus comprises four teeth with a long terminal tooth that fits between the two terminal teeth of the fixed ramus (see Text-fig. 103E). Again, the fixed ramus seems to correspond closely to the arrangement in the genus *Chaerilus* (see Vachon, 1963, p. 162).

The pedipalps are robustly developed and show all of the joints except the coxae. The trochanter is deeply sculptured with coarse granulations. This is followed by the femur, which is robust and barely granulated ventrally. On the dorsal side, a linear series of granules occurs at the central part. The tibia is ornamented with a linear series of granules on the dorsal side and with a row of granules across the ventral face. The hand is preserved in its entirety, showing it to be robust, but with long curved fingers. Apparently two or three ridges may have been present on the hand, but these are not sufficiently preserved for description as they are flattened. The fingers are curved, and at least the free finger



Text-figure 103.—*Palaeopisthacanthus schucherti* Petrunkevitch. Holotype, YPM 140. From the Upper Carboniferous (Pennsylvanian), Lower Francis Creek Shale, Mazon Creek, Grundy Co., IL. See foldout inside front cover for explanation of abbreviations.

A. Showing the dorsal surface. **B.** Ventral aspect. **C.** Left chelicera, drawn from the specimen immersed in alcohol. All four joints of the appendage are shown. **D.** The anterior carapace and glossate process, as well as the lateral eyes, are particularly well shown. **E.** Cheliceral detail, showing restored fixed finger, making use of parts and counterparts of the holotype.

has a well-developed keel running alone the outer face. The inner edges of both fingers are without denticles of any kind.

The location of the granules and limbated trichobothria are detailed on the pedipalp joints; ventral and dorsal are shown on Text-figures 104C–H. In comparing these with modern forms, the reader is cautioned that compression has occurred, but they are not entirely flattened.

Parts of the walking legs are preserved, but not sufficiently so for description. Heavy punctations occur on the ventral side of the femur of the third walking leg. The venter is preserved so as to reveal the inside; however, the combs are covered by the sternites, and only their outlines are discernible (see Text-figs. 103B, 104A–B).

The coxosternal region is clearly revealed and shows that the sternum is large and pentagonal. The anterior is not clear, but it definitely is triangular, giving a pentagonal shape to the sternum. In the center is an elliptical area that was sunk inward in life, undoubtedly for the attachment of muscles. A narrow doublure can be seen on the lateral margin. The first and second pairs of coxae occur exactly as in Recent scorpions; that is, maxillary lobes of the first two pairs of coxae are well developed, and the second pair meets at the midsection with the first pair immediately behind the maxillary lobes of the second pair of coxae. The third and fourth pairs abut against the sides of the pentagonal sternum. The first pair is spatulate, again as in the Chaerilidae.

The genital operculum consists of two lacrimiform plates with the blunt ends opposite one another. Vogel and Durden (1966) report two rounded areas within the genital opercula, but the rounded, circular structures are more probably areas of muscle attachment and are not part of the actual sclerite, which is distinctly lacrimiform. Of particular importance is the presence of a well-developed bilobate prepectinal plate. The large anvil-shaped pectinal plate, to which the pectines are attached has been jammed partly under the prepectinal plate. The relationship and normal position can be seen in Text-figures 104A–B.

The combs are almost completely covered, but the outline of the periphery can be noted, and on the left comb one of the teeth has been impressed through the sternite. The fulcra are large. The combs are revealed as long, wide structures, and it is estimated that there must have been more than ten teeth on each pectine. There is evidence of small, rounded, areoles or sclerites, such as occur in the middle lamella of the comb in Recent scorpions and in such fossil scorpions as *Eoscorpius.*

The four sternites are preserved. These are true sternites, without doublures, and show that they are orthosternous and with round stigmata. All eight stigmata have been seen, although two of the anterior sternites are not so well-preserved as those following. The round stigmata recall some of the living Chactidae, such as *Broteochactas,* and the Chaerilidae. The last preabdominal tergite does not have ridges ventrally and is ornamented with a series of punctations along the dorsal side.

The postabdomen is not preserved.

Measurements have been given by Petrunkevitch (1913) and Vogel and Durden (1966).

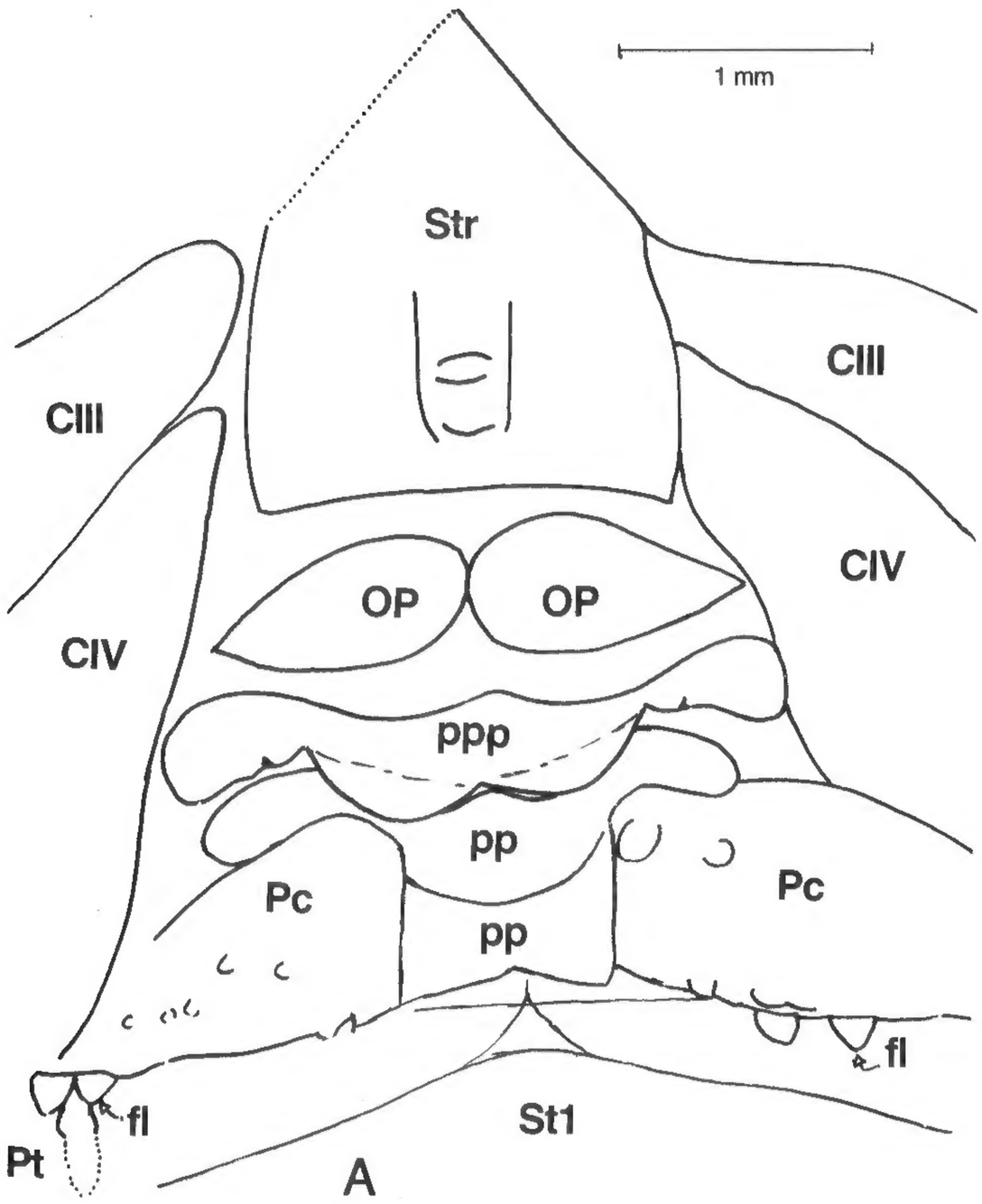
Type information.—Pennsylvanian, lower Francis Creek Shale, Mazon Creek, Grundy County, Illinois.

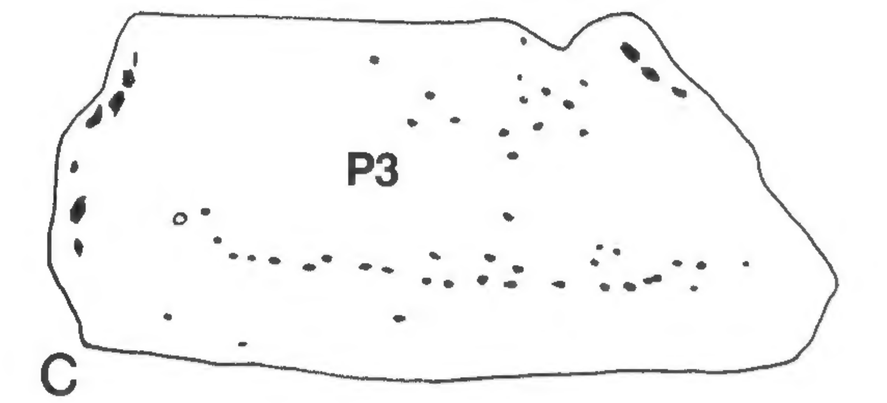
Remarks.—Vogel and Durden (1966, p. 657) assume that the holotype specimen is exuviae from ecdysis, but this does not seem to be the case. The preservation is very different from that of other Mazon Creek scorpions, and it appears to have been a dried specimen that had secondarily been swept into the water and later covered by sediments. This is based on the interesting fact that the ventral side of the scorpion is completely concave, fitting against the convex dorsal surface. The split of the nodule occurred through the integumental skin on the side, thus the dorsal side is on the side of one nodule, preserved from the inside, and the venter on the other, also preserved from the inside. Recent scorpions, when dried, also become concave on the ventral surface and become pressed or bowed upward against the convex dorsal surface. In the holotype, the venter is bowed outward, but this apparent convex surface is actually a concave surface as it is seen from the inside, and is not the actual ventral surface. The dorsal surface accordingly is concave, but, inasmuch as this is the concave inner surface, it is actually the inside of a dorsal surface.

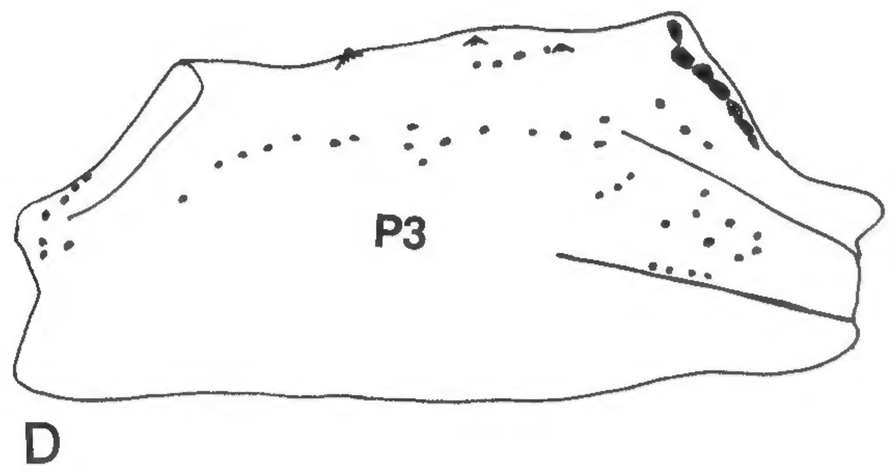
There is no question that this scorpion is a pulmonate, terrestrial form, which definitely belongs in a separate family from the living forms. The presence of spatulate maxillary lobes in the first pair of coxae, the type of chelicerae and stigmata seem to be significant

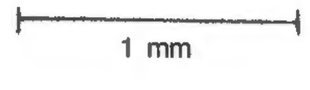
Text-figure 104.—*Palaeopisthacanthus schucherti* Petrunkevitch. Holotype, YPM 140. From the Upper Carboniferous (Pennsylvanian), Lower Francis Creek Shale, Mazon Creek, Grundy Co., IL. Figures C through H are drawn mainly from latex casts of the holotype. Trichobothria are represented by circles, pustules by black dots. See foldout inside front cover for explanation of abbreviations.

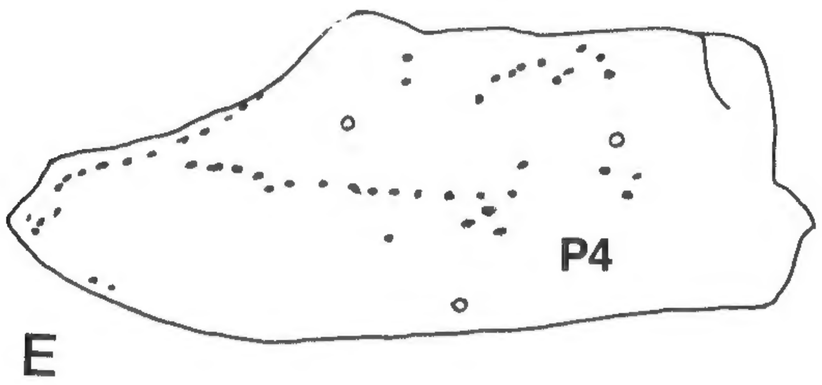
A. Showing the posterior coxosternal region and opercular and pectinal areas from the inside. **B.** A reconstruction of the coxosternal and pectinal areas; no restoration involved. **C.** Dorsal view of the femur of the right pedipalp. **D.** Ventral view of the femur of the right pedipalp. **E.** Dorsal view of tibia of right pedipalp. **F.** Ventral view of tibia of right pedipalp. No trichobothria are present over most of this surface. **G.** Dorsal view of hand and part of the fingers of right pedipalp. **H.** Ventral view of hand and part of fingers of right pedipalp.

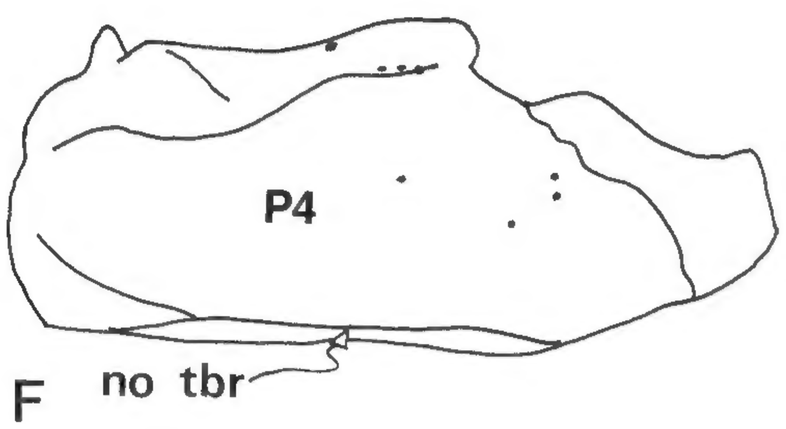

1 mm
Str
CIII
CIII
CIV
CIV
OP
OP
ppp
pp
pp
Pc
Pc
fl
fl
Pt
St1
A

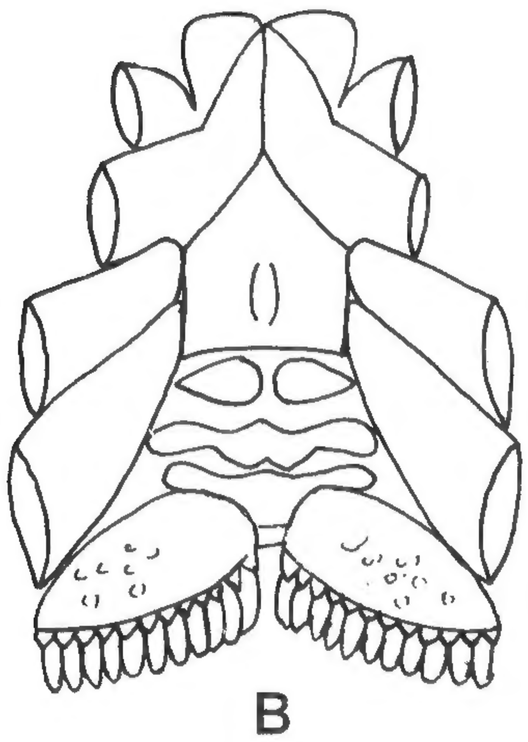

P3
C

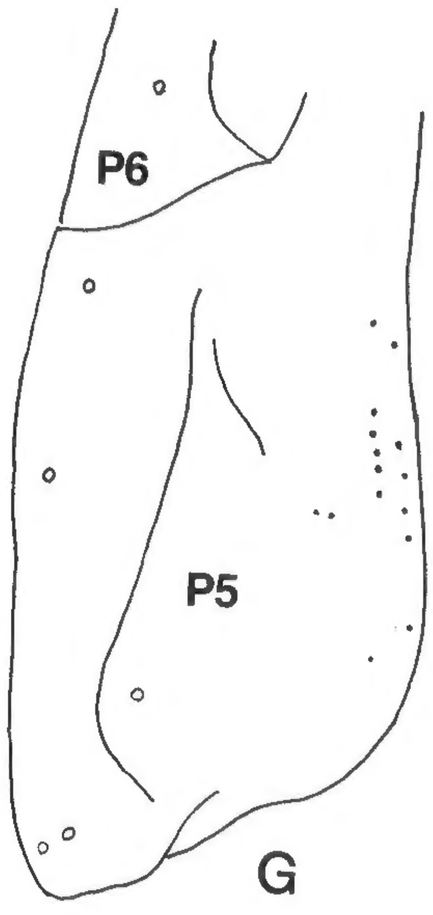

P3
D

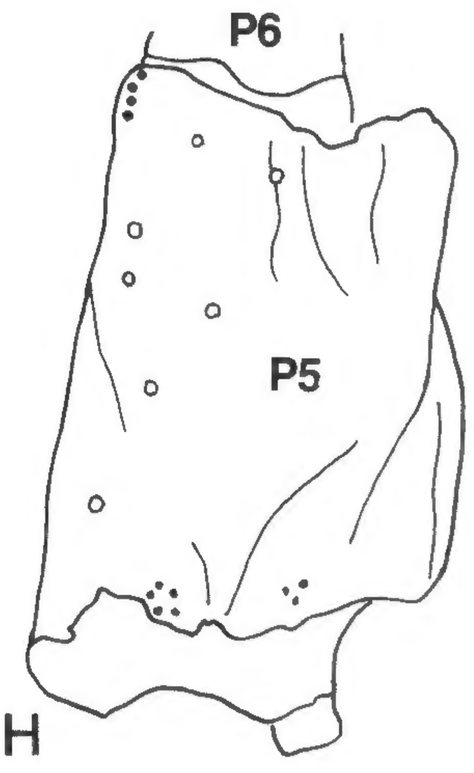

1 mm


P4
E


P4
no tbr
F


B


P6
P5
G


P6
P5
H

in showing the possibility of this scorpion being a forerunner of the Chaerilidae (see Text-figs. 103B and 104B).

Genus **COMPSOSCORPIUS** Petrunkevitch, 1949

Palaeopisthacanthidae having carapace with rounded anterior margin.

Type species.—*Compsoscorpius elegans* Petrunkevitch, 1949.

Geological range.—Upper Carboniferous (Coal Measures) of England.

Remarks.—The holotype of *Compsoscorpius elongatus* Petrunkevitch, 1949, is a male of *Compsoscorpius elegans* Petrunkevitch, 1949. The holotype specimen of *Compsoscorpius elegans* is a female. *Typhlopisthacanthus anglicus* Petrunkevitch, 1949, is merely a very poorly-preserved specimen of *Compsoscorpius elegans.* All three specimens, therefore, are synonymous and were described in the same publication by Petrunkevitch (1949). As first reviewer, I hereby select the genus and species of *Compsoscorpius elegans* Petrunkevitch to be the correct taxon to use for this scorpion.

The presence of three lateral eyes, indeed, of simple lateral eyes, whether one or five, is a character that occurs only on pulmonate or land-living scorpions. Therefore, although the underside of *Compsoscorpius* is unknown, I do not hesitate to consider it an Orthosternina.

Compsoscorpius elegans Petrunkevitch, 1949
Text-figures 105–107

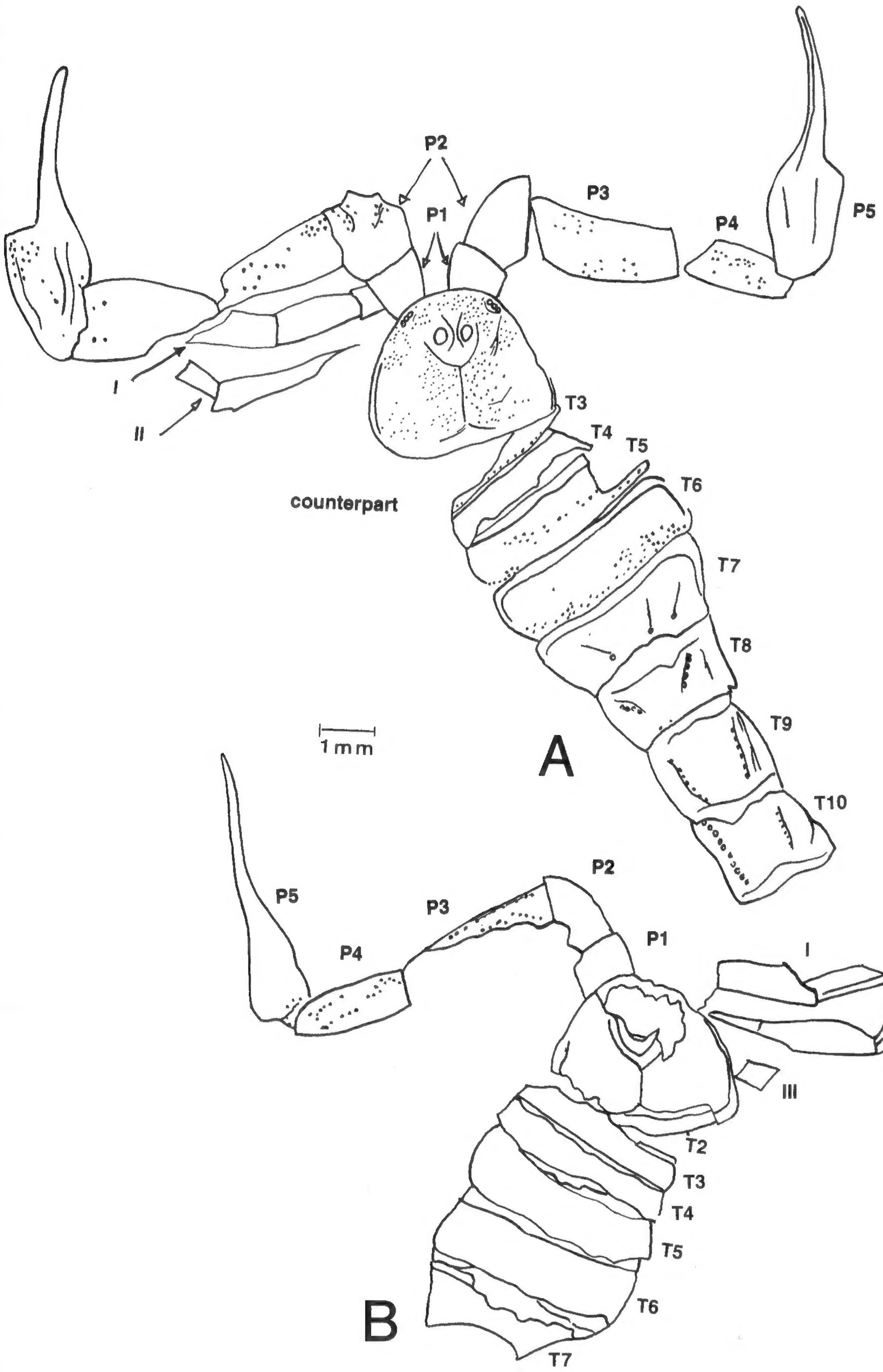
1911. *Anthracoscorpio buthiformis* Pocock (*partim*), p. 26, fig. 7.
1949. *Typhlopisthacanthus anglicus* Petrunkevitch, p. 145, figs. 143, 182.
1949. *Compsoscorpius elegans* Petrunkevitch, pp. 149–150, figs. 152–154, 183–185.
1949. *Compsoscorpius elongatus* Petrunkevitch, pp. 150–151, figs. 147–150, 186–188.
1953. *Compsoscorpius elegans* Petrunkevitch. Petrunkevitch, pp. 32–33.
1953. *Compsoscorpius elongatus* Petrunkevitch. Petrunkevitch, p. 33.
1953. *Typhlopisthacanthus anglicus* Petrunkevitch. Petrunkevitch, p. 34.
1955. *Compsoscorpius elegans* Petrunkevitch. Petrunkevitch, p. 75, fig. 44(1).
1962. *Compsoscorpius elegans* Petrunkevitch. Dubinin, p. 431, figs. 1235, 1253.

Petrunkevitch (1949, pp. 144–145) erected the genus *Typhlopisthacanthus,* with *T. mazonensis* (Petrunkevitch) as type species, for a rather poorly-preserved scorpion from the Mazon Creek area of Illinois. The genus was purported to be an eyeless scorpion with a very small tail, somewhat resembling a gigantic pseudoscorpion, or scorpions such as the living *Hormurus,* which are characterized by having small tails. He further referred a new species from the British Coal Measures to his new genus (*T. anglicus*). It has been shown in the review description of the holotype of *T. mazonensis,* given above, that the eyeless feature and the small tail were fictitious and that, furthermore, the holotype was nothing more than a poorly-preserved specimen of a female of *Eoscorpius carbonarius* Meek and Worthen and, therefore, the genus *Typhlopisthacanthus* Petrunkevitch, 1949, was an invalid genus, being a junior synonym of the genus *Eoscorpius* Meek and Worthen, 1868. *T. anglicus* Petrunkevitch also is based on imaginary characters and, as shown in the redescription and new figures, is nothing more than a very poorly-preserved specimen of *Compsoscorpius elegans* Petrunkevitch and, judging from its inflated state and sparse ornamentation, is a female of that species. It is also shown below that *Compsoscorpius elongatus* Petrunkevitch is a junior synonym of *C. elegans* Petrunkevitch, the latter being a female, whereas the former is a male. Both specimens, as well as the holotype of *Typhlopisthacanthus anglicus,* are from the same horizon and locality, namely, the Coseley area of Staffordshire, England. As stated under "Remarks" concerning the genus *Compsoscorpius, Compsoscorpius elegans* is the correct name for this species.

The description of the holotype of *Compsoscorpius elegans* Petrunkevitch given by Petrunkevitch (1949, p. 149) is mainly correct, although his figure is lacking in important details that would possibly have resulted in revealing that *C. elegans* and *C. elongatus* are synonymous. The two differ only in the presence of coarser pustules on the holotype of *C. elongatus,* and in the overall more slender aspect of the latter. Both of these traits can definitely be attributed to sex, as the holotype of *C. elongatus* is a male, a determination based on the great length of the twelfth tergite, the coarser ornamentation and the more slender aspect. On the other hand, the more robust aspect of the holotype of *C. elegans* and the finer pustules reveal that this is a female. These are good secondary characters for sexual determination. The three lateral eyes show that this scorpion was probably a land dweller that breathed through book-lungs, as present-day scorpions do, and is very likely related to the American species *Palaeopisthacanthus schucherti* Petrunkevitch, which has been shown to have stigmata and is a typical Orthosternina.

Text-figure 105.—*Compsoscorpius elegans* Petrunkevitch. Holotype (BM(NH) I.7883), part and counterpart. Female. From the Carboniferous, Upper Coal Measures, Coseley, Staffordshire, England. See foldout inside front cover for explanation of abbreviations.

A. External dorsal aspect. **B.** Internal dorsal aspect, except for ventral aspect of the right pedipalp.

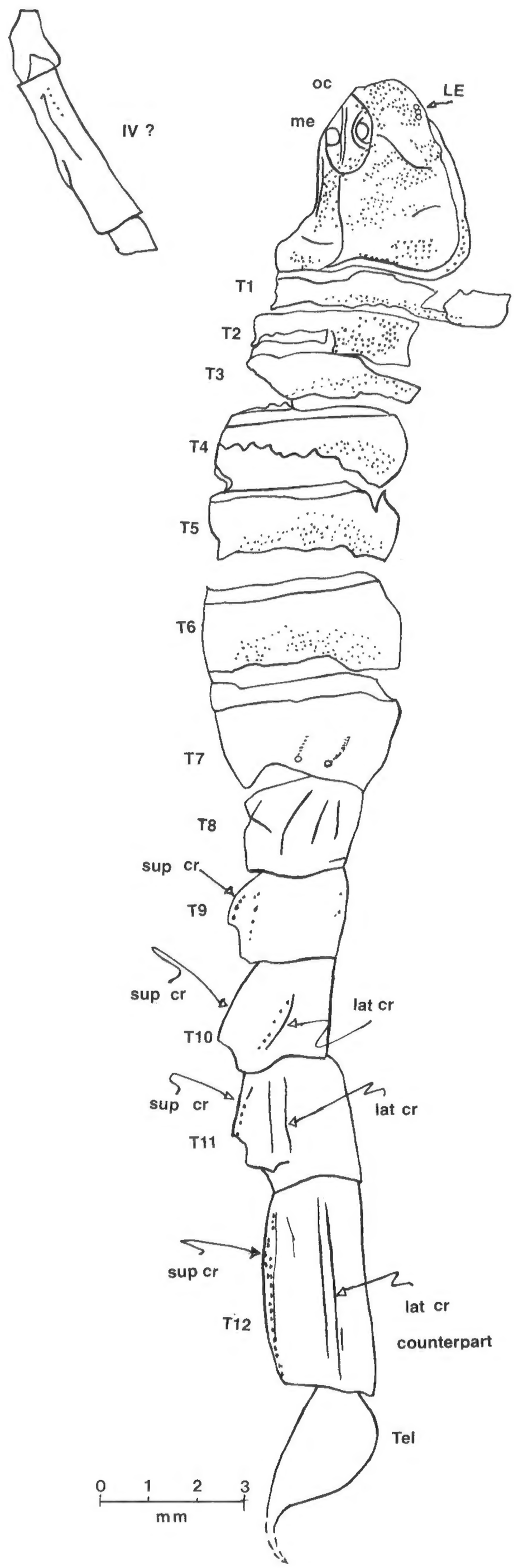

P2
P1
P3
P4
P5
I
II
T3
T4
T5
T6
T7
T8
T9
T10
counterpart
1 mm
A
P5
P4
P3
P2
P1
I
II
III
T2
T3
T4
T5
T6
T7
P5 ven
P4 ven
B

The marginal rim, shape of the carapace, shape of the median eyes and eye node, the presence of three lateral eyes on a side, the pattern of ornamentation, the details of the peculiar, large tubercle on the last preabdominal tergite, as well as the coarse pustulation surmounting the caudal carinae (note that the tail is turned in the holotype of *C. elongatus*), are identical in *C. elegans* and *C. elongatus,* so that the writer does not hesitate to refer them to the same species.

The holotype of *Typhlopisthacanthus anglicus* Petrunkevitch is so distorted and poorly preserved that there is considerable doubt as to the propriety of its ever having been described. Petrunkevitch's description is erroneous as well as the figure given (1949, pp. 145–146, figs. 143, 182). The figures given here (Text-figs. 107A, B) show the part and counterpart; it should be noted that the specimen is preserved in a curved position, therefore the figure has been "rolled over" to include all on a single plane. The carapace shows little, but has a median division or sulcus, which seems to separate it into halves. The eyes are not preserved, but would occur in the indicated ocellar mound. It is reckless to state that there were no eyes; there are none on the specimen, but that is entirely due to preservation. The tergites are greatly telescoped together, making the carapace appear to be huge, as noted by Petrunkevitch (1949, p. 145). However, of diagnostic value is the presence of two maxillary lobes, belonging to the first and second coxae and indicating a scorpion much like the living ones. Both narrow maxillary lobes reach the anterior to form a well-developed oral chamber as in modern scorpions. It would be safe to assume that the third and fourth coxae abut a sternum that very likely is pentagonal. This would give a coxosternal arrangement much as in present-day scorpions, but also like some present in the Pennsylvanian. The legs are preserved only as very small fragments.

The presence of a small tail such as occurs in some present-day scorpions (*Hormurus*) is entirely illusory. There are no caudal segments preserved and much less the telson.

The scorpion is identical to *Compsoscorpius elegans* Petrunkevitch, a determination which is based on the identification above of *C. elongatus* as the male and *C. elegans* as the female of a single species. The ornamentation on the carapace of the holotype of *Typhlopisthacanthus anglicus* is identical to that of the male of *C. elegans* (holotype of *C. elongatus*), including the row of larger punctae on the base of the cara-



Text-figure 106.—*Compsoscorpius elegans* Petrunkevitch. Paratype, BM(NH) In.15862 (holotype of *C. elongatus*). Male. From the Carboniferous, Upper Coal Measures, Coseley, Staffordshire, England. See foldout inside front cover for explanation of abbreviations.

pace; the punctations along the lower half of each tergite and the punctae (trichobothria?) developed into two rows on the ventral part of the femur of the pedipalp are also identical.

Type information.—All three specimens are from the Carboniferous, from the same horizon of concretions about ten feet above the Thick or Ten-foot Coal, Upper Coal Measures, Coseley, Staffordshire, England. All specimens are in the British Museum (Natural History): holotype, BM(NH) I.7883; paratypes, BM(NH) In.15862 and In.31261.

Family **SCORPIONIDAE** Leach, 1815

Scorpionoidea with third and fourth pairs of coxae grown together along lines of contact; single spur in intersegmental membrane between metatarsus and tarsus of first and second pairs of legs, no such spur on third and fourth pairs; three pairs of lateral eyes.

Genus **MIOSCORPIO**, new genus

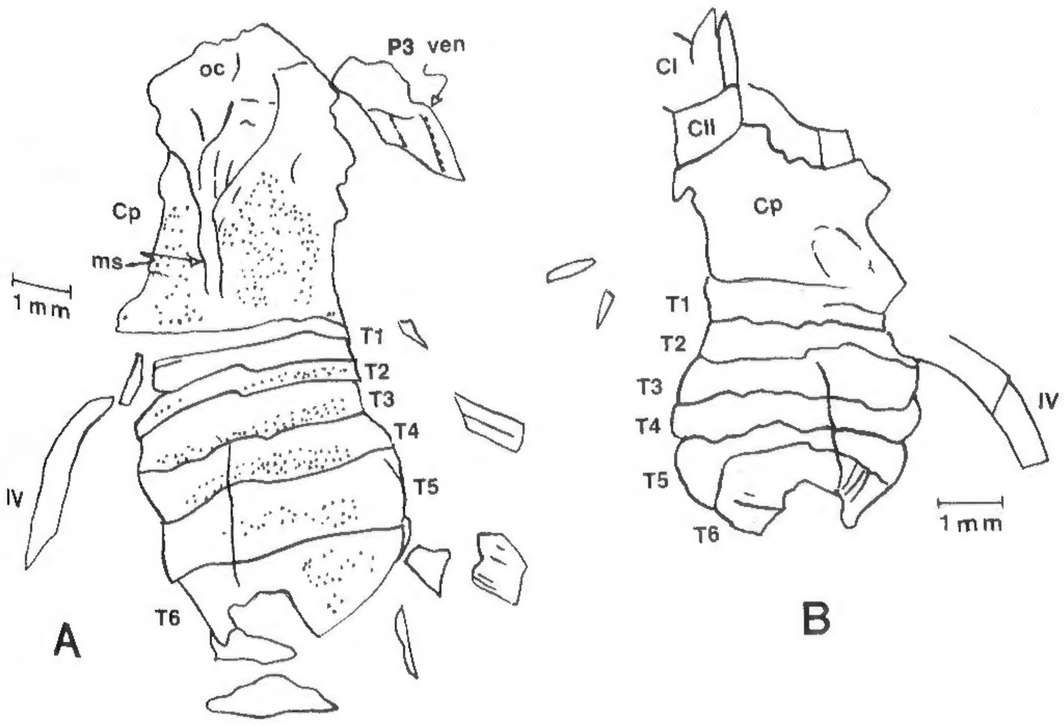
Scorpionidae having carapace rounded and protruding in front; sternum deeply divided by a median groove.

Derivatio nominis.—Scorpion from the Miocene.

Type species.—*Scorpio zeuneri* Hadži, 1931.

Geological range.—Miocene.

Remarks.—This is the only known Miocene scorpion genus. It differs from the genus *Scorpio* in lacking the deep anterior cleft that results in the bilobed anterior margin so characteristic of that genus. The Miocene form retains the produced anterior that recalls the older fossil scorpions and that is still retained by the living *Brachistosternus,* a Bothriuridae of the northern and western part of the South American continent, and by the troglobite *Typhlochactas* of Mexico, a Chactidae.



Text-figure 107.—*Compsoscorpius elegans* Petrunkevitch. Paratype (BM(NH) In.31261), part and counterpart (holotype of *Typhlopisthacanthus anglicus* Petrunkevitch). From the Carboniferous, Upper Coal Measures, Coseley, Staffordshire, England. See foldout inside front cover for explanation of abbreviations.

A. External dorsal aspect. **B.** Internal dorsal aspect.

Mioscorpio zeuneri (Hadži, 1931)

1931. *Scorpio zeuneri* Hadži, pp. 134–148, figs. 1–8.

Type information.—The holotype and paratypes come from the Upper Miocene Sprudelsinter at Böttingen, Swabian Alps, Germany, and are on deposit in the Staatliches Museum für Naturkunde (SMN), Stuttgart, West Germany.

Dr. Jovan Hadži kindly sent me the original casts used by him in his description of this interesting species. Later, in Nov. 1970, I was able to study the original specimens, which had been kindly sent to the Institut für Paläontologie der Rhein, at the Friedrich-Wilhelm University at Bonn by Dr. M. Warth of the Staatliches Museum für Naturkunde in Stuttgart, where the types are deposited. The scorpions are preserved as hollow external molds in the limestone, which apparently is a travertine deposit. It is necessary therefore to make casts before details are readily revealed. New silicone casts did not reveal any details not previously seen in the casts made by Hadži; however, there are a number of important details that have been determined by a review of the original specimens.

Hadži shows the first and second pairs of coxae meeting in front of the sternum, without the development of maxillary lobes in the second pair of coxae (Hadži, 1931, fig. 7a). This would result in a coxosternal arrangement more primitive than most of the Carboniferous scorpions and, indeed, would preclude the scorpion in question from being in the family Scorpionidae Leach, 1815, or even in the superfamily Scorpionoidea Leach, 1815.

I disagree with Hadži's excellent description of the arrangement of the coxae, at least in respect to the coxal maxillary lobes. My review clearly shows well-developed maxillary lobes in both the first and second coxae, and the latter meet at midsection and are squeezed in between the first coxae and their maxillary lobes. Thus they are identical to those of living scorpions.

The carapace is preserved on one specimen (object 88) and, although I was unable to determine the type of eyes, the outline of the carapace is clearly preserved. This is straight at the base, rounded at the anterolateral angles, and with a distinct protrusion along the anterior margin. The carapace is probably longer than wide, although the entire width has not been seen. It measures 5.2 mm in length. As stated above, this shape is an important taxonomic difference from that present in the genus *Scorpio,* which has a bilobed anterior. The surface of the carapace does not reveal any deep sulci,

although the basal margin, towards the sides, seems inflated. This would certainly be indicative of the Scorpionidae.

The sternum is small, deeply cleft at midsection, at least for the posterior three-fourths of the length. The base seems to be straight and the overall shape is pentagonal with parallel sides. The coxae of the last two pairs of legs abut the sides of the sternum.

I was unable to determine the type of stigmata[42] present, but there is no doubt that they are present and that the scorpion is an Orthosternina.

GENERA INCERTAE SEDIS

Genus **TITANOSCORPIO**, new genus

Very large scorpions with pedipalp having very short hand, both fingers curved inward, concave along the inner edge, and not joining along the edges. Edge armed with single (?) row of small denticles, at least on the distal part. The distal ends of both fingers hooklike. Tibia very short.

Type species.—*Titanoscorpio douglassi,* n. gen., n. sp.

Geological range.—Carboniferous of the Mazon Creek area of Illinois.

Remarks.—Although it is not possible to determine the family to which this unusual scorpion should be delegated, there is no doubt that on the generic level it is distinct. Unique morphological structures are found in the two long, hooklike terminations of the pedipalp fingers, as well as the opposable concavity of both fingers. In other scorpions, the fixed finger fits against the free one. The presence of very small denticles along the edge of the fingers, although well-known in various living scorpions, is an uncommon character in Palaeozoic scorpions. It would appear that the pedipalp would have a scissorlike action in closing, rather than that of nearly all scorpions where pressure is caused by the fitting of the curved or concave free finger against the convex fixed finger.

The size of this scorpion rivals that of *Gigantoscorpio willsi* Størmer and *Eoscorpius carbonarius* Meek and Worthen (see above, description of a new and very large specimen of the chela of a pedipalp, FMNH (PE) 32083, No. H-19 in the Herdina collection). A scorpion with pedipalps of this size would probably reach 30 cm in body length. The short tibia suggests that this was a burrowing scorpion, although the size of the scorpion indicates a water-dweller, as is the case with nearly all of the Mazon Creek scorpions.

[42] Hadži (1931, p. 139) claims to have noted traces of a slitlike stigma on one of the sternites of object 86. A.S.C.

Titanoscorpio douglassi, new species
Text-figure 108

DLD Specimen I.—Holotype: Specimen in the personal collection of David Lyon Douglass, Western Springs, Illinois,[43] consisting of three parts of an ironstone concretion showing ventral and dorsal sides of the chela and attached femur of the pedipalp, as well as a small piece of the inner filling representing the distal part of the free finger.

Type information.—Pennsylvanian, Francis Creek Shale of the Mazon Creek area, Illinois, collected by David Lyon Douglass, 1966.

The chela of the pedipalp comprises a wide, nearly quadrate hand, without any discernible ornamentation. The free finger is curved inward, convex rather than concave as in other Pennsylvanian scorpions, and is decidedly hooklike. The edge of the free finger contains at least one row of small, rather blunt denticles and presumably the same occur on the fixed finger, as in other scorpions. No pitting or other ornamentation was noted on the fingers.

The femur is very short, stout and subrectangular in general shape.

Measurements (in mm) of DLD unnumbered specimen (holotype: Specimen I).—

	length	width
Hand: (center)	17.5 (ventral) 22.5 (dorsal)	18.5
Free finger:	27.8 (inside)	5.5 (middle)
Immovable finger:	31.2 (inside)	5.3 (middle)
Tibia: (center)	20.2	11.2
Greatest length of chela:	52.0	

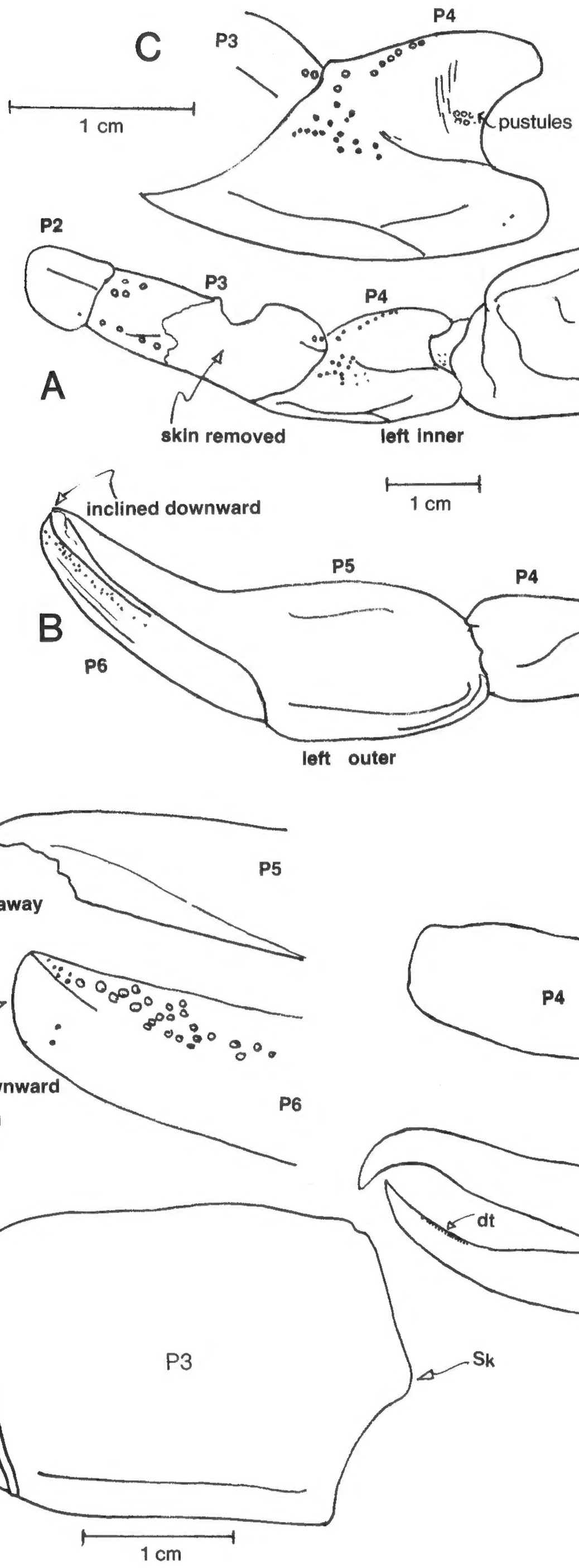
Text-figure 108.—*Titanoscorpio douglassi,* n. gen., n. sp. From the Upper Carboniferous (Pennsylvanian), lower Carbondale Formation, Lower Francis Creek Shale, Mazon Creek, Grundy Co., IL. Specimens represented by figures A to G are in the personal collection of David Lyon Douglass (DLD), Western Springs, Illinois.[43] See foldout inside front cover for explanation of abbreviations.

A–E. Details of the left pedipalp, paratype DLD Specimen III). Labelled "Bartowski Collection, write Gene Richardson" on the back of the drawings. **A.** Inner side showing joints **P2–6**. **B.** Outer side, segments **P4–6**. **C.** Detail of **P4** of figure A, showing the pustular organization. **D.** Enlargement of the end of the chela, inner side (fig. **A**), to show details of the fine linear pustulation and large pustules on the fixed finger. **E.** Detail, tip of segments **P5–6**, outer side.

F. Dorsal view of the terminus of the pedipalp, holotype (Specimen I). **G.** Ventral view of the same.

H. Paratype (RC Specimen II) in the private collection of Richard Cramer, Forest Park, IL 60130 U.S.A. Third segment of the pedipalp (**P3**).

[43] I spoke with Mr. Douglass, then of 95563 Highway 101, Yachats, OR 97498, U.S.A., on April 23, 1985. He said that a more permanent address would be: 1312 Chicago Avenue, Evanston, IL 60201, U.S.A. P.R.H.


C
P3
P4
1 cm
pustules
P2
P3
P4
P5
P6
A
skin removed
left inner
1 cm
inclined downward
P5
P4
B
P6
left outer
D
1 mm
P5
broken away
F
P4
P5
P6
P4
E
inclined downward
P6
1 mm
dt
P5
P6
G
1 cm
P3
Sk
H
1 cm

Derivatio nominis.—The species has been named in honor of the collector.

RC Specimen II.—Paratype: Specimen in the collection of Richard X. Cramer (1435 Marengo Ave., Forest Park, IL 60130, U.S.A.), collected August, 1975, in Pit 11, Will County, Illinois.

The paratype consists of the right humerus (**P3**) of the pedipalp. It is very stout, short, with only one superior carina on the posterior dorsal side. Socket for articulation of the brachium is present midway at the distal end. A raised area is present at the conjunction with the trochanter (see Text-fig. 108H), which would be overlain by the latter joint. The length of humerus is 21.8 mm, and the width is 20.0 mm. The paratype is smaller than the holotype, although still a formidable scorpion about 20 cm long. Little is left of the original skin.

DLD Specimen III.—Paratype: Specimen illustrated in Text-figures 108A–E, labelled on the back of the drawing "Bartowski Collection, write Gene Richardson" and accredited to the private collection of David Lyon Douglass in the figure description.[44]

Genus **WATTISONIA** Wills, 1960

Small scorpion with last preabdominal tergite having two low carinae. Corresponding ventral plate larger, with large median carina and two low lateral crests.

Type species.—*Wattisonia coseleyensis* Wills, 1960.

Geological range.—Upper Carboniferous.

Wattisonia coseleyensis Wills, 1960[45]

1960. *Wattisonia coseleyensis* Wills, pp. 319–322, pl. 56, figs. 2–4; text-figs. 26, 27.

Genus **PALAEOMACHUS** Pocock, 1911

Hand broad and oval, its width greatly exceeding that of the brachium, its length exceeding that of the fingers, which are short and in contact when closed. The length of the immovable digit about equals the width of the hand.

Type species.—*Eoscorpius anglicus* Woodward, 1876.

Geological range.—Upper Carboniferous.

Palaeomachus anglicus (Woodward, 1876)
Text-figure 109

1876. *Eoscorpius anglicus* Woodward, pp. 57–59, pl. VIII, fig. 3.
1911. *Palaeomachus anglicus* (Woodward). Pocock, pp. 16–17, fig. 2a.
1911. *Palaeomachus anglicus* (Woodward). Bather, p. 673, fig.
1913. *Palaeomachus anglicus* (Woodward). Petrunkevitch, pp. 33–34.
1953. *Palaeomachus anglicus* (Woodward). Petrunkevitch, p. 38, fig. 132.
1955. *Palaeomachus anglicus* (Woodward). Petrunkevitch, p. 79.
1962. *Palaeomachus anglicus* (Woodward). Dubinin, p. 433, fig. 1259.

Holotype.—BM(NH) I.944a and b. Upper Carboniferous Coal Measures, Skegby New Colliery, near Mansfield, Nottinghamshire, England. Two pieces showing part and counterpart of a pedipalp lacking its coxa, but otherwise complete.[46]

SCORPIONIDA, gen. et sp. indet. Størmer, 1969

1960. Eurypterid or scorpion. Størmer, p. 90, text-fig. 2.
1969. Scorpionida gen. et sp. indet., Størmer, p. 30, pl. 2, fig. 8.

The specimen consists of a well-preserved cauda, consisting of the last four segments and telson. The description is adequate, and all that can be added is that the long, twelfth tergite denotes the specimen is a male.

Type information.—From the Lower Devonian Klerfer beds of Willwerath, Eifel, Germany.

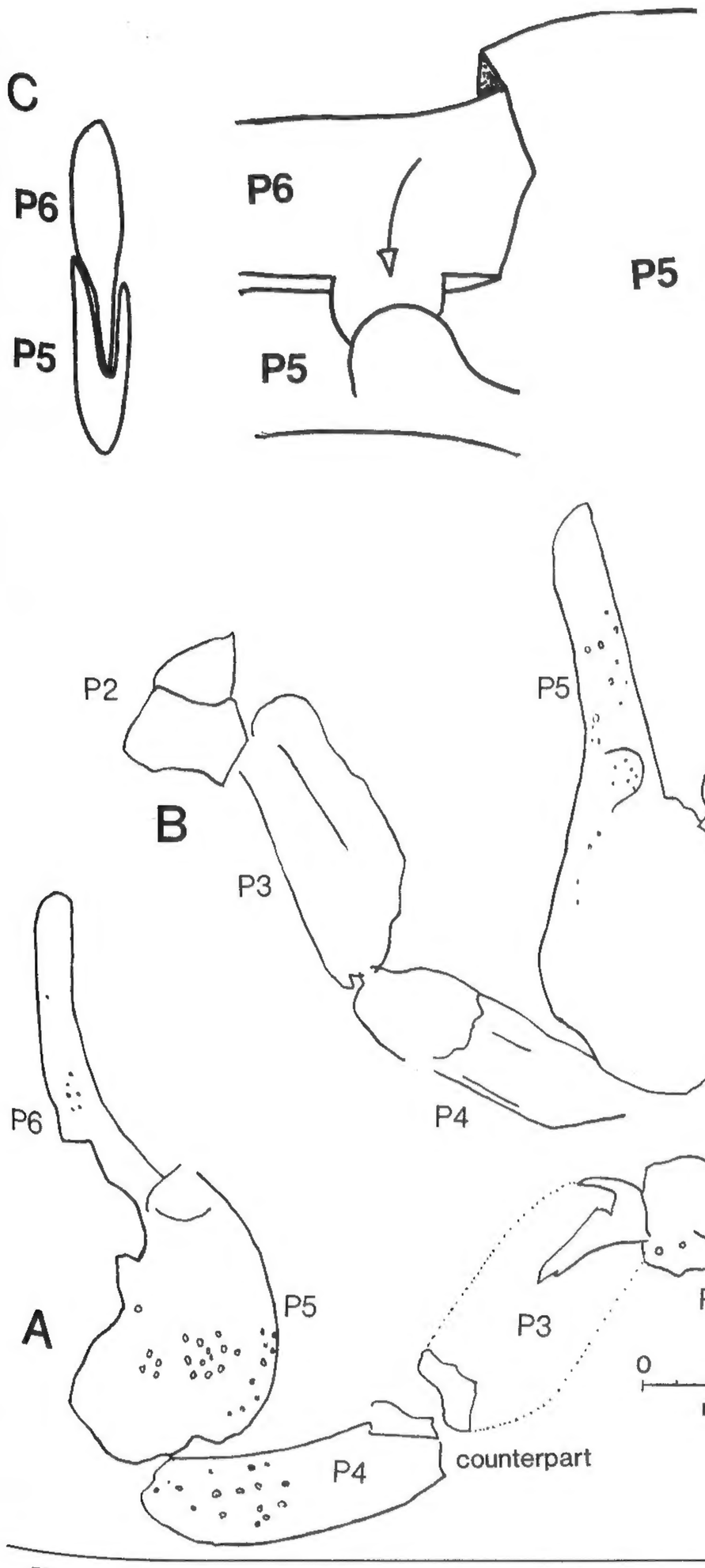
Text-figure 109.—*Palaeomachus anglicus* (Woodward). Holotype, BM(NH) I.944a,b. From the Upper Carboniferous, Coal Measures, Skegby New Colliery, near Mansfield, Nottinghamshire, England. See foldout inside front cover for explanation of abbreviations.

A. Fragmental pedipalp, counterpart. **B.** Fragmental pedipalp, part. **C.** Curious and unique interlocking of the base of the free dactylus (**P6**) and dactylus (**P5**) with a special sheath boss on **P5** to accommodate the blade boss of **P6**, and cross-section to show the interlocking bosses.

[44] No text was found about the specimen, and on the back of the drawing it was originally assigned to *Eoscorpius carbonarius.* A.S.C.

[45] Kjellesvig-Waering left no text on this species. The holotype, BU 722A,B, was collected by Mr. J. T. Wattison of Shrewsbury, almost certainly from the Ten-foot Measures above the Thick Coal, Coseley, South Staffordshire. It consists of two half-nodules with a small scorpion with normal, rather hairy tergites. The seventh ventral tergite is thickly coated by posteriorly-directed setae attached to small hair-bases. All other organs unknown. Nothing could be added to Wills' description. A.S.C.

[46] Other than the description of the text-figures, the author left no notes on this specimen. The dimensions are given by Petrunkevitch (1953, p. 38). The curious interlocking system of the base of the free dactylus (**P6**) and the immovable finger (**5**) with a special sheath boss on **P5** is diagrammed in Text-figure 109C. A.S.C.



Text-figure 110.—Coxosternal areas of the Holosternina (continued on Text-fig. 111).

A. Praearcturidae—*Praearcturus gigas* Woodward. **B.** Mesophonidae—*Mesophonus perornatus* Wills. [47]**C.** Anthracoscorpionidae—*Allobuthus macrostethus,* n. gen., n. sp. **D.** Anthracoscorpionidae—*Anthracoscorpio juvenis* Kušta. **E.** Phoxiscorpionidae—*Phoxiscorpio peachi,* n. gen., n. sp. **F.** Buthiscorpiidae—*Buthiscorpius buthiformis* (Pocock). **G.** Eoctonidae—*Eoctonus miniatus* Petrunkevitch. **H.** Gigantoscorpionidae—*Gigantoscorpio willsi* Størmer. **I.** Heloscorpionidae—*Heloscorpio sutcliffei* (Woodward). **J.** Centromachidae—*Centromachus euglyptus* (Peach). **K.** Archaeoctonidae—*Archaeoctonus glaber* (Peach) (after Størmer, 1963). **L.** Spongiophonidae—*Spongiophonus pustulosus* Wills. **M.** Stenoscorpionidae—*Stenoscorpio gracilis* (Wills). **N.** Acanthoscorpionidae—*Acanthoscorpio mucronatus,* n. gen., n. sp. **O.** Allopalaeophonidae—*Allopalaeophonus caledonicus* (Hunter). **P.** Mazoniidae—*Mazonia woodiana* Meek and Worthen.

[47] In the original figure description C was labelled "Anthracobuthidae—*Anthracobuthus*". We can only guess what he was referring to. A.S.C.

Text-figure 111.—Coxosternal areas. **A–E.** Holosternina.

A. Proscorpiidae—*Proscorpius osborni* (Whitfield). **B.** Waeringoscorpionidae—*Waeringoscorpio hefteri* Størmer. **C.** Labriscorpionidae—*Labriscorpio alliedensis* Leary (Kjellesvig-Waering's version). **D.** Labriscorpionidae—*Labriscorpio alliedensis* Leary (Leary's version). **E.** Palaeoscorpiidae—*Palaeoscorpius devonicus* Lehmann. **F.** Bilobosternina—Branchioscorpionidae—*Branchioscorpio richardsoni,* n. gen., n. sp. **G.** Orthosternina—Palaeopisthacanthidae—*Palaeopisthacanthus schucherti* Petrunkevitch. **H.** Meristosternina—Palaeobuthidae—*Palaeobuthus distinctus* Petrunkevitch. **I.** Meristosternina—Cyclophthalmidae—*Cyclophthalmus senior* Corda. **J.** Lobosternina—Loboarchaeoctonidae—*Loboarchaeoctonus squamosus,* n. gen., n. sp.

Text-figure 112.—Coxosternal areas of the Lobosternina (see also Text-figure 111J).

A. Paraisobuthidae—*Paraisobuthus prantli,* n. gen., n. sp. **B.** Eoscorpiidae—*Eoscorpius carbonarius* Meek and Worthen. **C.** Eobuthidae—*Eobuthus rakovnicensis* Frič. **D.** Isobuthidae—*Isobuthus kralupensis* (Thorell and Lindström). **E.** Opsieobuthidae—*Opsieobuthus pottsvillensis* (Moore). **F.** Telmatoscorpionidae—*Telmatoscorpio brevipectus,* n. gen., n. sp. **G.** Waterstoniidae—*Waterstonia airdriensis,* n. gen., n. sp. **H.** Kronoscorpionidae—*Kronoscorpio danielsi* (Petrunkevitch). **I.** Petaloscorpionidae—*Petaloscorpio bureaui,* n. gen., n. sp. **J.** Pseudobuthiscorpiidae—*Pseudobuthiscorpius labiosus,* n. gen., n. sp. **K.** Pareobuthidae—*Pareobuthus salopiensis* Wills. **L.** Anthracochaerilidae—*Anthracochaerilus palustris,* n. gen., n. sp.

Text-figure 113.—Morphological stages, but not necessarily in order of phylogenetic development, of the floor of the oral tube. The more primitive are at the bottom of the page, progressing upward to the completely-developed oral tube at the top of the page.

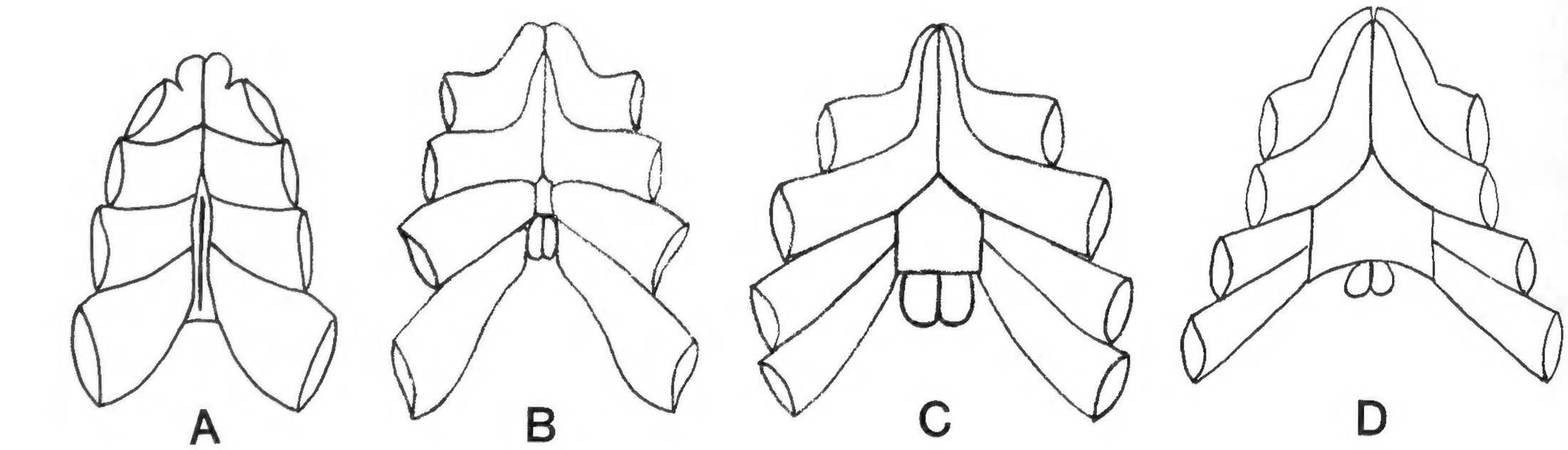
A. A group of holosternous scorpions: **1.** Centromachidae—*Centromachus euglyptus* (Peach). **2.** Mazoniidae—*Mazonia woodiana* Meek and Worthen. **3.** Mesophonidae—*Mesophonus perornatus* Wills. **4.** Heloscorpionidae—*Heloscorpio sutcliffei* (Woodward).

B. Another group of holosternous scorpions: **1.** Archaeoctonidae—*Archaeoctonus glaber* (Peach). **2.** Gigantoscorpionidae—*Gigantoscorpio willsi* Størmer. **3.** Anthracoscorpionidae—*Anthracoscorpio juvenis* Kušta. **4.** Anthracoscorpionidae—*Allobuthus macrostethus,* n. gen., n. sp.

C. Development, in ascending order, among a group of lobosternous scorpions in which the first pair of maxillary lobes was well-developed before the full lengthening of the second pair began, and displaced the first pair of coxae from the midline. **1.** Petaloscorpionidae—*Petaloscorpio bureaui,* n. gen., n. sp. **2.** Eoscorpiidae—*Eoscorpius carbonarius* Meek and Worthen. **3.** Isobuthidae—*Isobuthus kralupensis* (Thorell and Lindström). **4.** Paraisobuthidae—*Paraisobuthus prantli,* n. gen., n. sp.

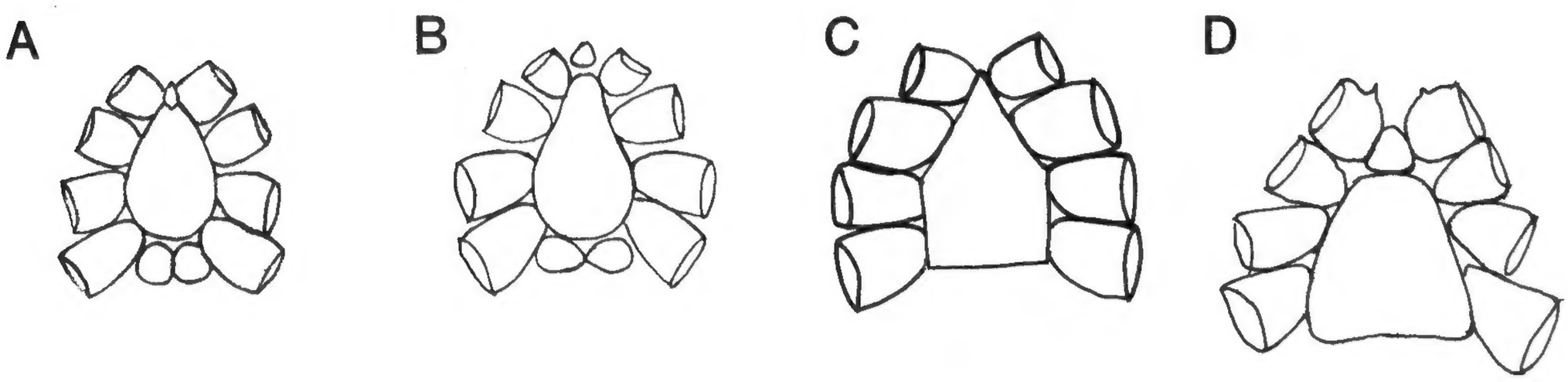
Text-figure 114.—Coxosternal region and oral tube conditions of some Recent scorpions, introduced for comparison (Figures D–H were kindly furnished by David Sissom).

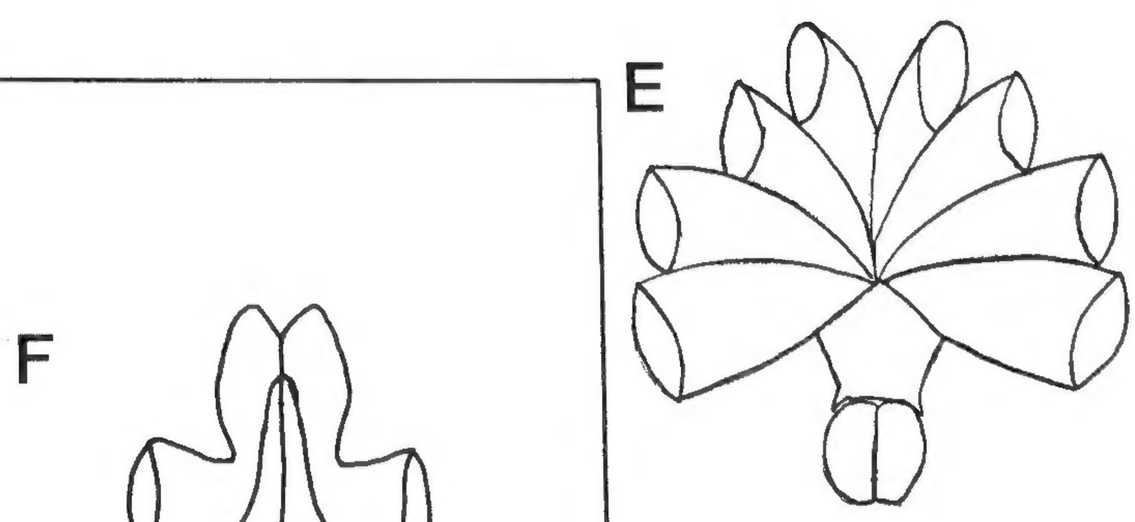
A. Chaerilidae—*Chaerilus celebensis* Pocock. **B.** Chactidae—*Broteochactas gollmeri* Karsh. **C.** Scorpionidae—*Scorpio maurus palmatus* Seuzet. **D.** Diplocentridae—*Diplocentrus bigbendensis* Stahnke. **E.** Iuridae—*Hadruroides lunatus* (Koch). **F.** Vaejovidae—*Vaejovis punctipalpi* (Wood). **G.** Bothriuridae—*Bothriurus araguayae* Vellard. **H.** Buthidae—*Parabuthus laevifrons* (Simon).

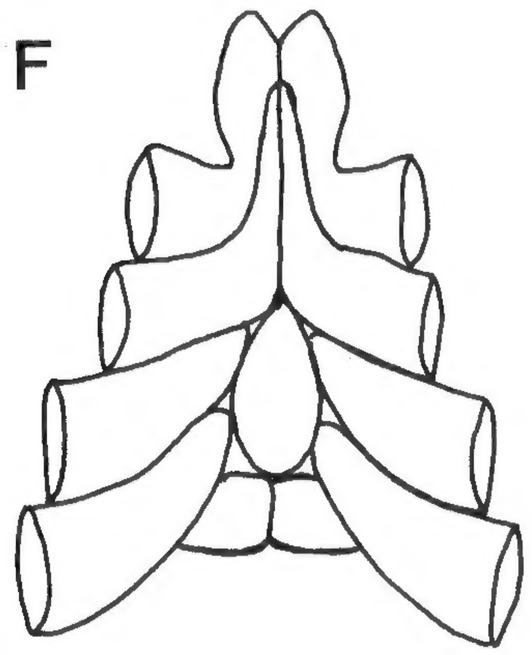


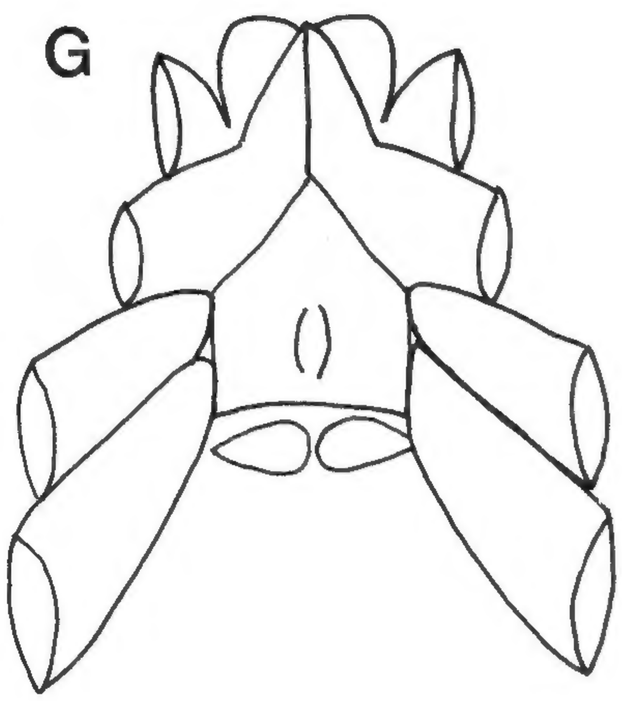
Holosternina

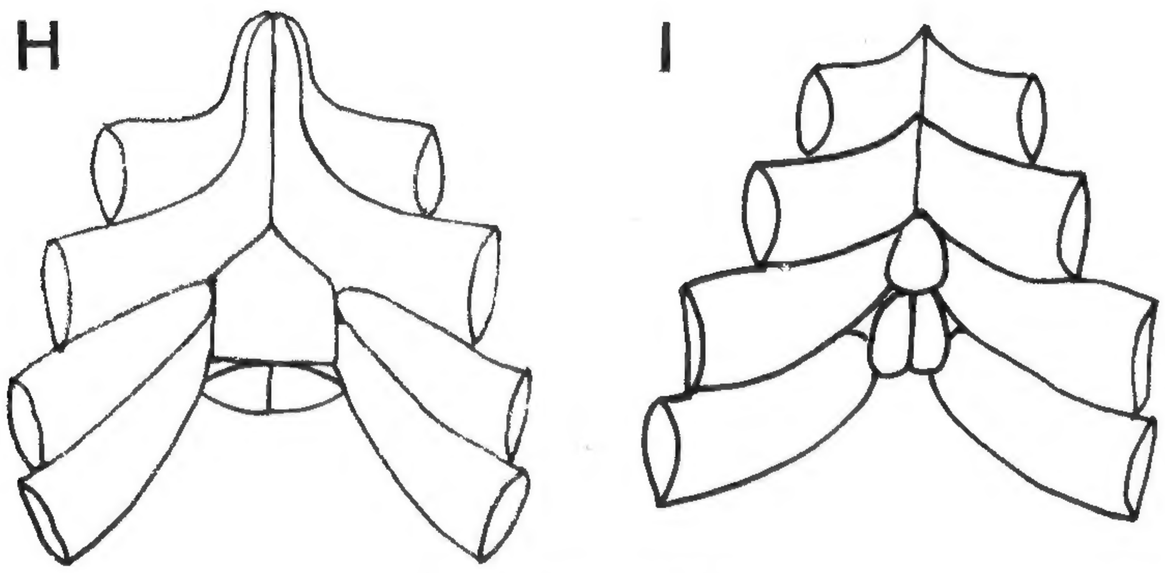
Text-figure 110.—(see p. 243)

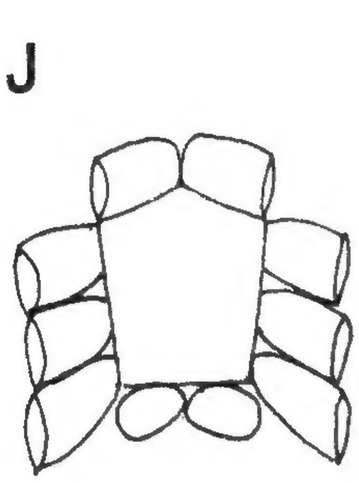




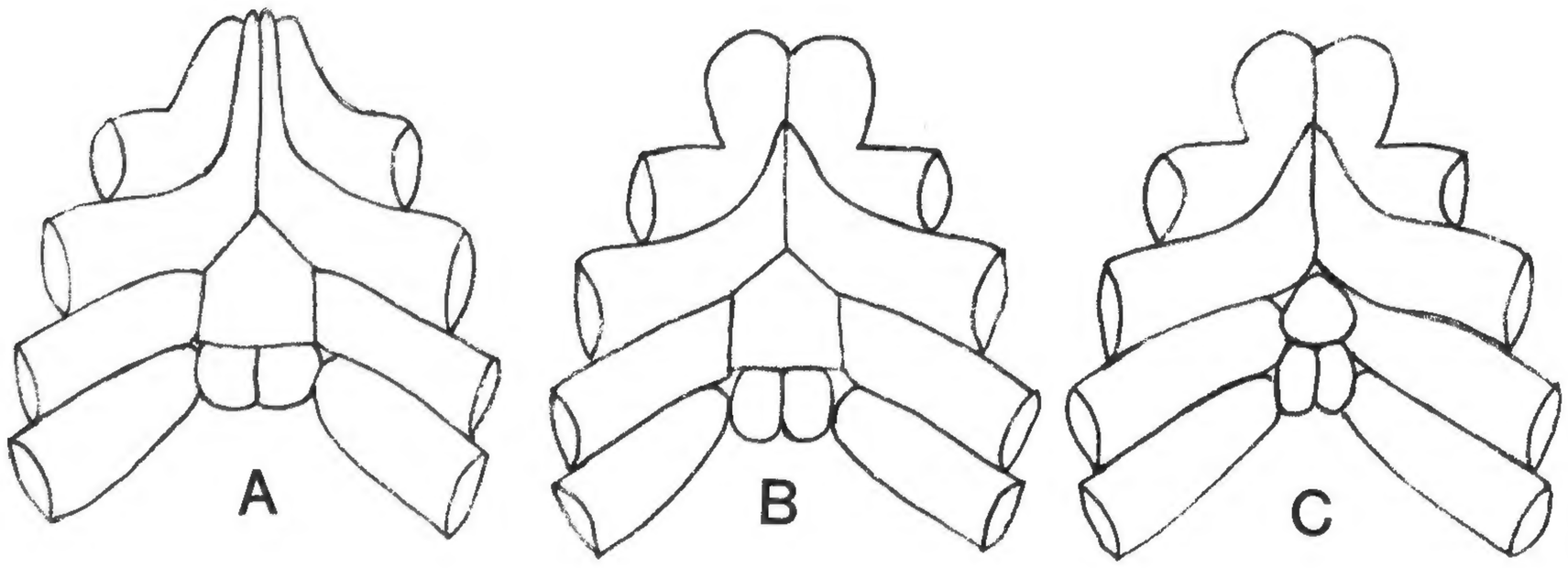


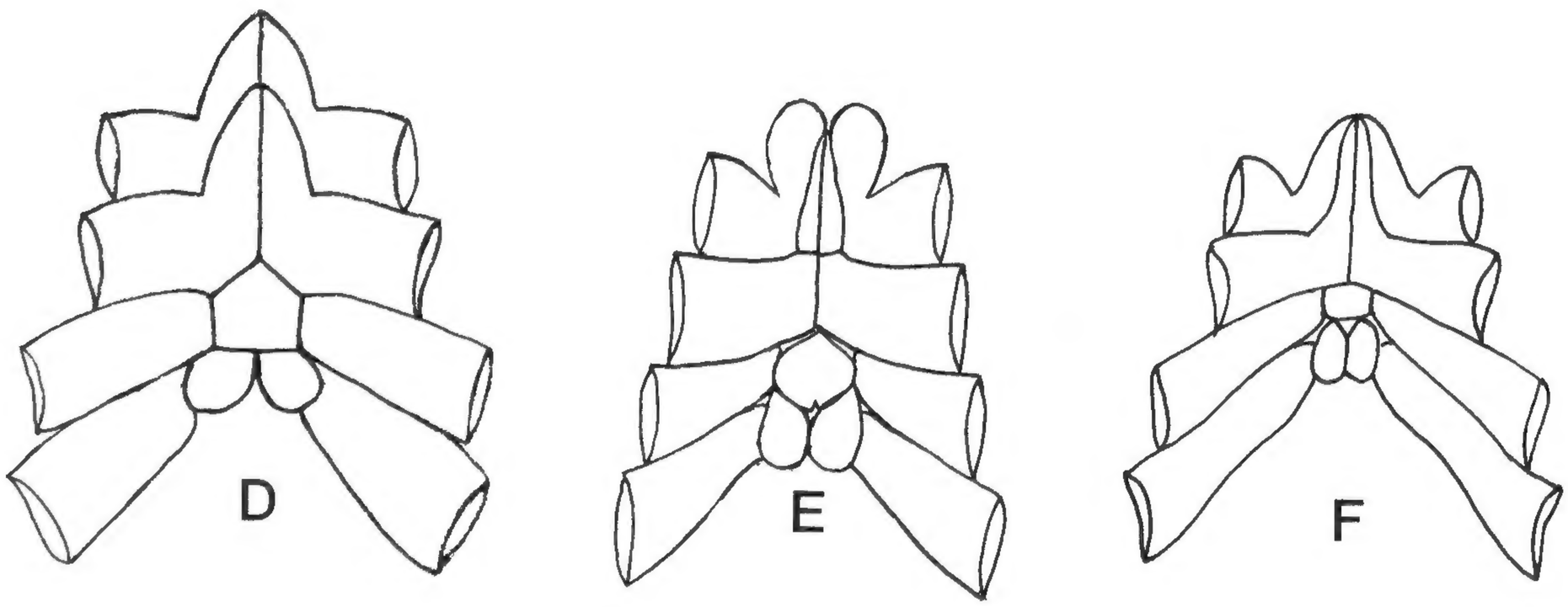


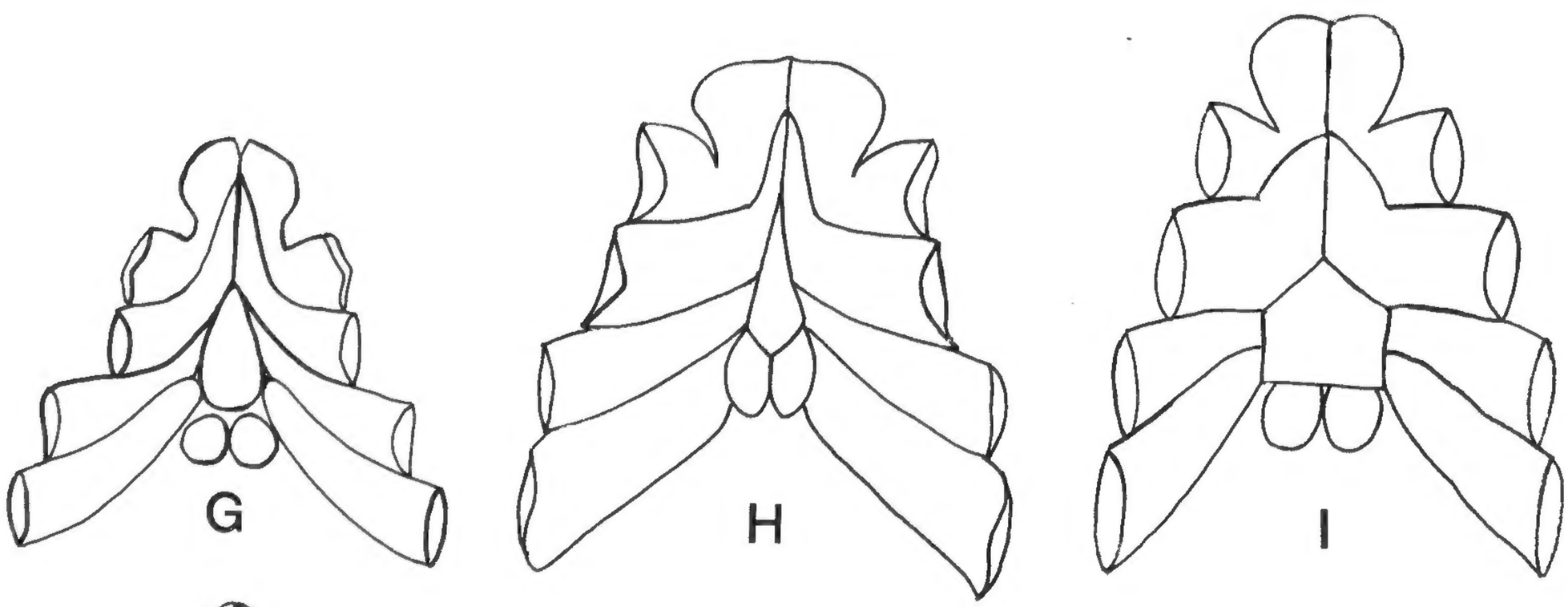


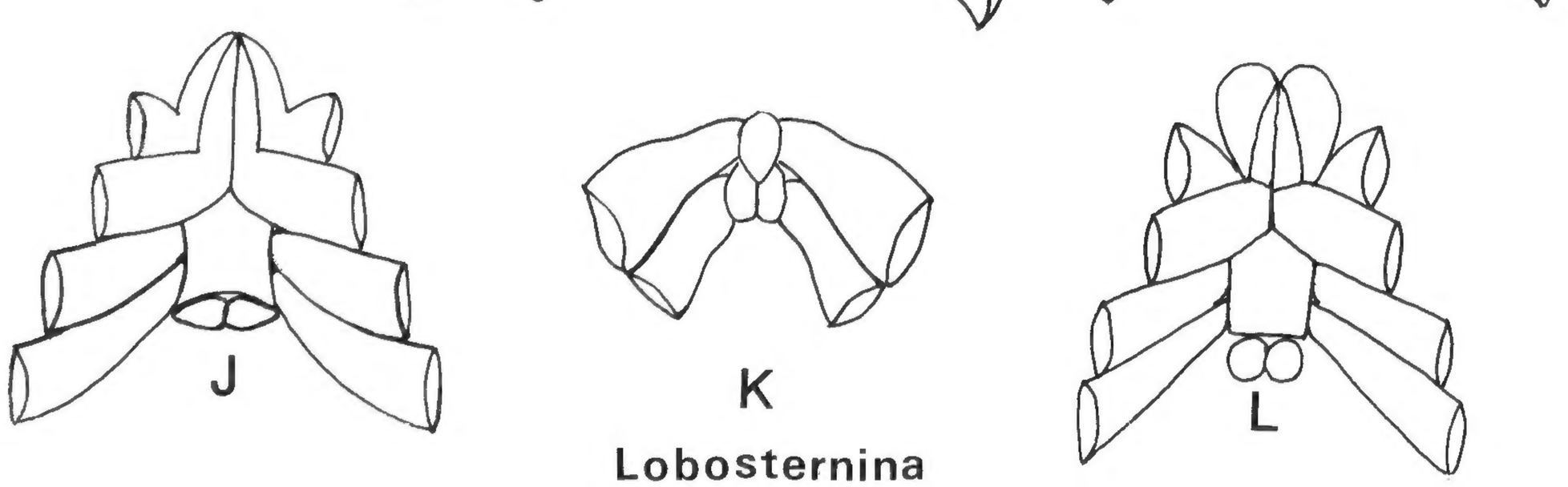


Text-figure 111.—(see p. 243)



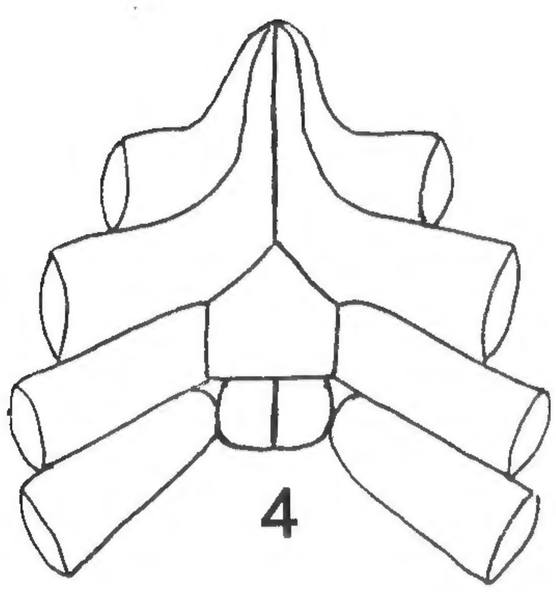


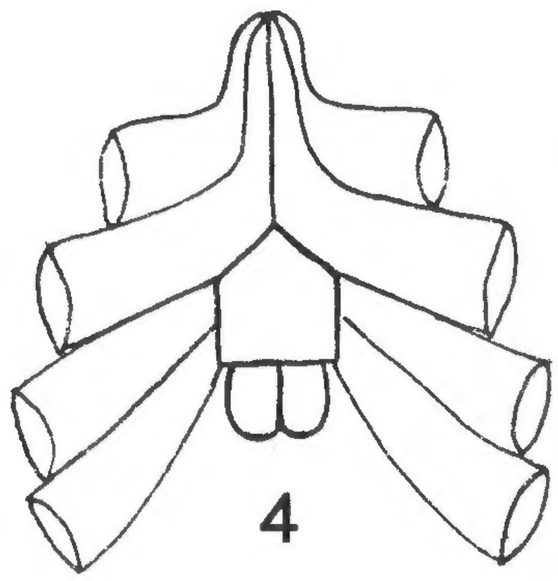


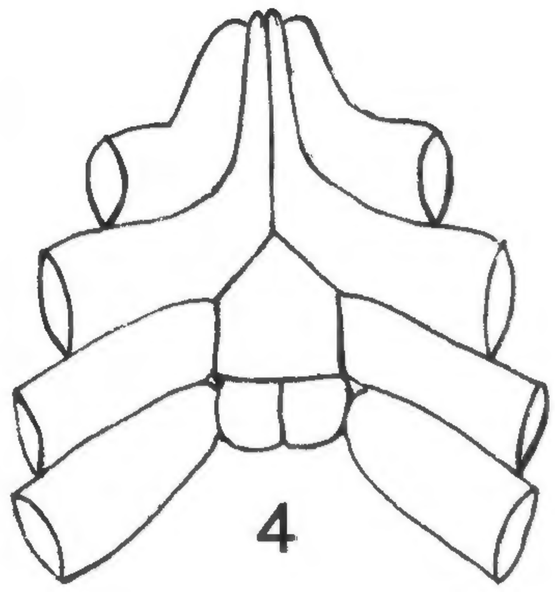


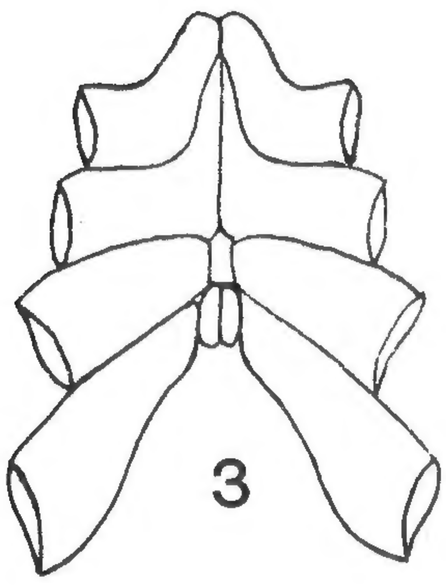
Lobosternina

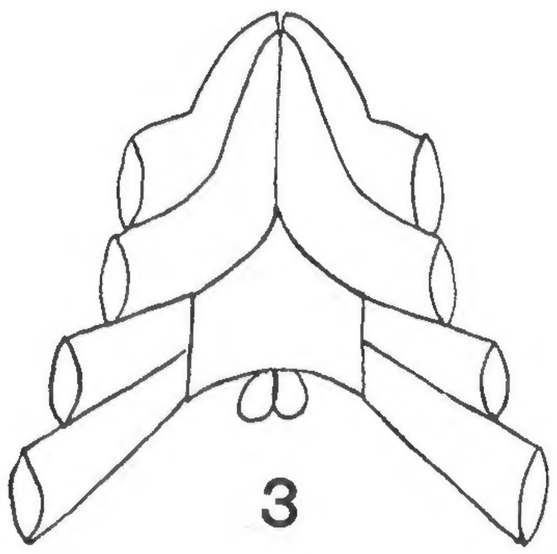
Text-figure 112.—(see p. 243)

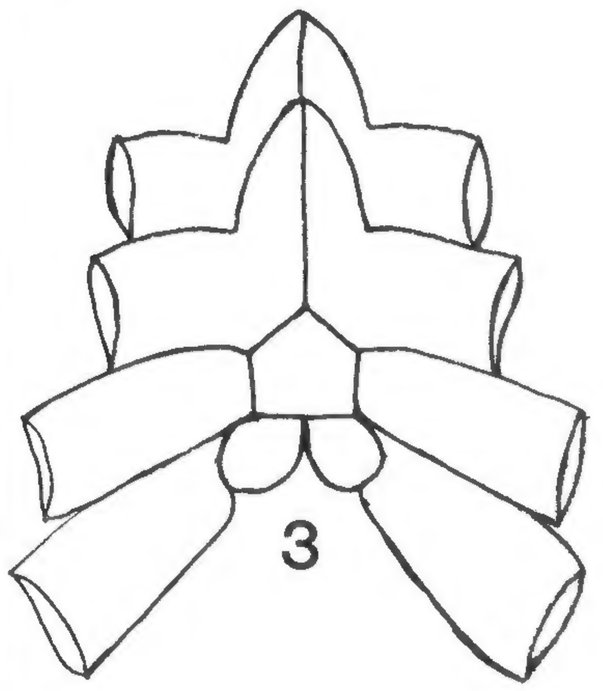


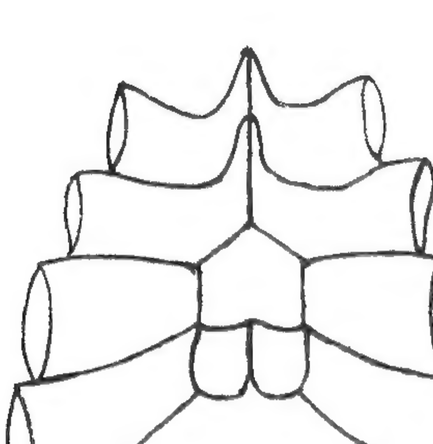


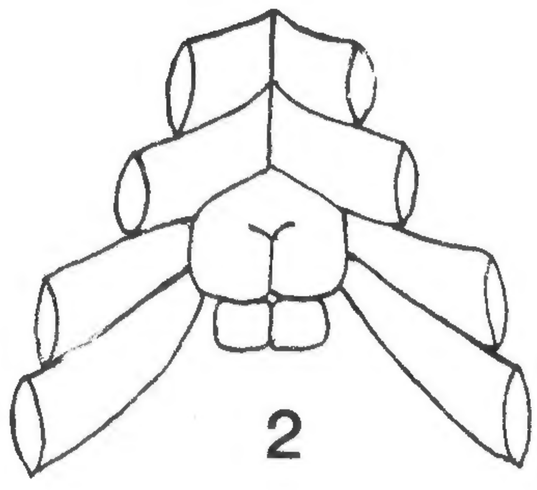


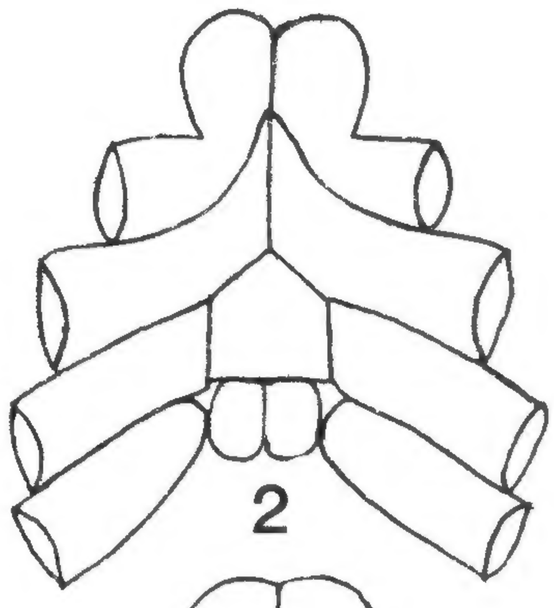


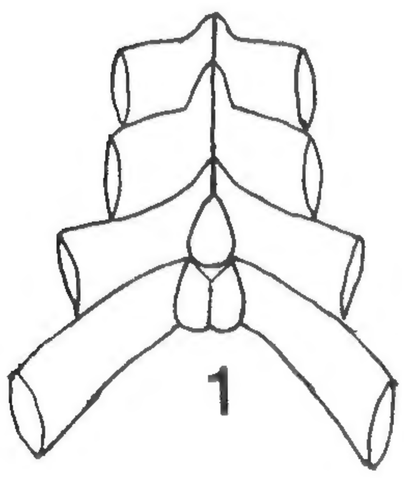


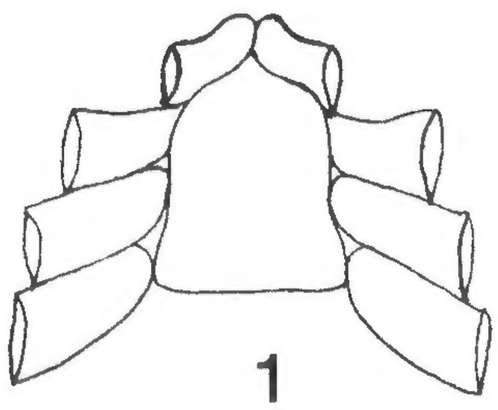


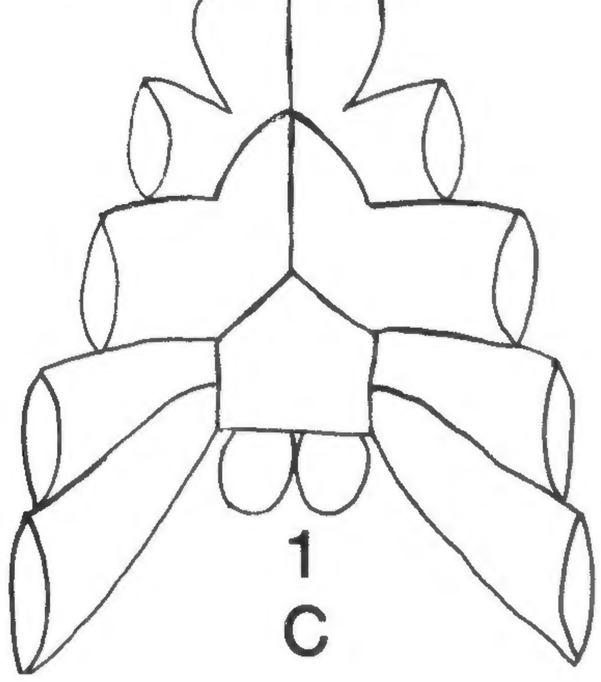




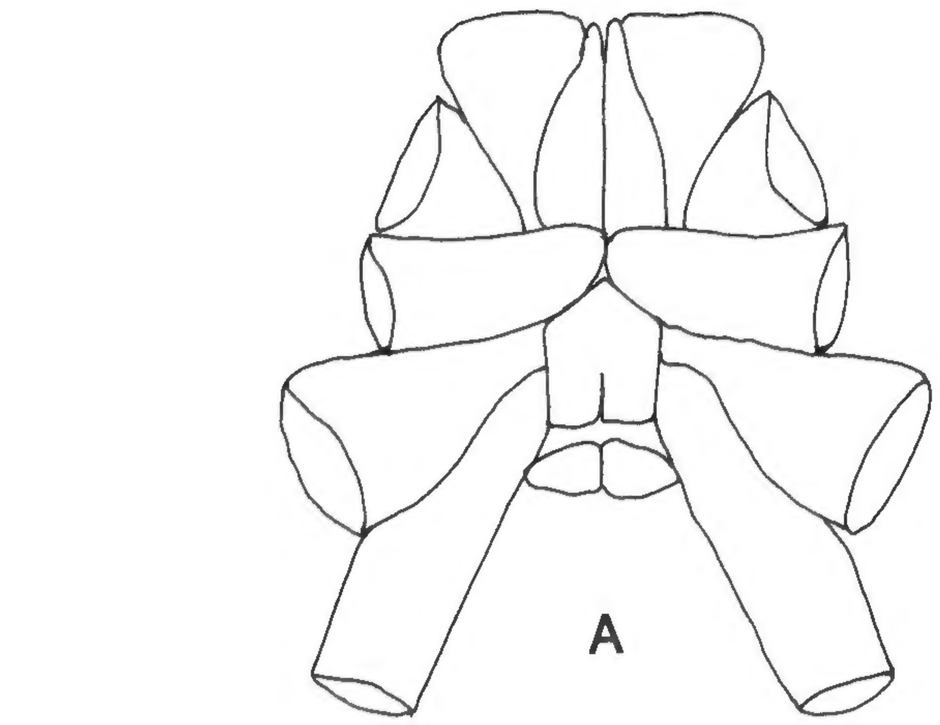


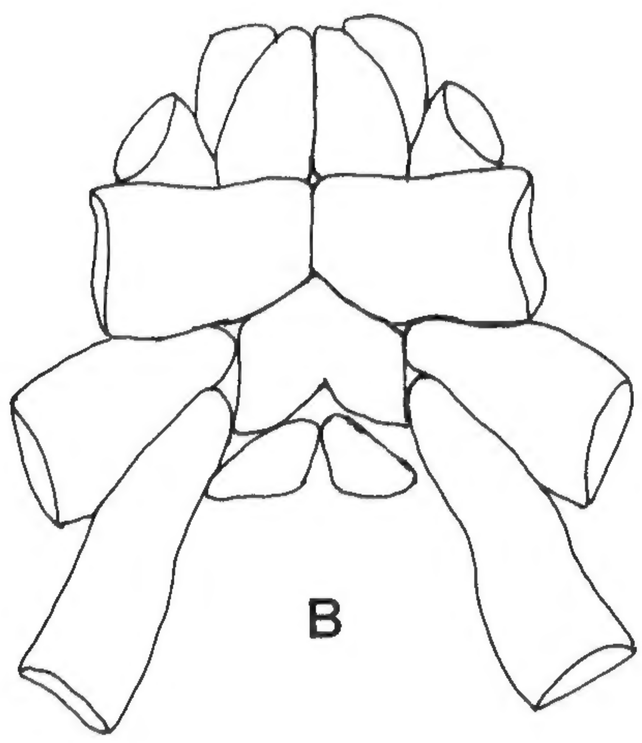


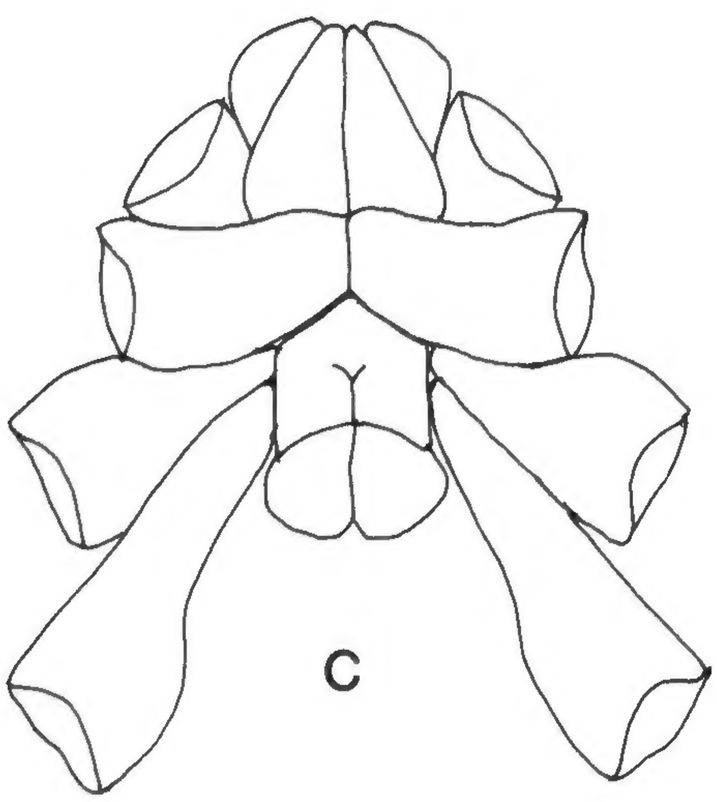


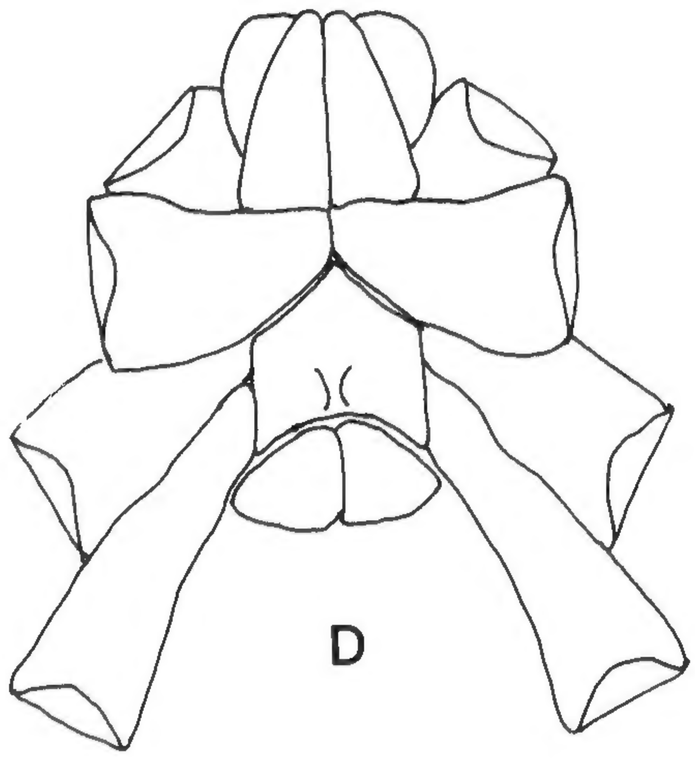


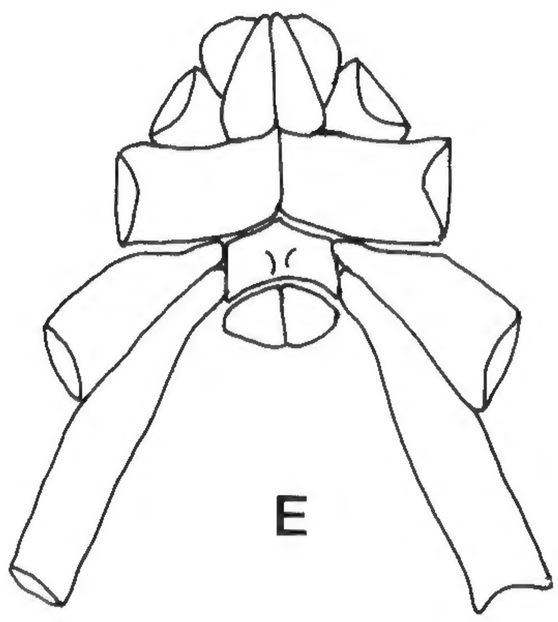
Text-figure 113.—(see p. 243)

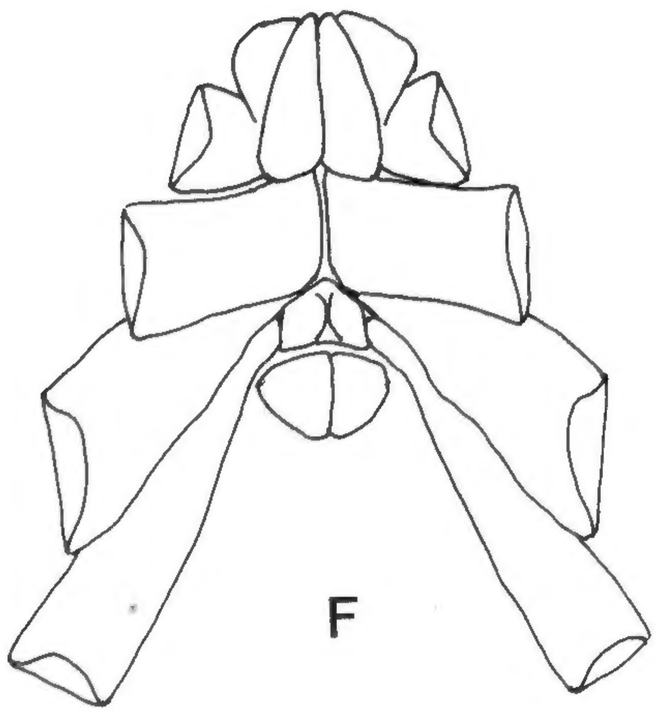


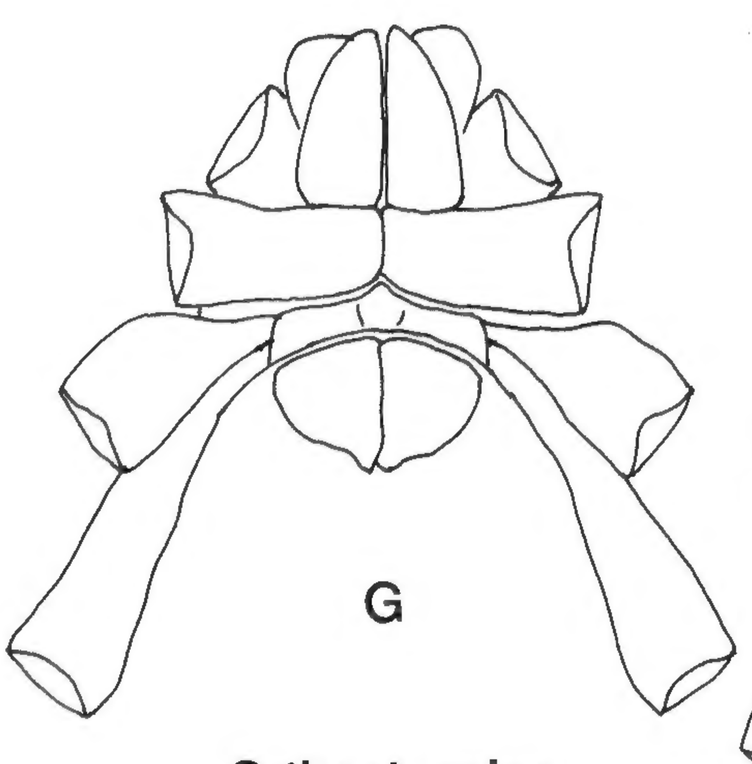


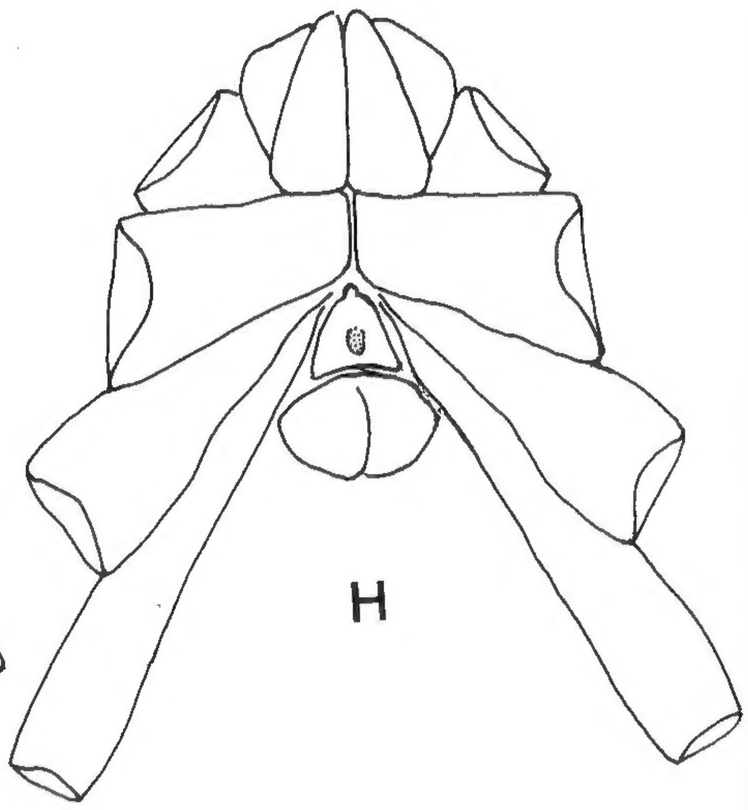












Orthosternina

Text-figure 114.—(see p. 243)

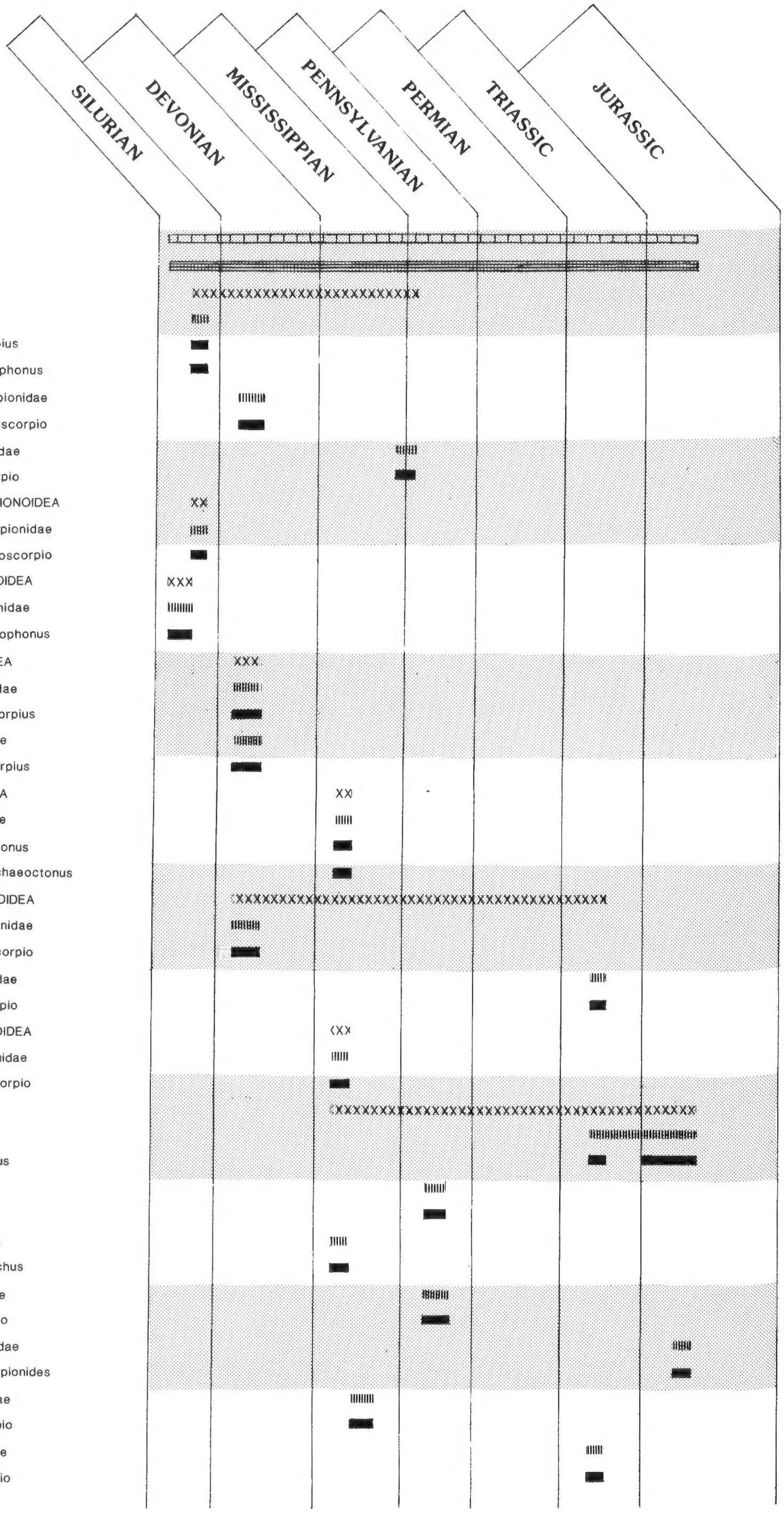
APPENDIX 1[48]

The stratigraphic distribution of orders, superfamilies, families and genera of fossil Scorpionida recognized in this monograph.

[48] Compiled by Anneliese S. Caster.

LEGEND:

- Suborder
- Infraorder
- XXX Superfamily
- Family
- Genus



BRANCHIOSCORPIONINA

HOLOSTERNINA

PROSCORPIOIDEA
- Proscorpiidae
  - Proscorpius
  - Archaeophonus
- Waeringoscorpionidae
  - Waeringoscorpio
- ? Labriscorpionidae
  - Labriscorpio

STOERMEROSCORPIONOIDEA
- Stoermeroscorpionidae
  - Stoermeroscorpio

ALLOPALAEOPHONOIDEA
- Allopalaeophonidae
  - Allopalaeophonus

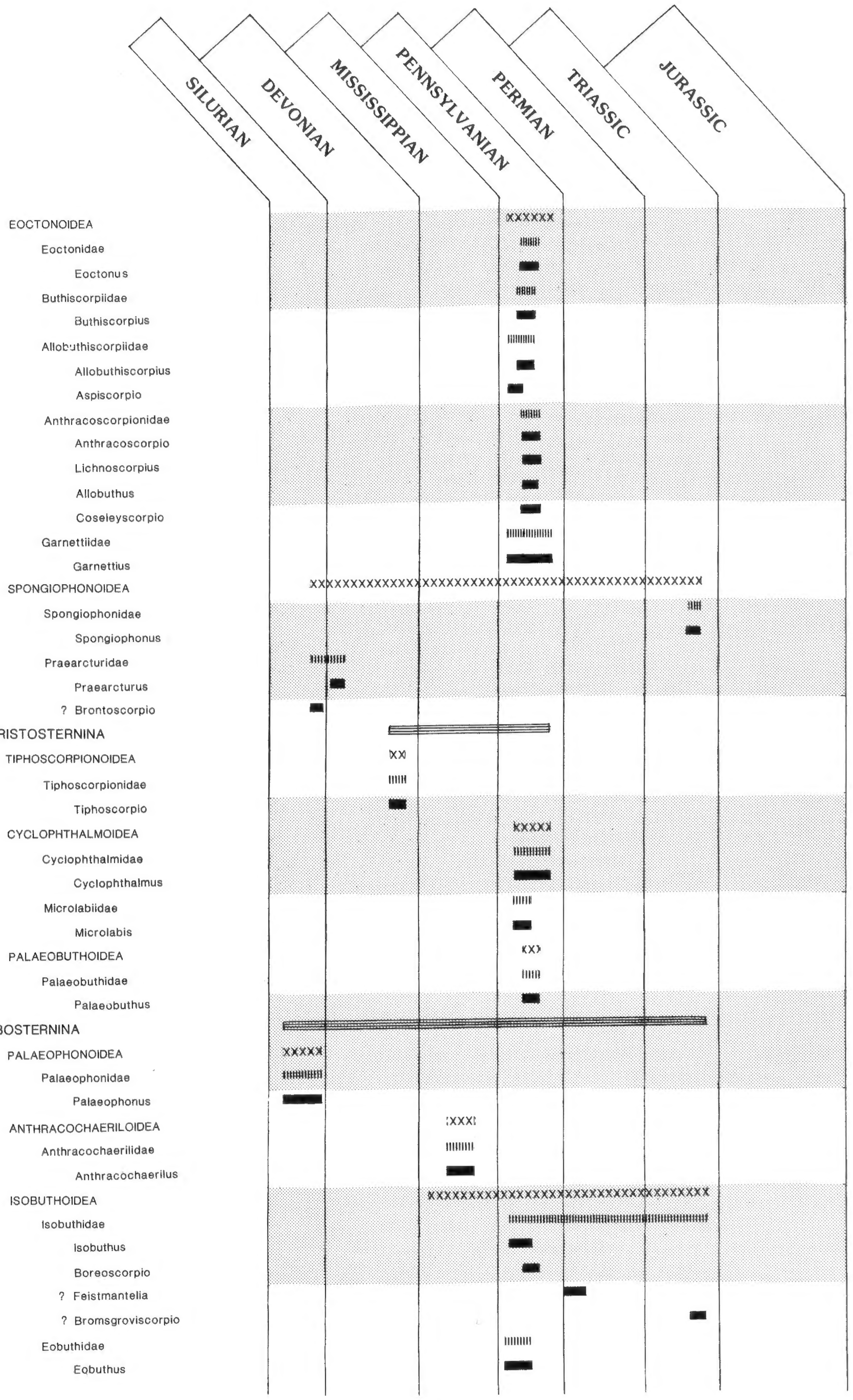
PALAEOSCORPIOIDEA
- Palaeoscorpiidae
  - Palaeoscorpius
- ? Hydroscorpiidae
  - Hydroscorpius

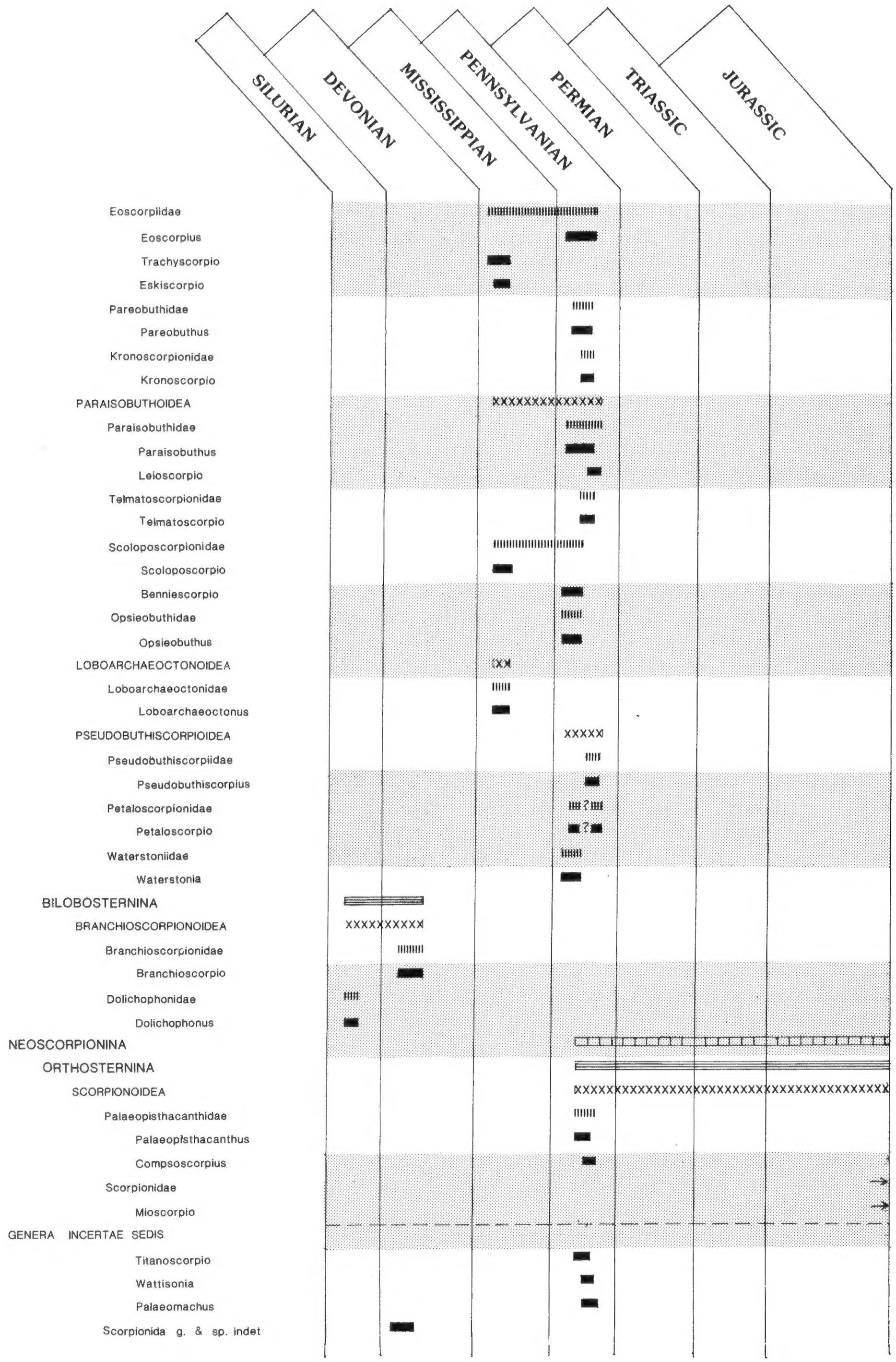
ARCHAEOCTONOIDEA
- Archaeoctonidae
  - Archaeoctonus
  - Pseudoarchaeoctonus

ACANTHOSCORPIONOIDEA
- Acanthoscorpionidae
  - Acanthoscorpio
- Stenoscorpionidae
  - Stenoscorpio

GIGANTOSCORPIONOIDEA
- Gigantoscorpionidae
  - Gigantoscorpio

MESOPHONOIDEA
- Mesophonidae
  - Mesophonus
- Mazoniidae
  - Mazonia
- Centromachidae
  - Centromachus
- Heloscorpionidae
  - Heloscorpio
- Liassoscorpionidae
  - Liassoscorpionides
- Phoxiscorpionidae
  - Phoxiscorpio
- Willsiscorpionidae
  - Willsiscorpio


SILURIAN
DEVONIAN
MISSISSIPPIAN
PENNSYLVANIAN
PERMIAN
TRIASSIC
JURASSIC
EOCTONOIDEA
Eoctonidae
Eoctonus
Buthiscorpiidae
Buthiscorpius
Allobuthiscorpiidae
Allobuthiscorpius
Aspiscorpio
Anthracoscorpionidae
Anthracoscorpio
Lichnoscorpius
Allobuthus
Coseleyscorpio
Garnettiidae
Garnettius
SPONGIOPHONOIDEA
Spongiophonidae
Spongiophonus
Praearcturidae
Praearcturus
? Brontoscorpio
MERISTOSTERNINA
TIPHOSCORPIONOIDEA
Tiphoscorpionidae
Tiphoscorpio
CYCLOPHTHALMOIDEA
Cyclophthalmidae
Cyclophthalmus
Microlabiidae
Microlabis
PALAEOBUTHOIDEA
Palaeobuthidae
Palaeobuthus
LOBOSTERNINA
PALAEOPHONOIDEA
Palaeophonidae
Palaeophonus
ANTHRACOCHAERILOIDEA
Anthracochaerilidae
Anthracochaerilus
ISOBUTHOIDEA
Isobuthidae
Isobuthus
Boreoscorpio
? Feistmantelia
? Bromsgroviscorpio
Eobuthidae
Eobuthus


SILURIAN
DEVONIAN
MISSISSIPPIAN
PENNSYLVANIAN
PERMIAN
TRIASSIC
JURASSIC
Eoscorpiidae
Eoscorpius
Trachyscorpio
Eskiscorpio
Pareobuthidae
Pareobuthus
Kronoscorpionidae
Kronoscorpio
PARAISOBUTHOIDEA
Paraisobuthidae
Paraisobuthus
Leioscorpio
Telmatoscorpionidae
Telmatoscorpio
Scoloposcorpionidae
Scoloposcorpio
Benniescorpio
Opsieobuthidae
Opsieobuthus
LOBOARCHAEOCTONOIDEA
Loboarchaeoctonidae
Loboarchaeoctonus
PSEUDOBUTHISCORPIOIDEA
Pseudobuthiscorpiidae
Pseudobuthiscorpius
Petaloscorpionidae
Petaloscorpio
Waterstoniidae
Waterstonia
BILOBOSTERNINA
BRANCHIOSCORPIONOIDEA
Branchioscorpionidae
Branchioscorpio
Dolichophonidae
Dolichophonus
NEOSCORPIONINA
ORTHOSTERNINA
SCORPIONOIDEA
Palaeopisthacanthidae
Palaeopisthacanthus
Compsoscorpius
Scorpionidae
Mioscorpio
GENERA INCERTAE SEDIS
Titanoscorpio
Wattisonia
Palaeomachus
Scorpionida g. & sp. indet

APPENDIX 2

Index of Synonyms

Alloscorpius Petrunkevitch, 1949 = *Eoscorpius* Meek and Worthen, 1868.

Alloscorpius danielsi Petrunkevitch = *Kronoscorpio danielsi* (Petrunkevitch).

Alloscorpius granulosus (Petrunkevitch)
holotype YPM 128 = *Eoscorpius carbonarius* Meek and Worthen; paratype YPM 129 = *Telmatoscorpio brevipectus* Kjellesvig-Waering; spec. YPM 132 = *Paraisobuthus virginiae* Kjellesvig-Waering.

Alloscorpius tuberculatus (Peach) = *Benniescorpio tuberculatus* (Peach).

Alloscorpius wardingleyi (Woodward) = *Mazonia wardingleyi* (Woodward).

Anthracoscorpii Thorell and Lindström, 1855, restricted = Anthracoscorpionidae Thorell and Lindström, 1855.

Anthracoscorpio buthiformis Pocock
holotype BM(NH) In.18596 = *Buthiscorpius buthiformis* (Pocock); paratype BM(NH) In.22832 = *Leioscorpio pseudobuthiformis* Kjellesvig-Waering; paratype BM(NH) In.7883 = *Compsoscorpius elegans* Petrunkevitch; paratype BM(NH) I.1555 = *Pseudobuthiscorpius labiosus* Kjellesvig-Waering; spec. BM(NH) In.31262 = *Coseleyscorpio lanceolatus* Kjellesvig-Waering; spec. BU 722 = *Wattisonia coseleyensis* Wills.

Anthracoscorpio minutus (Petrunkevitch) = *Lichnoscorpius minutus* Petrunkevitch.

Anthracoscorpio sparthensis (Baldwin and Sutcliffe) = *Eoscorpius sparthensis* Baldwin and Sutcliffe.

Apoxypoda Petrunkevitch, 1913 = superseded suborder based on tarsi terminating in a sharp point.

Archaeoctonus tuberculatus (Peach)
holotype GSE 9675, 9676 = *Benniescorpio tuberculatus* (Peach); paratype BM(NH) I.988 = *Loboarchaeoctonus squamosus* Kjellesvig-Waering.

Buthiscorpius buthiformis (Pocock), part only
paratype BM(NH) In.22832 = *Leioscorpio pseudobuthiformis* Kjellesvig-Waering; paratype BM(NH) I.1555 = *Pseudobuthiscorpius labiosus* Kjellesvig-Waering; spec. BM(NH) In.31262 = *Coseleyscorpio lanceolatus* Kjellesvig-Waering; spec. BU 720 = *Allobuthus macrostethus* Kjellesvig-Waering; spec. BU 722 = *Wattisonia coseleyensis* Wills.

Buthiscorpius major Wills = *Allobuthiscorpius major* (Wills).

Centromachoidea Petrunkevitch, 1953, included under Mesophonoidea Wills, 1910.

Centromachus euglyptus (Peach), part only
spec. BM(NH) In.12848 = *Loboarchaeoctonus squamosus* Kjellesvig-Waering.

Centromachus glaber (Peach) = *Arachaeoctonus glaber* (Peach).

Centromachus tuberculatus (Peach) = *Benniescorpio tuberculatus* (Peach).

Compsoscorpius elongatus Petrunkevitch = *Compsoscorpius elegans* Petrunkevitch.

Cyclophthalmus kralupensis Thorell and Lindström = *Isobuthus kralupensis* (Thorell and Lindström).

Cyclophthalmus senior Corda, part only
spec. NMP Inv. 837A,B = *Isobuthus kralupensis* (Thorell and Lindström).

Cyclophthalmus sternbergii (Corda) = *Microlabis sternbergii* Corda.

Dionychopoda Petrunkevitch, 1913 = superseded suborder based on tarsi terminating in two claws.

Eobuthus holti (?) Pocock = *Paraisobuthus duobicarinatus* Kjellesvig-Waering.

Eobuthus pottsvillensis Moore = *Opsieobuthus pottsvillensis* (Moore).

Eobuthus rakovnicensis Frič, part only
spec. BM(NH) I.2950 = *Paraisobuthus prantli* Kjellesvig-Waering.

Eobuthus sp. Wills = *Pareobuthus salopiensis* Wills.

Eoctonus miniatus Petrunkevitch, part only
paratype YPM 132 = *Paraisobuthus virginiae* Kjellesvig-Waering.

Eoscorpionidae Scudder, 1884 = Eoscorpiidae Scudder, 1884.

Eoscorpius anglicus Woodward = *Palaeomachus anglicus* (Woodward).

Eoscorpius buthiformis (Pocock)
holotype BM(NH) In.18596 = *Buthiscorpius buthiformis* (Pocock); paratype BM(NH) I.1555 = *Pseudobuthiscorpius labiosus* Kjellesvig-Waering.

Eoscorpius danielsi Petrunkevitch = *Kronoscorpio danielsi* (Petrunkevitch).

Eoscorpius dunlopi (Pocock) = *Anthracoscorpio dunlopi* Pocock.

Eoscorpius euglyptus Peach = *Centromachus euglyptus* (Peach).

Eoscorpius glaber Peach = *Archaeoctonus glaber* (Peach).

Eoscorpius granulosus Petrunkevitch
holotype YPM 128 = *Eoscorpius carbonarius* Meek and Worthen; paratype YPM 129 = *Telmatoscorpio brevipectus* Kjellesvig-Waering; paratype YPM 130 = *Palaeobuthus distinctus* Petrunkevitch.

Eoscorpius inflatus Peach = *Tribolbina carnegiei* Latham (*fide* Rolfe, 1963).

(?) Eoscorpius ornatus (Frič) = *Feistmantelia ornata* Frič.

Eoscorpius sparthensis Baldwin and Sutcliffe, part only
spec. BM(NH) I.2950 = *Paraisobuthus prantli* Kjellesvig-Waering.

Eoscorpius tuberculatus Peach = *Benniescorpio tuberculatus* (Peach).

Eoscorpius typicus Petrunkevitch
holotype USNM 37986, paratype USNM 37987 = *Eoscorpius carbonarius* Meek and Worthen; paratype YPM 126 = *Anthracoscorpio* (?) sp. Kjellesvig-Waering; paratype YPM 127 = *Palaeobuthus distinctus* Petrunkevitch.

Eoscorpius (Mazonia) wardingleyi Woodward = *Mazonia wardingleyi* (Woodward).

Eoscorpius (Mazonia) woodiana (Meek and Worthen) = *Mazonia woodiana* Meek and Worthen.

Eoscorpius sp. Copeland = *Boreoscorpio copelandi* Kjellesvig-Waering.

Europhthalmus Petrunkevitch, 1949 = *Eoscorpius* Meek and Worthen, 1868.

Europhthalmus longimanus Petrunkevitch = *Eoscorpius pulcher* (Petrunkevitch).

Eurypterus ? possibly **pygmaea Salter** = *Palaeophonus* (?) *lightbodyi* Kjellesvig-Waering.

Euscorpionina (Euscorpiones) Petrunkevitch, 1949 = superseded suborder based on seven tergites in the preabdomen and tarsi with two claws.

Euscorpius buthiformis (Pocock) in Petrunkevitch (1953, fig. 45) = *Pseudobuthiscorpius labiosus* Kjellesvig-Waering.

Geralinura ? sutcliffei Woodward = *Heloscorpio sutcliffei* (Woodward).

Isobuthus holti (Pocock) = *Eobuthus holti* Pocock.

Isobuthus ornatus (Frič) = *Feistmantelia ornata* Frič.

Isobuthus pottsvillensis (Moore) = *Opsieobuthus pottsvillensis* (Moore).

Isobuthus rakovnicensis (Frič) = *Eobuthus rakovnicensis* Frič.
Lichnophthalmus Petrunkevitch, 1949 = *Eoscorpius* Meek and Worthen, 1868.
Lichnophthalmus pulcher Petrunkevitch = *Eoscorpius pulcher* (Petrunkevitch).
Lichnophthalmus sp. Laurentiaux-Vieira and Laurentiaux = *Eoscorpius* sp.
Lobosterni Pocock, 1911, restricted = Lobosternina Pocock, 1911.
Mazonia hungerfordi Elias = *Garnettius hungerfordi* (Elias).
Mazonioidea Petrunkevitch, 1913, included under Mesophonoidea Wills, 1910.
Mazoniscorpio mazonensis Wills = *Palaeobuthus distinctus* Petrunkevitch.
Mesophonus bromsgroviensis Wills = *Willsiscorpio bromsgroviensis* (Wills).
Mesophonus gracilis Wills
Nos. 132 (lectotype), 11, 025, 102, 137, 147, 164, 185, 0191, 203, 228, 0257, 283, 327A = *Stenoscorpio gracilis* (Wills); No. 195 = *Willsiscorpio bromsgroviensis* (Wills); No. 0278 = *Stenoscorpio pseudogracilis* (Wills).
Mesophonus infans A (?) Mesophonus gracilis Wills, spec. 282 = *Stenoscorpio pseudogracilis* (Wills).
Mesophonus infans D Wills, spec. 0232B = *Stenoscorpio pseudogracilis* (Wills).
Mesophonus infans E Wills, spec. 0122 = *Mesophonus perornatus* Wills.
Mesophonus opisthophthalmus Wills = *Mesophonus perornatus* Wills.
Mesophonus pseudogracilis Wills
Nos. 231 (holotype), 012, 029, 052B, 065, 80, 184, 229, 0232B, 257, 279 = *Stenoscorpio pseudogracilis* (Wills); No. 094 = *Mesophonus perornatus* Wills.
Neoscorpii Thorell and Lindström, 1885 = Neoscorpionina Thorell and Lindström, 1885.
Ophismoblatta maculata (Brauer, Redtenbacher, and Ganglbauer) = *Mesophonus* (?) *maculatus* (Brauer, Redtenbacher, and Ganglbauer).
Orthosterni Pocock, 1911, restricted = Orthosternina Pocock, 1911.
Palaeomachus sp. Petrunkevitch = *Cyclophthalmus robustus* Kjellesvig-Waering.
Palaeopisthacanthus mazonensis Petrunkevitch = *Eoscorpius carbonarius* Meek and Worthen.
Palaeophonus caledonicus Hunter = *Allopalaeophonus caledonicus* (Hunter).
Palaeophonus hunteri Pocock = *Allopalaeophonus caledonicus* (Hunter).
Palaeophonus loudonensis Laurie = *Dolichophonus loudonensis* (Laurie).
Palaeophonus osborni Whitfield = *Proscorpius osborni* (Whitfield).
Palaeoscorpionidae Lehmann = Palaeoscorpiidae Lehmann.
Periplaneta maculatus Brauer, Redtenbacher, and Ganglbauer = *Mesophonus* (?) *maculatus* (Brauer, Redtenbacher, and Ganglbauer).
Protoscorpionina (Protoscorpiones) Petrunkevitch, 1949 = superseded suborder based on the erroneous observation of eight tergites in the preabdomen.
Scorpio zeuneri Hadži = *Mioscorpio zeuneri* (Hadži).
Scorpionides Leach, 1815 = Scorpionoidea Leach, 1815.
Spongiotarsus pustulosus Wills = *Spongiophonus pustulosus* Wills.
Trigonoscorpio Petrunkevitch, 1913 = *Eoscorpius* Meek and Worthen, 1868.
Trigonoscorpio americanus Petrunkevitch = *Eoscorpius carbonarius* Meek and Worthen.
Trigonoscorpio ? sutcliffei (Woodward) = *Heloscorpio sutcliffei* (Woodward).
Trigonoscorpionidae Dubinin, 1962 = family of doubtful standing.
Typhlopisthacanthus Petrunkevitch, 1949 = *Eoscorpius* Meek and Worthen, 1868.
Typhlopisthacanthus anglicus Petrunkevitch = *Compsoscorpius elegans* Petrunkevitch.
Typhlopisthacanthus mazonensis (Petrunkevitch) = *Eoscorpius carbonarius* Meek and Worthen.
Typhloscorpius Petrunkevitch, 1949 = *Eoscorpius* Meek and Worthen, 1868.
Typhloscorpius distinctus Petrunkevitch = *Eoscorpius distinctus* (Petrunkevitch).

APPENDIX 3

Index of Specimens by Repository

UNITED STATES OF AMERICA:

American Museum of Natural History, New York, NY
Proscorpius osborni (Whitfield), holotype No. ?, AMNH 28383.

Buffalo Museum of Science, Buffalo, NY
Proscorpius osborni (Whitfield), BMS E25162 (CIURCA 031966-1).

Field Museum of Natural History, University of Chicago, Chicago, IL
Acanthoscorpio mucronatus Kjellesvig-Waering, holotype FMNH (PE) 6177a,b; *Branchioscorpio richardsoni* Kjellesvig-Waering, holotype FMNH (PE) 6175a,b; *Buthiscorpius lemayi* Kjellesvig-Waering, holotype FMNH (PE) 21600; *Eoctonus miniatus* Petrunkevitch, FMNH (PE) 16498, (PE) 32202; *Eoscorpius carbonarius* Meek and Worthen, holotype FMNH (UC) 8949, FMNH (PE) 32083, (PE) 32084; *Hydroscorpius denisoni* Kjellesvig-Waering, holotype FMNH (PE) 6176; *Kronoscorpio danielsi* (Petrunkevitch), FMNH (PE) 32085; *Mazonia woodiana* Meek and Worthen, FMNH (PE) 39253; *Opsieobuthus pottsvillensis* (Moore), holotype FMNH (UC) 37984.

Illinois State Museum, Springfield, IL
Labriscorpio alliedensis Leary, holotype ISM 416899.

New York State Museum, Albany, NY
Archaeophonus eurypteroides Kjellesvig-Waering, holotype, NYSM 12947; *Proscorpius osborni* (Whitfield), NYSM 12948.

University of Illinois Geological Museum, Urbana, IL
Mazonia woodiana Meek and Worthen, holotype UI X-491.

University of Michigan Museum of Paleontology, Ann Arbor, MI
Eoscorpius carbonarius Meek and Worthen, UMMP 7224 (holotype of *Trigonoscorpio americanus* Petrunkevitch); *Kronoscorpio danielsi* (Petrunkevitch), holotype UMMP 7216 (under *Eoscorpius danielsi* Petrunkevitch).

U.S. National Museum of Natural History, Smithsonian Institution, Washington, DC
Eoscorpius carbonarius Meek and Worthen, USNM 37977, USNM 37986 (holotype of *E. typicus* Petrunkevitch), USNM 37987 (paratype of *E. typicus* Petrunkevitch); *Garnettius hungerfordi* (Elias), holotype USNM 125453a,b; *Kronoscorpio danielsi* (Petrunkevitch), plaster cast of holotype USNM 27921; *Tiphoscorpio hueberi* Kjellesvig-Waering, holotype USNM 252629, paratype USNM 252630.

Princeton University Museum, Princeton, NJ
Eoscorpius casei Kjellesvig-Waering, holotype PU 87266.

Yale Peabody Museum, New Haven, CT

Anthracoscorpio (?) sp. Kjellesvig-Waering, YPM 126 (paratype of *Eoscorpius typicus* Petrunkevitch); *Eoctonus miniatus* Petrunkevitch, holotype YPM 131; *Eoscorpius carbonarius* Meek and Worthen, YPM 128 (holotype of *Eoscorpius granulosus* Petrunkevitch), YPM 139 (cast of holotype of *Trigonoscorpio americanus* Petrunkevitch); *Palaeobuthus distinctus* Petrunkevitch, holotype YPM 133, YPM 127 (paratype of *Eoscorpius typicus* Petrunkevitch), YPM 130 (paratype of *Eoscorpius granulosus* Petrunkevitch); *Palaeopisthacanthus schucherti* Petrunkevitch, holotype YPM 140; *Paraisobuthus virginiae* Kjellesvig-Waering, holotype YPM 132 (paratype of *Eoctonus miniatus* Petrunkevitch); *Telmatoscorpio brevipectus* Kjellesvig-Waering, holotype YPM 129 (paratype of *Eoscorpius granulosus* Petrunkevitch).

Private collection of Samuel J. Ciurca, Rochester, NY

Archaeophonus eurypteroides Kjellesvig-Waering, CIURCA 062065-1; *Proscorpius osborni* (Whitfield), CIURCA 040564, 040668-1,2, 041771-1, 042570-1A, 072869-9B; *Stoermeroscorpio delicatus* Kjellesvig-Waering, holotype CIURCA 041771-1,2.

Private collection of Richard Cramer, Forest Park, IL

Titanoscorpio douglassi Kjellesvig-Waering, paratype RC unnumbered specimen.

Private collection of David Lyon Douglass, Western Springs, IL

Titanoscorpio douglassi Kjellesvig-Waering, holotype DLD unnumbered specimen.

CANADA:

Geological Survey of Canada, Ottawa, Ontario

Boreoscorpio copelandi Kjellesvig-Waering, holotype GSC 12778.

University of Laval, Quebec City, Quebec

Petaloscorpio bureaui Kjellesvig-Waering, holotype UL 1092.

UNITED KINGDOM:

Birmingham University, Birmingham, England

Allobuthus macrostethus Kjellesvig-Waering, holotype BU 720; *Palaeobuthus distinctus* Petrunkevitch, BU 721A,B (holotype of *Mazoniscorpio mazonensis* Wills); *Wattisonia coseleyensis* Wills, holotype BU 722A,B and slides W2A1,3; W2/2.

British Museum (Natural History), London, England

Anthracochaerilus palustris Kjellesvig-Waering, holotype BM(NH) In.39764; *Brontoscorpio anglicus* Kjellesvig-Waering, holotype BM(NH) In.31403, In.31404, In.31405; *Buthiscorpius buthiformis* (Pocock), holotype BM(NH) In.18596a,b; *Compsoscorpius elegans* Petrunkevitch, holotype BM(NH) I.4883, paratype BM(NH) In.15862 (holotype of *Compsoscorpius elongatus* Petrunkevitch), paratype BM(NH) In.31261 (holotype of *Typhlopisthacanthus anglicus* Petrunkevitch); *Coseleyscorpio lanceolatus* Kjellesvig-Waering, holotype BM(NH) In.31262; *Cyclophthalmus robustus* Kjellesvig-Waering, holotype BM(NH) In.13976 (under *Palaeomachus* sp. Petrunkevitch); *Eoscorpius distinctus* (Petrunkevitch), holotype BM(NH) In.13909, BM(NH) I.3172; *Eoscorpius pulcher* Petrunkevitch, holotype BM(NH) In.39772, BM(NH) In.39766 (holotype of *Europhthalmus longimanus* Petrunkevitch), BM(NH) In.39770; *Gigantoscorpio willsi* Størmer, counterpart of holotype BM(NH) In.42706a,b; *Heloscorpio sutcliffei* (Woodward), holotype BM(NH) In.18564; *Leioscorpio pseudobuthiformis* Kjellesvig-Waering, holotype BM(NH) In.22832; *Lichnoscorpius minutus* Petrunkevitch, holotype BM(NH) In.31266; *Loboarchaeoctonus squamosus* Kjellesvig-Waering, holotype BM(NH) I.988, paratype BM(NH) In.12848; *Mazonia wardingleyi* (Woodward), holotype BM(NH) In.18561; *Palaeomachus anglicus* (Woodward), holotype BM(NH) I.944a,b; *Paraisobuthus prantli* Kjellesvig-Waering, holotype BM(NH) I.2950; *Praearcturus gigas* Woodward, lectotype BM(NH) I.534, BM(NH) In.41782, In.60443; *Pseudobuthiscorpius labiosus* Kjellesvig-Waering, holotype BM(NH) I.1555; *Trachyscorpio squarrosus* Kjellesvig-Waering, holotype BM(NH) In.25985, paratypes BM(NH) In.25984, In.25986; *Trachyscorpio* (?) sp. Kjellesvig-Waering, BM(NH) In.39765.

Geological Survey Museum, London, England

Allobuthiscorpius major (Wills), holotype GSM Za 2926; *Eoscorpius mucronatus* Kjellesvig-Waering, holotype GSM PF 1392–1393 (formerly Wills' Za 2842); *Palaeophonus* (?) *lightbodyi* Kjellesvig-Waering, holotype GSM 89424; *Paraisobuthus duobicarinatus* Kjellesvig-Waering, holotype GSM 30245–30248; *Pareobuthus salopiensis* Wills, holotype GSM 87231.

Institute of Geological Sciences, Edinburgh, Scotland

Archaeoctonus glaber (Peach), holotype GSE 5858, 5859, GSE 2039; *Benniescorpio tuberculatus* (Peach), holotype GSE 9675(456), 9676(457); *Centromachus euglyptus* (Peach), holotype GSE 2142; *Eskiscorpio parvus* Kjellesvig-Waering, holotype GSE 2139; *Gigantoscorpio willsi* Størmer, holotype GSE 2137, GSE 2134, GSE 2174; *Phoxiscorpio peachi* Kjellesvig-Waering, holotype GSE 2140; *Pseudoarchaeoctonus denticulatus* Kjellesvig-Waering, holotype GSE 2038; *Scoloposcorpio cramondensis* Kjellesvig-Waering, holotype GSE 2173, paratype GSE 5862.

Kilmarnock Museum, Ayrshire, Scotland

Allopalaeophonus caledonicus (Hunter), holotype KM unnumbered specimen.

Manchester University Museum, Manchester, England

Aspiscorpio eagari Kjellesvig-Waering, holotype UMM L 8182; *Eoscorpius sparthensis* Baldwin and Sutcliffe, holotype UMM L 6271A,B.

Royal Scottish Museum, Edinburgh, Scotland

Anthracoscorpio dunlopi Pocock, holotype RSM 1957.1.4995a,b, RSM 1957.1.5000–5002; *Dolichophonus loudonensis* (Laurie), holotype RSM 1897.12.196; *Garnettius* (?) sp. Kjellesvig-Waering, RSM 1957.1.5007; *Waterstonia airdriensis* Kjellesvig-Waering, holotype RSM 1957.1.4996; *Waterstonia* (?) *brachistodactyla* Kjellesvig-Waering, holotype RSM 1978.5.1.

Sedgwick Museum, Cambridge, England

Bromsgroviscorpio willsi Kjellesvig-Waering, holotype Wills' No. 0163 (under *Mesophonus bromsgroviensis* ? Wills); *Mesophonus perornatus* Wills, SM 260 (lectotype), 7, 008, 011, 024, 034, 036, 039A, 040, 050, 85, 095, 0112, 0122, 125, 0128, 156, 0176, 0203, 205, 210, 0212, 213, 0266, 277, 284, 287, SM 094 (under *Mesophonus pseudogracilis* Wills), SM 0107, 0161, 0234 (under *Mesophonus opisthophthalmus* Wills); *Mesophonus* (?) *pulcherrimus* Wills, lectotype SM 201; *Mesophonus* (?) *pulcherrimus* var. *immaculatus* Wills, lectotype SM 212(G105); *Spongiophonus pustulosus* Wills, holotype Wills' No. 280, SM 059, 076, 0286; *Stenoscorpio gracilis* (Wills), SM 132 (lectotype), 11, 025, 102, 137, 147, 164, 185, 0191, 203, 228, 0257, 283, 327A; *Stenoscorpio pseudogracilis* (Wills), SM 231 (holotype), 012, 029, 052B, 065, 080, 184, 229, 231, 257, 279, SM 0278 (under *Mesophonus gracilis* Wills), SM 282 (under *Mesophonus infans* A Wills), SM 0232B (lectotype of *Mesophonus infans* D Wills); *Willsiscorpio bromsgroviensis* (Wills), SM 158 (lectotype), 9, 13, 18, 23, 35, 47, 074, 080, 098, 101, 208, 212, 213, 215, 220, 0235, 270, 273, 275, 0289, 295, SM 195 (under *Mesophonus gracilis* Wills).

CZECHOSLOVAKIA:

National Museum, Prague

Anthracoscorpio juvenis Kušta, holotype NMP Inv. 836 (Frič's Inv. P.3520); *Cyclophthalmus senior* Corda, holotype NMP Inv. 801; *Eobuthus cordai* Kjellesvig-Waering, holotype NMP Inv. 838, paratype NMP Inv. 834; *Eobuthus rakovnicensis* Frič, holotype NMP Inv. 822; *Feistmantelia ornata* Frič, holotype NMP Inv. 828 (CGH 1981, 1984); *Isobuthus kralupensis* (Thorell and Lindström), holotype NMP Inv. 837; *Microlabis sternbergii* Corda, holotype NMP Inv. 802 (Sternberg Collection No. 583); *Paraisobuthus frici* Kjellesvig-Waering, holotype NMP Inv. 827, paratype NMP Inv. 826, NMP GH 1973 (73).

WEST GERMANY:

Geol.-Paleo. Inst. und Museum, Georg-August Universität, Göttingen

Liassoscorpionides schmidti Bode, holotype GUM 525-1.

Inst. für Paläontologie, Friedrich-Wilhelm Universität, Bonn

Palaeoscorpius devonicus Lehmann, holotype FWU Egr 263.

Natur-Museum und Forschungs-Inst., Senckenberg, Frankfurt-am-Main

Waeringoscorpio hefteri Størmer, holotype SMF VIII 31.

Staatliches Museum für Naturkunde, Stuttgart

Mioscorpio zeuneri (Hadži), holotype and paratypes SMN unnumbered specimens.

SWEDEN:

Riksmuséet, Stockholm

Palaeophonus nuncius Thorell and Lindström, holotype SRM Ar. 32235, topotypes SRM Ar. 31591, Ar. 31818, Ar. 32242, Ar. 32243, Ar. 32067, Ar. 32236, Ar. 32244, Ar. 32270.

U.S.S.R.:

Paleontological Institute, Academy of Sciences, Leningrad

Cyclophthalmus (?) *sibiricus* Novojilov and Størmer, holotype LAS 638/1.

REFERENCES CITED

Baldwin, W., and Sutcliffe, W. H.

1904. Eoscorpius sparthensis *n. sp. from the Middle Coal Measures of Lancashire.* Q. J., Geol. Soc., London, vol. 60, pp. 395–398.

Bather, F. A.

1911. *The holotypes of fossil scorpions* Palaeomachus anglicus *and* Palaeophonus caledonicus. Ann. Mag. Nat. Hist. (8), vol. 8, pp. 673–677.

Birula, A. B.

1917. *Arachnoidea Arthrogastra Caucasica, pars 1, Scorpiones.* Mus. Caucase Tiflis, Mém., ser. A, No. 5. iv + 153 + VIII pp., 3 tables, 16 text-figs.[49]

Bode, A.

1951. *Ein liassischer Scorpionide.* Palaeon. Zeitschr., vol. 24, pp. 58–65, 1 fig.

Brauer, F., Redtenbacher, J., and Ganglbauer, L.

1889. *Fossile Insekten aus der Juraformation Ost-Siberiens.* Mém. de l'Acad. Imp. des Sci. de St. Pétersbourgh, VII sér., vol. 36, No. 15, ? pp., 2 pls.

Carroll, R. L., Belt, E. S., Dineley, D. L., Baird, D., and McGregor, D. C.

1972. *Vertebrate paleontology of Eastern Canada.* Guideb., Excursion A59, 24th Int. Geol. Congr., Montréal, pp. 1–113.

Caster, K. E., and Kjellesvig-Waering, E. N.

1964. *Upper Ordovician eurypterids of Ohio.* Paleontogr. Am., vol. 4, No. 32, pp. 297–358, pls. 43–53, text-figs. 1–33.

Clarke, J. M., and Ruedemann, R.

1912. *The Eurypterida of New York.* New York State Mus., Mem. 14, 2 vols. Vol 1, Text, 439 pp., 121 text-figs. Bibliography. Vol. 2, pp. 441–628, 88 pls.

Cloudsley-Thompson, J. L.

1962a. *Microclimates and the distribution of terrestrial arthropods.* Ann. Rev. Ent. (7), pp. 199–222.

1962b. *Some aspects of physiology of* Buthotus minax *(Scorpiones: Buthidae) with remarks on other African scorpions.* Ent. Mon. Mag. (98), pp. 243–246, figs. 1–2.

Copeland, M. J.

1957. *The Arthropod fauna of the Upper Carboniferous rocks of the Maritime Provinces.* Mem. Geol. Surv. Canada 286, pp. 1–110, pls. 1–21, figs. 1–2.

Corda, A. J. C.

1835. *Ueber den in der Steinkohlenformation bei Chomle gefundeden fossilen Scorpion.* Verhl. Gesell. Vaterl. Museums Böhmen, Prag, p. 36.

1839. *Ueber eine fossile Gattung der Afterscorpione.* Verhl. Gesell. Vaterl. Museums Böhmen, Prag, pp. 14–18, 1 pl., figs. 1–9.

Dubinin, W.

1962. *Handbook of the palaeontology and geology of the U.S.S.R., part Scorpionida.* Vol. 4, pp. 423–433, figs. 1220–1260.

Elias, M. K.

1936. *Character and significance of the late Paleozoic flora of Garnett, Kansas.* J. Geol., vol. 44, pp. 9–23.

1937. *A new scorpion from the Pennsylvanian Walchia beds near Garnett, Kansas.* J. Paleontol., vol. 11, pp. 335–336.

Frič [Fritsch], A.

1873. *Fauna der Steinkohlenformation Böhmens.* Archiv für Landesdurchforschung, vol. 2, Pt. 2, 16 pp., 4 pls.

1902. *Notizen ueber die Arachniden der Steinkohlenformation.* Zool. Anz., vol. 25, pp. 483–484.

1904. *Palaeozoische Arachniden (Scorpionida part).* Prag, pp. 63–83. pls. 7–12, text-figs. 78–99.

1907. *Miscellanea Palaeontologica. I. Palaeozoica.* Prag, 23 pp., 12 pls., 4 text-figs.

Gall, J.-C.

1971. [MS] *Faunes et paysages du Grès à Voltziá du Nord des Vosges. Essai paléoécologique sur le Buntsandstein supérieur.* Doctoral thesis, l'Université Louis Pasteur de Strasbourg.

Grabau, A. W.

1928. *Stratigraphy of China, pt. 2, Mesozoic.* 774 pp., pls. 7–10, text-figs. 307–755.

Grabau, A. W., and Shimer, H. W.

1910. *North American index fossils.* 2 vols., 909 pp., 1937 figs.

Hadži, J.

1931. *Skorpionenreste aus dem tertiären Sprudelsinter von Böttingen (Schwäbische Alb).* Pal. Zeit., Berlin, vol. 13, Nos. 1–2, pp. 134–148, 8 text-figs.

Handlirsch, A.

1906–1908. *Fossilen Insekten und die Phylogenie der rezenten Formen.* Leipzig, pp. i–vi, 1–1430.

Harrington, H. J.

1959. *General description of trilobites,* in *Treatise on invertebrate paleontology, Part O, Arthropoda I.* Geol. Soc. Am. and Univ. Kansas Press, pp. O38–O117.

Harrington, H. J., Moore, R. C., and Stubblefield, C. J.

1959. *Morphological terms applied to trilobites,* in *Treatise on invertebrate paleontology, Part O, Arthropoda I.* Geol. Soc. Am. and Univ. Kansas Press, pp. 117–126.

Hessler, R. R.

1969. *Arthropoda 4,* in *Treatise on invertebrate paleontology, Part R.* Geol. Soc. Am. and Univ. Kansas Press, vol. 1, p. 393.

[49] Translated from Russian to English (1965) by the Israel Program for Scientific Translations [N. Y. Nasonov, ed.]. In the English translation, which Kjellesvig-Waering evidently used, there are 154 pp., 3 pls., 21 figs. A.S.C.

Heubusch, C. A.
1962. *Preservation of the intestine in three specimens of* Eurypterus. J. Paleontol., vol. 36, pp. 222–224, pl. 39.
Hoffmann, C. C.
1931. *Monografias para la entomologia medica de Mexico, No. 2. Los scorpiones de Mexico. Primera parte: Diplocentridae, Chactidae, Vejovidae.* An. Inst. Biol. Mexico, vol. 2, No. 4, pp. 291–408, 43 figs.
Holl, F.
1829. *Handbuch der Petrefactenkunde, 1.* Dresden.
Holm, G.
1896. *Ueber eine neue Bearbeitung des* Eurypterus Fischeri *Eichw.* Acad. Imp. Sci. Bul. St. Pétersbourg (5), vol. 4, No. 4, pp. 369–372.
1897. *Om forekomsten af en* Pterygotus *i Dalarnes Öfversilur.* Geol. För. i Stockholm För., vol. 19, No. 181, pp. 475–478.
1898. *Ueber die Organisation des* Eurypterus Fischeri *Eichw.* Mém. Acad. Imp. Sci. St. Pétersbourg (8), vol. 8, No. 2, pp. 1–57, pls. i–x.
1899. *Palaeontologiska notiser 13. Om den yttre anatomien hos* Eurypterus Fischeri. Geol. För. i Stockholm För. vol. 21, pp. 83–127, pls. 1–4.
Hueber, F. M.
1960. [MS]—*Contribution to the fossil flora of the Onteora Red Beds (Upper Devonian) in New York State.* Ph.D. dissertation, Cornell Univ. (Arachnids are discussed on pp. 1–33 and 166–172.)
Hunter, J. R. S.
1886. *Notes on the discovery of a fossil scorpion (*Palaeophonus caledonicus*) in the Silurian strata of Logan Water.* Trans. Geol. Soc. Glasgow, vol. 8, pp. 169–170.
1888. *Notes on a new fossil scorpion (*Palaeophonus caledonicus*) from the Upper Silurian Shales, Logan Water, Lesmahagow.* Trans. Edinburgh Geol. Soc., vol. 5, pp. 185–191.
Kaestner, A.
1940. *Scorpiones,* in *Handbuch der Zoologie,* Kükenthal and Krumbach, (eds.) vol. 3 (2), pp. 117–240.
1968. *Invertebrate zoology, vol. 2,* translated by Levi and Levi. Intersci. Publs., John Wiley & Sons, New York, 472 pp.
King, W. W.
1934. *The Downtonian and Dittonian strata of Great Britain and Northwestern Europe.* Q. J. Geol. Soc. London, vol. 90, pp. 526–566.
Kingsley, J. S.
1900. *Zittel-Eastman Text-book of Palaeontology, Vol. 1, Malacostraca.* Macmillan and Co., London, New York, pp. 652–669, figs. 1369–1410.
Kjellesvig-Waering, E. N.
1951. *Downtonian (Silurian) Eurypterida from Perton-near-Stoke-Edith, Herefordshire.* Geol. Mag., vol. 88, pp. 1–24.
1954. *Note on a new Silurian (Downtonian) scorpion from Shropshire, England.* J. Paleontol., vol. 28, pp. 485–486, 1 text-fig.
1958a. *Some previously unknown morphological structures of* Carcinosoma newlini *(Claypole).* J. Paleontol., vol. 32, No. 2, pp. 295–303, pls. 41–43, 10 text-figs.
1958b. *The genera, species and subspecies of the family Eurypteridae, Burmeister, 1845.* J. Paleontol., vol. 32, No. 6, pp. 1107–1148, 6 pls., 27 text-figs.
1961. *The Silurian Eurypterida of the Welsh borderland.* J. Paleontol., vol. 35, pp. 789–835, pls. 94–96, 4 text-figs.
1964. *A synopsis of the family Pterygotidae Clarke and Ruedemann, 1912 (Eurypterida).* J. Paleontol., vol. 38, pp. 331–361, pls. 53–56, 26 text-figs.
1966. *Silurian scorpions of New York.* J. Paleontol., vol. 40, pp. 359–375, pls. 42–44, 18 text-figs.
1969. *Scorpionida: holotype of* Mazonia woodiana *Meek and Worthen, 1868.* Field Geol., vol. 12 (8/11), pp. 171–190.
1972. Brontoscorpio anglicus*; a gigantic Lower Paleozoic scorpion from central England.* J. Paleontol., vol. 46, pp. 39–42.
Krogh, A.
1941. *The comparative physiology of respiratory mechanisms.* Dover Publs., 172 pp.
Kušta, J.
1884. *Ein neuer Fundort von* Cyclophthalmus senior *Corda.* Sitz. Ber. K. Böhm. Ges. Wiss., pp. 48 and 401, fig. 4.
1885. *Neue fossile Arthropoden aus dem Noegerathienschiefer von Rakonitz.* Sitz. Ber. K. Böhm. Ges. Wiss., p. 7.
Lankester, E. R.
1881. Limulus*, an arachnid.* Q. J. Micros. Sci., vol. 21, pp. 1–87, 504–548, 609–649.
Laurentiaux-Vieira, F., and Laurentiaux, D.
1963. *Sur quelques restes nouveau d'Arachnides du terrain houiller.* Ann. Soc. Geol. Nord., vol. 83, pp. 23–29, pl. 3, text-figs. 1–4.
Laurie, M.
1899. *On a Silurian scorpion and some additional eurypterid remains from the Pentland Hills.* Trans. Royal Soc. Edinburgh, vol. 39, pt. 3, pp. 575–590, pls. 1–5.
Lawrence, R. F.
1953. *The biology of the cryptic fauna of forests.* A. A. Balkema, Cape Town, Amsterdam, 408 pp., 160 figs.
Leach, W. E.
1815. *A general arrangement of the classes Crustacea, Myriapoda and Arachnides . . . ordo II, Fam. II: Scorpionides.* Linnean Soc. London, Trans., vol. 11, pp. 390–391.
Leary, R. L.
1980. Labriscorpio alliedensis*: a new Carboniferous scorpion from Rock Island County, Illinois.* J. Paleontol., vol. 54, pp. 1255–1257, 1 pl., 2 text-figs.
Lehmann, W. M.
1944. Palaeoscorpius devonicus *n. g., n. sp., ein Skorpion aus dem rheinischen Unterdevon.* Neues Jahrbuch für Paläontologie, Monatsh., pt. B, pp. 177–185, figs. 1–4.
Levi, H. W.
1976. *On the evolution of tracheae in arachnids.* Bull. Brit. Arachnol. Soc. (7) vol. 3, pp. 187–188.
Levi, H. W., and Levi, L. R.
1968. *A guide to the spiders and their kin.* Golden Nature Guide, Golden Press, New York, 160 pp.
Meek, F. B., and Worthen, A. H.
1868a. *Preliminary notice of a scorpion, a* Eurypterus *? and other fossils from the Coal Measures of Illinois and Iowa.* Am. J. Sci. and Arts (2), vol. 45, p. 25.
1868b. *Geol. surv. of Illinois. Vol. 3, Arachnida,* pp. 560–563, figures.
Menge, A.
1869. *Lebenszeichen vorweltlicher, im Bernstein eingeschlossener Thiere.* Oeffentl. Progr. d. Petrischule in Danzig, 1856. Schr. Naturwiss. Gesellsch. Danzig, 2.
Miller, S. A.
1877. *The American Palaeozoic fossils: a catalogue of the genera and species, etc.* Cincinnati, Ohio, 253 pp.
1889. *North American geology and paleontology: Arachnida.* Cincinnati, Ohio, pp. 569–571.
Mitchell, R. W.
1968. Typhlochactas*, a new genus of eyeless cave scorpion, from Mexico (Scorpionida, Chactidae).* Ann. Spéléol., 23(4), pp. 753–777, 1 pl., 41 figs., 2 tabs.

Moore, J. I.
1923. *A review of the present knowledge of fossil scorpions, with the description of a new species from the Pottsville Formation of Clay County, Indiana.* Proc. Ind. Acad. Sci., vol. 38, pp. 125–134, pls. 1–2.

Moore, P. F.
1941. *On gill-like structures in the Eurypterida.* Geol. Mag., vol. 78, pp. 62–70.

Moore, R. C.
1964. *Paleoecological aspects of Kansas Pennsylvanian and Permian cyclothems,* in *Symposium on cyclic sedimentation,* Daniel F. Merriam (ed.), 2 vols., 636 pp., pp. 287–380.

Novojilov, N., and Størmer, L.
1963. *A new scorpion from the Upper Carboniferous of Siberia.* Norsk Geologisk Tidsskrift, vol. 43, pp. 83–87, 2 pls.

Peach, R. N.
1883. *A new species of fossil scorpions from the Carboniferous rocks of Scotland and the English borders, with a review of the genera* Eoscorpius *and* Mazonia *of Messrs. Meek and Worthen.* Trans. Roy. Soc. Edinb., vol. 30, pp. 397–412, pls. 22 and 23.
1885. *Ancient air-breathers.* Nature, vol. 31, pp. 295–298, 2 figs.

Petrunkevitch, A.
1913. *A monograph of the terrestrial Paleozoic Arachnida of North America.* Trans. Conn. Acad. of Arts and Sci., New Haven, vol. 18, pp. 1–137, pls. 1–13, 88 figs.
1949. *A study of Palaeozoic Arachnida.* Trans. Conn. Acad. Arts and Sci., vol. 37, pp. 69–315, figs. 1–271.
1953. *Paleozoic and Mesozoic Arachnida of Europe.* Mem. Geol. Soc. Am., vol. 53, 128 pp., 58 pls.
1955. *Arachnida,* in *Treatise on invertebrate paleontology, Part P.* Geol. Soc. Am. & Univ. Kansas Press, pp. 42–162, figs. 31–116.

Pocock, R. I.
1901. *The Scottish Silurian scorpions.* Q. J. Microsc. Sci., (2), vol. 44, pp. 291–311, pl. 19, text-figs. 1–3.
1911. *A monograph of the terrestrial Carboniferous Arachnida of Great Britain.* Palaeontogr. Soc., London, vol. 64, 84 pp., 3 pls., 42 text-figs.

Rolfe, W. D. I.
1963. Eoscorpius inflatus *Peach, 1882 (Arachnida): proposed suppression under the plenary powers, Z.N.(S.) 1588.* Bull. Zool. Nomencl., vol. 20, pt. 5, pp. 388–389.
1969. *Arthropoda — Incertae Sedis,* in *Treatise on invertebrate paleontology, Part R(2).* Geol. Soc. Am. & Univ. Kansas Press, pp. 620–625, fig.
1980. *Early invertebrate terrestrial faunas,* in *The terrestrial environment and the origin of land vertebrates,* A. L. Panchen (ed.), Academic Press, London and New York, pp. 117–157.
1982. *Ancient air breathers.* Bull. Field Mus. Nat. Hist. 53, pp. 12–16.

Ruedemann, R.
1919. *Preservation of alimentary canal in an Eurypterid.* Paleontologic Contributions from the New York State Museum. N.Y. State Mus. Bull. 227–228, pp. 92–95, figs. 33–35.

Salter, J. W.
1859. *On some new species of* Eurypterus*; with notes on the distribution of species.* Q. J. Geol. Soc., London, vol. 15, pp. 230–236.

Schawaller, W.
1979. *First record of a scorpion from Dominican Amber.* Stuttgarter Beitr. Naturk., Ser. B, No. 45, 15 pp., 8 figs.
1982. *Two further scorpions in Dominican Amber.* Stuttgarter Beit. Naturk., Ser. B, No. 82, 14 pp., 11 figs.

Scudder, S. H.
1884. *A contribution to our knowledge of Palaeozoic Arachnida.* Am. Acad. Arts Sci., Proc., vol. 20, pp. 15–22.
1885. *Arachnoidea, Spinnen, Skorpione,* in *Zittel's Handbuch der Palaeontologie, I Abth.,* vol. 2, pp. 732–746, figs. 906–928.
1886. *Systematic review of our present knowledge of fossil insects, myriapods and arachnids.* U.S. Geol. Surv. Bull. 31, 128 pp.

Shimer, H. W., and Shrock, R. R.
1944. *Index fossils of North America,* John Wiley and Sons, New York, 837 pp., 303 pls.

Størmer, L.
1934. *Eurypterid remains from the Ludlow zone 9d (Silurian) of Ringerike.* Norsk. Geol. Tidsskr., Bd. 14, H. 1–2, pp. 119–126, 3 figs.
1954. *New discoveries of ostracoderms and eurypterids at Ringerike, near Oslo.* Proc. Geol. Soc. London, No. 1505, pp. 21–22.
1955. *Chelicerata and Merostomata,* in *Treatise on invertebrate paleontology,* Geol. Soc. Am. & Univ. Kansas Press, Part P, pp. 1–41.
1960. *A scorpion-like eurypterid from the Lower Devonian of Germany.* Proc. International Paleontological Union; Rpt. of 21st Session, Norden, Copenhagen, pt. 22, pp. 87–91, 2 figs.
1963. Gigantoscorpio willsi*, a new scorpion from the Lower Carboniferous of Scotland and its associated preying microorganisms.* Skr. Norske Vid.-Akad. Oslo: Mat.-Naturv., Kl., Ny Ser., No. 8, 171 pp., 22 pls., 45 text-figs.
1969. *Eurypterids from the Lower Devonian of Willwerath, Eifel.* Senck. Lethaea, vol. 50, No. 1, pp. 21–35, 2 pls., 2 text-figs. Frankfurt-am-Main.
1970. *Arthropods from the Lower Devonian (Lower Emsian) of Alken an der Mosel, Germany, Part 1: Arachnida.* Senck. Lethaea, vol. 51 (4), pp. 335–369, 5 pls., 8 text-figs. Frankfurt-am-Main.
1976. *Arthropods from the Lower Devonian (Lower Emsian) of Alken an der Mosel, Germany. Part 5. Myriapoda and additional forms with general remarks on fauna and problems regarding invasion of land by arthropods.* Senck. Lethaea, vol. 57 (2/3), pp. 87–183, 10 pls., 107 text-figs., 2 tabs. Frankfurt-am-Main.

Stumm, E. C., and Kjellesvig-Waering, E. N.
1962. *A new eurypterid from the Upper Silurian of Southern Michigan.* Univ. Michigan Contr. Pal. Mus., vol. 17, No. 7, pp. 195–204, 1 pl., 1 fig.

Thorell, T.
1886. *On* Proscorpius osborni *Whitfield.* Am. Naturalist, vol. 20, pp. 269–270.

Thorell, T., and Lindström, G.
1884a. [*Note*] Acad. des Sciences de Paris, C.R., vol. 99, p. 984, (1 Dec. 1884).
1884b. *Discovery of a Silurian fossil scorpion.* The Glasgow Herald, Dec. 19, 1884.
1885. *On a Silurian scorpion from Gotland.* Kongl. Sv. Vet. Akad. Handl., vol. 21, No. 9, pp. 1–33, pl.

Vachon, M.
1963. *De l'utilité en systématique d'une nomenclature des dents des chélicères chez les scorpions.* Bull. Mus. Hist. Nat., 2 sér., vol. 35 (2), pp. 161–166, 9 figs.

Versluys, J., and Demoll, R.
1923. *Das Limulus-Problem. Die Verwandtschaftsbeziehungen der Merostomen und Arachnoiden unter sich und mit anderen Anthropoden.* Ergebn. u. Fortschr. d. Zoologie, 5, pp. 67–388.

Vogel, B. R., and Durden, C. J.
1966. *The occurrence of stigmata in a Carboniferous scorpion.* J. Paleontol., vol. 40, pp. 655–658, pl. 81, figs. 1, 2.

Waterston, C. D.
1975. *Gill structures in the Lower Devonian eurypterid* Tarsopterella scotica. Fossils and Strata, No. 4, pp. 241–254, pls. 1–2, 4 text-figs.

Werner, F.
1934. *Scorpiones,* in *Dr. H. G. Bronns: Klassen und Ordnungen,* vol. 5, pp. 1–316, text-figs. 1–289.

Whitfield, R. P.
1885a. *An American Silurian scorpion (*Palaeophonus osborni*).* Science, vol. 6, p. 87, fig.
1885b. *On a fossil scorpion from the Silurian rocks of America.* Bull. Am. Mus. Nat. Hist., vol. 1, No. 6, art. 9, pp. 181–190, pls. 19–20, 2 text-figs.
1886. *Professor Thorell and the American Silurian scorpion.* Science, vol. 7, pp. 216–217.

Wills, L. J.
1910. *On the fossiliferous Lower Keuper rocks of Worcestershire, with description of some of the plants and animals discovered therein.* Proc. Geol. Ass. London, vol. 21, pt. 5, pp. 249–331, pls. 10–26.
1925. *The morphology of the Carboniferous scorpion* Eobuthus *Fritsch.* J. Linnean Soc. Zool. London, vol. 36, pp. 87–98, pl. 3, text-figs. 1–3.
1934. *Notes on a rare Carboniferous scorpion from the Oranje Nassau Mine No. III.* Jaarverlag Geol. Bur. Nederlands, pp. 101–103, pl.
1947. *A monograph of the British Triassic scorpions.* Palaeontogr. Soc. London, vols. 100 and 101, 137 pp., 12 pls., 53 text-figs.
1959. *The external anatomy of some Carboniferous "scorpions", Part 1.* Palaeontology, vol. 1, pt. 4, pp. 261–282, pls. 49–50, figs. 1–8.
1960. *The external anatomy of some Carboniferous "scorpions", Part 2.* Palaeontology, vol. 3, pt. 3, pp. 276–332, pls. 46–57.
1964. *The ventral anatomy of the Upper Carboniferous eurypterid* Anthraconectes *Meek and Worthen.* Palaeontology, vol. 7, pt. 3, pp. 474–507, pls. 77–79, 11 text-figs.
1965. *A supplement to Gerhard Holm's "Ueber die Organisation des* Eurypterus Fischeri *Eichw." with special reference to the organs of sight, respiration and reproduction.* Arkiv fö Zoologi, ser. 2, vol. 18, No. 8, pp. 93–145, 8 pls., 19 text-figs.

Woodward, H.
1871. *On the remains of a giant isopod* Praearcturus gigas *(H. Woodward) from the Old Red Sandstone of Rowlestone Quarry, Hereford.* Trans. Woolhope Field Naturalist's Club, pp. 266–270, 7 text-figs.
1872. *A monograph of the British fossil Crustacea, belonging to the order Merostomata, Part IV (*Stylonurus, Eurypterus *and* Hemiaspis*).* Monographs Palaeontogr. Soc. London, vol. 19, pp. 121–180, pls. 21–30.
1876. *On the discovery of a fossil scorpion in the British Coal Measures.* Q. J. Geol. Soc. London, vol. 32, pp. 57–59, pl. 8.
1877. *Catalogue of the British Fossil Crustacea with their synonyms and the range in time of each genus and order.* British Mus. Nat. Hist., pp. 64–69.
1907. *Further notes on the Arthropoda of the British Coal Measures.* Geol. Mag., London, vol. 4, pp. 539–549.

PLATES

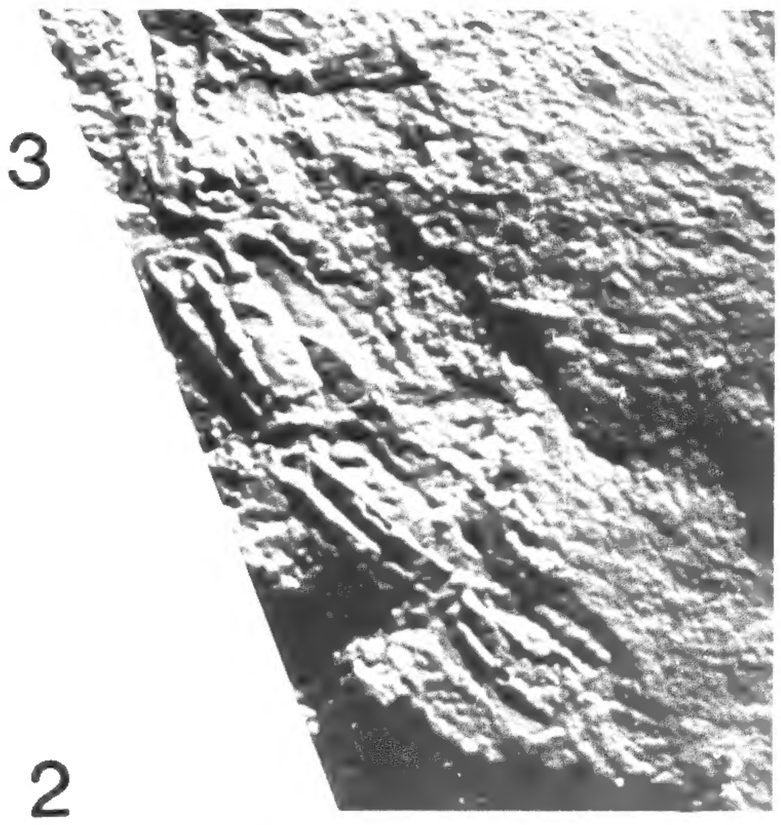
EXPLANATION OF PLATE 1

Page

Proscoprius osborni (Whitfield) 39

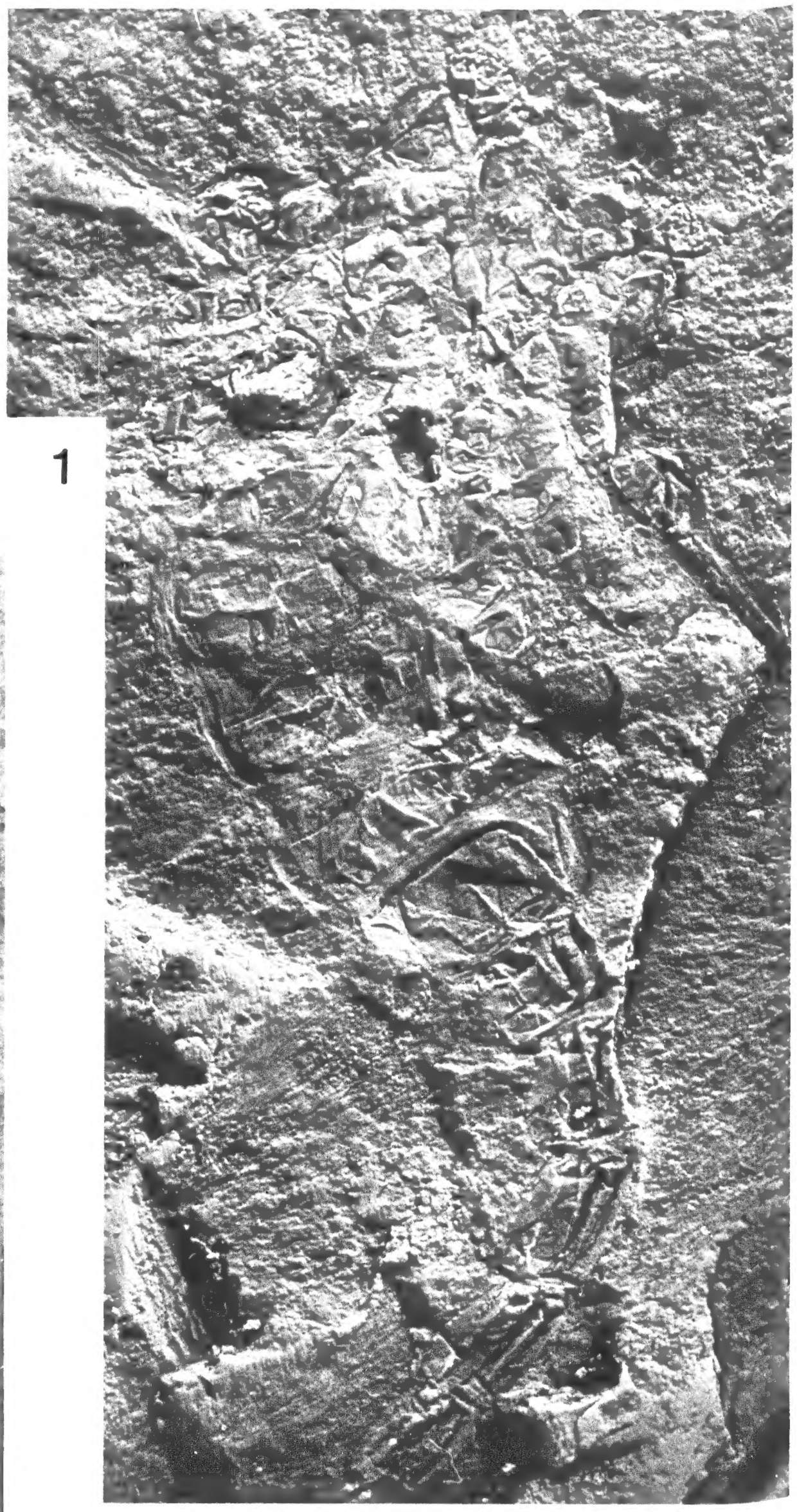
CIURCA 031966-1 [=BMS E 25162]. From the Upper Silurian, Ludlow, in the upper part of the Fiddler's Green Dolomite at Passage Gulf, near Litchfield, New York. ×5.

3

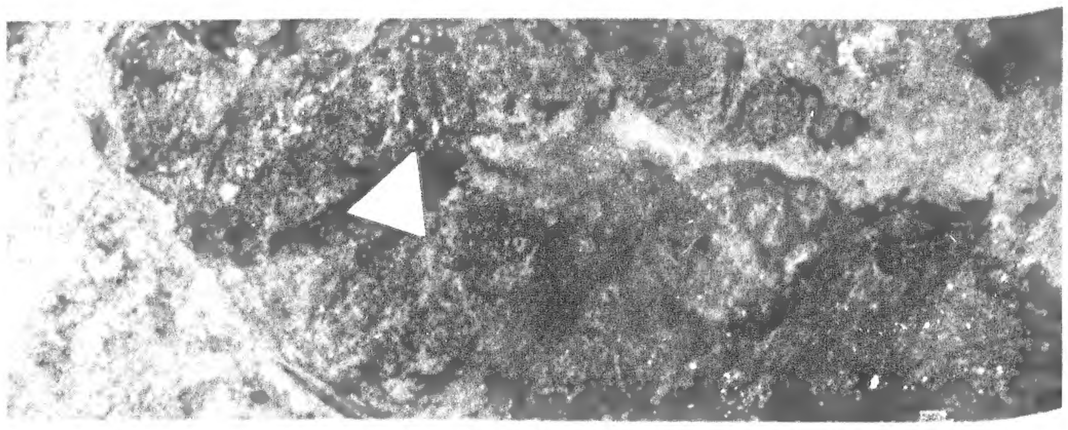


2

1



4



EXPLANATION OF PLATE 2

Figure — Page

1–4. ***Allopaleophonus caledonicus*** (Hunter) 57

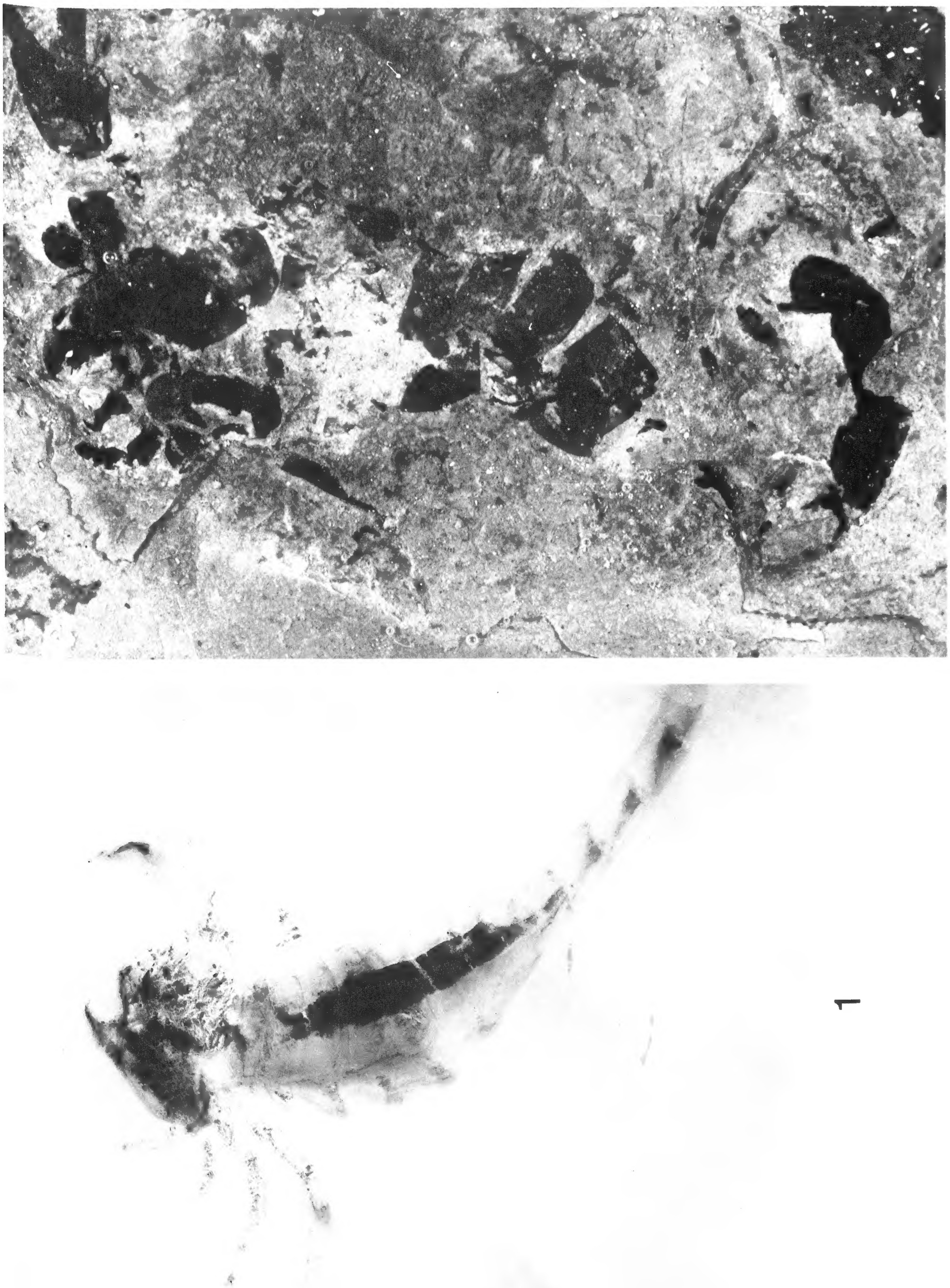
Holotype. KM unnumbered specimen. From the Silurian, Wenlock, Llandovery, at Dunside, Logan Water, Lesmahagow, Scotland (photographs by Ian Rolfe).

1. With light reversed to reveal various outstanding structures. ×5.
2. Immersed in alcohol. ×4.
3. The cauda with the film reversed to reveal the double lateral carinae. ×5.
4. Ventral part of the mesosoma. The arrow points to the peculiar median lobes (bifid plates) of the pectines. ×5.

EXPLANATION OF PLATE 3

Figure — Page

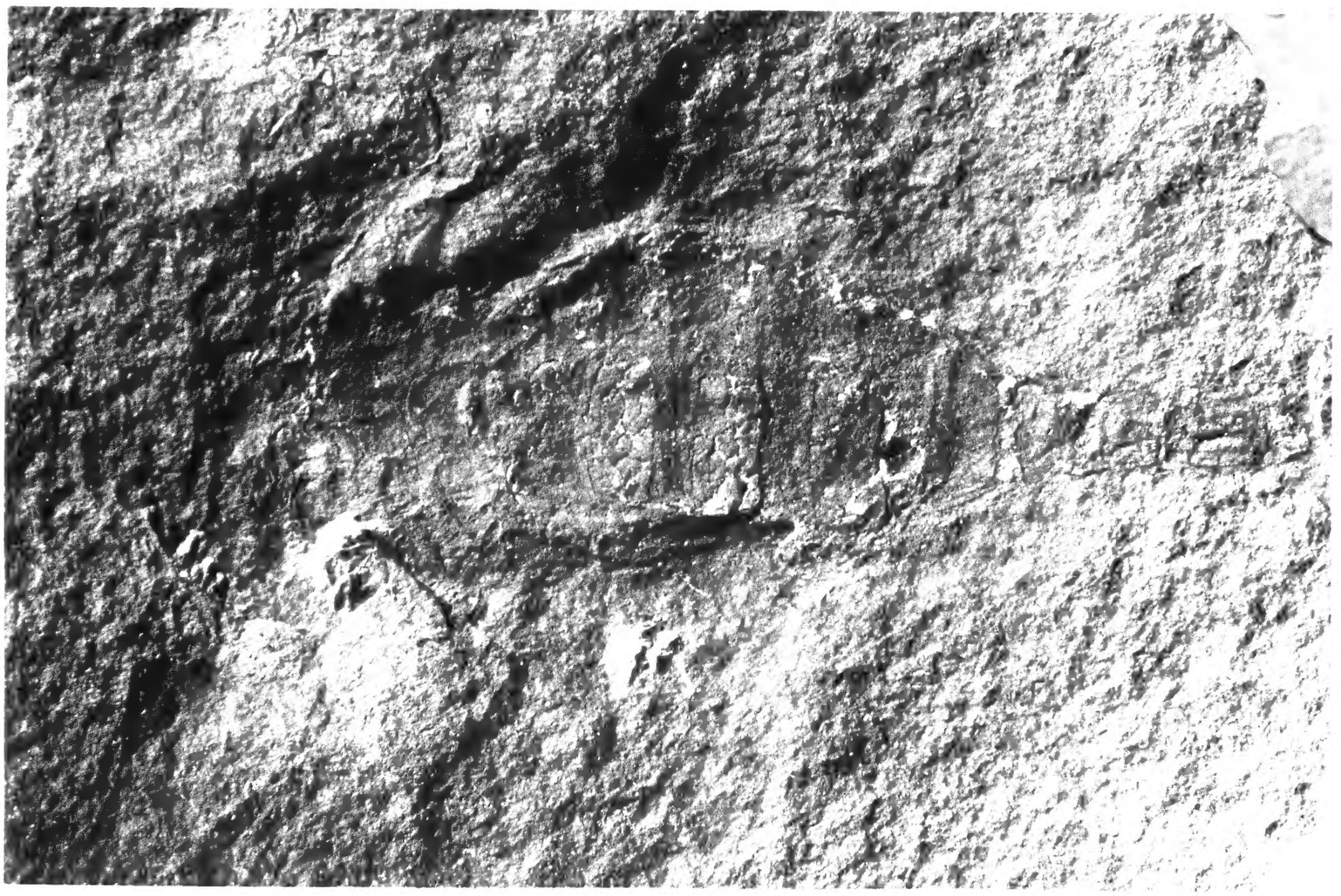
1. ***Palaeoscorpius devonicus*** Lehmann 61
   Holotype (FWV Egr 263). From the Lower Devonian, Hunsrück Shale, Pit I, Eschenbach, near Bundenbach (Hunsrück), West Germany. Natural size.
2. ***Hydroscorpius denisoni***, new genus and species 63
   Holotype (FMNH (PE) 6176). From the Lower Devonian, Beartooth Butte Formation, Cottonwood Canyon, Big Horn Mts., WY, U.S.A. ×4.



2

1

2



1

EXPLANATION OF PLATE 4

Figure — Page

1, 2. ***Eoctonus miniatus*** Petrunkevitch 96

Holotype (YPM 131). From the Pennsylvanian Carbondale Formation, Francis Creek Shale, at Mazon Creek, Grundy Co., IL.

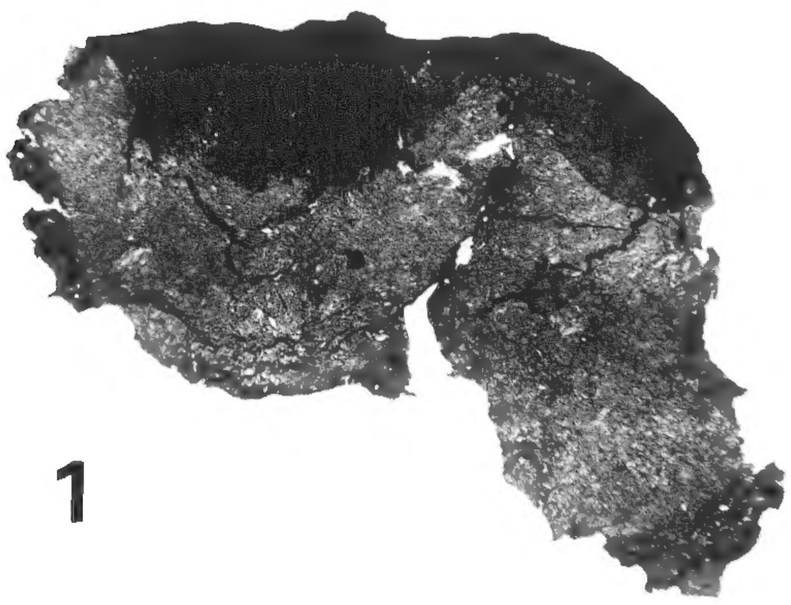
1. Ventral side. ×7.
2. Dorsal side. ×8.

EXPLANATION OF PLATE 5

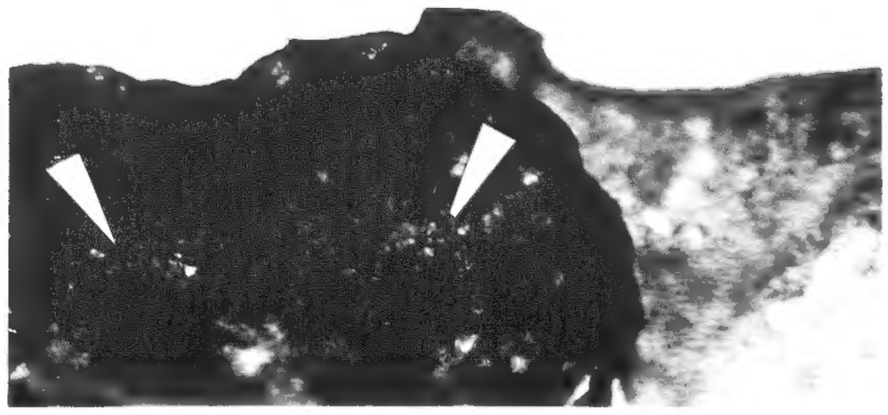
Figure — Page

1–9. ***Tiphoscorpio hueberi***, new genus and species 126
Holotype (USNM 252629). From the lower Upper Devonian (lower Frasnian), lower Onteora Formation at quarry on northwest slope of South Mountain, Schoharie Co., 1.1 mi west of Schoharie Co.–Green Co. line (Livingston 7′30″ map) at 74°16′30″E, 42°23′55″N, NY. Collected by F. M. Hueber.

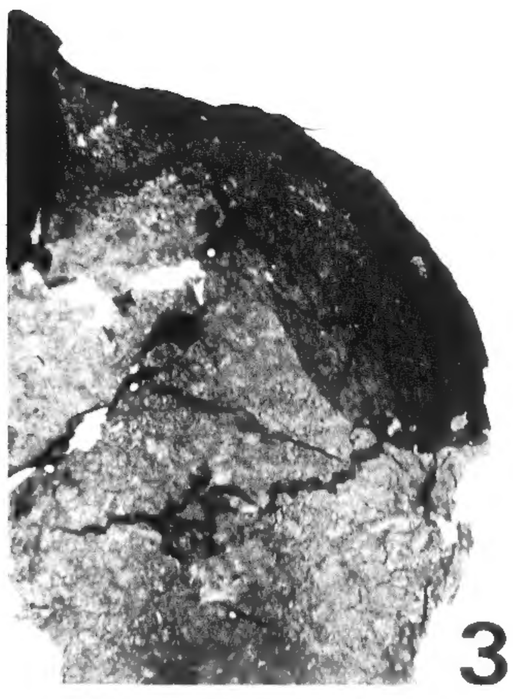
1. The carapace, showing the median eye node, with anterior glossate process turned under, and the lateral, facetted right eye. ×12.
2. The median eye node with the median eye indicated. ×128.
3. The facetted lateral right eye. ×30.
4. The tarsus, with movable spines on the inner edge. ×36.5.
5. The seventh tergite, showing two median carinae and the doublure at the posterior part. ×7.
6. Portion of tergite shown on figure 4, showing setal sites and seta on the site in the middle of the photograph. ×126.
7. Abdominal plate with pore system. ×108.
8. Abdominal plate with setal sites and pore system. ×58.
9. Serrations along inner edge of hand and possibly the chelicera. ×40.



1

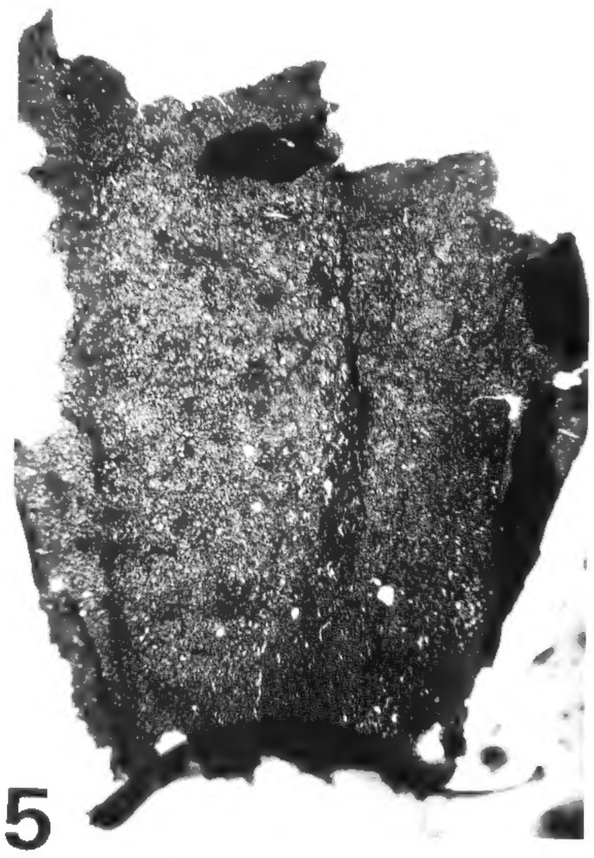


2

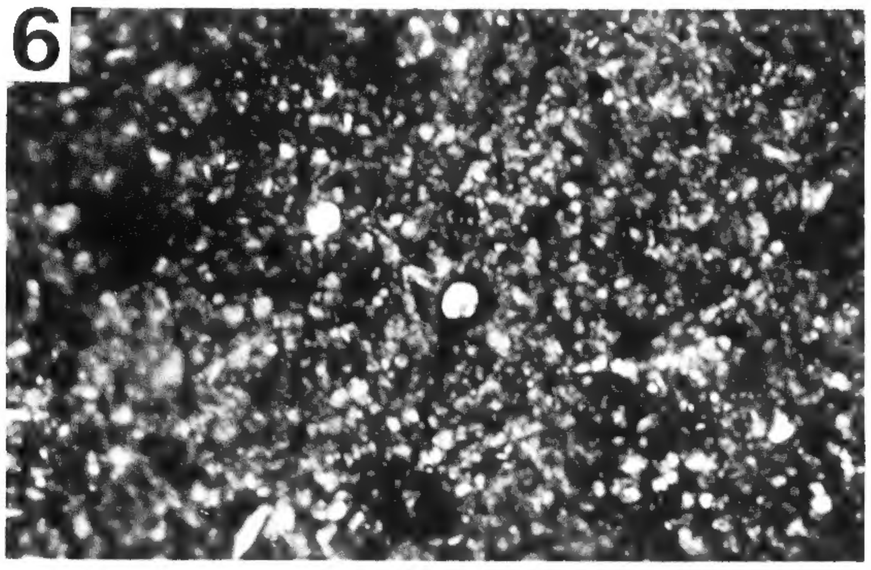


3

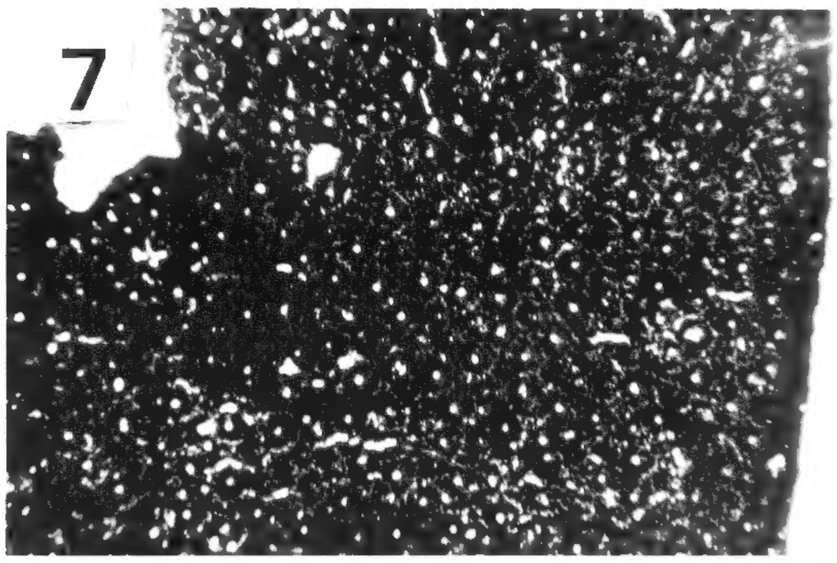
4



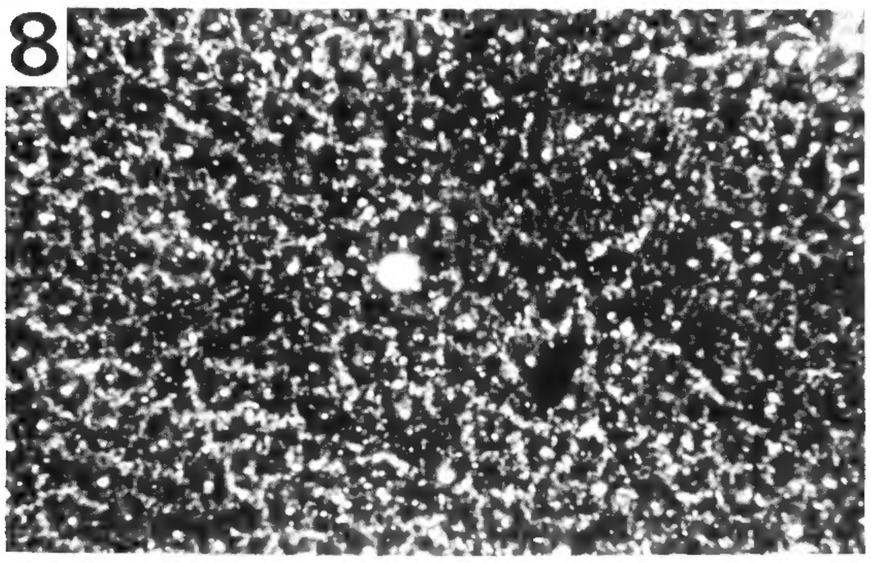
5



6

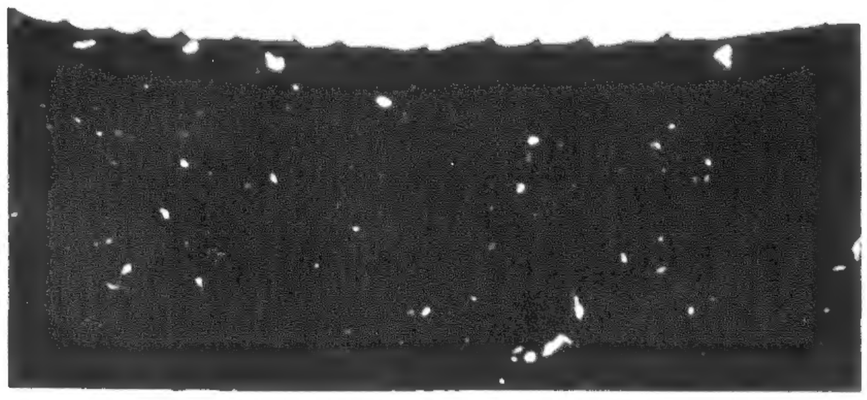


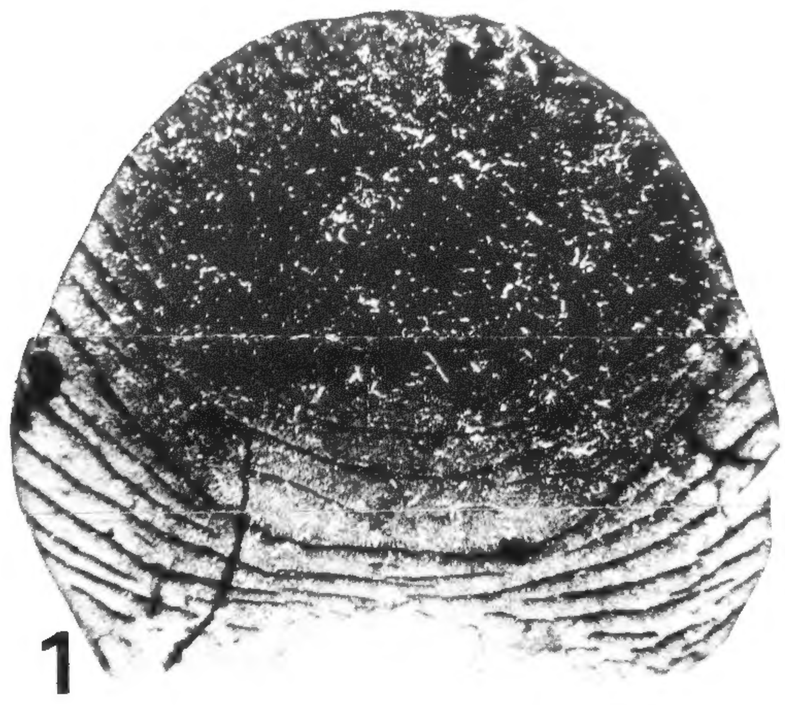
7



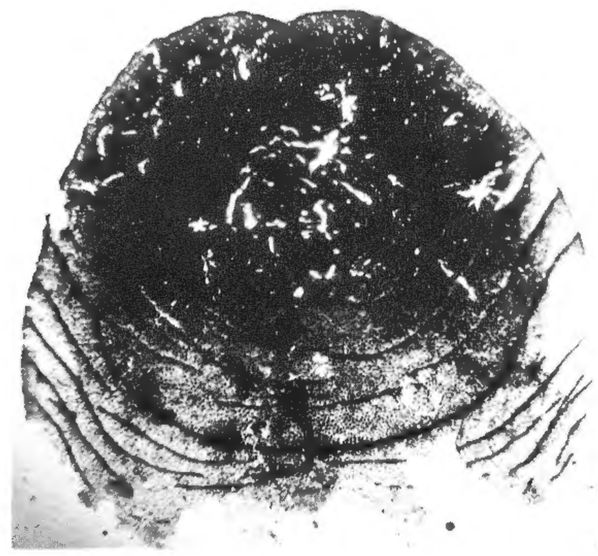
8

9

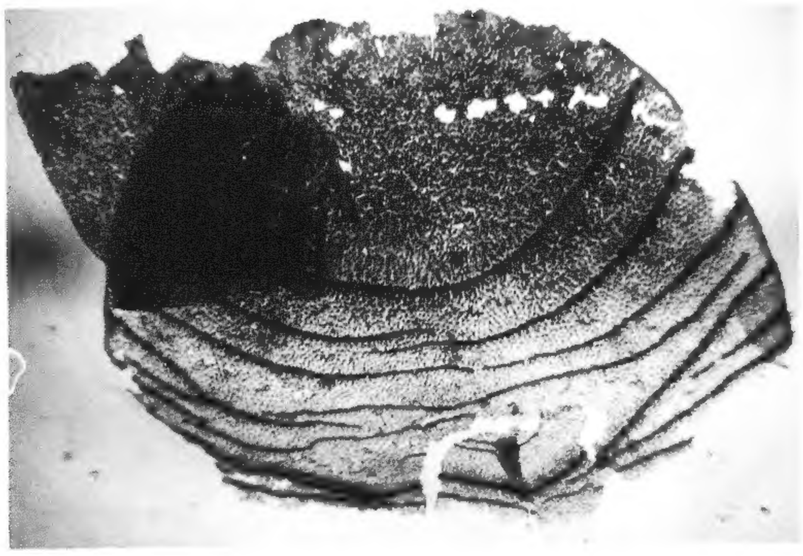




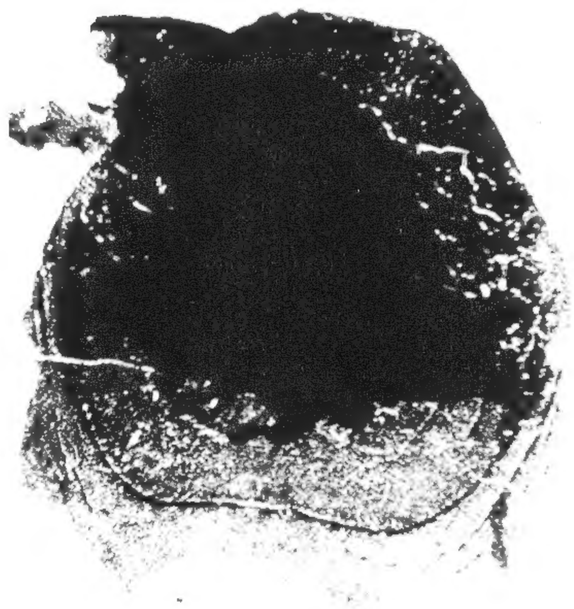
1



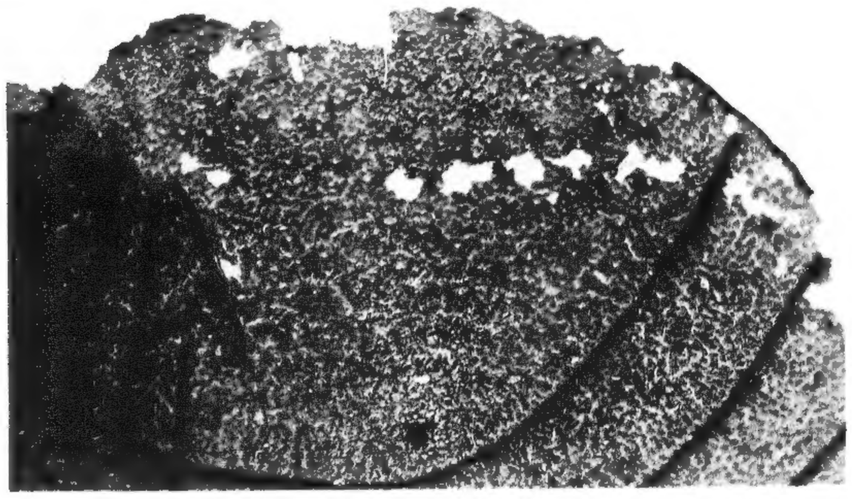
2



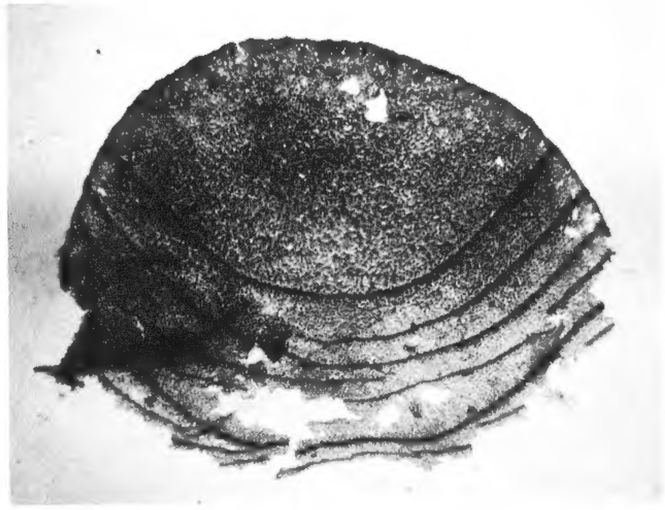
3



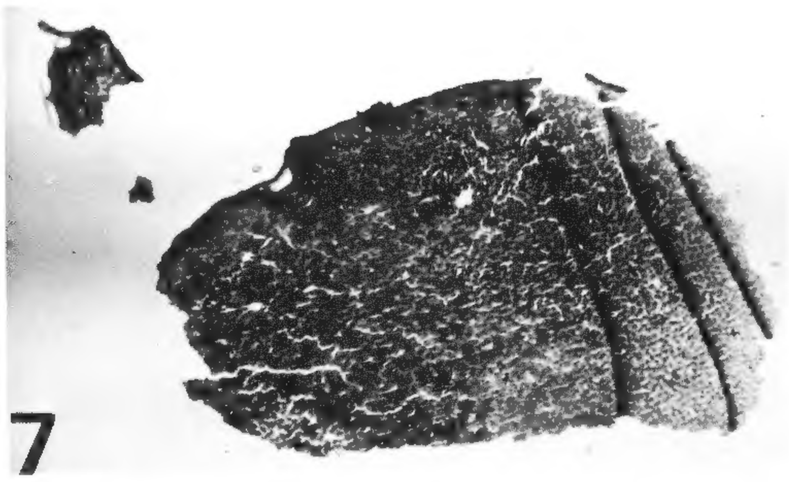
4



5



6



7

8

EXPLANATION OF PLATE 6

Figure

1–8. ***Tiphoscorpio hueberi***, new genus and species 126

Holotype (USNM 252629). From the Upper Devonian, Onteora Formation, at quarry on northwest slope of South Mountain, Schoharie Co., 1.1 mi west of the Schoharie Co.–Green Co. line (Livingston 7′30″ map) at 74°16′30″E, 42°23′55″N, NY. Collected by F. M. Hueber.

1–6. Gills of rounded type. The rounded end is considered to be the part facing the open posterior of the abdominal plate. Figures 1–4, ×72; figure 5, ×100; figure 6, ×72. Note small triangular spines pointing toward the round end.

7. Gill of the rectangular type. The hole at the anterior is where a large spine was located. ×48.

8. Gill of the rounded type with part of an irregular type gill with fringe of small spines. Setal sites are plainly visible. ×100.

EXPLANATION OF PLATE 7

Figure — Page

1–7. ***Tiphoscorpio hueberi***, new genus and species 126

From the Upper Devonian (lower Frasnian), lower Onteora Formation at quarry at northwest slope of South Mountain, Schoharie Co., 1.1 mi west of Schoharie Co.–Green Co. line (Livingston 7′30″ map) at 74°16′30″E, 42°23′55″N, NY. Collected by F. M. Hueber.

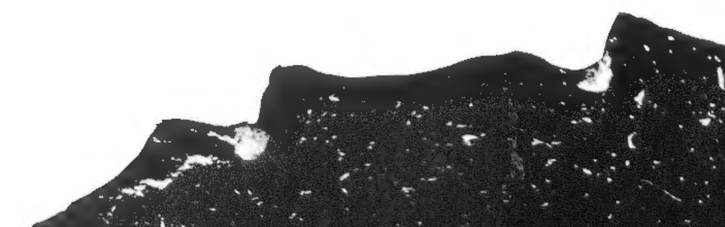
1. Paratype (USNM 252630). Gill of the rectangular type. Fine setal sites are seen as small holes. The large openings are the sites for large spines as seen in figures 3, 6, 7. ×47.

2, 3. Holotype (USNM 252629). Posterior end of gill of the rectangular type showing large spines on the anterior edge. ×37 and ×200, respectively.

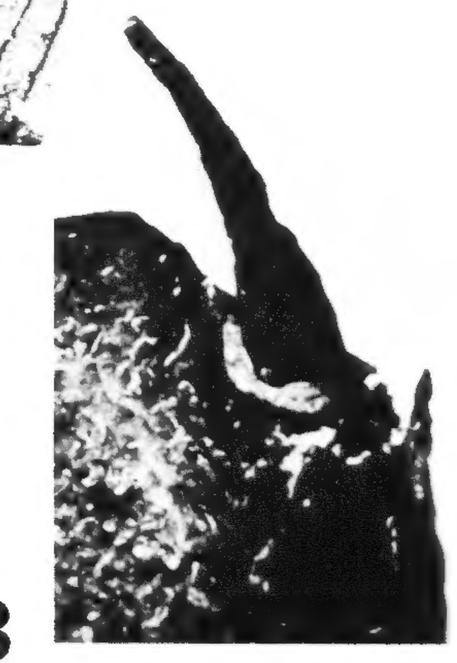
4, 5. Holotype (USNM 252629). Gills of the rectangular type with attached gills which are too incomplete to identify. ×48.

6, 7. Holotype (USNM 252629). Gills of the rectangular and irregular types. ×37 and ×72, respectively.

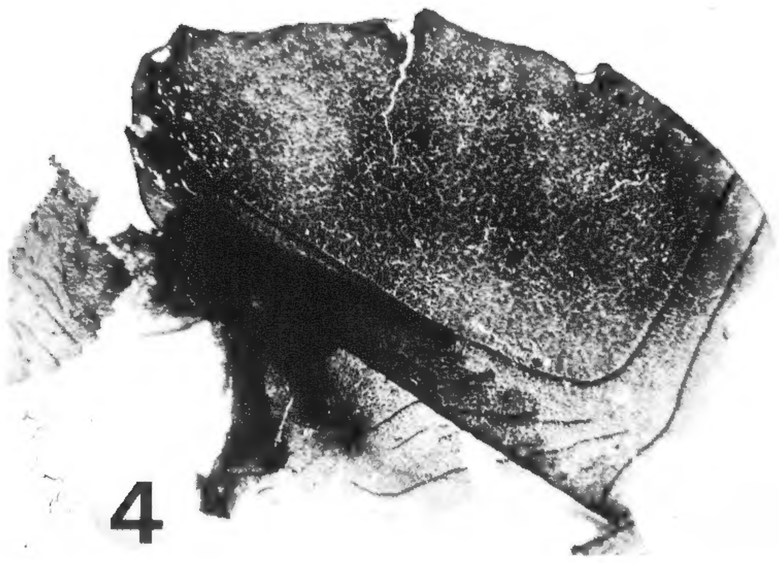
1



2



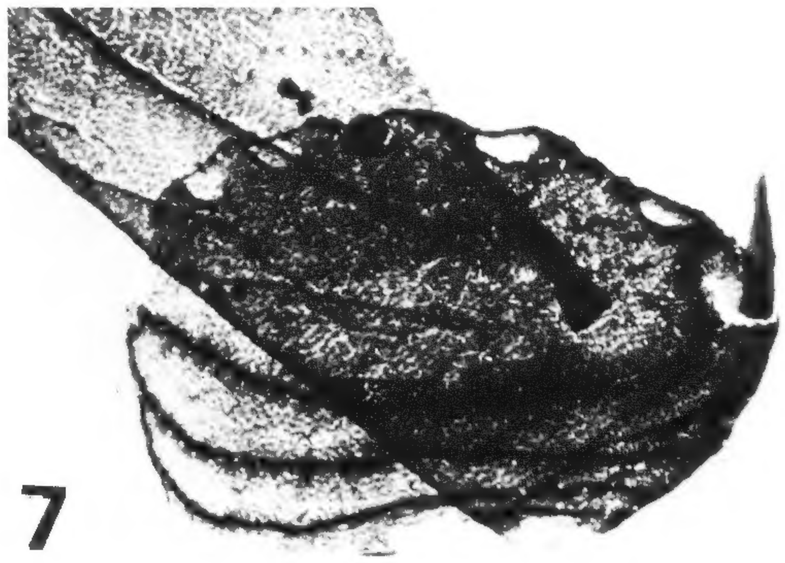
3



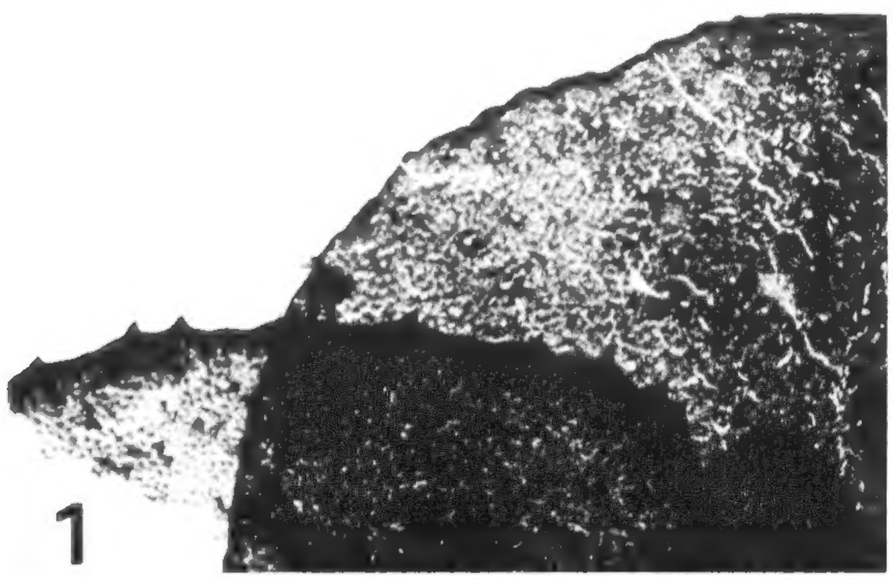
4

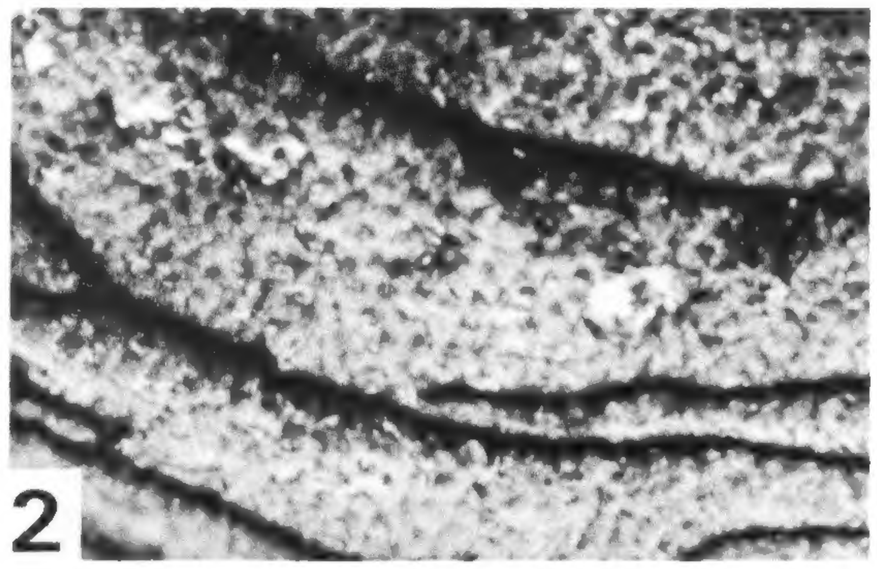
5

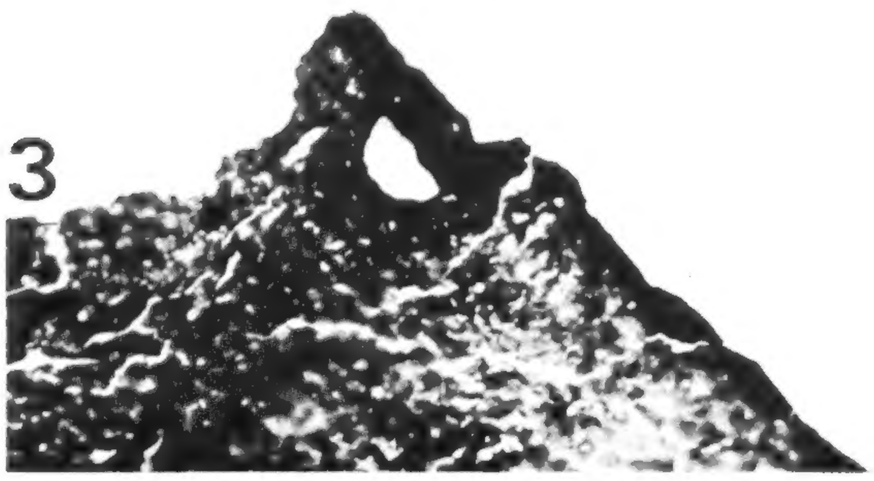
6

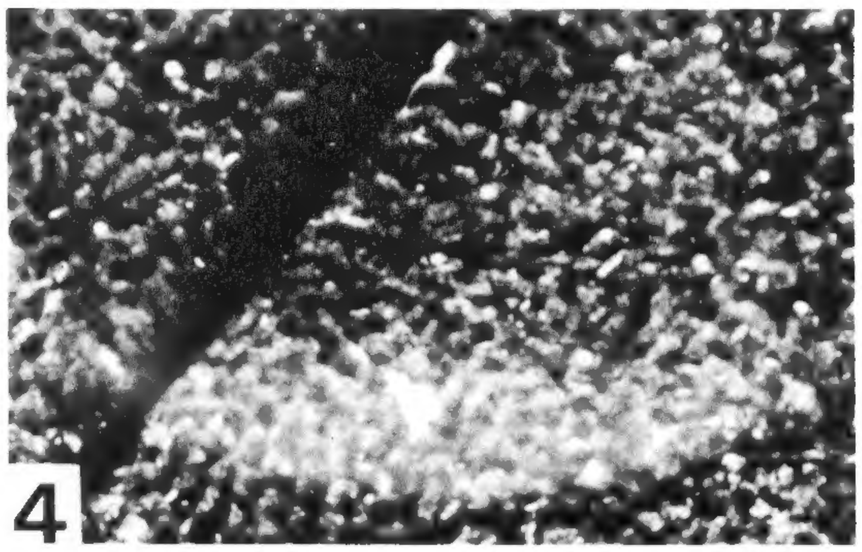


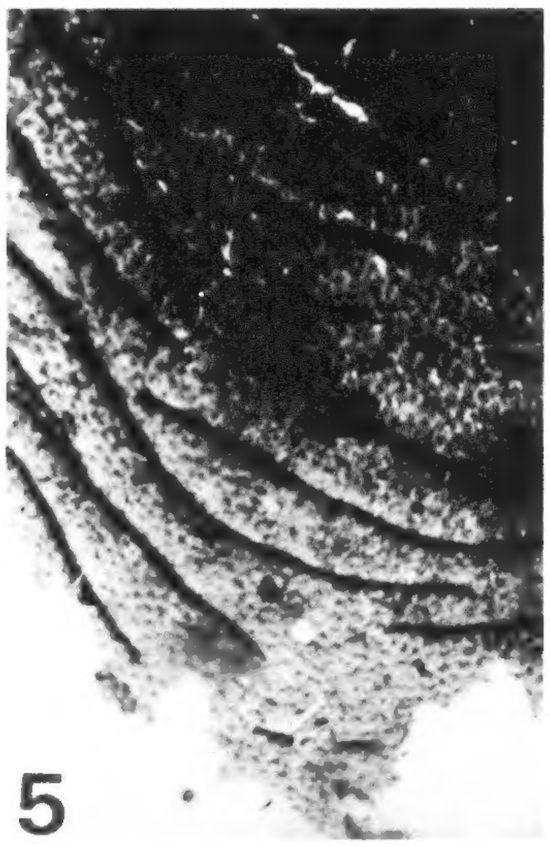
7

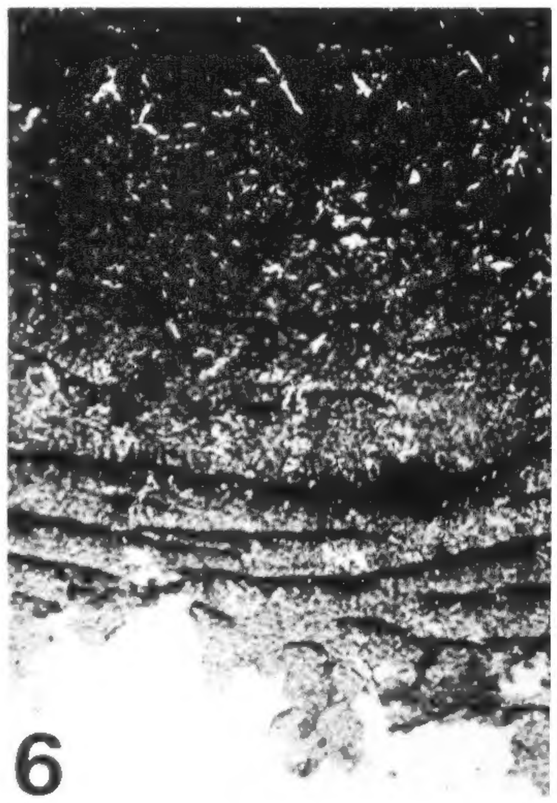

1


2

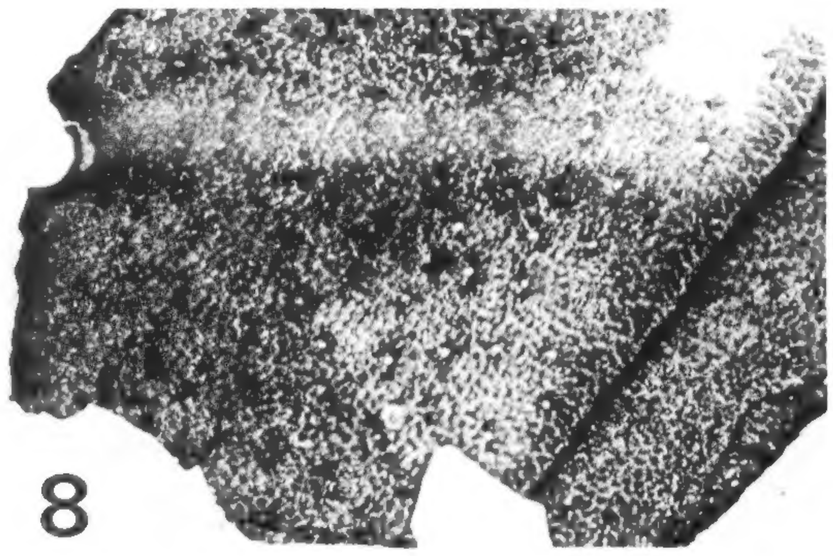

3


4


5


6

7


8

EXPLANATION OF PLATE 8

Figure

1–8. ***Tiphoscorpio hueberi***, new genus and species 126
Holotype (USNM 252629). From the lower Upper Devonian (lower Frasnian), lower Onteora Formation at quarry on northwest slope of South Mountain, Schoharie Co., 1.1 mi west of Schoharie Co.–Green Co. line (Livingston 7′30″ map) at 74°16′30″E, 42°23′55″N, NY. Collected by F. M. Hueber.

1. Serrated edge of irregular type gill associated with round type (see also Pl. 6, fig. 8). ×80.
2. Detail of gill showing the folds and subtriangular spinelets. ×250.
3. Site of one of the large fringe spines of triangular type gill (see also Pl. 7, fig. 2). ×220.
4. Detail of gill with fold and subtriangular spinelets. ×250.

5–7. Enlargement of the concentric folds of gill of the round type (see also Pl. 6, fig. 2). ×180.

8. Enlargement of rectangular type of gill showing the rounded holes and subtriangular spinelets. ×100.

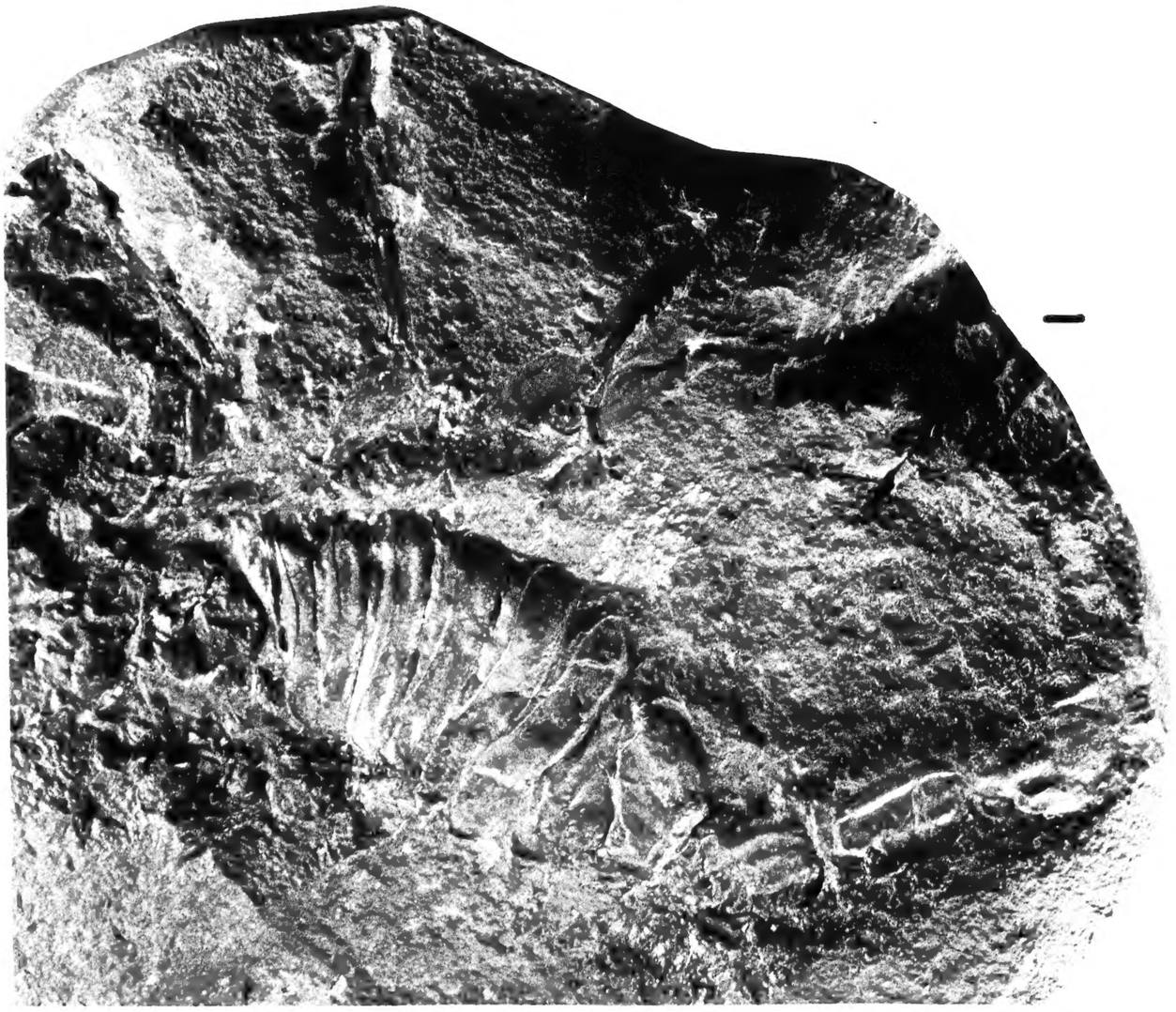
EXPLANATION OF PLATE 9

Page

Palaeophonus nuncius Thorell and Lindström 142

Holotype (SRM Ar. 32235). From the Middle Silurian, Lower Wenlock, top of the Högklintslager beds, at the Vattenfallet, Visby, Gotland, Sweden. ×4.

2



EXPLANATION OF PLATE 10

Figure — Page

1, 2. ***Eoscorpius carbonarius*** Meek and Worthen 163

Holotype (FMNH (UC) 8949). From the Pennsylvanian Carbondale Formation, lower Francis Creek Shale, Mazon Creek, Grundy Co., IL.

1. Obverse of the concretion. ×2.
2. Reverse of the concretion. ×2.

EXPLANATION OF PLATE 11

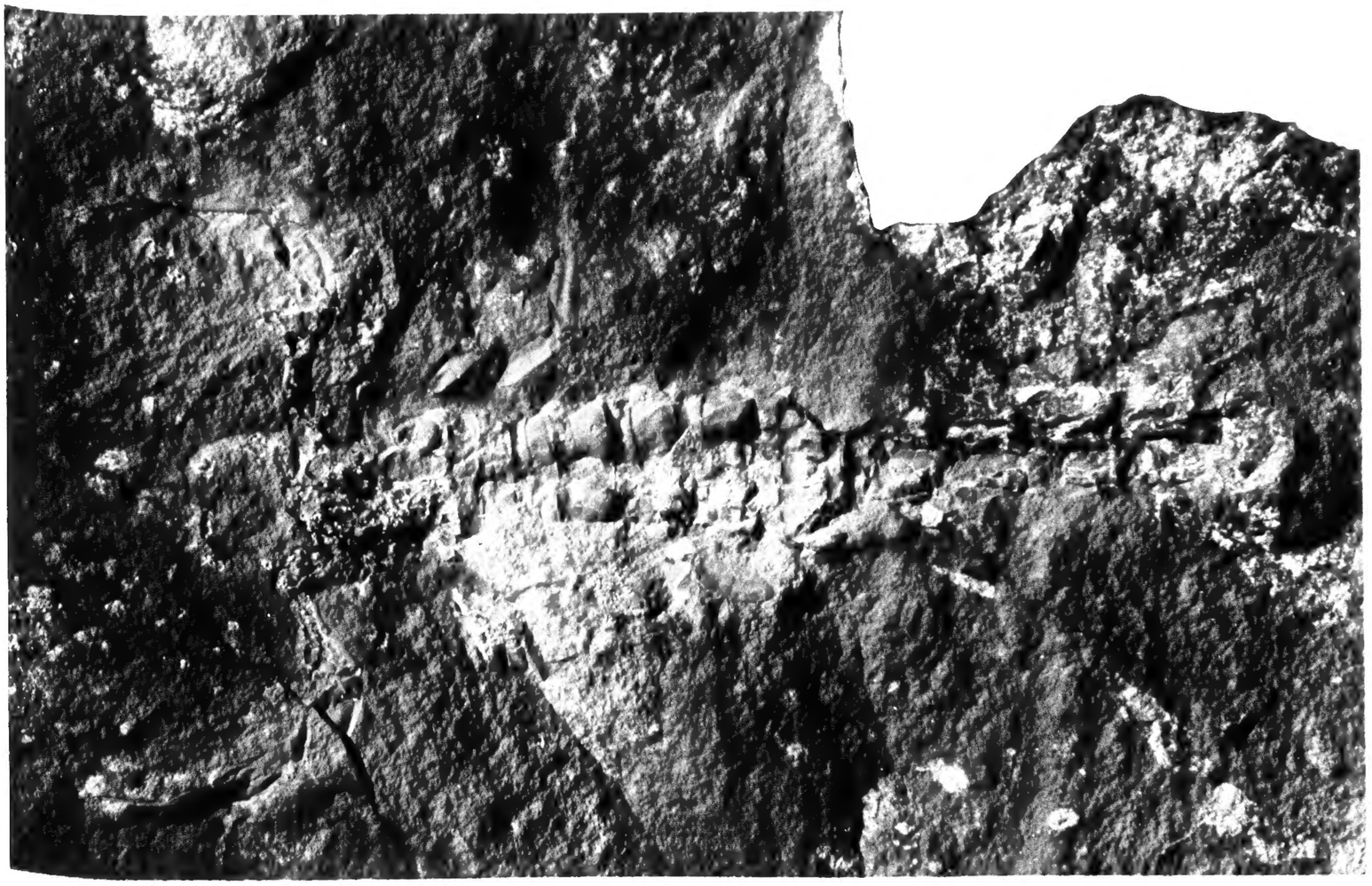
Figure — Page

1, 2. ***Eoscorpius carbonarius*** Meek and Worthen 163

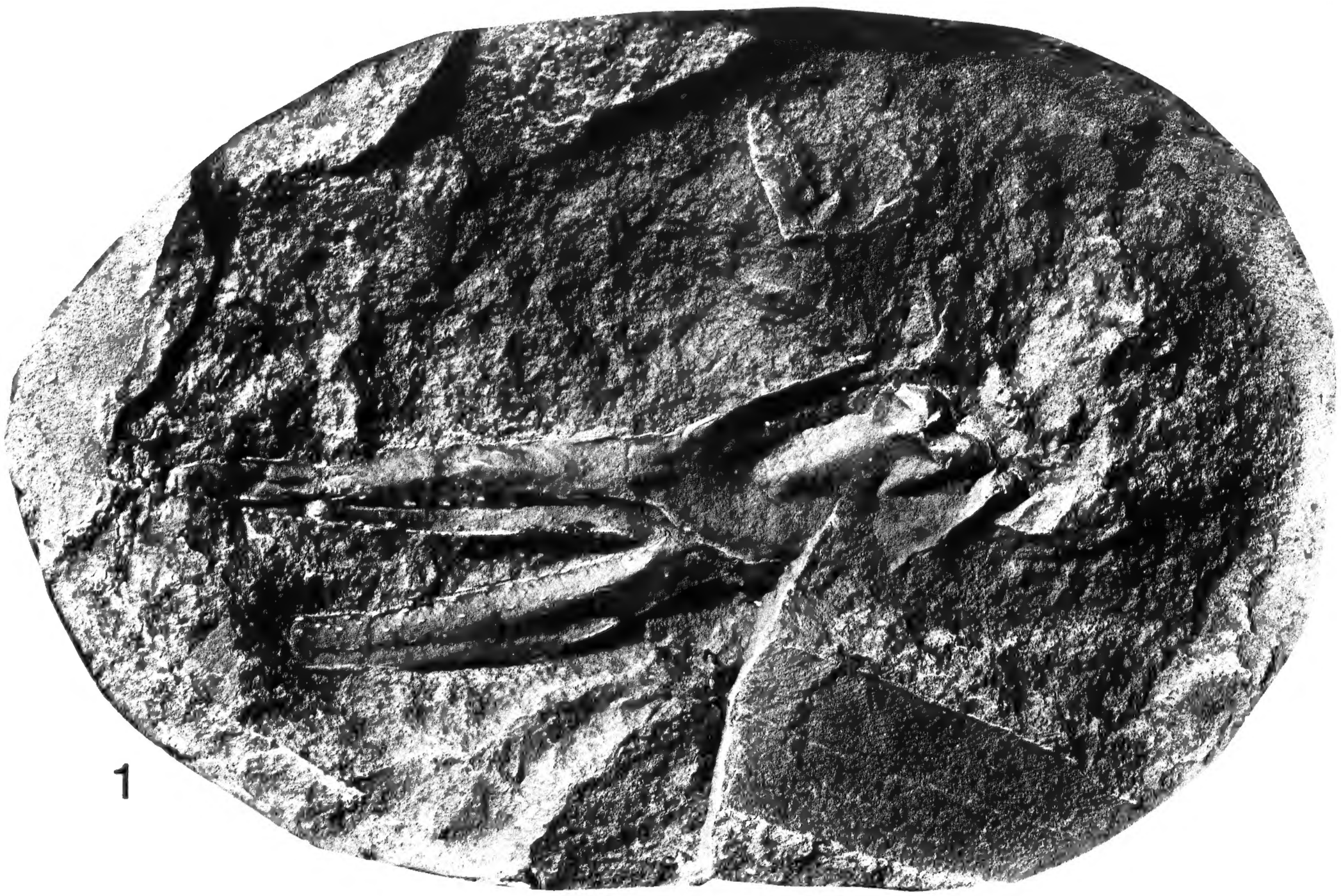
Specimen FMNH (PE) 32084. From the Pennsylvanian Carbondale Formation, lower Francis Creek Shale, Pit 1 of the Peabody Coal Company, on the Will Co.–Grundy Co. line, IL.

1. Obverse of the concretion. ×1.5.
2. Reverse of the concretion. ×1.5.

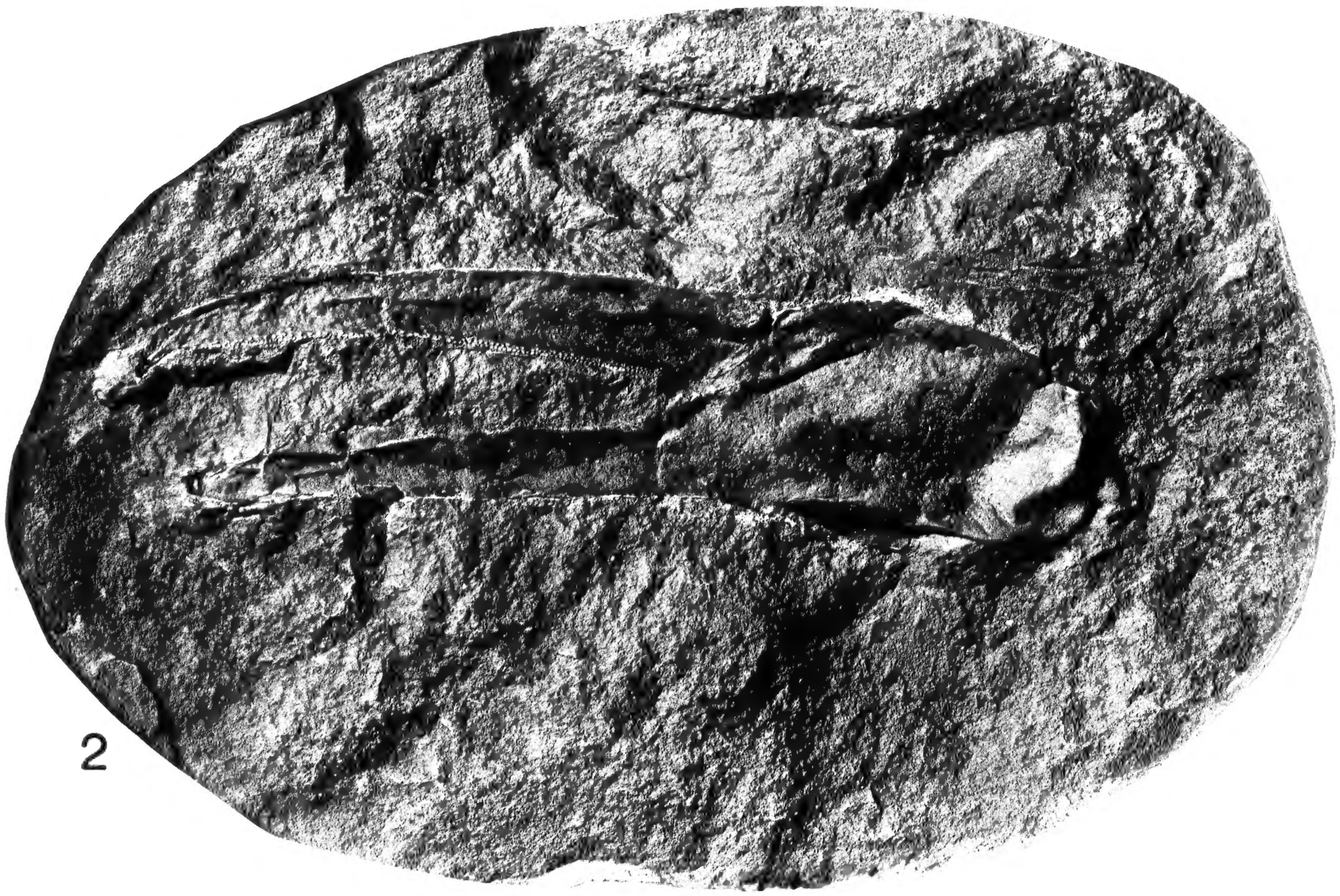
2



1



1



2

EXPLANATION OF PLATE 12

Page

Eoscorpius carbonarius Meek and Worthen 163

Specimen FMNH (PE) 32083. From the Pennsylvanian Carbondale Formation, lower Francis Creek Shale, Pit 1–6 undifferentiated, of the Peabody Coal Company, on the Will Co.–Grundy Co. line, IL. The two halves of the ironstone nodule. ×2.

EXPLANATION OF PLATE 13

Figure — Page

1–4. ***Eoscorpius distinctus*** (Petrunkevitch) 181

Holotype (BM(NH) In.13909). From the Carboniferous Upper Coal Measures of Coseley, England.

1. Specimen from the right side revealing the lateral compound eyes with well defined raised border and traces of ommatidial structures. ×6.
2. Lateral compound eyes from the left side. ×6.
3. Right eye greatly enlarged to further show the ommatidial structures and the raised marginal border. ×48.
4. The obverse. The large median ocelli and most of the ocellar node have been broken away, but are present in the counterpart. Note the two lateral compound eyes. ×6.

5, 6. ***Eoscorpius carbonarius*** Meek and Worthen 163

Holotype (FMNH (UC) 8949). From the Pennsylvanian Carbondale Formation, lower Francis Creek Shale at Mazon Creek, Grundy Co., IL.

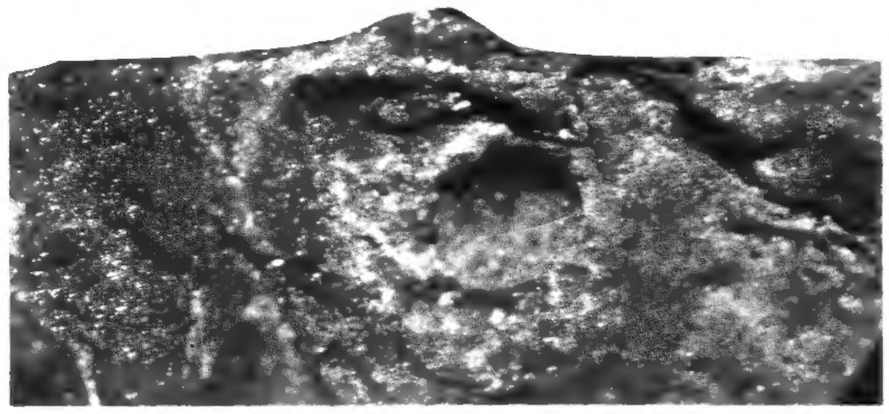
5. The left (reverse) median ocellus and the glossate anterior edge of the carapace. ×12.
6. The left lateral compound eye showing the ommatidia, with light reversed to accentuate the structure of the individual facets. ×25.

1

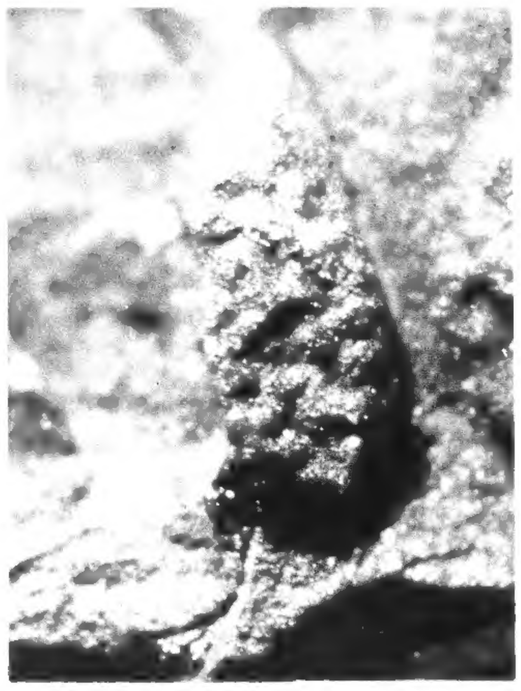
2

3

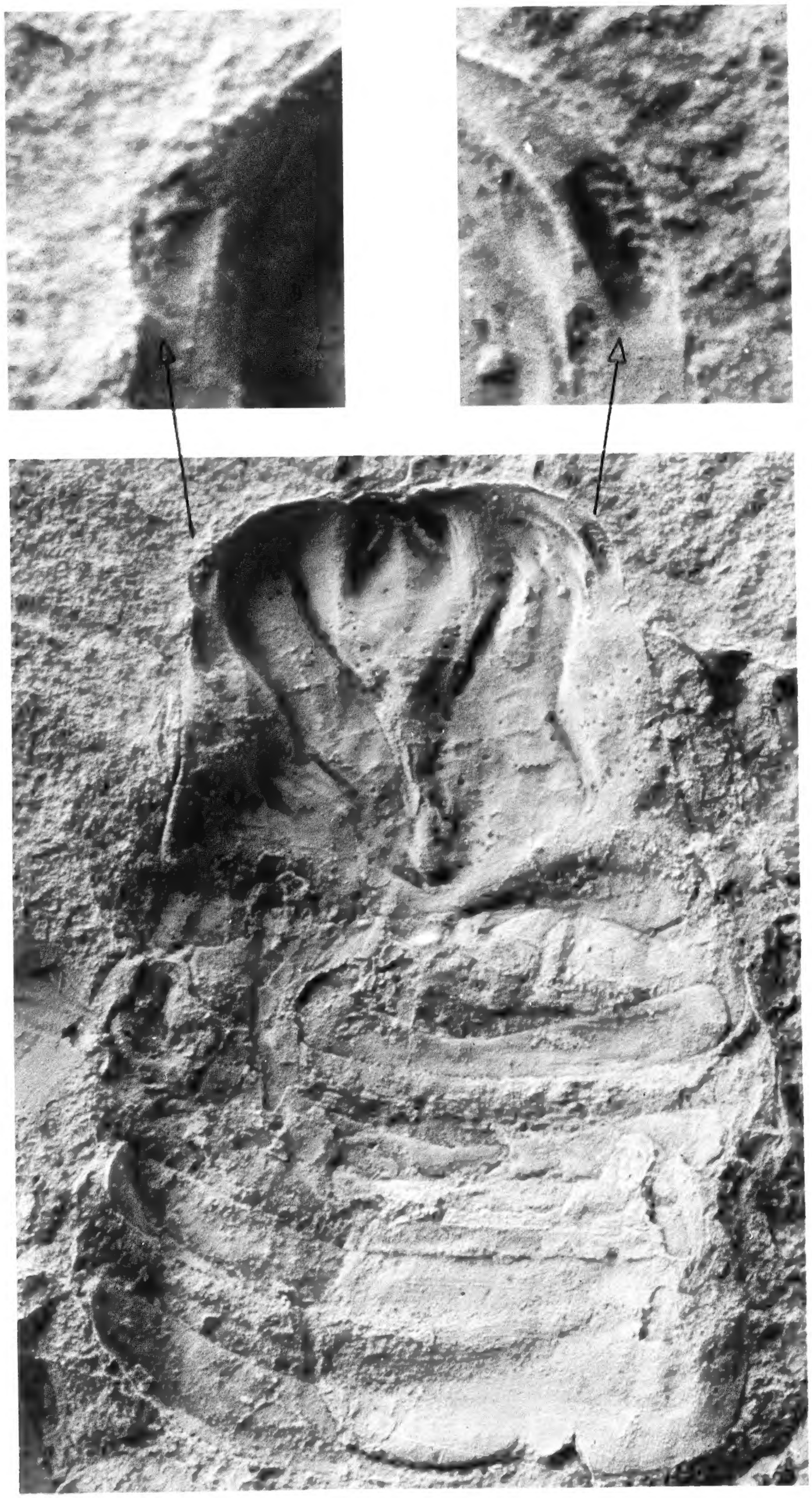
4



5



6



EXPLANATION OF PLATE 14

Page

Kronoscorpio danielsi (Petrunkevitch) 193

Holotype (UMMP 7216). From the Pennsylvanian Carbondale Formation, lower Francis Creek Shale, overlying Coal 2 at Mazon Creek, Grundy Co., IL. The carapace and dorsal side of the mesosoma from the original photograph by Alexander Petrunkevitch, ×5. The distinct ommatidia of the lateral compound eyes are clearly seen in the enlargement of the photograph, ×15.

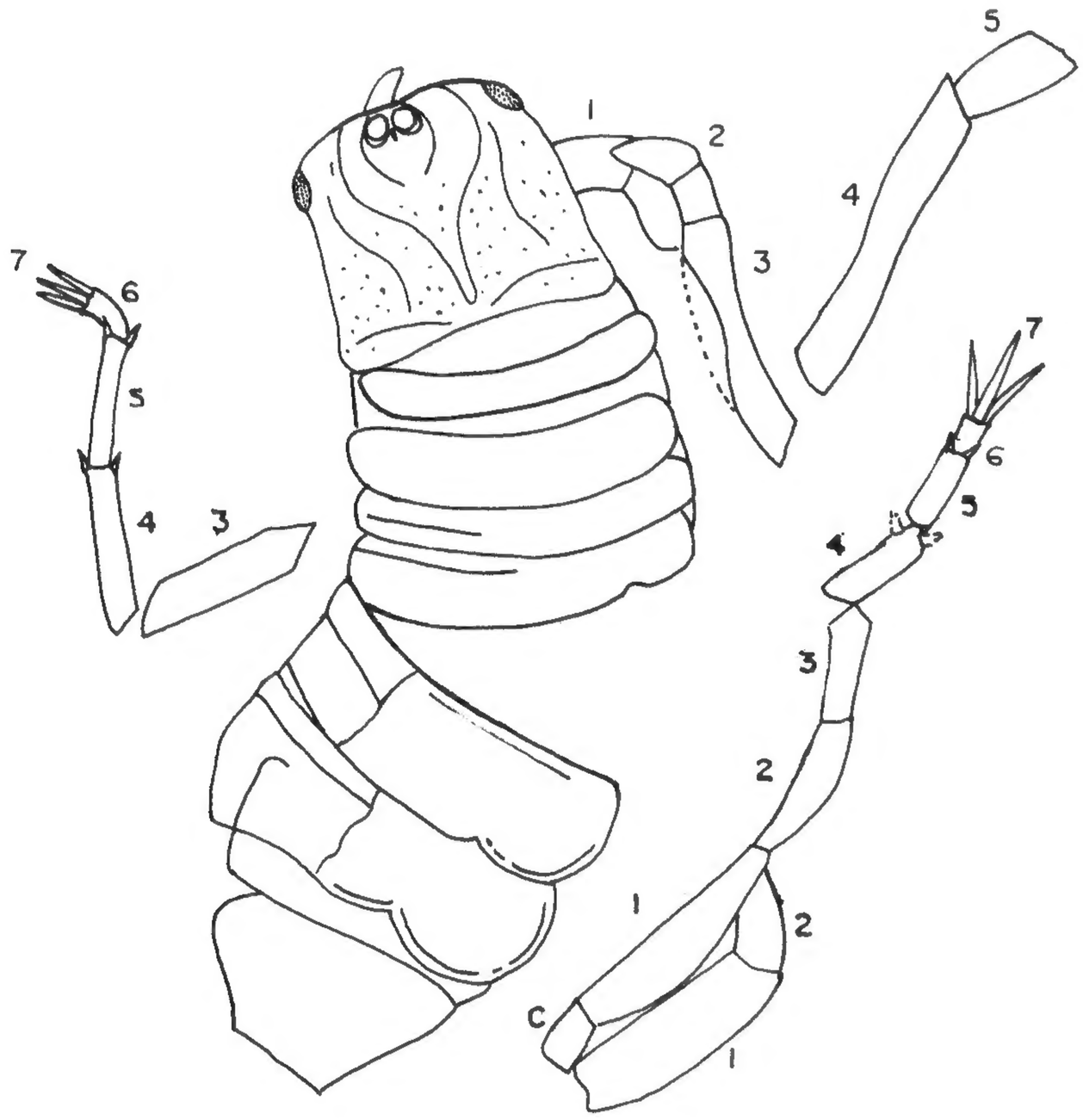
EXPLANATION OF PLATE 15

Figure — Page

1, 2. ***Kronoscorpio danielsi*** (Petrunkevitch) 193
Holotype (UMMP 7216). From the Pennsylvanian Carbondale Formation, lower Francis Creek Shale, overlying Coal 2 at Mazon Creek, Grundy Co., IL.

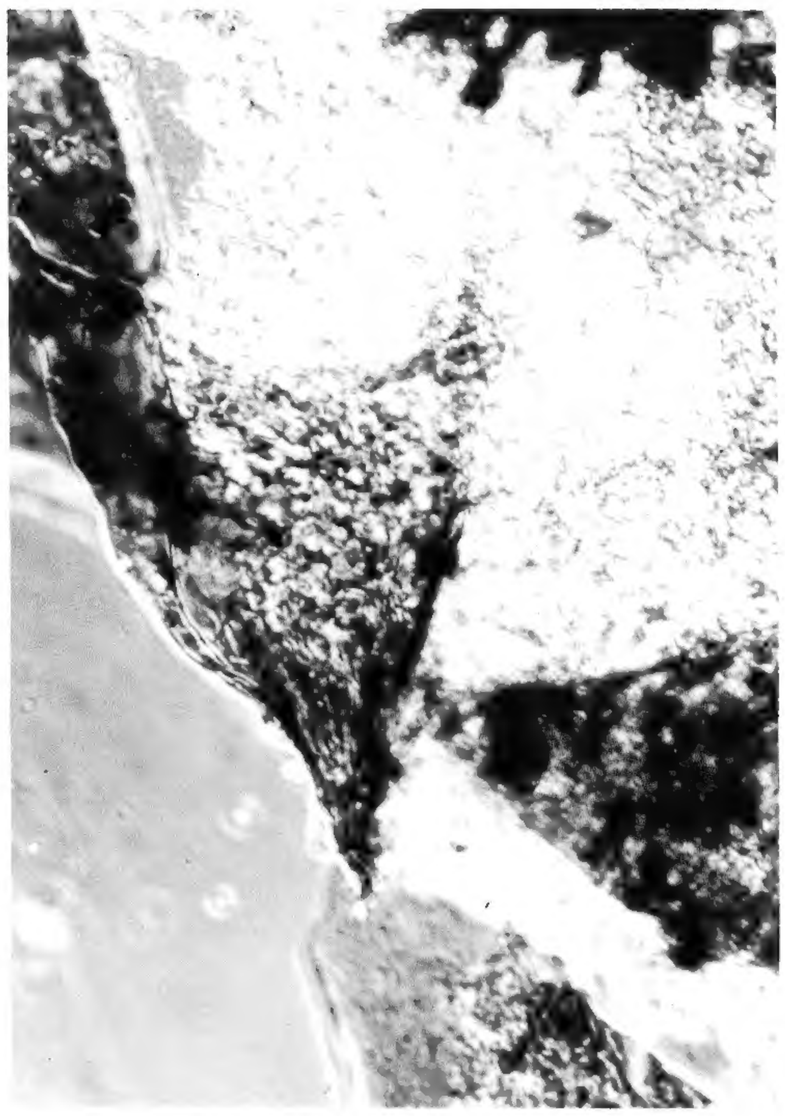
1. The original photograph by Petrunkevitch. ×2.
2. Line drawing from the plasto-holotype (USNM 27921). ×2.

1

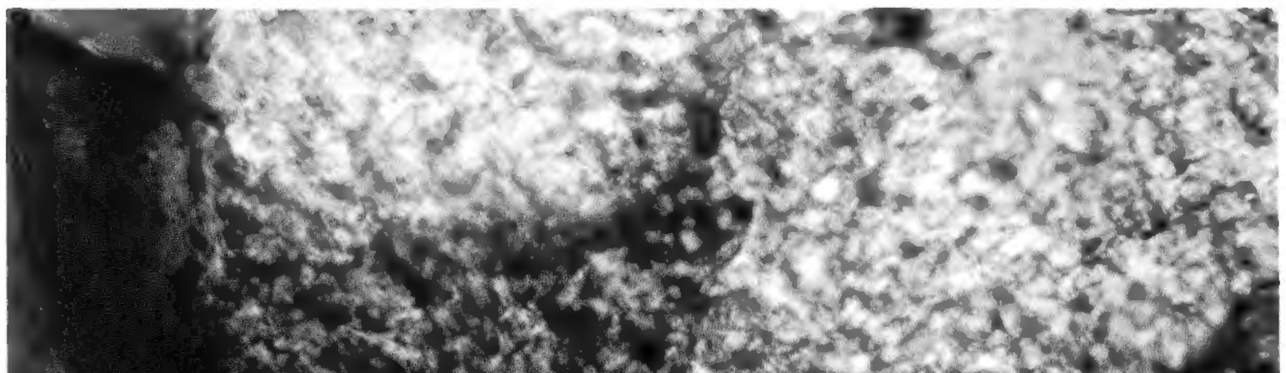


2

1



2



3

EXPLANATION OF PLATE 16

Figure — Page

1–3. ***Paraisobuthus duobicarinatus***, new species 204
Holotype (GSM 30245, 30246). From the Upper Carboniferous, Coal Measures, Shipley Clay Pit, Kimberley, Nottinghamshire, England.

1. The spongy white material represents the gill tract which has cone spines covering the outer (ventral) side. The darker chitin is brown colored and represents the lobosternous abdominal plates. ×90.
2. Enlargement of the white spongy gill tract showing the cone spines arising out of it and showing the striations that characterize the cone spines. ×220.
3. Further enlargement of the cone spines and the white spongy gill tract. ×330.

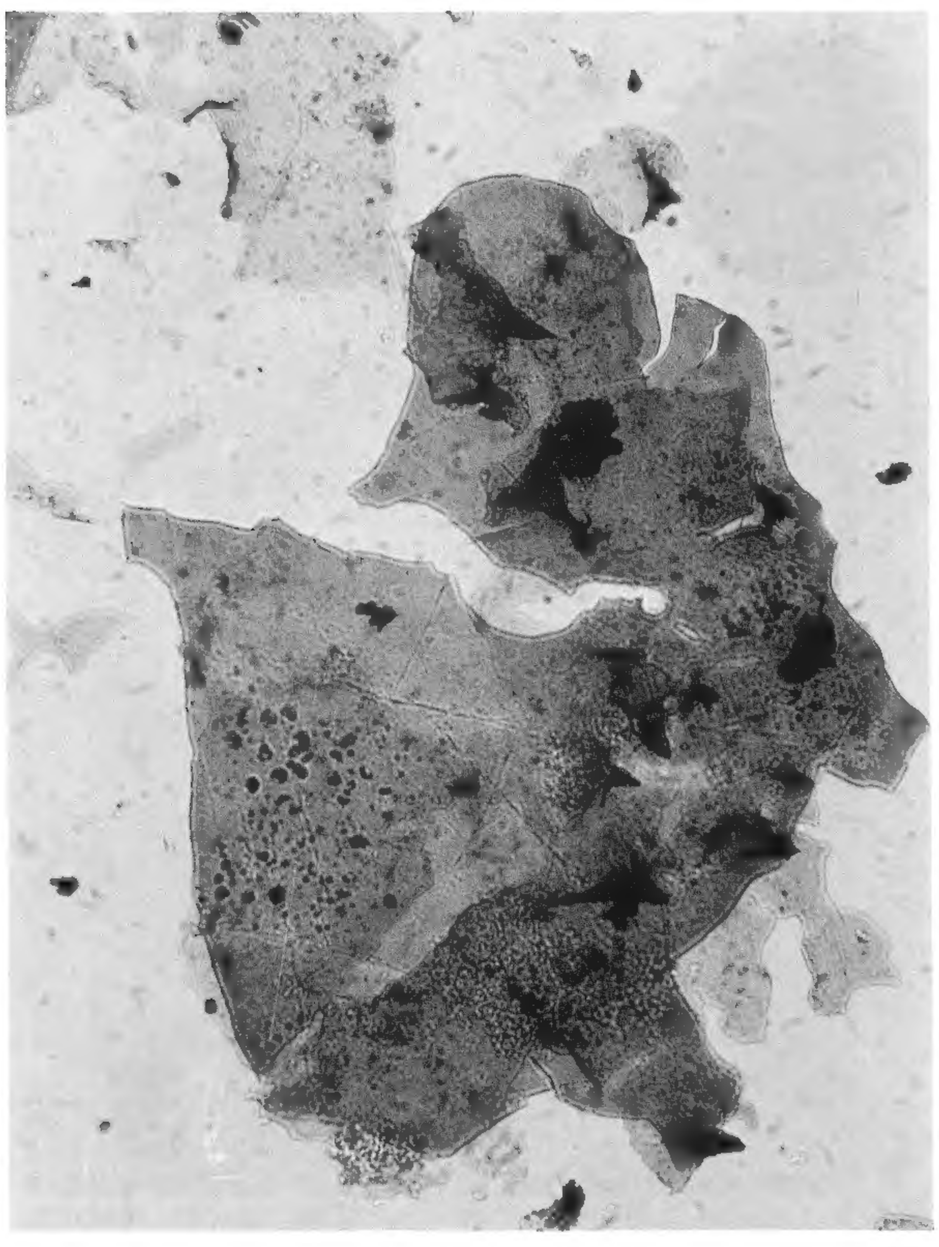
EXPLANATION OF PLATE 17

Figure — Page

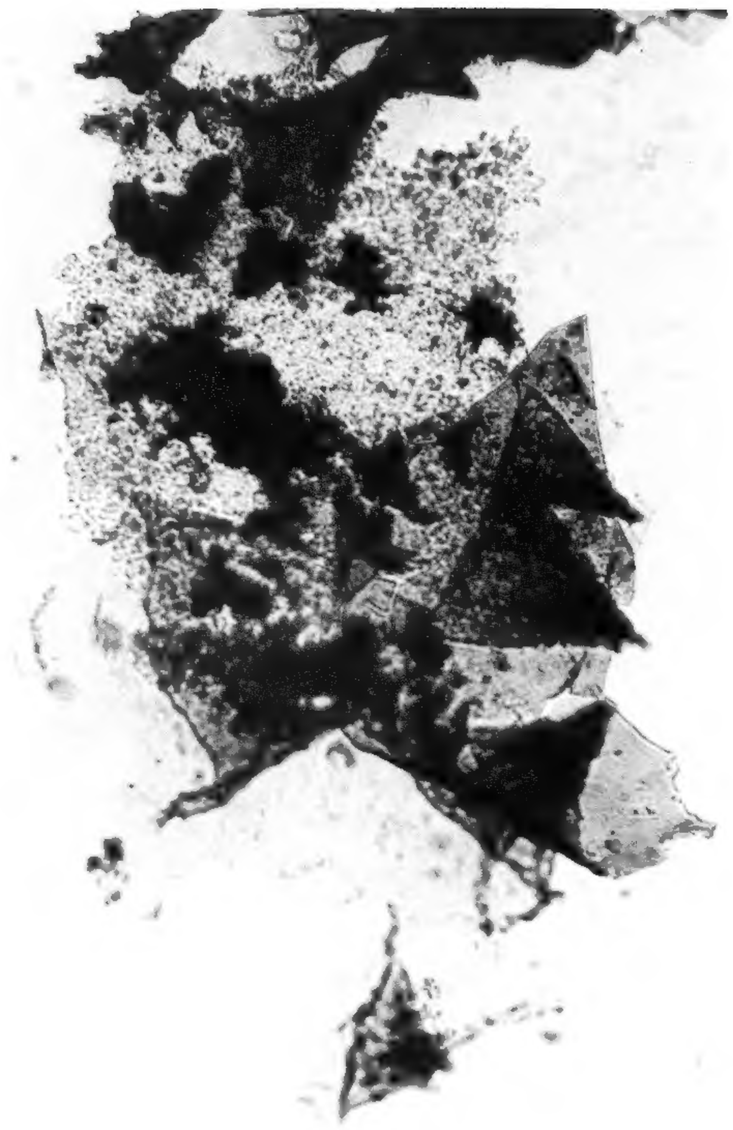
1–3. ***Paraisobuthus duobicarinatus***, new species 204

Holotype (GSM 30245, 30246). From the Upper Carboniferous, Coal Measures, Shipley Clay Pit, Kimberley, Nottinghamshire, England.

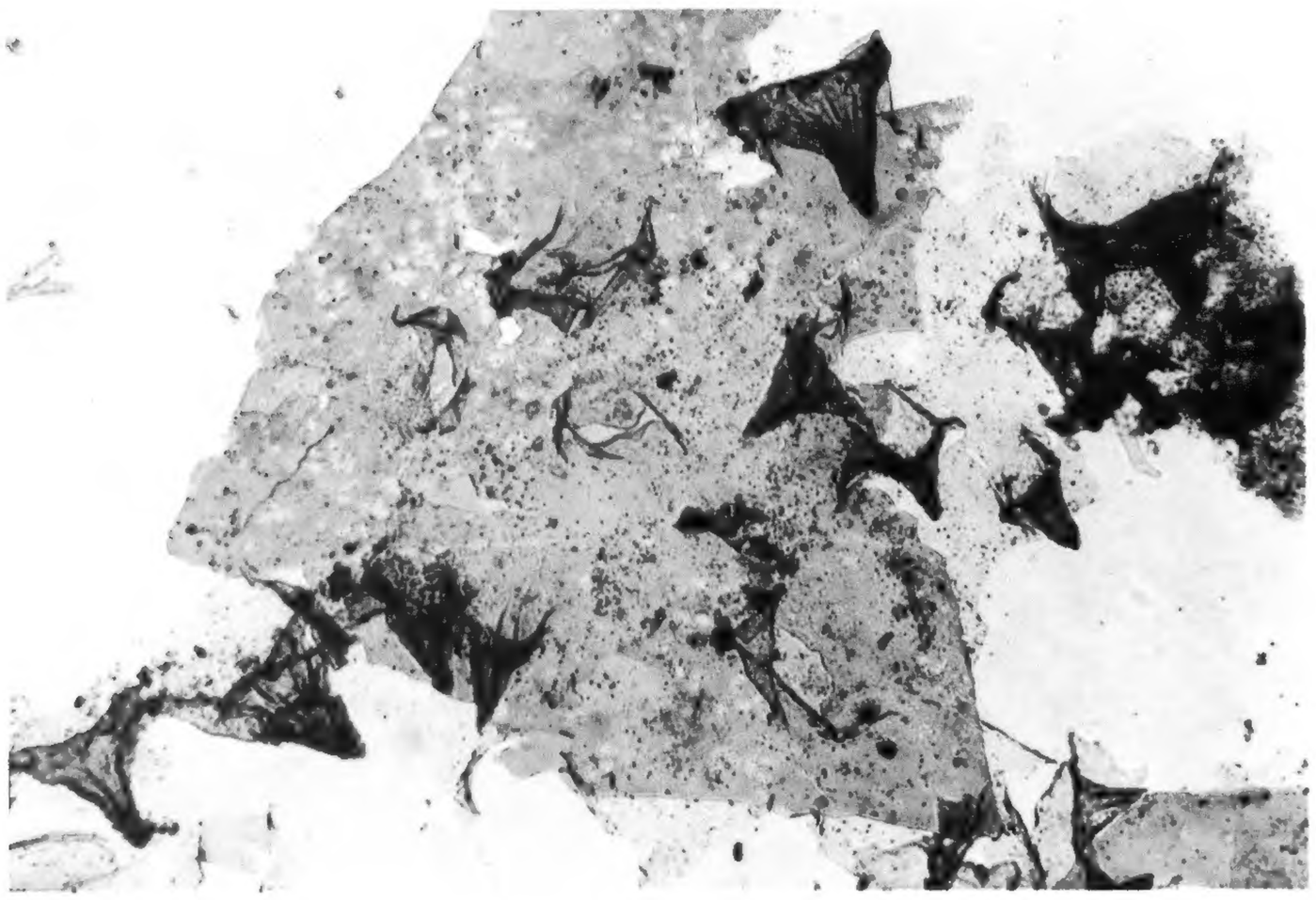
1. The spongy material is white and is the gill tract with its attached cone spines of various sizes. The clear darker material at the base is translucent chitin representing part of the abdominal plate. The dark shiny brown of the abdominal plate contrasts greatly with the overlying gill tract. The cone spines are also brown in color. ×90.
2. Cone spines attached to the white, spongy gill tract and covered by a piece of dark brown, translucent abdominal plate. ×90.
3. Cone spines and white spongy gill tract covered by a fragment of brown, translucent abdominal plate. ×90.



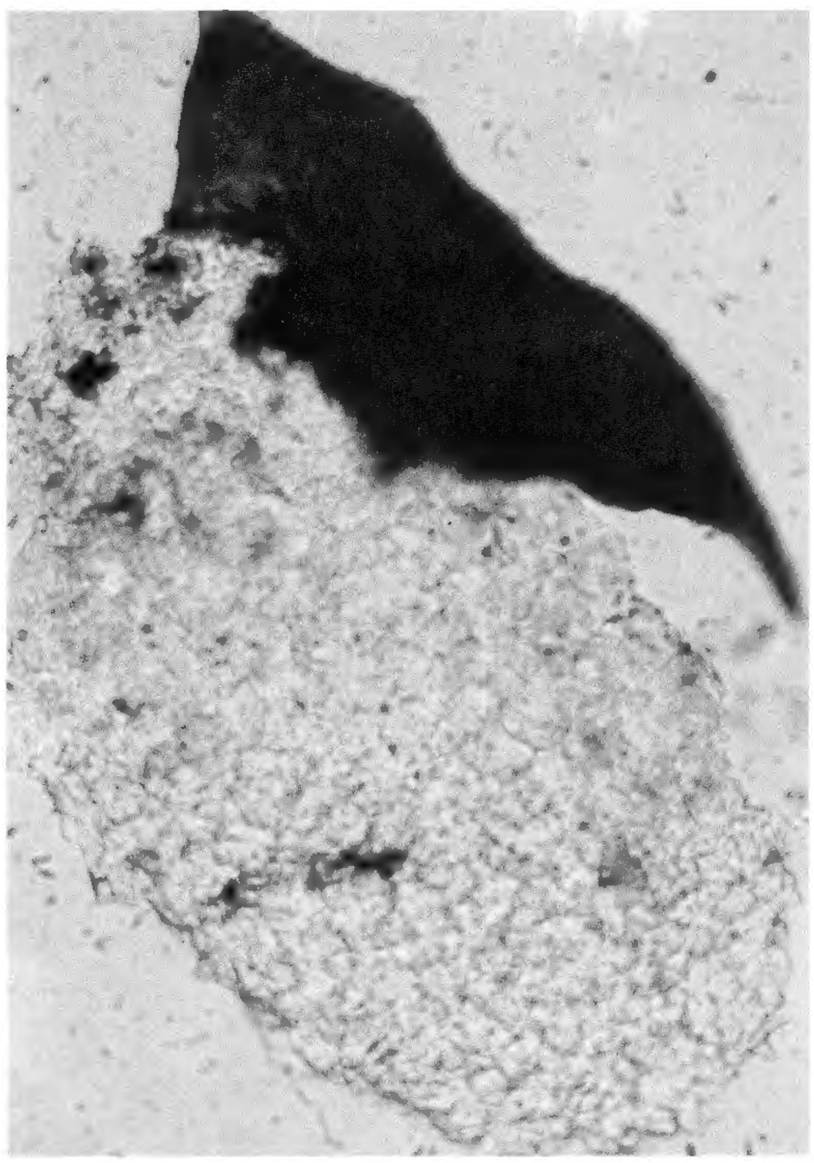
2



1

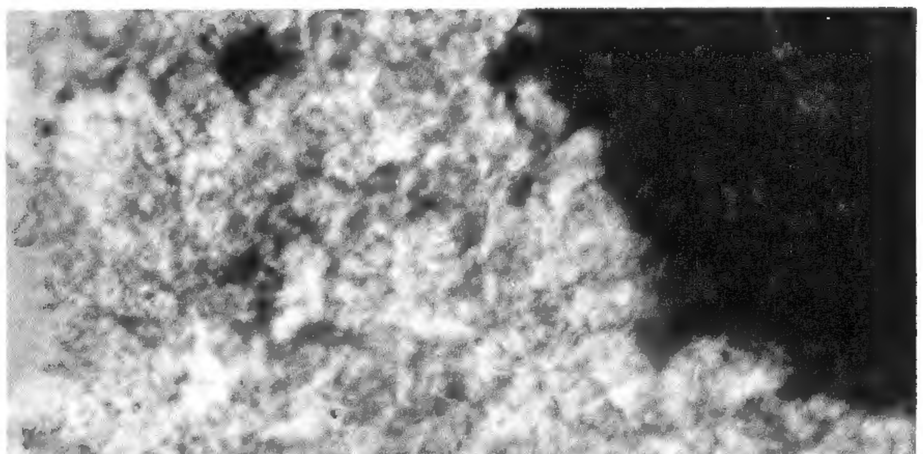


3

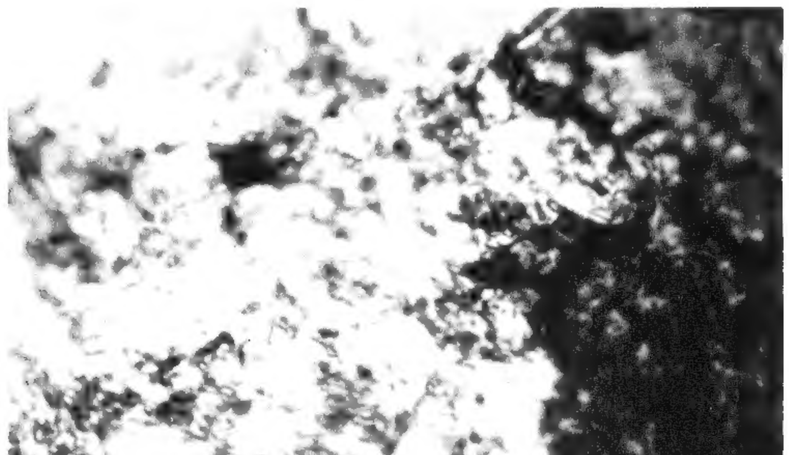


1

2



3



4

EXPLANATION OF PLATE 18

Figure — Page

1–4. ***Paraisobuthus duobicarinatus***, new species 204
Holotype (GSM 30245, 30246). From the Upper Carboniferous, Coal Measures, Shipley Clay Pit, Kimberley, Nottinghamshire, England.

1. Part of white, spongy gill tract with cone spine. ×220.
2. Same as figure 1, but with greater contrast. ×220.
3. Same. ×330.
4. Same with higher contrast. ×330.

INDEX

Note: Page numbers are in lightface; plate numbers are in **boldface** type; numbers in *italics* indicate principal discussions; **F** = foldout inside front cover; **B** = foldout inside back cover.

abdominal plates 23–24,28,29,31,32,36,37,82–83,96,157,227
Acanthoscorpio, n. gen. *70,*73,250
  mucronatus, n. sp. *70,*125,243,244
Acanthoscorpionidae, n. fam. *70,*73,243,244,250,**B**
Acanthoscorpionoidea, n. superfam. 34,*70,*250,**B**
aculeus, very short 191
airdriensis, Waterstonia 13,142,*222–224,*225,243,246
alliedensis, Labriscorpio *53,*243,245
Allobuthiscorpiidae, n. fam. *105,*106,251
Allobuthiscorpius, n. gen. *105,*251
  major (Wills, 1960) *105–106*
Allobuthus, n. gen. *112,*251
  macrostethus, n. sp. 102,*112–113,*243,244,247
Allopalaeophonidae, n. fam. *56,*60,243,244,250,**B**
Allopalaeophonoidea, n. superfam. 18,*56,*250,**B**
Allopalaeophonus, n. gen. 16,17,19,*56,*66,146,148,250
  caledonicus (Hunter, 1886) ..... **2** 29,*57–61,*142, 146,148,243,244
Alloscorpius Petrunkevitch, 1949 ... 162,163,172,176,177,196,253
  danielsi (Petrunkevitch, 1913) 177,193,196,253
  granulosus (Petrunkevitch, 1913) 100,163,*168–170,*172, 175,176,207,210,253
  tuberculatus (Peach, 1883) 177,214,253
  wardingleyi (Woodward, 1907) 84,176,253
amber 12
Amblypygida 24
American Museum of Natural History [AMNH] 254,**F**
americanus, Trigonoscorpio 163,*173–174,*175,176,254
Ananteris 20
anglicus,
  Brontoscorpio 31,78,*126,*188
  Palaeomachus *242–243*
  Typhlopisthacanthus 30,236,238,239,254
anterior (glossate) process 31
Anthracochaerilidae, n. fam. 15,16,*149,*156,243,246,251,**B**
Anthracochaeriloidea, n. superfam. *149,*218,251,**B**
Anthracochaerilus, n. gen. 15,19,20,*149–150,*158,251
  palustris, n. sp. *150–151,*192,243,246
Anthracoscorpii Thorell and Lindström, 1885 151,253
Anthracoscorpio Kušta, 1885 ..... 19,101,102,*107,*108,110,112, 151,162,163,186,251
  buthiformis Pocock, 1911 101,113,209,219,236,253
  dunlopi Pocock, 1911 ..... *108–109*
  juvenis Kušta, 1885 ..... *107–108,*110,150,151,243,244,247
  minutus (Petrunkevitch, 1949) 110,253
  sparthensis (Baldwin and Sutcliffe, 1904) 184,198,253
  Anthracoscorpio (?) sp. *109–110,*172,176
Anthracoscorpionidae, n. fam. *107,*110,112,113,243, 244,247,251,**B**
Apoxypoda Petrunkevitch, 1913 253
Arachnida 196
Archaeoctonidae Petrunkevitch, 1949 ..... 28,*66,*243,244, 247,250,**B**
Archaeoctonoidea Petrunkevitch, 1949 ..... 18,53,*66,*70, 216,250,**B**
Archaeoctonus Pocock, 1911 ..... 15,*66,*68,70,250
  glaber (Peach, 1883) 21,53,*66–68,*70,192,243,244,247
  tuberculatus (Peach, 1883) 214,216,217,253
Archaeophonus Kjellesvig-Waering, 1966 ..... 14,15,18,28,*48–50,* 52,56,149,250
  eurypteroides Kjellesvig-Waering, 1966 ..... *50–52,*196
Arthropleurida 125
Aspiscorpio, n. gen. *106,*251
  eagari, n. sp. *106–107*
Asteropyge 197

Baldwin and Sutcliffe (1904) 184,186
Baltoeurypterus 13,20,144
  serratus (Jones and Woodward) 146
  tetragonophthalmus (Fischer) 13
basal plate of the combs 86
Bather (1911) 57,242
Benniescorpio Wills, 1960 ..... 177,213,*214,*252
  tuberculatus (Peach, 1883) 213,*214*
Bertie Waterlime 39
Bilobosternina, n. infraorder 16,21–22,25,27,*36,*37,142, 193,*225,*243,245,252,**B**
Birmingham University [BU] 255,**F**
Birula (1917) 38
Bode (1951) 90,92
Boreoscorpio, n. gen. *154,*251
  copelandi, n. sp. 18,*154–156*
Bothriuridae 15,16,22,150,239,243,248
Bothriurus 20
  araguayae Vellard 243,248
  bonariensis (Koch) 22,23
brachistodactyla, Waterstonia (?) *224–225*
Brachistosternus 12,20,28,150,239
Branchioscorpio, n. gen. 15–20,35,158,192,*225–226,*252
  richardsoni, n. sp. 20,24,25,46,73,79,125,199,222, *226–229,*231,243,245
Branchioscorpionidae, n. fam. *225,*243,245,252,**B**
Branchioscorpionina, n. suborder 27,35,36,*38,*90,92,225,250
Branchioscorpionoidea, n. superfam. *225,*252,**B**
Brauer, Redtenbacher, and Ganglbauer (1889) 81
breathing mechanisms 25–30
brevipectus, Telmatoscorpio 208,*210–212,*243,246
British Museum (Natural History) [BM(NH)] 255,**F**
bromsgroviensis,
  Mesophonus 32–34,80,94,157,254
  Willsiscorpio 26,*94,*158
Bromsgroviscorpio, n. gen. *157*
  willsi, n. sp. 34,*157–158,*190,251
Brontoscorpio Kjellesvig-Waering, 1972 17,251
  anglicus Kjellesvig-Waering, 1972 ..... 31,78,*126,*188
Broteas 76
  gravimanus Pocock 22
Broteochactas 12,18,60,76,110,115,167,232,234
  gollmeri Karsh 243,248
Buffalo Museum of Science [BMS] 254,**F**
Buffalopterus 167
bureaui, Petaloscorpio *220–222,*243,246,247
Burgessia 197
burrowing scorpions 31
Buthidae 15,16,22,29,79,137,166,211,243,248
buthids, New World 22–23,126

buthiformis,
Anthracoscorpio 101,113,209,219,236,253
Buthiscorpius 13,101,*102–103,*105,107,112, 113,219,243,244,253
Eoscorpius 102,219,253
Euscorpius 253
Buthiscorpiidae, n. fam. 86,*101–102,*106,109, 190,243,244,251,**B**
Buthiscorpius Petrunkevitch, 1953 ..... 14,30,101,*102,*106,112, 162,163,219,228,251
buthiformis (Pocock, 1911) 13,101,*102–103,*105,107,112, 113,209,219,243,244,253
lemayi, n. sp. 102,*103–105,*219
major Wills, 1960 105,253
Buthus (*Scorpio* ? *Eoscorpius* ?) *carbonarius* Meek and Worthen, 1868 163,175
Buthus trilineatus Peters 23

calcareous deposits (travertine) 12
Calchas 100
caledonicus,
Allopalaeophonus 29,*57–61,*142,146,148,243,244
Palaeophonus 56,57,148,254
Canada
Miguasha, Bonaventure Co., Quebec 220
Stellarton Coalfield, Nova Scotia 155,156
West Bay, Cumberland Co., Nova Scotia 186,188
Canthon 113
carapace, fossil and living 12
carbonarius,
Buthus (*Scorpio* ? *Eoscorpius* ?) 163,175
Eoscorpius 13–15,78,86,88,100,159,160,*163–177,*184, 186,196,208,210,236,242,243,246,247
Carboniferous
Anthraconaia modiolaris Zone 181,193
Anthracosia similis–Anthraconaia pulchra Zone ... 110,112,113, 133,182,204
Autunian, lower 186
Coal Measures, unspecified 162,183,242
Crow Coal 177,179
Escuminac Formation 220
Etruria Marl Group 209,236,238,239,242
Namurian E, Limestone Coal Group 225
Pictou Group 155,156
Pottsville Series 86,87,215
Stanton Group, Missourian Series 114,116
Stephanian 133
Upper Gray Formation 157
Viséan, lower
Cementstone Group 188
Glencartholm Volcanic Beds 66,68,77,78,86,150,188, 190,191,217
Lower Oil Shale Group 213
Viséan, middle 93
Westphalian A
communis Zone of the Ammanian .. 84,88,102,105,106,108, 109,116,162,184,223,224
Parrsboro Formation 186,188
Westphalian B/C, Radnice Group (Lower Gray Formation) 107,130,134,153,159,161,199,203
Westphalian C, Lower Francis Creek Shale 81,95,98, 101,104,109,136,138,140,163,164,169,171, 173,174,194,196,207,211,233,240
Carcinosoma 20
newlini (Claypole) 61
Carcinosomidae 27,218
Carroll *et al.* (1972) 186
casei, Eoscorpius *186–188*
Caster and Kjellesvig-Waering (1964) 48
Centromachetes obscurus Mello-Leitão 23
Centromachidae Petrunkevitch, 1953 ..... 79,*84–86,*93,243,244, 247,250,**B**
Centromachoidea Petrunkevitch, 1953 ..... *84,*93,253
Centromachus Thorell and Lindström, 1885 ..... 19,34,84,*86,*250
euglyptus (Peach, 1883) 22,78,84,*86–87,*94,192, 218,243,244,247,253
glaber (Peach, 1883) 66,253
tuberculatus (Peach, 1883) 214,216,253
Centruroides Marx 12,110
beynai Schawaller, 1979 12
gracilis (Latreille) 22–23
keysi Muma = *C. guanensis* Franganillo 22–23
margaritatus (Gervais) 22–23
Ceraurus 197
Chactas 76
Chactidae 15,22,29,31,60,99,110,116,232,234,239,243,248
Chaerilidae 12,15,22,29,31,150,232,233,234,236,243,248
Chaerilus 100,158,233
celebensis Pocock 23,243,248
truncatus Karsh 23
chelicerae 16–17,28,32,33,90–92,115
Ciurca, S. J. [CIURCA] 39–51,53,255,**F**
Clarke and Ruedemann (1912) 13,15,20,39,57
classification, key to 34–38,**B**
claws 18–19
trifid or tridactyl 18,19,60,62,63,194,196,197
Cloudsley-Thompson (1962) 35
combs 26
comparison of scorpions and eurypterids 26–27
Compsoscorpius Petrunkevitch, 1949 ..... 12,15,17,28,162,163, 232,*236,*252
elegans Petrunkevitch, 1949 ..... 30,102,*236–239*
elongatus Petrunkevitch, 1949 30,236,238,253
Copeland (1957) 154
copelandi, Boreoscorpio 18,*154–156*
Copris 12,113
"coprolites" 48
Corda (1835) 129
Corda (1839) 133,134
cordai, Eobuthus 160–162
coseleyensis, Wattisonia *242*
Coseleyscorpio, n. gen. *113,*251
lanceolatus, n. sp. 101,102,112,*113,*220
coxosternal area 15–16,28,86–87,174–175
diagrams ... 62,74,80,88–89,108,116,122,150,220,234,243–248
Cramer, R. [RC] 242,255,**F**
cramondensis, Scoloposcorpio *213–214*
Cryptolithus 197
Cyclophthalmidae Thorell and Lindström, 1885 .... *129,*243,245, 251,**B**
Cyclophthalmoidea Thorell and Lindström, 1885 ..... *129,*133, 135,251,**B**
Cyclophthalmus Corda, 1835 ..... 15,17,126,*129,*132,151,160,251
kralupensis Thorell and Lindström, 1885 151,153,253
robustus, n. sp. *132–133*
senior Corda, 1835 ..... 107,*129–132,*133,153,160, 175,203,243,245,253

Cyclophthalmus
(?) *sibiricus* Novojilov and Størmer, 1963 ..... *133*
sternbergii (Corda, 1839) 134,253
Czechoslovakia
Červená Hůrka Hill, Kralupy 153,161,203
Chomle, near Radnice 130,134
Rakovnik 107,159,199
Studnoves 157

danielsi,
Alloscorpius 177,193,196,253
Eoscorpius 13,193,196,253
Kronoscorpio 15,60,168,186,*193–197*,208,209,243,246
delicatus, Stoermeroscorpio *53–56*
denisoni, Hydroscorpius ..... **3** 12,*63–66*,125
denticulatus, Pseudoarchaeoctonus *68–70*,192
desert existence, evidence 30,35
Devonian
Beartooth Butte Formation 63,70,125,226
Hunsrück Shale 61
Klerfer Beds 242
Nellenköpfchen Beds (Lower Emsian) 52
Old Red Sandstone 122
Onteora Red Beds (Lower Frasnian) 126
devonicus, Palaeoscorpius 22,60,*61–63*,64,243,245
Dionychopoda Petrunkevitch, 1913 253
Diplocentridae 15,22,99,211,243,248
Diplocentrus 167
bigbendensis Stahnke 243,248
distinctus,
Eoscorpius 14,15,*181–184*,186,196,197
Palaeobuthus 21,*135–141*,172,176,177,180,243,245
Typhloscorpius 13,15,182–183,254
Dolichophonidae Petrunkevitch, 1953 ..... *229–230*,252,**B**
Dolichophonus Petrunkevitch, 1949 ..... 15,18,*230*,252
loudonensis (Laurie, 1899) 70,216,*230–231*
doublures 24,29,31,32,82,83
Douglass, D. L. [DLD] 240,242,255,**F**
douglassi, Titanoscorpio 78,*240–242*
Dubinin (1962) 21,32,34,39,57,61,66,79,80,81,86,90,96,102,107,109,110,113,120,121,132,134,135,142,154,162,163,177,181,210,214,216,230,232,236,242
dunlopi,
Anthracoscorpio *108–109*
Eoscorpius 109,253
duobicarinatus, Paraisobuthus 24,26,31,*204–207*

eagari, Aspiscorpio *106–107*
ecdysis 29
elegans, Compsoscorpius 30,102,*236–239*
Elias (1936) 113,114,115
Elias (1937) 114
elongatus, Compsoscorpius 30,236,238,253
England
Bromsgrove Quarry, near Birmingham 74,75,80,81,94,121,157
Charford Mills, Birmingham 29,30,94,121
Coseley, Staffordshire 110,112,113,133,182,209,219,236,238,239,242
Dodsworth, near Barnsley, Yorkshire 181
Dudley 183
Eastham Bridge, Trimpley, Worcestershire 126
Kimberley, Nottinghamshire 204
Ludlow, Shropshire 149
Mansfield, Nottinghamshire 242
Rowlestone, Herefordshire 122
Ryton-on-Tyne, Durham 177,179
Trowell Colliery, Nottinghamshire 105
Weston Rhyn, Shropshire 193
environments 35
Eobuthidae 16,152,153,*158*,162,214,243,246,251,**B**
Eobuthus Frič, 1904 ..... 15,19,151,152,153,156,*158*,186,192,204,251
cordai, n. sp. *160–162*
holti Pocock, 1911 ..... *162*,207
holti (?) Pocock, 1911 193,204,253
pottsvillensis Moore, 1923 214,253
rakovnicensis Frič, 1904 ..... 151,152,153,*158–160*,162,186,198,202,243,246,253
sp. Wills, 1934 193,253
Eobuthus (?) sp. Wills, 1934 ..... *162*
Eocarcinosoma 31,183
Eochaerilus 86
Eoctonidae, n. fam. 15,16,94,*96*,102,243,244,251,**B**
Eoctonoidea, n. superfam. *94–95*,101,107,109,110,113,251,**B**
Eoctonus Petrunkevitch, 1913 ..... 14,15,30,31,*96*,251
miniatus Petrunkevitch, 1913 ..... **4** 13,*95–101*,207,208,243,244,253
Eoscorpiidae Scudder, 1884 .... 16,101,126,151,152,153,158,*162*,163,190,211,212,219,243,246,247,252,**B**
Eoscorpionidae Scudder, 1884 253
Eoscorpius Meek and Worthen, 1868 ... 14,16,18,19,20,30,31,90,96,101,109,150,151,152,154,156,158,*162–163*,176,178,182,184,186,190,208,209,210,213,219,228,233,234,236,252
anglicus Woodward, 1876 242,253
buthiformis (Pocock, 1911) 102,219,253
carbonarius Meek and Worthen, 1868 .... **10-13** 13,14,15,78,86,88,100,159,160,162,*163–177*,184,186,196,208,210,236,242,243,246,247
casei, n. sp. *186–188*
danielsi Petrunkevitch, 1913 13,193,196,253
distinctus (Petrunkevitch, 1949) ..... **13** 14,15,*181–184*,186,196,197
dunlopi (Pocock, 1911) 109,253
euglyptus Peach, 1883 86,253
glaber Peach, 1883 66,68,253
granulosus Petrunkevitch, 1913 135,139–140,163,176,210,211,253
inflatus Peach 253
mucronatus, n. sp. *181*
(?) *ornatus* (Frič, 1904) 156,253
pulchra (Petrunkevitch, 1949) 21,22,139,163,*177–181*,197,212
sparthensis Baldwin and Sutcliffe, 1904 ..... 106,*184–186*,202,253
tuberculatus Peach, 1883 213,214,253
typicus Petrunkevitch, 1913 .... 109–110,135,137–138,162,163,*171–173*,175,176,253
(*Mazonia*) *wardingleyi* Woodward, 1907 84,253
(*Mazonia*) *woodiana* (Meek and Worthen, 1868) 81,253
sp. Carroll *et al.,* 1972 186
sp. Copeland, 1957 253
sp. *186*
Erieopterus 14,168
hypsophthalmus 14
turgidus 14
Eskiscorpio, n. gen. 68,*190–191*,252
parvus, n. sp. *191–192*

Estheria 29,30
eurypteroides, Archaeophonus *50–52*,196
euglyptus,
Centromachus 22,78,84,*86–87*,94,192,218,243,244,247,253
Eoscorpius 86,253
Europhthalmus Petrunkevitch, 1949 162,163,178,253
longimanus Petrunkevitch, 1949 18,177,178,179,180,253
Eurypterida 21,23,24,26–27,31,48,96,144,196
Eurypteridae 144,166
Eurypterida Zone 53
Eurypterina 13,14
Eurypterus 20,144,167
? possibly *pygmaea* Salter 253
Euscorpionina (Euscorpiones) Petrunkevitch, 1949 253
Euscorpius 115
buthiformis (Pocock) 253
evolution 24–25,27–28
external morphology ..... **F**
exuviae, ecdysial 29–30
eyes *12–15*,196–197
holochroal (compound) 13
schizochroal (aggregate) 13
"sexual dimorphism" 79,94
size relationships of median and lateral 14–15,52,144

Feistmantelia Frič, 1904 ..... 151,152,*156*,251
ornata Frič, 1904 ..... 151,*156–157*
Field Museum of Natural History [FMNH] 254,**F**
fixative 149
Florida State University [FSU] 3,86,**F**
fossil scorpions, characteristics and nature of 11–21
France
Aumance Basin 186
North of Vosges 30
Francke (pers. commun.) 15,19
Frič (1873) 129,134,153,154,160,203
Frič (1902) 129
Frič (1904) 39,57,107,129,134,142,151,152,153,154,156,158,160,163,198,202,203,232
Frič (1907) 39
frici, Paraisobuthus *203–204*,206
fulcra 74

Gall (1971) 30
Garnettiidae Dubinin, 1962 ..... *113*,163,251,**B**
Garnettius Assemblage 115
Garnettius Petrunkevitch, 1953 ..... 16,17,*113*,162,163,166,189,251
hungerfordi (Elias, 1936) 12,15,*114–120*,196
(?) sp. 116,*120*
Genera Incertae Sedis 126,240–242,252
Geological Survey of Canada [GSC] 255,**F**
Geological Survey Museum, London [GSM] 255,**F**
Geralinura ? *sutcliffei* Woodward, 1907 86,88,253
Gerard Holm Collection 13
Gerufa 14
Gigantoscorpio Størmer, 1963 ..... 15,17,18,20,*76*,158,233,250
willsi Størmer, 1963 ..... 19,22,31,75,*76–79*,125,189,192,199,218,243,244,247
Gigantoscorpionidae, n. fam. *76*,243,244,247,250,**B**
Gigantoscorpionoidea, n. superfam. *75*,250,**B**
gigas, Praearcturus 78,*121–125*,243,244
gills **5-8**, **16-18** 23–24,26,28–32,34,35,95–97,101,126–128,157,206,229
openings 33,82–83,157,226,229
pouches or chambers 31,96–97,139,206
glaber,
Archaeoctonus 21,53,*66–68*,70,192,243,244,247
Centromachus 66,253
Eoscorpius 66,68,253
gnathobase 16,48,226
Göttingen University Museum [GUM] 256,**F**
Grabau (1928) 81
Grabau and Shimer (1910) 81
gracilis,
Mesophonus 32,34,74,80,94,254
Stenoscorpio 34,73,*74*,75,90,243,244
granulosus,
Alloscorpius 100,163,*168–170*,172,175,176,207,210,253
Eoscorpius 135,139–140,163,176,210,211,253
Grosphus 60

Hadogenes 115,167
troglodytes (Peters) 22
Hadruroides lunatus (Koch) 243,248
Hadži (1931) 12,239,240
Handlirsch (1906) 81
Harrington (1959) 13
Harrington, Moore, and Stubblefield (1959) 13
hefteri, Waeringoscorpio 26,31,48,*52*,229,243,245
Heloscorpio, n. gen. *86–88*,250
sutcliffei (Woodward, 1907) *88–90*,243,244,247
Heloscorpionidae, n. fam. *86*,243,244,247,250,**B**
Hennig (1922) 121
Herdina specimens 174,175,196
Hessler (1969) 121,125
Heterometrus 17,31,144
Heubusch (1962) 61
Hoffman (1931) 229
Holl (1929) 12
Holm (1896) 20
Holm (1897) 20
Holm (1898) 20
Holm (1899) 20
Holm–Wills technique 92–93
holochroal (compound) eyes, definition 13
Holosternina, n. infraorder ... 14,15,16,21–22,24,26–28,31,33,34,36–37,*38*,92,94,97,142,151,163,212,243,244,245,247,250,**B**
holti,
Eobuthus *162*,207
(?) *Eobuthus* 193,204,253
Isobuthus 162,253
Hormurus 236,238
Hueber (1960) 126
hueberi, Tiphoscorpio 26,31,*126–129*
Hughmilleria 31,216
banksii Salter 12,182,183
hungerfordi,
Garnettius 12,15,*114–120*,196
Mazonia 113,114
Hunter (1886) 56,57
Hunter (1888) 57
hunteri, Palaeophonus 57,254
Hydroscorpiidae, n. fam. *63*,250,**B**
Hydroscorpius, n. gen. *63*,106,250
denisoni, n. sp. ..... **3** 12,*63–66*,125

Illinois
Mazon Creek Area 109,163
Grundy Co. 95,136,138,164,169,171,173, 196,207,211,233,240
Pit 1, Peabody Coal Co., Grundy Co.–Will Co. line 174
Pit 6, Peabody Coal Co. near Braidwood 104
Pit 11, Peabody Coal Co., Will Co.–Kankakee Co. line .. 81, 98,194,242
Strip mines, Will Co.–Grundy Co. line 101
Illinois State Museum [ISM] 254,**F**
Indiana
Clay City, Owen Co. 86,87,215
infans A, Mesophonus 32,74,254
infans D, Mesophonus 32,74,254
infans E, Mesophonus 32,80,254
inflatus, Eoscorpius 253
infraorders 35–37
Inst. für Paläontologie, Friedrich Wilhelm Univeristät, Bonn [FWU] 256,**F**
Institute of Geological Sciences, Edinburgh [GSE] 255,**F**
intestinal canal, preservation **3** 61,90
Ischnurus ochropus Koch 22
Isobuthidae Petrunkevitch, 1913 ..... 133,151,*152–153,*156,158, 162,198,243,246,247,**B**
Isobuthoidea Petrunkevitch, 1913 ..... 135,*151–152,*158,162,190, 192,193,198,212,213,218,251,**B**
Isobuthus Frič, 1904 ..... 19,29,151,152,*153,*156,192,251
holti (Pocock, 1911) 162,253
kralupensis (Thorell and Lindström, 1885) .. 152,*153–154,*160, 168,192,203,204,243,246,247
ornatus (Frič, 1904) 156,253
pottsvillensis (Moore, 1923) 214,253
Isotoma 14
Iuridae 15,243,248

juvenis, Anthracoscorpio *107–109,*110,150,151,243,244,247
Jurassic
Irkutsk Basin of Siberia 81
Lias epsilon marl pit 90,92

Kaestner (1940) 19,23
Kaestner (1968) 19
Kansas
Rock Lake Shale member of Stanford Group 114,116
Kilmarnock Museum [KM] 255,**F**
King (1934) 57
Kingsley (1900) 121
Kjellesvig-Waering, E. N. 3,9–10
Kjellesvig-Waering (1951) 21,125
Kjellesvig-Waering (1954) 39
Kjellesvig-Waering (1958a) 20
Kjellesvig-Waering (1958b) 14
Kjellesvig-Waering (1961) 53,149,228
Kjellesvig-Waering (1964) 166
Kjellesvig-Waering (1966) 13,18,22,39,46,48,50,57, 63,196,225,231
Kjellesvig-Waering (1969) 13,17,21,23,34,81–82, 84,144,168,176
Kjellesvig-Waering (1972) 76,126
kralupensis,
Cyclophthalmus 151,153,253
Isobuthus 152,*153–154,*160,168,192,203,204,243,246,247
Krogh (1941 (1968)) 26

Kronoscorpio, n. gen. ... 15,18,19,20,48,150,177,182,183,*193,*252
danielsi (Petrunkevitch, 1913) ..... **14**,**15** 15,60,168, 186,*193–197,*208,209,243,246
Kronoscorpionidae, n. fam. *193,*243,246,252,**B**
Kušta (1884) 107
Kušta (1885) 107,108

labiosus, Pseudobuthiscorpius 101,102,112,*219–220,*243,246
Labriscorpio Leary, 1980 ..... *52–53,*250
alliedensis Leary, 1980 ..... *53,*243,245
Labriscorpionidae, n. fam. *52,*243,245,250,**B**
labrum 48,52,56
lanceolatus, Coseleyscorpio 101,102,112,*113,*220
Lankester (1881) 24
lateral eyes 28,30,31
Laurentiaux-Vieira and Laurentiaux (1963) 186
Laurie (1899) 39,216,230,231
Lawrence (1953) 13,14,124
Lawrence (pers. commun.) 32,197
Leach (1815) 38,152,232,238
Leary (1980) 52,53
legs, walking 17–19,28
differentiation 113,115,116–120
fossorial 113
Lehmann (1944) 15,39,57,61,63,81,154
Leioscorpio, n. gen. *209,*252
pseudobuthiformis, n. sp. 101,102,*209–210,*220
Leiurus quinquestriatus 60
lemayi, Buthiscorpius 102,*103–105,*219
Lepisma 14
Levi (1976) 26
Levi and Levi (1968) 19
Liassoscorpionidae, n. fam. *90,*250,**B**
Liassoscorpionides Bode, 1951 ..... *90,*166,250
schmidti Bode, 1951 ..... **3** *90–93*
Lichnophthalmus Petrunkevitch, 1949 ..... 162,163,177,178, 181,254
pulcher Petrunkevitch, 1949 13,14,19,177,180,181,254
sp. Laurentiaux-Vieira and Laurentiaux, 1963 186,254
Lichnoscorpius Petrunkevitch, 1949 ..... *110,*251
minutus Petrunkevitch, 1949 ..... *110–112*
lightbodyi, Palaeophonus (?) *149*
Limulus 13,14,48
Liobuthus 30
Loboarchaeoctonidae, n. fam. 66,*216,*243,245,252,**B**
Loboarchaeoctonoidea, n. superfam. 52,*216,*252,**B**
Loboarchaeoctonus, n. gen. 52,70,*216,*252
squamosus, n. sp. 53,66,*216–218,*243,245
Lobosterni Pocock, 1911 35,36,141,151,254
Lobosternina Pocock, 1911 ..... 14–16,21–22,24–28,31,33,34,*36,* 37,94,97,*141–142,*157,193,198,212, 243,245,246,247,251,**B**
longimanus, Europhthalmus 18,*177–180,*253
loudonensis,
Dolichophonus 70,216,*230–231*
Palaeophonus 230,254
lungs 23–24,26,28–32,34,35,101

macrostethus, Allobuthus 102,*112–113,*243,244,247
maculatus,
Mesophonus (?) *81*
Ophismoblatta 81,254
Periplaneta 81,254

major,
Allobuthiscorpius *105–106*
Buthiscorpius 105,253
Manchester University Museum [UMM] 255,**F**
Marco-cast 181
Marrella 197
maxillary lobes 28,243,247
mazonensis,
Mazoniscorpio 135,140,254
Palaeopisthacanthus 163,254
Typhlopisthacanthus 15,163,169,*170–171*,175,176,236,254
Mazonia Meek and Worthen, 1868 ... 15,17,23,34,52,*81*,84,131, 151,176,233,250
hungerfordi Elias, 1936 113,114,254
wardingleyi (Woodward, 1907) 16,*84–85*
woodiana Meek and Worthen, 1868 ..... 12,21,28,*81–84*,110,168,214,243,244,247
Mazoniidae Petrunkevitch, 1913 ..... 34,79,*81*,212,243, 244,247,250,**B**
Mazonioidea Petrunkevitch, 1913 254
Mazoniscorpio Wills, 1960 177,228
mazonensis Wills, 1960 135,140,254
median eyes 28,31
median organ, appendage 22,52,78,86,226,229
Meek and Worthen (1868a) 163,175
Meek and Worthen (1868b) 81,162,163,167,168,175
Megacormus granosus Gervais 229
Megalograptidae 218
megalograptids 27
Megalograptus 31,88
ohioensis Caster and Kjellesvig-Waering 48,229
Menge (1869) 12
Meristosternina, n. infraorder 15,16,21–22,25–27,*36*,37,86, *126*,153,243,245,251,**B**
Mesobuthus gibbosus (Brulle) 22–23
Mesophonidae Wills, 1910 ..... 32,34,*79*,90,196,243, 244,247,250,**B**
Mesophonidea Wills, 1910 32
Mesophonoidea Wills, 1910 ..... 32,34,53,*79*,82,90,92, 94,110,250,**B**
Mesophonus Wills, 1910 ..... 12,13,23,32,33,34,*79*,90,94,226,250
bromsgroviensis Wills, 1910 32,33,34,80,94,157,254
gracilis Wills, 1910 32,34,74,80,94,254
infans forms A, B, C, D, E Wills, 1947 32
infans A (?) *Mesophonus gracilis* Wills, 1947 74,254
infans A Wills, 1947 74
infans D Wills, 1947 74,254
infans E Wills, 1947 80,254
(?) *maculatus* (Brauer, Redtenbacher, and Ganglbauer, 1889) *81*
opisthophthalmus Wills, 1947 32,34,79,80,254
perornatus Wills, 1910 ..... 26,32,33,34,74,79,*80*, 122,243,244,247
pseudogracilis Wills, 1947 32,33,34,80,254
(?) *pulcherrimus* Wills, 1947 ..... 32,34,*80*
(?) *pulcherrimus* var. *immaculatus* Wills, 1947 .... 32,34,*80–81*
sp. Wills, 1947 33,74,80,94
Mesophonus fauna 90
Microlabiidae, n. fam. *133*,251,**B**
Microlabis Corda, 1839 ..... 126,*133–134*,151,152,251
sternbergii Corda, 1839 ..... 22,*134–135*,175,232
Miocrotityus rickyi Kjellesvig-Waering 22–23
Miller (1877) 81
Miller (1889) 81
miniatus, Eoctonus 13,*95–101*,207,208,243,244,253
minutus,
Anthracoscorpio 110
Lichnoscorpius *110–112*
Miocene 12,17
Sprudelsinter 239
Mioscorpio, n. gen. 17,*239*,252
zeuneri (Hadži, 1931) 12,*239–240*
Mitchell (1968) 12
Mixopteridae 27,218
Mixopteroidea 13,21
Mixopteroidea–Pterygotina assemblage 149
Mixopterus 31,88,183
kiaeri Størmer 20
Moore, J. I. (1923) 158,162,184,198,214,216
Moore, P. F. (1941) 229
Moore, R. C. (1964) 115
morphology, external ..... **F**
mouth, position of 48
mucronatus,
Acanthoscorpio *70*,125,243,244
Eoscorpius *181*
mucrones 73

Naraoia 197
National Museum, Prague, Czechoslovakia [NMP] 255,**F**
Natur-Museum und Forschungs-Institut Senckenberg, Frankfurt-am-Main, West Germany [SMF] 256,**F**
Nebo hierichonticus Simon 22
neonates and juveniles 75
Neoscorpii Thorell and Lindström, 1885 97,231,254
Neoscorpionina Thorell and Lindström, 1885 ..... 27,35,36,90, *231*,252
Netherlands
Orange Nassau Mine III, Heerlerheide 162
New York
Passage Gulf, Herkimer Co. 39,42,45,46,50,53
South Mountain, Schoharie Co. 126
Waterville, Oneida Co. 39
New York State Museum, Albany, NY [NYSM] 254,**F**
Novojilov and Størmer (1963) 133
nuncius, Palaeophonus 29,56,*142–149*,232

Olenoides 197
Oligocene 12
operculum 19,27,28,77,78
Ophismoblatta maculata (Brauer, Redtenbacher, and Ganglbauer, 1889) 81,254
Opisthacanthus 12,15,31,115
laevipes Pocock 22
Opisthophthalmus 12,15
opisthophthalmus, Mesophonus 32,34,79,80,254
Opsieobuthidae, n. fam. *214*,243,246,252,**B**
Opsieobuthus, n. gen. *214*,252
pottsvillensis (Moore, 1923) 22,78,86–87,*214–216*,243,246
oral chamber or tube 16,24,28,35,48,56,193,195,243,247
orbital ridges 57
ornamentation 21
ornata, Feistmantelia 151,*156–157*
(?) *Eoscorpius* 156,253
Isobuthus 156,253
Orthosterni Pocock, 1911 35,36,38,151,231,254
Orthosternina Pocock, 1911 ..... 16,21,23,25,27,*36*,37,163,*231*, 232,243,245,252,**B**

osborni,
Palaeophonus 39,254
Proscorpius 20,22,28,*39–48,*53,63,150,196,197
ostracodes 148

Palaeobuthidae, n. fam. *135,*153,243,245,251,**B**
Palaeobuthoidea, n. superfam. *135,*251,**B**
Palaeobuthus Petrunkevitch, 1913 ..... 96,126,*135,*151–154, 177,251
distinctus Petrunkevitch, 1913 ..... 21,*135–141,*172,176,177, 180,243,245
Palaeocharinidae 196
Palaeomachus Pocock, 1911 ..... 17,132,133,*242,*252
anglicus (Woodward, 1876) *242–243*
sp. Petrunkevitch, 1949 132,254
Paleontological Institute, Academy of Sciences, Leningrad, U.S.S.R. [LAS] 256,**F**
Palaeophonidae Thorell and Lindström, 1885 ... 18,60,*142,*251,**B**
Palaeophonoidea Thorell and Lindström, 1885 ..... 18,*142,*251,**B**
Palaeophonus Thorell and Lindström, 1884 ..... 14,17,28,66,*142,* 144,146,251
caledonicus Hunter, 1886 ..... **2** 56,57,148,254
hunteri Pocock, 1901 57,254
(?) *lightbodyi* Kjellesvig-Waering, 1954 ..... *149*
loudonensis Laurie, 1899 230,254
nuncius Thorell and Lindström, 1884 ..... **9** 29,56, *142–149,*232
osborni Whitfield, 1885 39,254
sp. Peach, 1885 57
Palaeopisthacanthidae, n. fam. 35,*232,*236,243,245,252,**B**
Palaeopisthacanthus Petrunkevitch, 1913 ..... 12,15,17,19,29,30, 31,90,162,163,*232,*252
mazonensis Petrunkevitch, 1913 163,254
schucherti Petrunkevitch, 1913 ..... 29,31,96,*232–236,*243,245
Palaeoscorpiidae Lehmann, 1944 ..... *61,*243,245,250,**B**
Palaeoscorpioidea Lehmann, 1944 ..... *61,*250,**B**
Palaeoscorpionidae Lehmann, 1944 254
Palaeoscorpius Lehmann, 1944 ..... 15,17,18,*61,*66,250
devonicus Lehmann, 1944 ... **3** 22,60,*61–63,*64,243,245
palustris, Anthracochaerilus *150–151,*192,243,246
Pandinus viatoris (Pocock) 22
Parabuthus
laevifrons (Simon) 243,248
villosus Peters 23
Paracarcinosoma sp. Kjellesvig-Waering 21
Parahughmilleria 12
Paraisobuthidae, n. fam. *198,*209,243,246,247,252,**B**
Paraisobuthoidea, n. superfam. *198,*208,210,212,213,252,**B**
Paraisobuthus, n. gen. 17,19,20,156,*198,*204,207,208,209,252
duobicarinatus, n. sp. ..... **16-18** 24,26,31,*204–207*
frici, n. sp. *203–204,*206
prantli, n. sp. 17,22,158,*198–203,*206,207,243,246,247
virginiae, n. sp. 96,97,100,*207–209*
Pareobuthidae, n. fam. *192,*243,246,252,**B**
Pareobuthus Wills, 1959 ..... *192,*252
salopiensis Wills, 1959 ..... 192,*193,*243,246
Paruroctonus mesaensis Stahnke 22–23
parvus, Eskiscorpio *191–192*
Peach (1883) 66,68,81,86,213,214
Peach (1885) 57,59,60,163
peachi, Phoxiscorpio *93–94,*243
pectinal plate 22,158,215,216
pectines 19–20,59–60,86–87,160
pedipalps 17,26
bifurcating tip 200,202
interlocking fingers 242–243
Periplaneta maculatus Brauer, Redtenbacher, and Ganglbauer, 1889 81,254
perornatus, Mesophonus 26,32–34,74,79,*80,*122,243,244,247
Petaloscorpio, n. gen. *220,*252
bureaui, n. sp. *220–222,*243,246,247
Petaloscorpionidae, n. fam. *220,*243,246,247,252,**B**
Petrunkevitch (1913) 15,21,22,39,57,66,81,86,96,97,100,102, 109,129,134,135,137,142,151,152,154,156,162,163, 168,171–173,176,184,186,193,194,196,197,204, 207,208,210,214,219,230,232,234,242
Petrunkevitch (1949) 15,21,22,39,57,66,81,86,96,102,107, 109–111,114,129,132,135,142,148,150,151,153, 154,158,163,168,172,176–178,180–184,193, 196,210,214,216–219,230,232,236,238
Petrunkevitch (1953) ... 13,15,21,22,32,34,37,39,57,59–61,66,74, 79,81,84,86,88,90,92,96,100–102,106,107,109, 110,113–115,118,121,129,131,132,134, 135,142,144,146,148–154,156,158,160, 162,163,168,176,177,181,184,186, 193,196,198,203,207,209,210,213, 214,219,230,231,232,236,242
Petrunkevitch (1955) 15,21,22,25,32,34,37,39,57,60,61,66,79, 81,84,86,90,96,101,102,107,114,121,129, 132–135,142,152–155,158,162,163,168, 176,177,181,196–198,203,210, 219,230,232,236,242
Phacopina 14
Phacops 197
Phalangiotarbida 23
Phanaeus 12,113,118
Phoxiscorpio, n. gen. *93,*250
peachi, n. sp. *93–94,*243,244
Phoxiscorpionidae, n. fam. *93,*243,244,250,**B**
Pinotus 12,118
Pocock (1901) 39,57,59,60,142
Pocock (1911) 35,36,66,81,86,101–103,109,113,141,148, 151–154,158,161,184,186,198,204, 207,209,210,214,219,236,242
poison glands in eurypterids 26–27,31
pottsvillensis,
Eobuthus 214,253
Isobuthus 214,253
Opsieobuthus 22,78,86–87,*214–216,*243,246
prantli, Paraisobuthus .. 17,22,158,*198–203,*206,207,243,246,247
preabdomen 20–21
Praearcturidae, n. fam. *121,*243,244,251,**B**
Praearcturus Woodward, 1871 ..... *121,*125,251
gigas Woodward, 1871 ..... 78,*121–125,*243,244
pregenital tergite 121,122
preoral chamber—see: oral chamber or tube
prepectinal plate 22–23,27–28,77,78,177,215–216
preservation 12
Princeton University Museum [PU] 254,**F**
Proscorpiidae Scudder, 1885 ..... 14,*39,*225,243,245,250,**B**
Proscorpioidea Scudder, 1885 ..... *39,*69,250,**B**
Proscorpius Whitfield, 1885 ..... 14,16–18,21,23,28,*39,*48,52,56, 146,149,183,230,250
osborni (Whitfield, 1885) ..... **1** 20,22,28,*39–48,*53, 63,150,196,197,231,243,245
prosomal appendages 16–19
Protocarus crani Hirst 197

protolobosternous abdominal plates 25,27,*36*,37,142,149, 218,219
Protoscorpiones Petrunkevitch, 1953 231
Protoscorpionina (Protoscorpiones) Petrunkevitch, 1949 254
protosternite (hypothetical) 25,37
Pseudoarchaeoctonus, n. gen. *68*,250
denticulatus, n. sp. *68–70*,192
pseudobuthiformis,
Leioscorpio 101,102,*209–210*,220
Mesophonus 32–34,80,254
Pseudobuthiscorpiidae, n. fam. 162,163,170,209,*218*,220, 243,246,252,**B**
Pseudobuthiscorpioidea, n. superfam. 95,178,*218–219*,220, 222,252,**B**
Pseudobuthiscorpius, n. gen. 209,*219*,252
labiosus, n. sp. 101,102,112,*219–220*,243,246
pseudogracilis, Stenoscorpio 34,*74–75*
Pterygotidae 166
Pterygotus mcgrewi Kjellesvig-Waering and Richardson 73
pulcher,
Eoscorpius 21,22,139,163,*177–181*,197,212
Lichnophthalmus 13,14,19,177,180,181,254
pulcherrimus, Mesophonus (?) 32,34,*80*
pulcherrimus var. *immaculatus, Mesophonus* (?) 32,34,*80–81*
pustulosus,
Spongiophonus 32,34,79,*121*,243,244
Spongiotarsus 121,254

rakovnicensis, Eobuthus 151–153,*158–160*,162,186,198, 202,243,246,253
repositories 254–255,**F**
Rhinocarcinosoma 183
Rhopalurus borelli 33
richardsoni, Branchioscorpio 20,24–25,46,73,79,125,199,222, *226–229*,231,243,245
robustus, Cyclophthalmus *132–133*
Rolfe (1963) 253
Rolfe (1969) 121,125
Rolfe (1980) 121
Rolfe (1982) 129
Royal Scottish Museum [RSM] 255,**F**
Ruedemann (1919) 61

salopiensis, Pareobuthus 192,*193*,243,246
Salter (1859) 12,149,182,183
Schawaller (1979) 12
Schawaller (1982) 12
schizochroal (aggregate) eyes 13
schmidti, Liassoscorpionides *90–93*
schucherti, Palaeopisthacanthus 29,31,96,*232–236*,243,245
Scoloposcorpio, n. gen. *212*,252
cramondensis, n. sp. *213–214*
Scoloposcorpionidae, n. fam. *212*,214,252,**B**
Scorpio 12,17,31,239
maurus palmatus Seuzet 243,248
schweigeri Holl, 1829 12
zeuneri Hadži, 1931 239,254
scorpionid type eurypterids 31,218
Scorpionida Latreille, 1817 14,26–27,34
g. and sp. indet. Størmer, 1969 ..... *242*,252
incertae sedis Petrunkevitch 90
Scorpionidae Leach, 1815 ..... 15,22,29,59,116,211,231, *239*,243,248,252,**B**
Scorpionides Leach, 1815 232,254
Scorpionlike eurypterid ? gen. et spec. indet. Størmer, 1960 ... 52
Scorpionoidea Leach, 1815 ..... 32,38,152,162,*232*,239,**B**
Scorpiops 31
Scotland
Airdrie, Lanarkshire 108,109,116,223
Cramond near Edinburgh 213
Crookhill-Beigh, North Ayrshire 225
Dalmeny railroad cutting near Edinburgh 93
Dysart, Fife 214
Foulden, Berwickshire 188
Gutterford Burn, Pentland Hills 230
Lesmahagow 57
River Esk, Langholm, Dumfriesshire 66,68,77,78,86,150, 188,190,191,217
Scudder (1884) 152,153,162
Scudder (1885) 39
Scudder (1886) 39
Sedgwick Museum [SM] 255,**F**
senior, Cyclophthalmus 107,*129–132*,133,153,160,175, 203,243,245,253
Shimer and Shrock (1944) 81
sibiricus, (?) *Cyclophthalmus* *133*
Silurian
Downtonian 126,149
Fiddlers Green Dolomite (Ludlow age) 39,42,45,46,50,53
Llandovery–Wenlock 57,230
lower Wenlock, top of Högklintslager beds 143
Smithsonian Institution 254,**F**
sparthensis,
Anthracoscorpio 184,198,253
Eoscorpius 106,*184–186*,202,253
spine on maxillary lobe 195–196
Spongiophonidae, n. fam. 34,73,*121*,243,244,251,**B**
Spongiophonoidea, n. superfam. 34,*120–121*,251,**B**
Spongiophonus Wills, 1947 ..... 15,28,32,34,79,*121*,251
pustulosus Wills, 1947 ..... 32,34,79,*121*,243,244
Spongiotarsus Wills (in error) 32,121
pustulosus Wills (in error) 121,254
spurs, tibial and basitarsal 28
squamosus, Loboarchaeoctonus 53,66,*216–218*,243,245
squarrosus, Trachyscorpio *188–190*
Staatliches Museum für Naturkunde, Stuttgart, West Germany [SMN] 256,**F**
Stenoscorpio, n. gen. 34,*73–74*,250
gracilis (Wills, 1910) 34,73,*74*,75,90,243,244
pseudogracilis (Wills, 1947) 34,*74–75*
Stenoscorpionidae, n. fam. 34,*73*,243,244,250,**B**
sternbergii,
Cyclophthalmus 134,253
Microlabis 22,*134–135*,175,232
sternites 23–24,28,29,31,32,33,36,37,227
sternum 15–16,27,28,193,195
stigmata 23–24,28,29,31,32,232
Størmer (1934) 125
Størmer (1954) 216
Størmer (1955) 20,88
Størmer (1960) 52
Størmer (1963) 17,19,20,22,23,57,76–78,81,84,86, 87,94,167,192,197,218
Størmer (1969) 242
Størmer (1970) 26,31,48,52,229
Størmer (1976) 23,24
Stoermeroscorpio, n. gen. 14,28,*53*,56,250
delicatus, n. sp. *53–56*

Stoermeroscorpionidae, n. fam. *53*,250,**B**
Stoermeroscorpionoidea, n. superfam. *53*,250,**B**
stratigraphic distribution 249–252
stridulating organ or area 33,122–124,226
Stumm and Kjellesvig-Waering (1962) 14
Stylonuroidea 13
suborders 35–36
sutcliffei,
Geralinura ? 86,88,253
Heloscorpio *88–90*,243,244,247
Trigonoscorpio ? 88,254
Svensk Riksmuséet, Stockholm [SRM] 256,**F**
Sweden
Vattenfallet, Visby, Gotland 143
synonyms, index of 253–254

Tarsopterella scotica (Woodward) 24,97
tarsus 28
taxobases 34–38
Telmatoscorpio, n. gen. 20,30,31,209,*210*,252
brevipectus, n. sp. 208,*210–212*,243,246
Telmatoscorpionidae, n. fam. *210*,214,243,246,252,**B**
telson, poison-bearing 218
Teuthrautes 76
Thelyphonida 88
Thorell (1886) 22,39
Thorell and Lindström (1884a) 142
Thorell and Lindström (1884b) 142
Thorell and Lindström (1885) 56,66,86,129,134,142,146,148,149,151,153,214
tibial spine 18
Tiphoscorpio, n. gen. 26,*126*,251
hueberi, n. sp. ..... **5-8** 26,31,*126–129*
Tiphoscorpionidae, n. fam. *126*,251,**B**
Tiphoscorpionoidea, n. superfam. *126*,251,**B**
Titanoscorpio, n. gen. 17,*240*,252
douglassi, n. sp. 78,*240–242*
Tityus 12,17,20,60,110,167,206
ambarensis Schawaller, 1982 12
eogenus Menge, 1869 12
melanostictus Pocock 156,199
pictus Pocock 22
rufofuscus Pocock 23
serrulatus 19
smithi Pocock 23
trinitatis Pocock 22–23,86–87
Trachyscorpio, n. gen. *188*,252
squarrosus, n. sp. *188–190*
(?) sp. *190*
tracheae 26
"triangular sternum" 187
Triarthrus 197
Triassic
Lower Keuper Sandstone Series 29,30,74,75,80,81,94,121,157
Upper Bunt Sandstone 30
Triassic scorpions (British) 23,24,26,28–34
trichobothria 17,76,99,103,164,226,228,232,234,239
trichogen cells 17,103
Trigonoscorpio Petrunkevitch, 1913 88,162,163,254
americanus Petrunkevitch, 1913 .... 163,*173–174*,175,176,254
(?) *sutcliffei* (Woodward, 1907) 88,254
Trigonoscorpionidae Dubinin, 1962 254
trilobation of preabdominal tergites 88
trochanter, double 18,48,93,226
tuberculatus,
Alloscorpius 177,214,253
Archaeoctonus 214,216,217,253
Benniescorpio *213–214*
Centromachus 214,216,253
Eoscorpius 213,214,253
Typhlochactas 12,28,144,239
Typhlopisthacanthus Petrunkevitch, 1949 90,162,163,236,254
anglicus Petrunkevitch, 1949 30,236,238,239,254
mazonensis (Petrunkevitch, 1913) ... 15,163,169,*170–171*,175,176,236,254
Typhloscorpius Petrunkevitch, 1949 162,163,254
distinctus Petrunkevitch, 1949 ..... 13,15,181,*182–183*,254
typicus, Eoscorpius 109,110,135,137,138,162,163,*171–173*,175,176,253

ungues 28
U. S. National Museum of Natural History, Smithsonian Institution [U.S.N.M] 254,**F**
University of Illinois Geological Museum [UI] 254,**F**
University of Kansas Geological Museum [KU] 114,**F**
University of Laval, Quebec [UL] 255,**F**
University of Michigan Museum of Paleontology [UMMP] 254,**F**
Urodacus 167
Uroplectes triangulifer marchalli (Pocock) 22,23
U.S.S.R.
Kemerov region, Siberia 133
Ust Balei region, Siberia 81

Vachon (1963) 17,38,233,234
Vaejovidae 15,22,59,243,248
Vaejovis punctipalpi (Wood) 243,248
Versluys and DeMoll (1923) 57
virginiae, Paraisobuthus 96,97,100,*207–209*
Vogel and Durden (1966) 29,35,232
volcanic ash 12

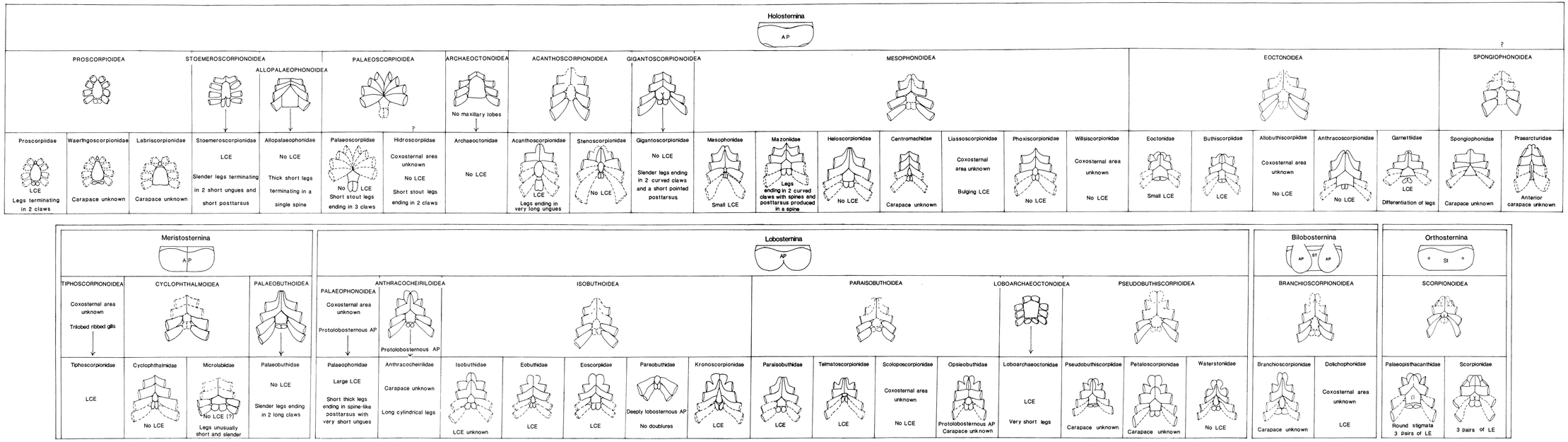
Waeringoscorpio Størmer, 1970 ..... 15,18,48,*52*,56,136,149,250
hefteri Størmer, 1970 ..... 26,31,48,*52*,229,243,245
Waeringoscorpionidae Størmer, 1970 ..... *52*,243,245,250,**B**
wardingleyi,
Alloscorpius 84,176,253
Eoscorpius (*Mansonia*) 84,253
Mazonia 16,*84–85*
waterlimes 56
Waterston (1975) 24,97,206
Waterstonia, n. gen. 15,19,156,158,*222*,225,228,252
airdriensis, n. sp. 13,142,*222–224*,225,243,246
(?) *brachistodactyla,* n. sp. *224–225*
Waterstoniidae, n. fam. 220,*222*,243,246,252,**B**
Wattisonia Wills, 1960 ..... *242*,252
coseleyensis Wills, 1960 ..... *242*
Weinbergina opitzi 61
Werner (1934) 33,79
West Germany
Alkan an der Mosel 52
Böttingen, Swabian Alps 239
Eschenbach, near Bundenbach 61
Hondelage bei Braunschweig 90,92
Willwerath, Eifel 242
Whitfield (1885a) 39
Whitfield (1885b) 39,196
Whitfield (1886) 39
Wild Drawing Tube 61

Wills (1910) 28,32,33,34,74,79,80,92,94
Wills (1925) 192,193
Wills (1934) 163
Wills (1947) 12,13,23,25,26,28,29,30,32,33,34,46,73,74, 75,79,80,90,92,94,121,122,157, 158,190,196,197,226
Wills (1959) 19,35,37,38,66,154,167,176,177,178, 179,181,192,193,197
Wills (1960) 25,35,38,42,66,81,101,102,105,112,113, 135,140,177,181,213,214,242
Wills (1964) 38
Wills (1965) 13,181,206
Wills (1967) 181
willsi,
Bromsgroviscorpio 34,*157–158*,190
Gigantoscorpio 19,22,31,75,*76–79*,125,189,192, 199,218,243,244,247
Willsiscorpio, n. gen. 34,*94*,250
bromsgroviensis (Wills, 1910) 26,*94*,158
Willsiscorpionidae, n. fam. 34,*94*,250,**B**
woodiana,
Eoscorpius (*Mazonia*) 81,253
Mazonia 13,21,28,*81–84*,110,168,214,243,244,247
Woodward (1871) 121
Woodward (1872) 121
Woodward (1876) 242
Woodward (1877) 121
Woodward (1907) 84,86,88
Wyoming
Cottonwood Canyon, Big Horn Mts. 63,70,125,226

Xiphosura 13,19,24,196

Yale Peabody Museum [YPM] 255,**F**

zeuneri,
Mioscorpio 12,*239–240*
Scorpio 239,254



Text-figure 5.—Key to the classification of the Scorpionida, showing the relationship of the higher taxa, infraorders through families [prepared by A.S.C.]. See foldout inside front cover for explanation of abbreviations.

PREPARATION OF MANUSCRIPTS

Palaeontographica Americana currently appears irregularly, on an average of about one monograph each year. This series is a publication outlet for significant longer paleontological monographs for which high quality photographic illustrations and the large quarto format are a requisite.

Manuscripts submitted for publication in this monograph series must be typewritten, and double-spaced *throughout* (including direct quotations and references). All manuscripts should contain a table of contents, lists of text-figures and (or) tables, and a short, informative abstract that includes names of all new taxa. Format should follow that of recent numbers in the series. All measurements must be stated in the metric system, alone or in addition to the English system equivalent. The maximum dimensions for photographic plates are 178 mm × 229 mm (7″ × 9″; outlined on this page). Single-page text-figures should be drafted for reproduction as single column (82 mm; 3¼″) or full page (178 mm; 7″) width, but arrangements can be made to publish text-figures that must be larger. Any lettering in illustrations should follow the recommendations of Collinson (1962).

Authors must provide three (3) copies of the text and accompanying illustrative material. The text and line-drawings may be reproduced xerographically, but glossy prints at publication scale must be supplied for all half-tone illustrations and photographic plates. These prints should be identified clearly on the back.

All dated text-citations must be referenced. Additional references may be listed separately if their importance can be demonstrated by a short general comment, or individual annotations. Referenced publication titles must be spelled out in their entirety. Citations of illustrations within the monograph bear initial capitals (*e.g.*, Plate, Text-figure), but citations of illustrations in other articles appear in lower-case letters (*e.g.*, plate, text-figure).

Original plate photomounts should have oversize cardboard backing and strong tracing paper overlays. These photomounts should be retained by the author until the manuscript has been formally accepted for publication. Explanations of text-figures should be interleaved on separate numbered pages within the text, and the approximate position of the text-figure in the text should be indicated. Explanations of plates follow the Bibliography.

Authors are requested to enclose $10 with each manuscript submitted, to cover costs of postage during the review process.

Collinson, J.
1962. *Size of lettering for text-figures.* Journal of Paleontology, vol. 36, p. 1402.

Gilbert Dennison Harris
(1864 - 1952)

Founder of *Palæontographica Americana* (1916)

ISBN 0-87710-401-8