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Re-examination of diagnostic traits for the higher classification of Dermaptera (Insecta) and a new classification system for Neodermaptera based on a revised dataset

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ABSTRACT

Suborder Neodermaptera (Dermaptera) includes over 2,000 species of extant earwig species. To revise the higher classification of this group, the morphologies of the neck, epiproct, and male and female terminal structures, all of which have been considered important to define higher neodermapteran taxa, were re-evaluated for representative species in the light of contemporary advances in their phylogenetic analyses. As the result, the definitions of blattoid- and forficuloid necks are redefined based on the shape of the posterior end of the posterior lateral cervical sclerites, which is either acutely bent inward or only gently curved. This dichotomy is correlated with the penis configuration immediately after imaginal eclosion, providing more stable definitions to Protodermaptera (with a blattoid-neck and two penises bent to the anterior) and Epidermaptera (with a forficuloid-neck and one or two penises point posteriorly). Accordingly, Apachyidae, Gonolabinidae (= Gonolabininae), Allostethidae (= Allostethinae) are proposed to be transferred to Protodermaptera, while Hemimeridae should be placed in Eudermaptera, as well as Arixeniidae. After several rearrangements (removal of Allostethinae and Gonolabininae to Protodermaptera, and inclusion of Isolaboidinae to Anisolabididae), it is challenging to delineate Labiduroidea (Labiduridae) from Anisolabidoidea (Anisolabididae). Polyphyly of Eudermaptera and Spongiphoridae, suggested by several previous molecular works, could be an artifact while the latter could be paraphyletic, as well as the placement of neodermapteran root on the branch to Apachyidae. Although still under debate, the root of Neodermaptera is likely situated within the redefined Protodermaptera, which appears to be paraphyletic, while Epidermaptera and Eudermaptera are likely monophyletic.

KEYWORDS cervical sclerites, earwigs, Epidermaptera, genitalia, neck structure, Polyneoptera, Protodermaptera

1. INTRODUCTION

Dermaptera de Geer, 1773, an insect order within Polyneoptera Martynov, 1923, comprises over 2,000 species predominantly found in tropical, subtropical, and warm temperate regions (Popham 2000; Grimaldi and Engel 2005; Haas 2018; Hopkins et al. 2023). Commonly known as earwigs, these insects are typically omnivorous or carnivorous and inhabit a variety of natural and semi-natural environments (Günther and Herter 1974; Renz and Kevan 1991; Haas 2018). Engel and Haas (2007) conducted a comprehensive revision of family-level and higher taxonomic names within Dermaptera and proposed a new classification system, in which Dermaptera is categorized into three suborders: Archidermaptera Bey-Bienko, 1936 and Eodermaptera Engel, 2003, both consisting exclusively of fossil species, and Neodermaptera Engel, 2003, which includes both fossil and extant species. The classification system of Neodermaptera, as proposed by Engel and Haas (2007), is presented in Table 1. Subsequently, in Engel et al. (2017), Engel separated genus *Haplodyplatys* Hincks, 1955 from the Diplatyinae (Diplatyidae Verhoeff, 1902), establishing family Haplodyplatyidae Engel, 2017; the definition of this family was revised by Kamimura and Ferreira (2018). Kamimura and Ferreira (2017) transferred Cylindrogastrinae Maccagno, 1929 and Diplatymorphinae Boeseman, 1954 from Pygidicranidae Verhoeff, 1902 to Diplatyidae. However, with recent advances in phylogenetic analyses of

Table 1 Higher classification of the Neoermaptera proposed by Engel and Haas (2007).

- Order DERMAPTERA de Geer, 1773
  - Suborder Neodermaptera Engel, 2003
    - Infraorder Protodermaptera Zacher, 1910
        - Superfamily Karschielloidea Verhoeff, 1902
          - Family Karschiellidae Verhoeff, 1902
        - Superfamily Pygidicranoidea Verhoeff, 1902
          - Family Diplatyidae Verhoeff, 1902
          - Family Pygidicranidae Verhoeff, 1902
            - Subfamily † Burmapygiinae Engel & Grimaldi, 2004
            - Subfamily Anataeliinae Burr, 1909
            - Subfamily Blandicinae Burr, 1915
            - Subfamily Brindlensiinae Srivastava, 1985
            - Subfamily Challiinae Steinmann, 1973
            - Subfamily Cylindrogastrinae Maccagno, 1929
            - Subfamily Diplatymorphinae Boeseman, 1954
            - Subfamily Echinosomatinae Burr, 1910
            - Subfamily Esphalmeninae Burr, 1909
            - Subfamily Pygidicraninae Verhoeff, 1902
            - Subfamily Pyragrinae Verhoeff, 1902
    - Infraorder Epidermaptera Engel, 2003
      - Parvorder Paradermaptera Verhoeff, 1902
          - Superfamily Hemimeroidea Sharp, 1895
            - Family Hemimeridae Sharp, 1895
          - Superfamily Apachyoidea Verhoeff, 1902
            - Family Apachyidae Verhoeff, 1902
      - Parvorder Metadermaptera Engel, 2003
          - Superfamily Anisolabidoidea Verhoeff, 1902
            - Family Anisolabididae Verhoeff, 1902
              - Subfamily † Cretolabiinae Engel & Haas, 2007
              - Subfamily Anisolabidinae Verhoeff, 1902
              - Subfamily Anophthalmolabidinae Steinmann, 1975
              - Subfamily Antisolabidinae Brindle, 1978
              - Subfamily Brachylabidinae Burr, 1908
              - Subfamily Gonolabininae Popham and Brindle, 1966
              - Subfamily Idolopsalinae Steinmann, 1975
              - Subfamily Isolabidinae Verhoeff, 1902
              - Subfamily Palicinae Burr, 1910
              - Subfamily Parisolabidinae Verhoeff, 1904
              - Subfamily Titanolabidinae Srivastava, 1982
      - Parvorder Eteodermaptera Engel, 2003
        - Nanorder Plesiodermaptera Engel, 2003
          - Superfamily Labiduroidea Verhoeff, 1902
            - Family Labiduridae Verhoeff, 1902
              - Subfamily Allostethinae Verhoeff, 1904
              - Subfamily Labidurinae Verhoeff, 1902
              - Subfamily Nalinae Steinmann, 1975
        - Nanorder Eudermaptera Verhoeff, 1902
          - Superfamily Forficuloidea Latreille, 1810
            - Family Arixeniidae Jordan, 1909
            - Family Spongiphoridae Verhoeff, 1902
              - Subfamily Caecolabiinae Steinmann, 1990
              - Subfamily Cosmogeracinae Brindle, 1982
              - Subfamily Geracinae Brindle, 1971
              - Subfamily Isolaboidinae Brindle, 1978
              - Subfamily Isopyginae Hincks, 1951
              - Subfamily Labiinae Burr, 1909
              - Subfamily Nesogastrinae Verhoeff, 1902
              - Subfamily Pericominae Burr, 1911
              - Subfamily Ramamurthiinae Steinmann, 1975
              - Subfamily Rudracinae Srivastava, 1995
              - Subfamily Sparattinae Verhoeff, 1902
                - Tribe Auchenomini Burr, 1909
                - Tribe Chaetospaniini Steinmann, 1990
                - Tribe Sparattini Verhoeff, 1902
              - Subfamily Spongiphorinae Verhoeff, 1902
              - Subfamily Strongylopsalinae Burr, 1911
              - Subfamily Vandicinae Burr, 1911
            - Family Chelisochidae Verhoeff, 1902
              - Subfamily Chelisochinae Verhoeff, 1902
              - Subfamily Genitalatinae Steinmann, 1987
              - Subfamily Kinesinae Srivastava, 2003
            - Family Forficulidae Latreille, 1810
              - Subfamily Allodahliinae Verhoeff, 1902
              - Subfamily Ancistrogastrinae Verhoeff, 1902
              - Subfamily Anechurinae Verhoeff, 1902
              - Subfamily Diaperasticinae Burr, 1907
              - Subfamily Forficulinae Latreille, 1810
              - Subfamily Neolobophorinae Burr, 1907
              - Subfamily Opisthocosmiinae Verhoeff, 1902
              - Subfamily Skendylinae Burr, 1907

† Taxa with fossil species

dermapterans, the classification system proposed by Engel and Haas (2007) requires further revision.

For example, Engel and Haas (2007) included Apachyidae Verhoeff, 1902 (the sole family constituting the superfamily Apachyoidea Verhoeff, 1902) and Hemimeridae Sharp, 1895 (the sole family constituting the superfamily Hemimeroidea Sharp, 1895) in their parvorder Paradermaptera Verhoeff, 1902. Members of Hemimeridae, which are exclusively found in sub-Saharan Africa, live phoretically on murid mammals (Nakata and Maa 1974). Conventionally, this family was treated as either an independent insect order (Diploglossata de Saussure, 1879) or a suborder of Dermaptera (as Dermodermaptera Verhoeff, 1902 or Hemimerina Burr, 1911). However, recent advancements in molecular phylogenetics suggest that Hemimeridae is part of Eudermaptera Verhoeff, 1902, a potentially monophyletic clade at the nanorder level within the Engel and Haas (2007) system, along with families Spongiphoridae Verhoeff, 1902, Chelisochidae Verhoeff, 1902, Forficulidae Latreille, 1810, and Arixeniidae Jordan, 1909 (Jarvis et al. 2005; Kočárek et al. 2013; Naegle et al. 2016; Wipfler et al. 2020). Conversely, accumulating evidence suggests that Apachyidae exhibits several presumably plesiomorphic traits of extant Dermaptera, such as the maternal care of eggs attached to substrates, more than five nymphal instars (Shimizu and Machida 2024), and distinct wing structures (Haas and Kukalová-Peck 2001). Phylogenetic studies that have included both Apachyidae and Hemimeridae provide no support for either the monophyly or paraphyly of Apachyidae + Hemimeridae (Jarvis et al. 2005; Kočárek et al. 2013; Naegle et al. 2016; Wipfler et al. 2020).

In the present study, I revised the classification of Neodermaptera based on my re-examination of three traits: the neck structure, epiroct (opisthomeres), and penis configuration. These traits have been considered crucial in defining higher taxa within Neodermaptera. For example, Steinmann's classification system (1986, 1989a, b, 1990, 1993) categorizes free-living, extant earwigs (Neodermaptera excluding Hemimeridae and Arixeniidae) into two suborders: Catadermaptera Steinmann, 1986, which is characterized by earwigs with two penis lobes in the male genitalia, featuring a deep posterior incision (Fig. 1 A–E), and Eudermaptera, which comprises earwigs with a single penis lobe (Fig. 1F). Steinmann further categorized Catadermaptera into three sections: Protodermaptera, Mesodermaptera Steinmann, 1986, and Paradermaptera, as described below.

Section 1, Protodermaptera: The neck is of the blattoid type, characterized by a small, distinct posterior ventral cervical sclerite located anterior to the prosternum. The posterior margin of this sclerite either does not reach or just touches the anterior margin of the prosternum. The anterior ventral cervical sclerite never contacts the posterior ventral cervical sclerite or only meets it along a broad section.

Section 2, Mesodermaptera: The neck is of the forficuloid type, with a large posterior ventral cervical sclerite located anterior to the prosternum. Its posterior margin touches the prosternum along a wide section, and the anterior ventral cervical sclerite typically touches the posterior ventral cervical sclerite. In both sexes, abdominal tergite 10 appears normal and is not extended posteriorly into a tabular appendage between the cerci.

Section 3, Paradermaptera: The neck is of the forficuloid type, with a large posterior ventral cervical sclerite lying anterior to and in contact with the prosternum along a wide section, and an anterior ventral cervical sclerite typically in contact with the posterior ventral cervical sclerite. However, abdominal tergite 10 in both sexes is elongated posteriorly into a tabular appendage, known as the anal process, which projects between the cerci.

Following Crampton's (1926) pioneering research comparing neck structures across insect orders, Popham (1959) and Giles (1963) examined these structures in numerous dermapteran groups, although their interpretations and terminology left many inconsistencies. Nonetheless, the classification of Neodermaptera (Table 1), based on the size of the posterior cervical sclerite relative to the anterior cervical sclerite, or their relative positions (whether or not in contact), has been widely adopted without much criticism (Srivastava 1988, 2003, 2013; Haas 1995; Haas and Kukalová-Peck 2001), as reflected in Steinmann's system (1986, 1989a, b, 1990, 1993). Additionally, there remain many dermapteran taxa for which detailed neck morphology descriptions remain unavailable.

As Giles (1963) noted, "the terminology and homologies of the terminal plates between the forceps of the Dermaptera have been the subject of much discussion". In this context, these sclerites, formerly referred to as opisthomeres, are collectively termed epiprocts, regardless of their developmental origins. According to Klass (2001, 2003), in Dermaptera, the epiproct consists of two sclerites: tergum XI (the pygidium) and the dorsal sclerite of the telson. The pygidium is typically visible from the dorsal side and exhibits notable variability in shape among species within certain pygidicranids (e.g., *Echinosoma* Audinet-Serville, 1839 spp.) and many spongiphorids, making it a valuable character for species diagnosis (Steinmann 1986, 1990; Srivastava 1988, 2013). Conversely, the dorsal sclerite of the telson is located ventrally behind the anal region, usually concealed beneath the "penultimate sternite", which is sternum IX in adult males or nymphs and sternum VII in adult females. In some

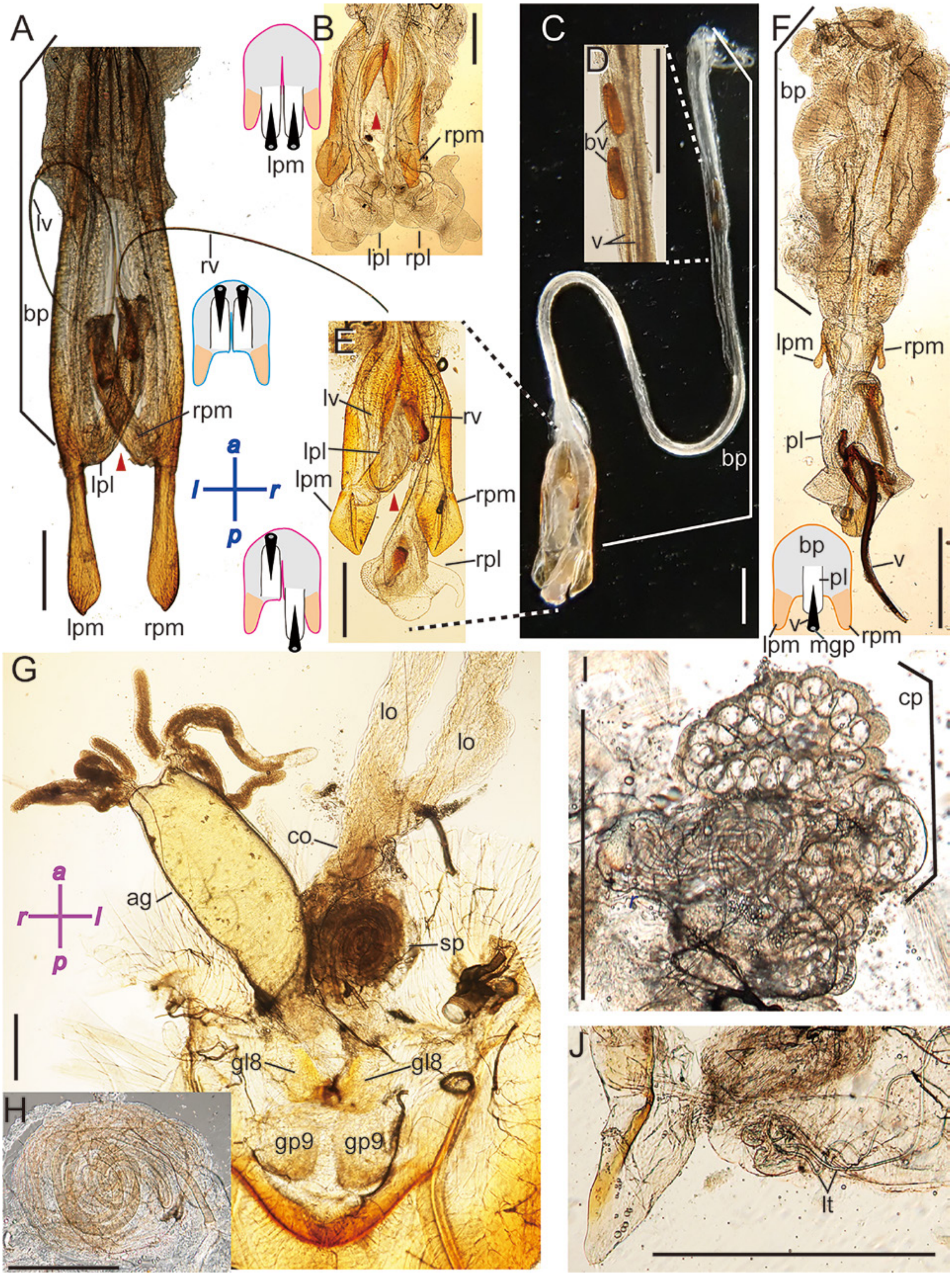

Fig. 1 Male (A–F) and female (G–J) genital structures of *Apachyus chartaceus* (A, G, H: spermatheca), *Euborellia annulipes* (B–E), *Labia minor* (F), and *Parapsalis infernalis* (I: spermatheca, J: lateral tubes), with the schematics of male genital configurations (in A, B, E, F). In B (before flipping of a penis lobe) and E (after flipping of the left penis lobe), only the posterior distal part is shown. The red arrowheads (in A, B, E) indicate the deep posterior incision of the basal piece. The anterior (*a*)-posterior (*p*) and right (*r*)-left (*l*) axes for A–F (dorsal views) and G–J (ventral views) are indicated in A and G, respectively. The explanations of schematics are given in that of F. ag: accessory gland, bp: basal piece, bv: basal vesicle, co: common oviduct; cp: coiled part of spermatheca, gl8: gonoplac VIII, gp9: gonapophysis IX, lo: lateral oviduct, lpl: left penis lobe, lpm: left paramere, lt: lateral tube, lv: left virga, mgp: male gonopore, pl: penis lobe, rpl: right penis lobe, rpm: right paramere, rv: right virga, sp: spermatheca, v: virga. Scales = 0.5 mm.

pygidicranids, three distinct parts can be identified within the epiproct, and early studies suggested that three different abdominal segments contribute to its formation as a plesiomorphic trait of Dermaptera (Verhoeff 1903; Burr 1916b; Matsuda 1976). The pygidium is fused with tergum X in two groups of free-living (i.e., non-epizoic) earwigs: Apachyidae, which includes *Apachyus* Audinet-Serville, 1831 (12 described species) and *Dendroiketes* Boeseman, 1954 (three species) (Steinmann 1989a, b; Sakai 1990; Srivastava 2013; Hopkins et al. 2023), and Gonolabininae Popham et Brindle, 1966 (formerly Gonolabinae, as corrected by Engel and Haas 2007), which encompasses only three species of *Gonolabina* Verhoeff, 1902 from Chile and Peru (Brindle 1967; Steinmann 1989a,b; Hopkins et al. 2023). Interestingly, previous studies have not explored the possibility that these two groups are closely related, despite their sharing of the fused terminal sclerite as an apomorphy.

Dermaptera is characterized by the unique morphology of the male genitalia. In some groups of Neodermaptera, males possess two penis lobes, each enclosing a sclerotized terminal portion of the ejaculatory duct, known as the virga, located at the posterior end of a plate-like structure, between the right and left parameres (also referred to as external parameres or metaparameres) (Fig. 1 A–E). Conversely, males of species belonging to the Spongiphoridae, Chelisochidae, Forficulidae, Arixeniidae, and Hemimeridae possess a single penis and thus a single virga (Fig. 1F). This distinct feature led Verhoeff (1902) to classify Neodermaptera (excluding Apachyidae) into two groups, the "Diandria" and "Monandria". The condition of possessing two penises has been regarded as plesiomorphic in Dermaptera: Ramamurthi (1959), Popham (1965a) and Kamimura (2006, 2007) demonstrated that a rudimentary ejaculatory duct is present on the seminal vesicle in species of the Spongiphoridae, Chelisochidae, and Forficulidae. Furthermore, in earwigs with two penises (i.e., Catadermaptera as classified by Steinmann 1986), both penises are reflexed and point anteriorly in Protodermaptera (sensu Steimann 1986), except in Karschiellinae Verhoeff, 1902, where the left penis is largely reduced. In other groups, the penises are bidirectional, with one pointing straight backwards and the other bending, as seen in the Paradermaptera and Mesodermaptera (Steinmann 1989a) (Fig. 1). Conventionally, the former condition has been considered more primitive among the Dermaptera (Popham 1965a).

Similar to several other sexually reproducing animals that engage in copulation, male genital structures of the Dermaptera exhibit high interspecific diversity (Kamimura 2014; Kamimura et al. 2023b). As a result, nearly all contemporary taxonomic studies describing new species of the Dermaptera include detailed descriptions of male genitalia to determine their placement at the genus, family, or even higher taxonomic levels. However, these descriptions are typically based on wild-caught male specimens with unknown mating histories, similar to taxonomic studies of many other insect groups. The post-embryonic changes in the paired penis configuration, whether unidirectional or bidirectional, have received limited attention (Kamimura 2006). In the present study, the importance of penis configuration in naïve males (i.e., prior to their first copulation or immediately after imaginal eclosion) is discussed, providing valuable insights into the evolutionary biology of the Dermaptera.

The terminology used in the present study for the dermapteran neck, wings, epiproct, and female genital structures largely follows conventions established by Giles (1963), Haas and Kukalová-Peck (2001), Klass (2001), and Klass (2003), respectively. For male genitalia, a modified terminology system based on Kamimura (2014) is also proposed.

2. MATERIALS AND METHODS

In addition to a comprehensive review of key references on dermapteran classification, phylogeny, and morphology, including monographs, catalogues, and compilations by Sakai (1985, 1987, 1990, 1991, 1992, 1993, 1994, 1995a, b, c, d, 1996), Steinmann (1986, 1989a, b, 1990, 1993), and Srivastava (1988, 2003, 2013), the present study re-examined the morphology of the neck, epiproct, and male and female genitalia in selected taxa of the Neodermaptera (Table 2).

To examine neck structures (specifically the arrangement of the cervical sclerites), the head and prothorax of each male sample was amputated, parallel to the cross-sectional planes using a micro-scissor designed for iris surgery (G-38240; Geuder, Heidelberg, Germany) attached to a handgrip (G-38246; Geuder). The cervical samples were cleared in 10% potassium hydroxide at 56°C for 5–40 min, depending on the sample size. After neutralisation in lactic acid, thorough washing in distilled water three times, and removal of the dorsal integument, each sample was mounted in a hole (depth, 0.6 mm) on a glass slide using glycerol. A BZ-X800 fluorescent microscope (Keyence, Osaka, Japan) equipped with a ×4 objective lens was used to observe autofluorescence from the sclerotized parts of the exoskeletons (Michels and Gorb 2012), with a filter set for red fluorescence (for tetramethylrhodamine-isothiocyanate staining: excitation, 545 nm; dichroic mirror, > 565 nm; absorbance filter, > 605 nm). Deconvoluted, fully-focused images were obtained using the sectioning module and analyzer software of the

Table 2 Samples used to examine the neck and terminal structures. The species names are followed by the family (and subfamily) names of the new system proposed in the present study in the parentheses.

Species	Locality	No. samples examined (F: female, M: male)			
		Cervical sclerites	Epiproct and associated structures	Spermatheca and associated structures	Genitalia
Allostethus indicum (Burmeister, 1838) (Allostethidae)	Penang, Malaysia	M1			
Anechura harmandi (Burr, 1904) (Forficulidae: Anechurinae)	Kanagawa, Japan		M1		
Anisolabella marginalis (Dohrn, 1864) (Anisolabididae: Anisolabidinae)	Kagoshima, Japan				M1*
Anisolabella marginalis (Dohrn, 1864) (Anisolabididae: Anisolabidinae)	Kanagawa, Japan				M1*
Anisolabella ryukyuensis (Nishikawa, 1969) (Anisolabididae: Anisolabidinae)	Kagoshima, Japan				M1*
Anisolabella ryukyuensis (Nishikawa, 1969) (Anisolabididae: Anisolabidinae)	Okinawa, Japan				M1*
Anisolabis martima (Bonelli, 1832) (Anisolabididae: Anisolabidinae)	Niigata, Japan	M1	M1		
Anisolabis seirokui Nishikawa, 2008 (Anisolabididae: Anisolabidinae)	Tokushima, Japan	M1			M1*
Apachyus chartaceus (de Haan, 1842) (Apachyidae)	Singapore	M1	F1	F1	M1*
Challia imamurai Nishikawa, 2006 (Pygidicranidae: Challiinae)	Kagoshima, Japan	M1			
Diplatys flavicollis Shiraki, 1908 (Diplatyidae: Diplatyinae)	Okinawa, Japan	M1			
Echinosoma denticulatum Hincks, 1959 (Pygidicranidae: Echinosomatinae)	Penang, Malaysia	M1	M1		
Eparchus yezoensis (Matsumura and Shiraki, 1905) (Forficulidae: Opisthocosmiinae)	Tokyo, Japan	M1			
Euborellia annulipes (Lucas, 1847) (Anisolabididae: Anisolabidinae)	Okinawa, Japan				M1*
Euborellia annulipes (Lucas, 1847) (Anisolabididae: Anisolabidinae)	Shizuoka, Japan				M2**
Euborellia annulipes (Lucas, 1847) (Anisolabididae: Anisolabidinae)	Tokyo, Japan				M6*
Euborellia pallipes (Shiraki, 1906) (Anisolabididae: Anisolabidinae)	Kanagawa, Japan				M1*
Euborellia pallipes (Shiraki, 1906) (Anisolabididae: Anisolabidinae)	Niigata, Japan				M1*
Euborellia pallipes (Shiraki, 1906) (Anisolabididae: Anisolabidinae)	Shizuoka, Japan				M2*
Labia minor (Linnaeus, 1758) (Spongiphoridae: Labiinae)	Hyogo, Japan	M1			M1
Labidura riparia (Pallas, 1773) (Labiduridae: Labiduridnae)	Niigata, Japan	M1	F1		
Parapsalis infernalis (Burr, 1913) (Pygidicranidae: Prolabiscinae)	Pahang, Malaysia			F1	
Platylabia major Dohrn, 1867 (Anisolabididae: Platylabiinae)	Penang, Malaysia	M1			
Proreus simulans (Stål, 1860) (Chelisochidae: Chelisochinae)	Kagoshima, Japan	M1			
Pyragra fuscata fuscata Audinet-Serville, 1831 (Pygidicranidae: Pyragrinae)	Montsinéry-Tonnegrande, French Guiana		M1		

* Naïve male
** 1 naïve + 1 mature

BZ-X800 microscope. Additionally, several samples were photographed under a differential interference contrast (DIC) microscope (BX53, ×100–400; Olympus, Tokyo, Japan) equipped with an Olympus Pen e-pl1s digital camera. Based on these photographs, selected parts of each image in focus were combined using Combine ZP Image Stacking Software (Hadley 2010). Composite images of intact specimens were also obtained using the microscope mode and focus-stacking sub-mode of a Tough-TG5 digital camera (Olympus).

To observe the epiproct and surrounding structures, after clearing and air-drying, composite images were captured using a Tough-TG5 digital camera, following the same procedure as described for neck structures.

Male and female genital structures were examined and photographed under a DIC microscope, following the methods described by Kamimura et al. (2023a) for male structures and those described by Kamimura and Lee (2017) for female structures.

3. RESULTS

3.1. Cervical sclerites

As reported by several previous authors (e.g., Popham 1959; Giles 1963), two large sclerites, the anterior and posterior ventral cervical sclerites, are present on the ventral side of the neck in all 12 examined earwig species (Figs 2, 3). These sclerites are positioned posterior to the gular sclerite of the head and anterior to the prosternum of the thorax. Traditionally, species with a blattoid neck type (e.g., members of the Haplodiplatyidae, Diplatyidae, and Pygidicranidae) are thought to have anterior and posterior ventral cervical sclerites of nearly equal size, whereas species with a forficuloid neck type (e.g., other families of the Neodermaptera) have a notably larger posterior sclerite. However, in the species examined, the variation was found to be more continuous, with a nearly identical sclerite size ratio observed in *Echinosoma denticulatum* Hincks, 1959 (Pygidicranidae) and *Eparchus yezoensis* (Matsumura et Shiraki, 1905) (Forficulidae) (Fig. 2A, K).

Both Popham (1959) and Giles (1963) noted the presence of two pairs of lateral sclerites on each side of the dermapteran neck. The anterior lateral cervical sclerite is an elongated plate, accompanied by an accessory sclerite with sparse setae, referred to as a latero-ventral sclerite by Popham (1959). This accessory sclerite is termed "associated sclerites of anterior lateral cervical sclerite" in the present study. The anterior end of the anterior lateral cervical sclerite is articulated to the flange extending from the head (Fig. 2). The posterior end of the anterior lateral cervical sclerite, which is partially covered by the posterior lateral cervical sclerite, forms an outward hairpin curve before connecting to the posterior lateral cervical sclerite (Figs 2, 3). In species such as *Ec. denticulatum*, *Challia imamurai* Nishikawa, 2006 (Pygidicranidae), *Diplatys flavicollis* Shiraki, 1908 (Diplatyidae), *Allostethus indicum* (Burmeister, 1838) (Allostethidae Verhoeff, 1904; see Discussion), and *Apachyus chartaceus* (de Haan, 1842) (Apachyidae), the posterior end of the posterior lateral cervical sclerite bends inward at an acute angle, thus V-shaped, near the humeral angle of the prosternum (Figs 2A–C, E, F, 3C, C'; schematically illustrated in Fig. 3A). Similar V-shaped structures have been illustrated by Matsuda (1970) for *Al. indicum* and by Nishikawa (1976) for *Parapsalis infernalis* (Burr, 1913) (Pygidicranidae). In other species examined in the present study such as *Anisolabis maritima* (Bonelli, 1832), *Anisolabis seirokui* Nishikawa, 2008 (Anisolabididae), *Platylabia major* Dohrn, 1867 (Anisolabididae), *Labidura riparia* (Pallas, 1773) (Labiduridae), *Labia minor* (Linnaeus, 1758) (Spongiphoridae), *Proreus simulans* (Stål, 1860) (Chelisochidae), and *Ep. yezoensis* (Forficulidae), as well as *Arixenia jacobsoni* Burr, 1912 (Arixeniidae), *Hemimerus talpoides* Walker, 1871 (Hemimeridae), and *Forficula auricularia* Linnaeus, 1758 (Forficulidae), which were previously studied by Crampton (1926), Henson (1953), Popham (1959), and Giles (1963), the posterior end of the posterior lateral cervical sclerite, which is bilobated to form an accessory sclerite, curves gently posteriorly towards the prosternal midline (Figs 2D, G–K, 3D, D'; schematically illustrated in Fig. 3B).

These fundamental structures are modified in certain species. Notably, the anterior and posterior lateral cervical sclerites appear fused in *Ap. chartaceus* (Fig. 2C). In species such as *Ec. denticulatum*, *C. imamurai*, *D. flavicollis*, and *Al. indicum*, the prosternum is divided into two distinct parts: a small anterior section and a larger posterior section (Fig. 2A, B, E, F). Matsuda (1970) referred to the anterior section in *Al. indicum* as the presternum. In *Ec. denticulatum*, the anterior and posterior sections are clearly separated (Fig. 2A), and a pair of distinct, triangular sclerites are present at the humeral angles of the prosternum (Figs 2A, 3E, E'). Giles (1963), who observed similar structures in *Echinosoma afrum* Palisot de Beauvois, 1805, suggested that these may represent another set of accessory sclerites associated with the anterior lateral cervical sclerites. Note that Popham (1959) reported a pair of similar sclerites for *Diplatys macrocephalus* (Palisot de Beauvois, 1805) (Diplatyidae) and *Bormansia africana* Verhoeff, 1902 (Pygidicranidae). Although Giles' (1963) interpretation is plausible, these structures appear to develop on the distal part of the posterior lateral cervical sclerites, i.e., the inner portion of the V-shaped ends (Fig. 3E, E'). Another possibility is that they are separated parts of the posterior ventral cervical sclerite.

3.2. Epiproct

The present study corroborates the observations of previous authors regarding the epiproctal structures of selected dermapteran species (Fig. 4). Although early studies claimed that the epiproct consists of three sclerites, i.e., pygidium, metapygidium, and telson, in some pygidicranids (Verhoeff 1903; Burr 1915a), it is composed of two sclerites both in *Pyragra fuscata fuscata* Audinet-Serville, 1831 (Pygidicranidae: Pyragrinae Verhoeff, 1902) and *Echinosoma denticulatum* (Pygidicranidae: Echinosomatinae Burr, 1910), similar to *Anisolabis maritima* (Anisolabididae) and *Anechura harmandi* (Burr, 1904) (Forficulidae) (Fig. 4). According to Klass' interpretation (2001, 2003), these sclerites are tergum XI (11th abdominal tergite or pygidium) positioned dorsally and the dorsal sclerite of the telson located ventrally, connected each other by a narrow membranous region. In *Py. fuscata fuscata*, the dorsal sclerite of telson appears to be further divided into two sections by a constriction, although without articulation by a membranous region (Fig. 4A, A'), as similarly concluded by Klass (2001).

In *Apachyus chartaceus* (Apachyidae), terga X and XI are fully fused, forming a tabular anal process (Fig. 4E, E'), as noted in many previous studies (e.g., Zacher 1915). Ventrally, the lateral and anal plates, which are commonly present in both male and female earwigs (Klass 2003; Schneider and Klass 2013; Fig. 4F, F'), appear to be fused with tergum X and the epiproct, creating a large capsule that houses the muscles responsible for cercal movements (Fig. 4E, E').

3.3. Male and female genitalia

Male genitals were examined in several representative species, particularly focusing on naïve males, to illustrate differences prior to copulatory experiences. As an addition to the terminology system established by Kamimura (2014), the term "basal piece" is proposed in the present study for the main body of the dermapteran male genitalia. Either a single or two

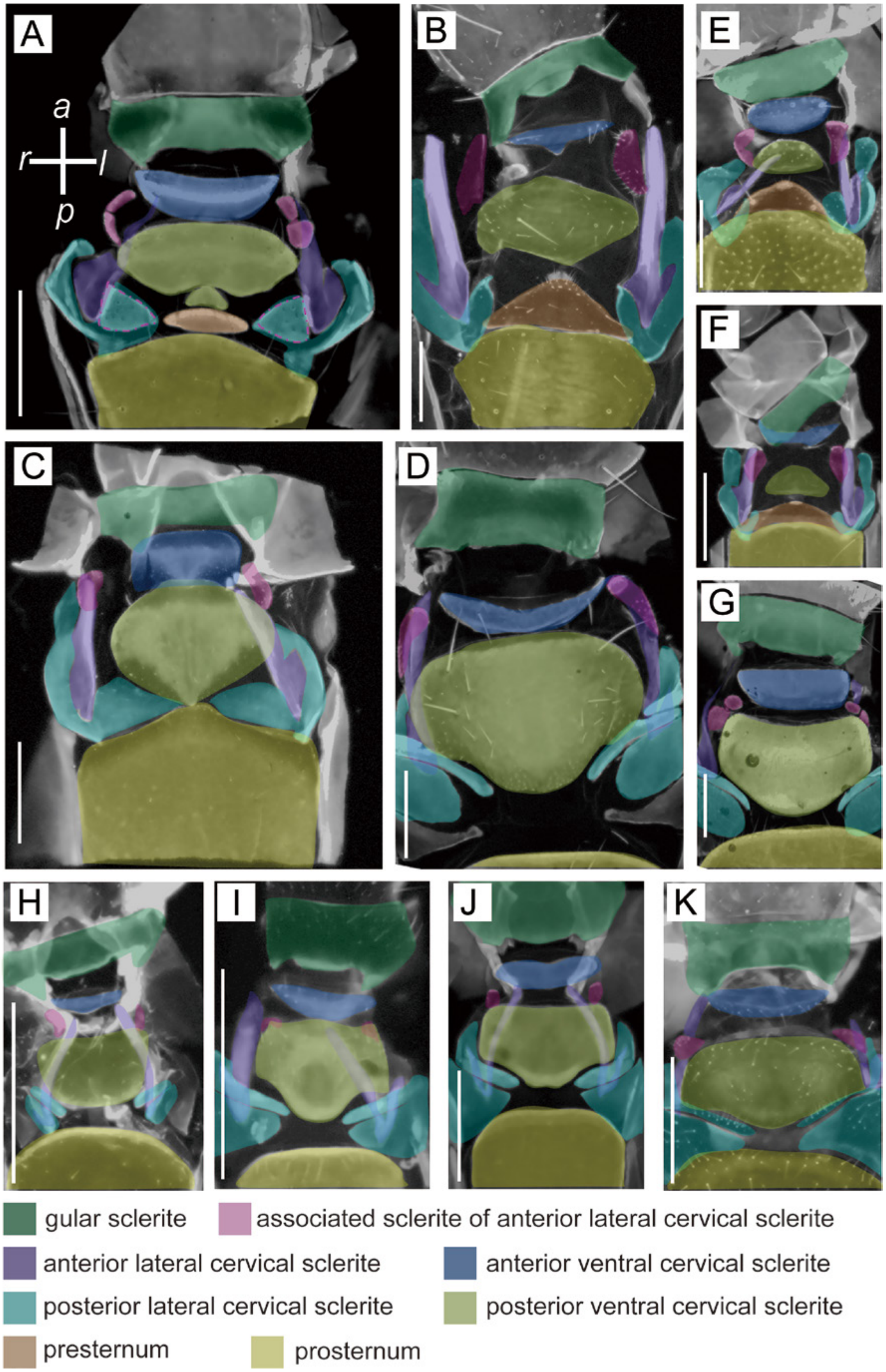

Fig. 2 Auto-fluorescence micrograph images (ventral views) of the cervical structures of 11 species of Neodermaptera. A. *Echinosoma denticulatum*. B. *Allostethus indicum*. C. *Apachyus chartaceus*. D. *Anisolabis maritima*. E. *Challia imamurai*. F. *Diplatys flavicollis*. G. *Labidura riparia*. H. *Platylabia major*. I. *Labia minor*. J. *Proreus simulans*. K. *Eparchus yezoensis*. Additional sclerites of an unknown origin of *Ec. denticulatum* are delineated with the magenta broken lines. The anterior (*a*)-posterior (*p*) and right (*r*)-left (*l*) axes are indicated in A. Scales = 0.5 mm.

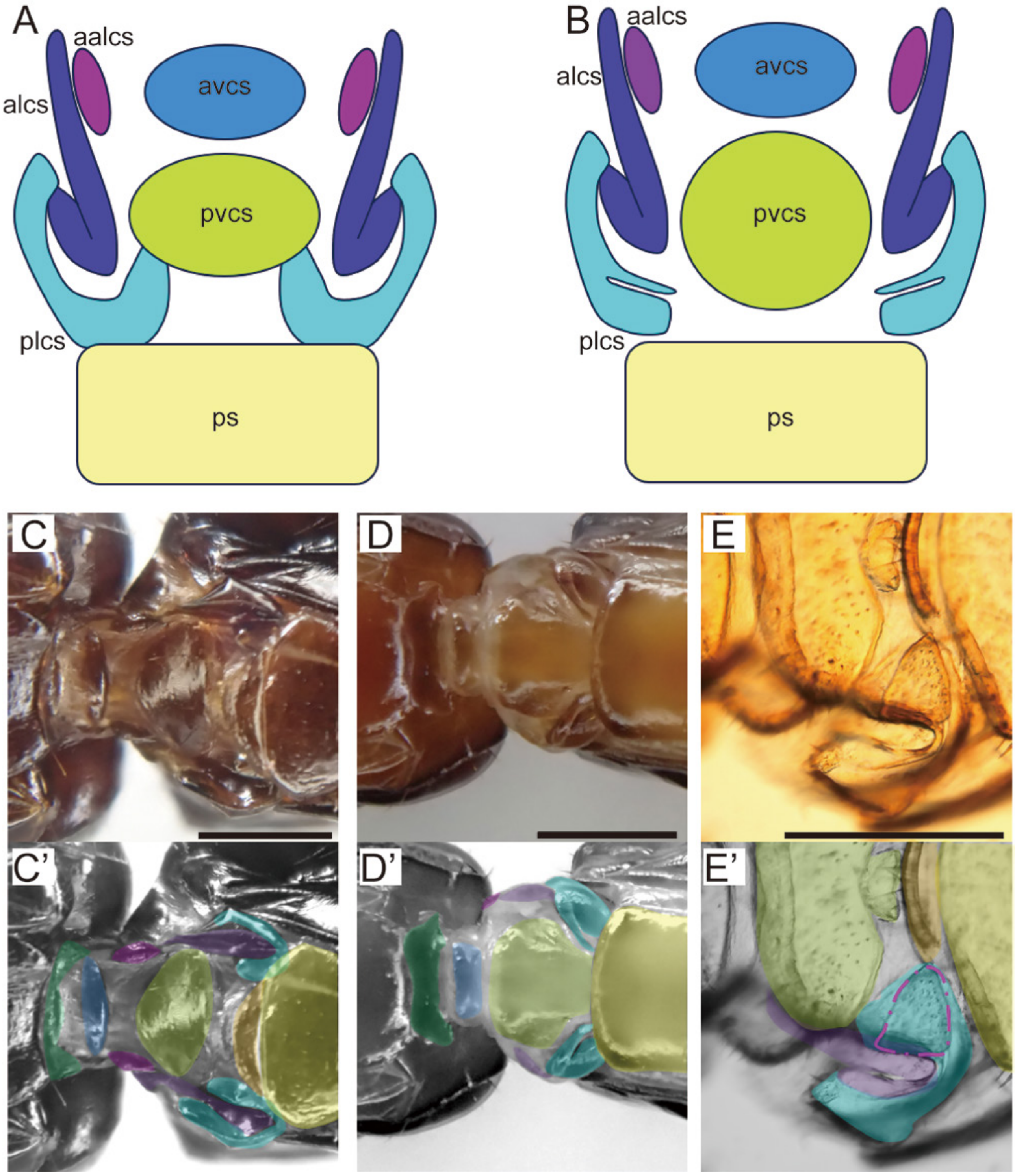

Fig. 3 Schematics of the blattoid (A) and forficuloid (B) type necks based on the revised definitions. Each structure is drawn in a color similar to those of Fig. 2. The neck (ventral views) of intact *Allostethus indicum* (C) and *Anisolabis seirokui* (D), and a DIC micrograph of the right-side neck (ventral view) of *Echinosoma denticulatum* (E) with each structure highlighted/delineated in a color corresponding to those of Fig. 2 (C', D', E'). aalcs: associated sclerite of anterior lateral cervical sclerite, alcs: anterior lateral cervical sclerite, avcs: anterior ventral cervical sclerite, plcs: posterior lateral cervical sclerite, ps: prosternum, pvcs: posterior ventral cervical sclerite. Scales = 0.5 mm.

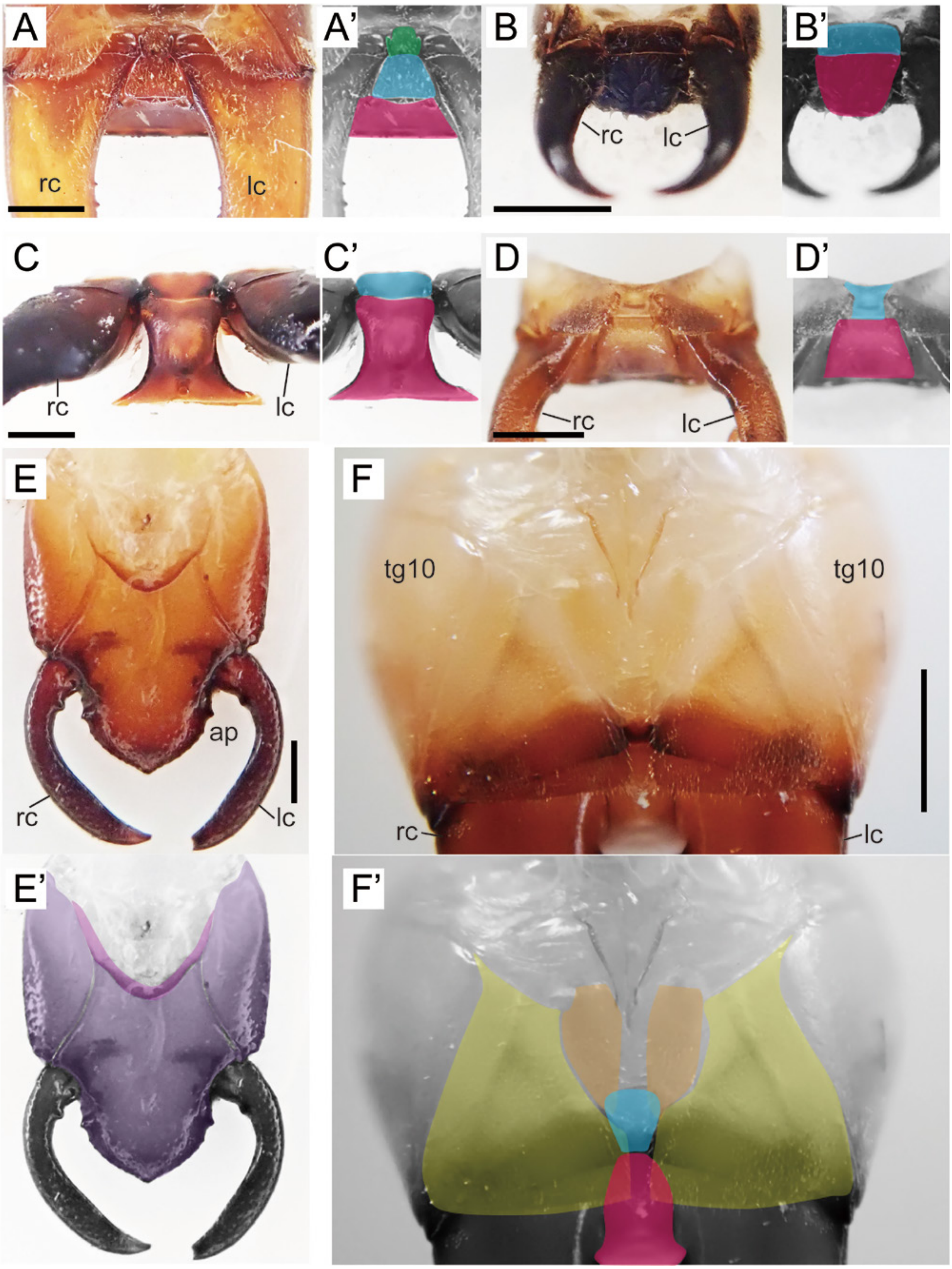

Fig. 4 The epiproct (caudoventral views) of *Pyragra fuscata fuscata* (A, A’), *Echinosoma denticulatum* (B, B’), *Anisolabis maritima* (C, C’) and *Anechura harmandi* (D, D’), and female terminalia (ventral views) of *Apachyus chartaceus* (E, E’), and *Labidura riparia* (F, F’). In A’–F’, the tergum XI (pygidium) and the dorsal sclerite of telson are highlighted in magenta and light blue (also green in A’), respectively. In E’, a large capsule-shaped sclerite, which includes the fused terga X and XI, is highlighted in purple (main part) and red purple (anterior flange). The main part likely includes the lateral plates (highlighted in yellow in F’), while the anterior flange may homologous to the anal plates (highlighted in orange in F’). ap: anal process, tg10: tergum X, lc: left cercus (left branch of forceps), rc: right cercus (right branch of forceps). Scales = 1 mm.

penises and laterally paired parameres extend from the posterior end of this tabular structure (Fig. 1A–F) (see “4.10. Exploring the root of Neodermaptera”).

The genitals of a male *Apachyus chartaceus* that died after imaginal eclosion without any cohabitation with conspecific females (and therefore no courtship or mating experience) were observed. Although many previous authors have noted that one of the paired penises points posteriorly in Apachyidae, both the right and left penises flexed to point anteriorly in this male (Fig. 1A). In contrast, in 5 species (*N* = 17, in total) of the Anisolabidinae (Anisolabididae), both penis lobes pointed posteriorly without bending in males examined within 24 h after their imaginal eclosion (Table 2; Fig. 1E). A similar condition was reported for male *Labidura riparia* (Labiduridae) in Kamimura (2006).

Kamimura and Lee (2014b) reported that a male *Allostethus indicum*, examined 12 days after imaginal eclosion, exhibited “both bending” status even after cohabitating with a virgin female for 24 h without inseminating her (possibly involving courtship but not copulation). Interestingly, Sakai (1987) published a micrograph of the male genitalia of *Gonolabina kuhlgatzi* Verhoeff, 1902 (holotype), a species later synonymized with *Gonolabina spectabilis* (Philippi, 1863) (Gonolabinidae Popham and Brindle, 1966: see Discussion) by Brindle (1967), in which both penis lobes flexed anteriorly. Although this configuration may have resulted from an artifact during slide preparation, it suggests their penis configuration before mating experiences.

Nishikawa (1976) illustrated the female terminalia of *Parapsalis infernalis*, including their moderately developed gonapophyses. Further examination in the present study revealed that this species possesses a pair of long, thin tubes near the gonapophyses of abdominal segment IX (Fig. 1J). Klass (2003) reported similar structures, termed lateral tubes, for many haplodiplatyid and pygidicranid genera, as well as Kamimura and Lee (2014b) for *Al. indicum*. The spermatheca of *Pa. infernalis* consists of a long single tube without internal branching, with the basal part conspicuously coiled (Fig. 1I). In the present study, lateral tubes and coiled parts of the spermatheca were not detected in females of *Ap. chartaceus* (Fig. 1G, H). Instead, a large, voluminous accessory gland, likely responsible for the secretion of egg-attaching substances (Shimizu and Machida 2024) was observed (Fig. 1G), along with moderately developed ovipositor components, as previously reported by Kaidel and Klass (2011).

4. DISCUSSION

4.1. Revised definitions of infraorders and parvorders

Based on the results of the present study and information from the recent literature, a new classification system for Neodermaptera is proposed (Table 3). Taking into account recent advances in the phylogenetic studies of this group, the higher taxa are arranged to avoid polyphyly to the extent possible. However, due to uncertainties, several groups are likely paraphyletic (e.g., Protodermaptera and Pygidicranidae).

The name Protodermaptera has been adopted by many previous authors as a higher taxon of Neodermaptera, with variable ranks, definitions, and delineations. Unlike the Protodermaptera of Engel and Haas (2007) (Table 1) and Steinmann (1986; see Introduction), Burr (1911) classified Protodermaptera as a superfamily-level taxon, which includes not only members of the present Haplodiplatyidae, Diplatyidae, and Pygidicranidae, but also those of Anisolabididae and Labiduridae. Sakai (1982) and Srivastava (1988, 2003, 2013) basically followed Steinmann's system, but used the names Pygidicranoidea Verhoeff, 1902, Apachyoidea, and Anisolabidoidea Verhoeff, 1902 [Anisolaboidea (sic) in Srivastava] for Protodermaptera, Paradermaptera, and Mesodermaptera, respectively. In these three groups, the neck of Protodermaptera members is referred to as the blattoid type, which is described as having “anterior and posterior cervical sclerites anterior to the prosternum separated from each other, but the hind margin of the posterior sclerite may be separate or fused with the apical margin of the prosternum” (Srivastava 1988). However, as revisited in the present study, the relative sizes and positions of the cervical sclerites alone cannot provide definitive diagnostic traits for discriminating between Protodermaptera and Epidermaptera, as defined by Engel and Haas (2007). Instead, the posterior ends of posterior lateral cervical sclerites are always curved and V-shaped in Protodermaptera, in which Apachyidae and Allostethidae Verhoeff, 1904 (Allostethinae in Table 1) may be included, whereas it is only gently curved in the newly defined Epidermaptera. Additionally, considering the penis configuration of naïve males from *Apachyus* (Apachyidae) and *Allostethus* (Allostethidae), revised definitions of the two infraorders, two parvorders, and six superfamilies are provided below, along with explanations of the rationales for changes from the Engel and Haas (2007) system.

Infraorder Protodermaptera

The basal piece of the male genitalia has an inverted V or Y shape due to a posterior incision. Both

Table 3 Revised higher classification of Neodermaptera. Taxa changed/transferred from that of Engel and Haas (2007) are shown in bold.

- Order DERMAPTERA de Geer, 1773
  - Suborder Neodermaptera Engel, 2003
    - Infraorder Protodermaptera Zacher, 1910
        - Superfamily Pygidicranoidea Verhoeff, 1902
          - **Family Haplodiplatyidae Engel, 2017**
          - Family Diplatyidae Verhoeff, 1902
            - **Subfamily Cylindrogastrinae Maccagno, 1929**
            - Subfamily Diplatyinae Verhoeff, 1902
            - **Subfamily Diplatymorphinae Boeseman, 1954**
          - Family Pygidicranidae Verhoeff, 1902
            - Subfamily Anataeliinae Burr, 1909
            - **Subfamily †Astreptolabidinae Engel, 2011**[*]
            - Subfamily Blandicinae Burr, 1915
            - Subfamily Brindlensiinae Srivastava, 1985
            - Subfamily † Burmapygiinae Engel et Grimaldi, 2004
            - Subfamily Challiinae Steinmann, 1973
            - Subfamily Echinosomatinae Burr, 1910
            - Subfamily Esphalmeninae Burr, 1909
            - **Subfamily Karschiellinae Verhoeff, 1902**
            - **Subfamily Prolabiscinae Bey-Bienko, 1959**
            - Subfamily Pygidicraninae Verhoeff, 1902
            - Subfamily Pyragrinae Verhoeff, 1902
            - **Subfamily †Stonychopygiinae Engel et Huang, 2017**[**]
        - **Superfamily Apachyoidea Verhoeff, 1902**
          - **Family Apachyidae Verhoeff, 1902**
          - **Family Gonolabinidae Popham et Brindle, 1966**
        - **Superfamily Allostethoidea Verhoeff, 1904**
          - **Family Allostethidae Verhoeff, 1904**
    - Infraorder Epidermaptera Engel, 2003
      - **Parvorder Mesodermaptera Steinmann, 1986**
        - Superfamily Anisolabidoidea Verhoeff, 1902
          - Family Anisolabididae Verhoeff, 1902
            - Subfamily Anisolabidinae Verhoeff, 1902
            - Subfamily Anophthalmolabidinae Steinmann, 1975
            - Subfamily Antisolabidinae Brindle, 1978
            - Subfamily Brachylabidinae Burr, 1908
            - Subfamily † Cretolabiinae Engel et Haas, 2007
            - Subfamily Idolopsalinae Steinmann, 1975
            - Subfamily Isolabidinae Verhoeff, 1902
            - **Subfamily Isolaboidinae Brindle, 1978**
            - Subfamily Parisolabidinae Verhoeff, 1904
            - **Subfamily Platylabiinae Burr, 1911**
            - Subfamily Titanolabidinae Srivastava, 1982
        - Superfamily Labiduroidea Verhoeff, 1902
          - Family Labiduridae Verhoeff, 1902
            - Subfamily Labidurinae Verhoeff, 1902
            - Subfamily Nalinae Steinmann, 1975
      - Parvorder Eudermaptera Verhoeff, 1902
        - Superfamily Forficuloidea Latreille, 1810
          - Family Arixeniidae Jordan, 1909
          - **Family Hemimeridae Sharp, 1895**
          - Family Spongiphoridae Verhoeff, 1902
            - Subfamily Caecolabiinae Steinmann, 1990
            - Subfamily Cosmogeracinae Brindle, 1982
            - Subfamily Geracinae Brindle, 1971
            - Subfamily Isopyginae Hincks, 1951
            - Subfamily Labiinae Burr, 1909[***]
            - Subfamily Nesogastrinae Verhoeff, 1902
            - Subfamily Pericominae Burr, 1911
            - Subfamily Ramamurthiinae Steinmann, 1975
            - Subfamily Sparattinae Verhoeff, 1902
              - Tribe Auchenomini Burr, 1909
              - Tribe Chaetospaniini Steinmann, 1990
              - Tribe Sparattini Verhoeff, 1902
            - Subfamily Spongiphorinae Verhoeff, 1902
            - Subfamily Strongylopsalinae Burr, 1911
            - Subfamily Vandicinae Burr, 1911
          - Family Chelisochidae Verhoeff, 1902
            - Subfamily Chelisochinae Verhoeff, 1902
            - Subfamily Genitalatinae Steinmann, 1987
            - Subfamily Kinesinae Srivastava, 2003
          - Family Forficulidae Latreille, 1810
            - Subfamily Allodahliinae Verhoeff, 1902
            - Subfamily Ancistrogastrinae Verhoeff, 1902
            - Subfamily Anechurinae Verhoeff, 1902
            - Subfamily Diaperasticinae Burr, 1907
            - Subfamily Forficulinae Latreille, 1810
            - Subfamily Neolobophorinae Burr, 1907
            - Subfamily Opisthocosmiinae Verhoeff, 1902
            - Subfamily Skendylinae Burr, 1907

† Taxa only with fossil species

[*] See Engel (2011)

[**] See Engel et al. (2017)

[***] See ICZN (2005)

of two penis lobes (although one is sometimes reduced) bend to point anteriorly in repose or immediately after imaginal eclosion. The neck is of the blattoid type, such that the posterior ends of the posterior lateral cervical sclerites are acutely bent inward and V-shaped. The tergum XI (pygidium) is articulated with the tergum X (ultimate tergite) in the Pygidicranoidea and Allostethoidea, or completely fused with it in both sexes in the Apachyoidea. The thoracic mesosternum is distinctively narrowed towards the metasternum in the Allostethoidea, or truncated (not distinctively narrowed) in the Pygidicranoidea and Apachyoidea.

Allostethoidea: Allostethidae; Apachyoidea: Apachyidae, Gonolabinidae; Pygidicranoidea: Diplatyidae, Haplodiplatyidae, Pygidicranidae.

Infraorder Epidermaptera

In the male genitalia, there are a single or two penis lobes. In the members with two penis lobes (although sometimes one is reduced), the basal piece has an inverted V or Y shape with a posterior incision. At least one penis lobe points posteriorly when in repose from immediately after imaginal eclosion. The necks are of the forficulid-type, meaning the posterior end of the posterior lateral cervical sclerites is only gently curved. The tergum XI (pygidium) is not fused with the tergum X (ultimate tergite) (except for Hemimeridae).

Parvorder Mesodermaptera

The male genitalia possess two penis lobes (although one is sometimes reduced) and a basal piece of inverted V- or Y-shape with a posterior incision. At least one penis lobe points posteriorly in repose from immediately after imaginal eclosion. The virga contains a sinuated tube in the Labiduroidea, but lacks this structure in the Anisolabidoidea. In winged species, the head of the fustis is not separated from its base.

Anisolabidoidea: Anisolabididae; Labiduroidea: Labiduridae.

Parvorder Eudermaptera (= Forficuloidea)

The male genitalia possess a single penis lobe and a basal piece without an incision posteriorly. The penis lobe permanently points posteriorly from imaginal eclosion. In winged species, the head of the fustis is separated from its base by a groove.

Forficuloidea: Arixeniidae, Chelisochidae, Forficulidae, Hemimeridae, Spongiphoridae.

4.2. General remarks on the new classification system

Several additional traits can be used to differentiate the newly defined Protodermaptera from the Epidermaptera. Notably, the components of the female ovipositor, particularly the gonapophyses of abdominal segments VIII and/or IX, are generally well developed (Klass 2003; Kamimura and Lee 2014b). Spermathecae with internal or external branching, a pair of lateral tubes and a large accessory gland, the latter of which are likely for secreting adhesive substances to affix eggs, have been identified in only some members of the redefined Protodermaptera (Klass 2003; Kamimura and Lee 2014b) (Fig. 1). In winged species, the combined basivenalia of anal anterior 3+4 (BAA3+4), anal posterior (BAP), and jugal basivenale (BJ) are either not twisted or only slightly twisted in the Protodermaptera (Haplodiplatyidae, Diplatyidae, Pygidicranidae, Allostethidae, and Apachyidae), whereas in the Epidermaptera (Anisolabididae, Labiduridae, Spongiphoridae, Chelisochidae, and Forficulidae) these structures are strongly twisted (Haas and Kukalová-Peck 2001).

Recent comprehensive studies on the embryonic and post-embryonic development of free-living neodermapterans have revealed six or more nymphal instars in the Protodermaptera (no data are available for the Allostethidae, Gonolabinidae, and Haplodiplatyidae), but five (Mesodermaptera) or four (Eudermaptera) in the Epidermaptera (Shimizu and Machida 2024). Additionally, during the anatrepsis period, the elongation ratio of embryos is 160% or less in epidermapterans, whereas it is 210% or more in protodermapterans (Shimizu and Machida 2024). These findings represent a significant morphological gap between the Protodermaptera and Epidermaptera, although the former group is likely paraphyletic, as discussed below.

Since the seminal works of Verhoeff (1902) and Burr (1915a, b, 1916a), the number and resting positions of penises have been considered crucial traits for understanding the higher classification of the Dermaptera. The evidence presented in the present study strongly suggests the existence of two distinct configurations in dermapteran bidirectional penises: in some species, one of the paired penises shifts its orientation from anterior to posterior, and in others, the opposite shift occurs after imaginal eclosion. The species showing the former configuration changes have been classified with the Protodermaptera. Observing the changes in penis direction shortly after imaginal eclosion basically requires rearing nymphal insects under laboratory conditions, which reduces its practicality as a diagnostic trait. However, with advancements in observational techniques, such as confocal laser scanning microscopy (e.g., Kamimura et al. 2021; Matsumura et al. 2021) and micro-computed tomography (Kamimura and Lee 2023), further exploration is needed to identify additional differences in male genital structures to better distinguish the Protodermaptera and the Epidermaptera.

In contrast to the numerous morphological and developmental gaps distinguishing the newly defined Protodermaptera from the Epidermaptera, epiproct structures alone do not offer reliable diagnostic traits for these taxa, despite Zacher's (1910) original definition of Protodermaptera as having a "metapygidium and telson composed of distinct chitinous plates". Instead, the shape of the posterior ends of the posterior lateral cervical sclerites (V-shaped vs. gently curved) is more strongly correlated with the original direction of the penises (anterior vs. posterior). The V-shaped posterior ends of these sclerites likely restrict the downward movement of the head, contributing to the prognathous nature observed in species with a blattoid neck type.

4.3. Members included in the Haplodiplatyidae and Diplatyidae, and treatment of Karschiellinae

After the proposal of the Engel and Haas (2007) system, Engel et al. (2017) established family Haplodiplatyidae to include a single genus, *Haplodiplatys*. In adult Neodermaptera specimens, the cerci are consistently present as unsegmented forceps. However, segmented cerci are observed in the nymphal stages of the Haplodiplatyidae (de Bormans and Krauss 1900), Diplatyidae (e.g., Shimizu and Machida 2011b), and Karschiellinae (at least in the distal part: Verhoeff 1903; Haas et al. 2012). Among these taxa, the members of Haplodiplatyidae are particularly noteworthy due to their multiple, presumably plesiomorphic features such as laterally symmetrical tegmina and the absence of a spiny ridge (a component of the tegmina-locking device) on the dorsal side of the mesothorax (Haas and Kukalová-Peck 2001). Kamimura and Ferreira (2017) suggested that the Cylindrogastrinae (*Cylindrogaster* Stål, 1855) and Diplatymorphinae (*Diplatymorpha* Boeseman, 1954) should be placed in Diplatyidae together with Diplatyinae if the latter is treated as a family separate from the Pygidicranidae. This proposal is followed in the system outlined in the present study (Table 3).

The Karschiellinae include large, robust earwigs from two genera: *Bormansia* Verhoeff, 1902 (eight species) and *Karschiella* Verhoeff, 1902 (four species), both exclusively recorded from tropical Africa (Brindle 1973). These species are thought to be predatory, particularly on ants (Hincks 1959). In addition to the segmented cerci observed in nymphs, they possess unique male genitalia within the Protodermaptera, where the left penis is significantly reduced and vestigial (Steinmann 1986). Consequently, some studies, including Engel and Haas (2007), have treated them as a superfamily-level taxon (Karschielloidea; Popham 1965b), or as a distinct family within Protodermaptera (Verhoeff 1902). Other studies have treated them as a subfamily of Pygidicranidae (Burr 1911; Hincks 1959; Brindle 1973; Sakai 1982, 1985; Steinmann 1975, 1986, 1989b). Recently, Kočárek et al. (2024) published the first molecular phylogenetic study including this unique group. In their molecular tree, based on both mitochondrial and nuclear genes (totalling 5,164 bp), *Karschiella* sp. and *Bormansia africana* Verhoeff, 1902 formed a monophyletic clade deeply embedded within the Pygidicranidae, suggesting that Karschiellinae should be placed within the paraphyletic Pygidicranidae. Thus, in the system proposed in the present study, these members are treated as a subfamily-level taxon (Karschiellinae of Pygidicranidae: Table 3). Like the Arixeniidae and Hemimeridae, which are phoretic on or associated with mammals (see "4.7. Transfer of the Hemimeridae to Eudermaptera"), the distinct and unusual morphologies of *Karschiella* and *Bormansia* likely represent adaptations to their specific life histories.

4.4. Treatment of the Prolabiscinae

The subfamily Prolabiscinae, originally established as Protolabinae by Bey-Bienko (1959a) within Pygidicranidae, is a monotypic group, with the type species *Parapsalis infernalis* (Bey-Bienko 1959b; Nishikawa 1976). Although some studies, beginning with Steinmann (1973), placed this species in the Echinosomatinae alongside the type genus *Echinosoma* (e.g., Sakai 1982; Steinmann 1986, 1989b; Popham 2000; Engel and Haas 2007), Srivastava (1988) reinstated Prolabiscinae, arguing that *Pa. infernalis* represents a "transitional stage between Pygidicranoidea and Carcinophoroidea (= Anisolabidoidea)".

In addition to the smooth, glabrous body (as opposed to the dense characteristic setation of *Echinosoma*), ecarinate femora (unlike the femora with distinctive carina in *Echinosoma*), and a non-projecting, vertical pygidium (in contrast to that which projects posteriorly in *Echinosoma*), several distinctive differences support the view that the Echinosomatinae and Prolabiscinae are largely different groups within Pygidicranidae. Nishikawa (1976) examined the cervical sclerites, pygidium, and female terminalia of *Pa. infernalis*, and concluded that, although the structures of the first two traits clearly indicate that this species should be classified within the Pygidicranidae, the females possess less-developed ovipositor components. In contrast, *Echinosoma* species are characterized by a notably developed gonapophysis VIII and gonoplac IX (Klass 2003; Kamimura and Lee 2014a).

Representatives of the Diplatyidae, Apachyidae, and some pygidicranid subfamilies (particularly Pygidicraninae and Echinosomatinae) attach their eggs to substrates (Matzke and Klass 2005; Shimizu and Machida 2011b, 2024). In these groups, a large accessory gland, which is thought to produce material for forming the adhesive substance or egg stalk, has also been identified (Klass 2003; Kaidel and Klass 2011; Kamimura and Lee 2014b). However, Shimizu and Machida (2024) observed maternal care in *Pa. infernalis* and found that the eggs are not adhered to the substrate. In this species, the accessory gland is also absent. Given these multiple differences, Prolabiscinae is reinstated within Pygidicranidae in the proposed classification system (Table 3).

4.5. Apachyidae and Gonolabinidae

Apachyidae is a small family distributed in the tropical parts of Ethiopian, Oriental and Indo-Australian faunal regions (Popham 2000). Although its members possess bidirectional penises similar to those of the Anisolabididae and Labiduridae, and Allostethidae (see "4.6. Family-level treatment of Allostethidae"), their unique anal process morphology (Fig. 4E, E') has led to their classification as a distinct higher taxon within the Dermaptera, either as Paradermaptera by Verhoeff (1902), Burr (1911), and Steinmann (1986, 1989a, b), or as Apachyoidea by Sakai (1982) and Srivastava (2013). The examination of dermapteran wing structures and cladistic analyses based on morphological traits by Haas and Kukalová-Peck (2001) indicated that Apachyidae represents a second basal offshoot of Paradermaptera of Epidermaptera sensu Engel and Haas (2007). However, Wipfler et al. (2020) suggested that Apachyidae is the most basal offshoot of neodermapteran families, which recalls Verhoeff's (1902) dichotomy of extant free-living earwigs into the Paradermaptera (= Apachyidae) and Eudermaptera (all other families). Thus, the placement of Apachyidae is of particular interest when considering the evolution of the Dermaptera.

As pointed out by Haas and Kukalová-Peck (2001), the wing structures of Apachyidae members indicate their affinity with the taxa Haplodiplatyidae, Diplatyidae, Pygidicranidae, and Allostethidae (see "4.2. General remarks on the new classification system"). Shimizu and Machida (2024) revealed that the embryonic development of *Apachyus chartaeus* is similar to that of diplatyids and pygidicranids, and their six nymphal instars fall within the number range observed in these protodermapteran families. They also reported that female *Ap. chartaceus* use adhesive substances to fix their eggs to a substrate, corresponding to the discovery of a large accessory gland in the females of this species (Kaidel and Klass 2011) (Fig. 1G). Additionally, the discovery of a unidirectional configuration of paired penises (pointing anteriorly) in a naïve male (Fig. 1A) provides further support for the view that Apachyidae (or Apachyoidea) should be placed within the Protodermaptera.

In contrast to this view, Klass (2001) and Kaidel and Klass (2011) suggested some similarities between the Apachyidae and Hemimeridae, of which the latter group is now considered a member of the Eudermaptera (see "4.7. Transfer of the Hemimeridae to Eudermaptera"). The inclusion of the Hemimeridae within the Paradermaptera in the Engel and Haas (2007) system follows this perspective (Table 1). In females of both the Apachyidae and Hemimeridae, tergum X (ultimate tergite), tergum XI (pygidium), and the dorsal telson sclerite are fused (Klass 2001). The extent of development and configuration of the ovipositor components are also similar between these two taxa (Kaidel and Klass 2011). However, the presence of developed gonapophyses is not exclusive to the Protodermaptera (which now include the Apachyidae, Gonolabinidae, and Allostethidae). Although Schneider and Klass (2013) revealed that the absence of ovipositor-like structures is usual for females of the Spongiphoridae, Chelisochidae, and Forficulidae, Kamimura et al. (2016) detected a pair of well-developed lobes resembling the gonoplac IX of *Echinosoma* spp. (Klass 2003; Kamimura and Lee 2014a) in *Pseudovostox brindlei* Srivastava, 2003 (Spongiphoridae: Geracinae Brindle, 1971). Additionally, the Hemimeridae are characterized by the loss of the anterior lateral cervical sclerites (Giles 1963). Thus, the fusion of terminal structures likely represents unique adaptations of this epizoic insect group, resulting in reduced body flexibility (Popham 1985, Klass 2001; see also"4.7. Transfer of the Hemimeridae to Eudermaptera").

Among extant, free-living earwigs, another group exhibits conspicuous modifications of tergum IX (pygidium) in both males and females: genus *Gonolabina*, which comprises three described species (Brindle 1967). Burr (1911) placed this genus in subfamily Esphalmeninae Burr, 1909, alongside *Esphalmenus* Burr, 1909 within "Labiduridae", focusing on their prosternum strongly narrowed posteriorly. Later, based on the male genitalia, which feature both penises bent to point anteriorly in repose, Hincks (1959) transferred the Esphalmeninae (including *Esphalmenus*) to Pygidicranidae, leaving *Gonolabina* as an isolated genus. Popham and Brindle (1966) subsequently placed this genus in a separate subfamily, Gonolabininae (incorrectly referred to as "Gonolabinae" in Popham and Brindle 1966; corrected in Engel and Haas 2007) of Carcinophoridae (= Anisolabididae), based on the bidirectional penis configuration. Many subsequent studies have followed this classification (e.g., Steinmann 1989a, b; Sakai 1982, 1987).

Recently, Vera (2021) observed the male and female reproductive structures of *Gonolabina spectabilis* and discovered the spermatheca with multiple openings, as well as well-developed gonapophyses and gonoplacs. Along with the unidirectional penises of the holotype *Gonolabina kuhlgatzi* (which is considered synonymous with *G. spectabilis*; see "3. Results"), these characteristics strongly support the view that *Gonolabina* should be placed in Protodermaptera, similar to cases in the Apachyidae discussed in this section and Allostethidae (see "4.6. Family-level treatment of Allostethidae"). However, in the absence of contemporary studies of their phylogenetic position, it is advisable to treat this group as a family-level taxon, Gonolabinidae, placed in Apachyoidea alongside the Apachyidae.

Although these two families can be characterized by the fusion of tergum XI (pygidium) to tergum X (ultimate tergite), the structural organization of their terminal abdomens is not identical. The pygidium of female *Ap. chartaceus* appears to be fused also with the anal plates, lateral plates, and telson sclerite, forming a large capsule that accommodates the muscles used to move the forceps (Fig. 4). In contrast, according to Vera (2021), the pygidium and lateral plates (referred to as anal lobes in that study) of female *G. spectabilis* are not fused. Additionally, female *G. spectabilis* do not adhere eggs to substrates and show no indication of an accessory gland (Vera 2021). Therefore, the Gonolabinidae are only tentatively included in the Apachyoidea, for convenience. An alternative possibility is that the Gonolabinidae are closely related to the Esphalmeninae (e.g., genus *Esphalmenus*), with members of the latter primarily occurring in neotropical regions (Brindle 1984; Steinmann 1986), as suggested by Burr's (1911) original treatment. Molecular studies are needed to elucidate this unique group, as well as examination of their cervical sclerites.

4.6. Family-level treatment of Allostethidae

Allostethidae erected by Verhoeff (1904) includes members of three genera: *Allostethella* Zacher, 1910, *Allostethus* Verhoeff, 1904, and *Gonolabidura* Zacher, 1910. Regarding the enigmatic genus *Protolabidura* Steinmann, 1985, the present study aligns with Srivastava's (1993) view that it is a synonym of *Gonolabidura*. All of these genera are characterized by the peculiar shape of the thoracic mesosternum, which is distinctly narrowed toward the metasternum (Burr 1911; Brindle 1965; Popham 1965b; Matsuda 1970; Günther and Herter 1974; Steinmann 1989a). Burr (1915a) classified them as Allostethinae in Pygidicranidae within his Protodermaptera, considering their well-developed gonapophyses. Later, Hincks (1951a) transferred this subfamily to Labiduridae, based on their neck structure (enlarged posterior ventral cervical sclerite: see Figs 2B, 3C, C') and bidirectional penises, a treatment that has been followed by many subsequent authors (e.g., Brindle 1965; Popham 1965b; Sakai 1982, 1990; Steinmann 1989a, b; Srivastava 2003).

However, based on their detailed examination of dermapteran wing structures, Haas and Kukalová-Peck (2001) revealed that the hindwing structures of *Allostethus indicum* exhibit multiple presumably plesiomorphic characteristics. These include an anojugal fulcalare with an almost elliptical head, a narrow neck, and a broad, weakly sclerotized tail, as well as the position of the third anal anterior far from the anal anterior 1+2 basivenale. Consequently, *Allostethus* was placed as the most basal taxon within the paraphyletic group Mesodermaptera (comprising the Labiduridae and Anisolabididae) in their cladistic analysis. Kamimura and Lee (2014b) examined the mating and reproductive organs of this species and found an internally branched spermatheca and a pair of lateral tubes, in addition to well-developed gonapophyses. These characteristics indicate strong affinity to protodermapterans (Klass 2003; Kamimura and Lee 2014b). Interestingly, Kamimura and Lee (2014b) also reported a unidirectional penis configuration, oriented towards the anterior in a naïve male (see "3. Results"). Furthermore, recent molecular phylogenetic studies on dermapterans have confirmed its closer relationship to Pygidicranidae or Apachyidae, rather than to Labiduridae s. str (Labidurinae Verhoeff, 1902 and/or Nalinae Steinmann, 1975) (Wipfler et al. 2020; Kočárek et al. 2024).

Therefore, if we place Apachyidae and Gonolabinidae within the Protodermaptera, then members of Allostethinae should be treated similarly. However, considering the distinctive differences in epiproct morphology, Allostethidae is proposed as a single family forming the superfamily Allostethoidea Verhoeff, 1904 (Table 3). The Allostethoidea can be distinguished from species of the Apachyoidea by the fact that tergum XI (pygidium) is not fused with tergum X (ultimate tergite), from species of the Pygidicranoidea by a typically bidirectional penis (possibly following mating experience), and from both groups by its mesosternum, which is distinctly narrowed towards the metasternum.

4.7. Transfer of the Hemimeridae to Eudermaptera

Neodermaptera of Engel and Haas (2007) includes two unique groups of earwigs that are phoretic on or associated with mammal species. Arixeniidae comprises two genera: *Arixenia* Jordan, 1909 (two species) and *Xeniaria* Maa, 1974 (three species), both of which have been recorded exclusively from Southeast Asia (Nakata and Maa 1974). These completely apterous insects are associated with the roosts of bats (*Cheiromeles* Horsfield, 1824 spp. and occasionally *Mops plicatus* Buchanan, 1800), and are thought to feed on skin and gland secretions of their bat hosts, as well as guano and guano-associated arthropods (Cloudsley-Thompson 1957; Nakata and Maa 1974; Marshall 1977; Encinares et al. 2024). Members of the Hemimeridae, which are completely wingless and eyeless, are more closely associated with mammals. The genus *Hemimerus* Walker, 1871 (nine species) and *Araeomerus* Maa, 1974 (two species) are phoretic on the rodents *Cricetomys* Waterhouse, 1840 and *Baemys* Thomas, 1909, respectively (Nakata and Maa 1974). Although the ecology of *Araeomerus* spp. is largely unknown, *Hemimerus* spp. are thought to be commensal, feeding primarily on dead skin or fungi growing on the host's skin in sub-Saharan Africa (Nakata and Maa 1974). Both arixeniids and hemimerids are viviparous, which is an apparent adaptation to their phoretic/epizoic lifestyle on mammals (Heymons 1912; Hagan 1951; Tworzydło et al. 2013b).

Although these two unique groups have traditionally been treated as independent orders of insects or suborders of the Dermaptera, Engel and Haas (2007) placed Arixeniidae in the Eudermaptera, following Popham (1985), who examined the detailed morphology of the Arixeniidae. However, as discussed in "4.5. Apachyidae and Gonolabinidae", they classified Hemimeridae [as Hemimerina (Hemimeroidea)] within Paradermaptera, along with Apachyidae (Apachyoidea) (Table 1).

As with Arixeniidae, there is strong evidence supporting the inclusion of Hemimeridae in Eudermaptera. First, in estimated phylogenetic trees based on various molecular datasets, hemimerids are consistently placed within Eudermaptera (Jarvis et al. 2005; Kočárek et al. 2013; Naegle et al. 2016; Wipfler et al. 2020). Interestingly, Haas and Gorb (2004) noted that *Hemimerus vosseleri* (Rehn et Rehn, 1936) (Hemimeridae) possesses well-developed setae for attachment on all three tarsomeres, similar to those found in the Chelisochidae and Forficulidae. Additionally, hemimerids share several morphological characteristics with the Spongiphoridae, Chelisochidae, Forficulidae, and Arixeniidae, including short ovarioles attached to markedly elongated lateral oviducts, the elongation of embryos resulting in their posterior ends extending beyond the anterior pole of the egg, the egg tooth with an anteriorly-pointed, central major process, and only four nymphal instars before imaginal eclosion (Heymons 1912; Hagan 1951; Cloudsley-Thompson 1959; Tworzydło et al. 2010, 2013a; Biliński et al. 2014, 2017; Shimizu and Machida 2024). These findings are considered to outweigh the similarities shared by Hemimeridae and Apachyidae. Although the placement of both Hemimeridae and Arixeniidae in Eudermaptera has not been definitively settled (reviewed in Wipfler et al. 2020), Eudermaptera appears to form a monophyletic clade (see "4.9. Possible polyphyly and paraphyly of Spongiphoridae" and "4.10. Exploring the root of Neodermaptera").

4.8. Reactivation of the infraorder Mesodermaptera to include Labiduridae and Anisolabididae

After removing Allostethinae and Gonolabininae from the Labiduridae and Anisolabididae of Engel and Haas (2007), respectively, the remaining members of these two families exhibit relatively uniform external features. They are typically medium-sized to large earwigs, often apterous (particularly in Anisolabididae), with a simple, almost vertical pygidium (Sakai 1987, 1990; Steinmann 1989a; Srivastava 2003). These two families, s. str, include earwig species characterized by a forficuloid neck type (revised definition) and bidirectional penises that are straight immediately after imaginal eclosion, although the latter characteristic has only been examined in a few representatives (Fig. 1B, E).

Given the revised definitions of Anisolabididae and Labiduridae, many studies based on molecular datasets have indicated the relationship [Anisolabididae, (Labiduridae, Eudermaptera)], supporting the monophyly of the parvorder Eteodermaptera Engel, 2003, which includes Labiduroidea Verhoeff, 1902 (= Labiduridae) and Eudermaptera (Colgan et al. 2003; Kamimura 2004; Kočárek et al. 2013; see also "4.9. Possible polyphyly and paraphyly of Spongiphoridae" and "4.10. Exploring the root of Neodermaptera"). This relationship is further supported by an analysis conducted by Haas and Kukalová-Peck (2001) based on a large morphological dataset, which identified four traits that support a sister relationship between Eudermaptera and Labiduridae (excluding Allostethinae).

Nevertheless, the present study proposes the tentative use of the term Mesodermaptera, a name introduced by Steinmann (1986) to encompass Anisolabididae and Labiduridae, for the following two reasons. First, several recent studies of the molecular phylogeny of Dermaptera have indicated alternative topologies, such as [Labiduridae, (Anisolabididae, Eudermaptera)] (Kočárek et al. 2024) and [(Labiduridae, Anisolabididae), Eudermaptera] (Wipfler et al. 2020) (Fig. 5). Second, and more importantly, it is often difficult to discriminate between Anisolabididae and Labiduridae based on morphological characters. For example, in the key provided by Steinmann (1989a), Labiduridae is separated from Anisolabididae (referred to as Carcinophoridae) based on the observations that

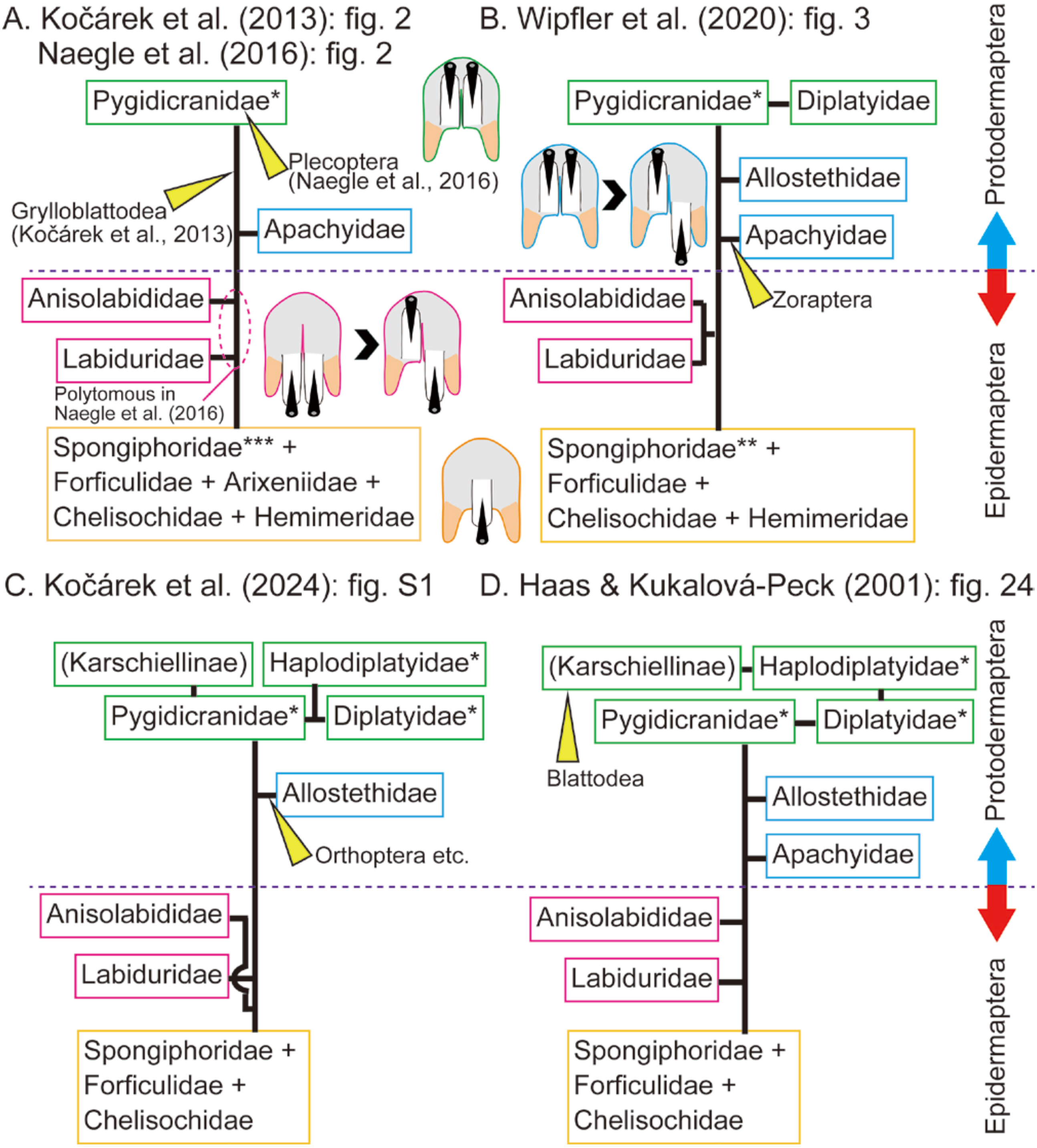

Fig. 5 Unrooted ingroup relationships of Neodermaptera estimated in five comprehensive studies based on molecular (A–C) and morphological (D) datasets. Taxonomic names are provided according to new definitions presented in the present study (Table 3). Family or subfamily (in parentheses) names are enclosed in rectangles of different colors, corresponding to their respective penis configurations: green indicates two penises unidirectionally bent to the anterior in repose (except for Karschiellinae); light blue indicates two penises unidirectionally bent to the anterior at imaginal eclosion but later changing to bidirectional; magenta indicates two penises unidirectionally straight to the posterior at imaginal eclosion but later changing to bidirectional; orange indicates one penis permanently straight, pointing to the posterior. Schematics of male genitalia (see Fig. 1F for explanations) with the outline of the basal piece and parameres of respective colors are also shown. Purple dotted lines delineate the newly defined boundary between Protodermaptera and Epidermaptera. Yellow arrowheads indicate the estimated root position, accompanied by the nearest outgroup taxa used. * paraphyletic; ** polyphyletic; *** polyphyletic only in Naegle et al. (2016).

"tarsal joint 2 is distally slightly elongated and distinctly originates from the ventral surface of joint 3 (metatarsus)" and "virgae are invariably present, with the base always containing a smaller or larger, but easily recognisable, basal vesicle". However, Haas (1995) pointed out that the shape of the second tarsomere is quite variable among labidurid species. Nishikawa (2007) also noted that in nymphal Anisolabidinae, the distal end of the second tarsal segment can protrude under the third segment. To my knowledge, all species of the Anisolabididae possess virgae for sperm transfer, and many also have a vesicle at the base of each virga, although their basal piece, which is often elongated, complicates detailed examinations by taxonomists (Hudson 1973; Sakai 1987; Kamimura 2000, 2014) (Fig. 1C, D). Female Labiduridae specimens are characterized by a small, triangular gonapophysis VIII, located posterior to the gonopore (Kamimura and Lee 2014b). However, Kamimura et al. (2016) detected a similar structure in *Platylabia major* (Anisolabididae: Platylabiinae Burr, 1911); the subfamilial name has been discussed in previous studies (Engel and Haas 2007; Kočárek 2010; ICZN 2017).

Srivastava (2003), who likely encountered these challenges, focused on a sinuous tube present in the basal vesicle or throughout the entire virgae, a feature found in Labiduridae but absent in Anisolabididae. To my knowledge, after the removal of Allosthethinae, this trait is shared among all members of the remaining two subfamilies of Labiduridae: Nalinae (the species of *Nala* Zacher, 1910) and Labidurinae (the species of *Labidura* Leach, 1815 and *Forcipula* Boliver, 1897; excluding the monotypic genus *Tomopygia* Burr, 1904, for which male genitalia are unknown). No Anisolabididae members are known to exhibit this characteristic, supporting the idea that Nalinae and Labidurinae are closely related, as indicated by molecular (plus morphology) data (Colgan et al. 2003; Jarvis et al. 2005; Kočárek et al. 2013; Naegle et al. 2016). However, this presumption does not guarantee the monophyly of Anisolabididae, which comprises ten subfamilies with extant species (Tables 1, 3) and appears to be less significant in distinguishing the superfamilies Anisolabidoidea and Labiduroidea.

Therefore, these two superfamilies are tentatively retained in the system proposed in the present study (Table 3). Once the monophyly of both (Labiduroidea + Eudermaptera) and Anisolabidoidea is confirmed with high accuracy, Eteodermaptera (= Labiduroidea + Eudermaptera) and Metadermaptera (= Anisolabidoidea) (Table 1), which were erected by Engel (2003) as parvorder-level taxa, should be reinstated with clear indications of the diagnostic character states.

4.9. Possible polyphyly and paraphyly of Spongiphoridae

Although Eudermaptera included all families of free-living, extant earwigs except for apachyids (i.e., Paradermaptera) when Verhoeff (1902) first proposed this name, many researchers later adopted Burr's (1911) revised definition, which limits Eudermaptera to the families Spongiphoridae, Chelisochidae, and Forficulidae (Sakai 1982; Steinmann 1989b, 1990, 1993; Srivastava 2013). Arixeniidae and Hemimeridae have also been included in this group (see "4.7. Transfer of the Hemimeridae to Eudermaptera"). Within this classification, Chelisochidae and Forficulidae are characterized by the second tarsal joint, which is either elongate and reaching the third joint but not lobated (Chelisochidae) or elongate and lobate (Forficulidae) (Haas and Gorb 2004). As previously discussed, Arixeniidae and Hemimeridae exhibit numerous special modifications related to their unique ecologies associated with mammals. In contrast, Spongiphoridae potentially encompasses a diverse array of free-living earwigs that possess a single penis and normal tarsal joints.

Steinmann (1989b, 1990) and Engel and Haas (2007) classified Isolaboidinae Brindle, 1978, which comprises five (plus two uncertain) species of *Isolaboides* Brindle, 1978 (according to Srivastava 1996, 2003), as members of the Spongiphoridae (Table 1). Although the males of Isolaboidinae exhibit unique genitalia characterized by a single, well-developed penis and a conspicuous spirally coiled virga (Brindle 1978; Steinmann 1990; Srivastava 1996, 2003), Srivastava (1996) argued that the right penis lobe is either atrophied, with or without a rudimentary virga, whereas the left penis is well developed with a spirally coiled virga. Illustrations by Brindle (1978) and a photograph of paratype genitalia in Sakai (1987) clearly demonstrate that in *Isolaboides burri* Borelli, 1909, the basal piece is deeply incised posteriorly. Consequently, Srivastava (1996, 1999, 2003, 2013) placed Isolaboidinae within Anisolabididae, as a classification adopted in the present classification system (Table 3). Recently, Nishikawa and Yoshitomi (2024) argued that *Rudrax brindlei* Srivastava, 1995, the unique type of Rudracinae Srivastava, 1995 (originally proposed as Rudraxinae, corrected by Engel and Haas 2007), is a junior synonym of *Nesogaster lewisi* (de Bormans, 1903) (Spongphoridae: Nesogastrinae). This treatment is also followed (Table 3).

Regardless of the placement of Isolaboidinae, Günther and Herter (1974) and Popham (1985, 2000) suggested that Spongiphoridae is closely related to Anisolabididae, whereas Chelisochidae and Forficulidae are sister to Labiduridae, opposing the notion of a monophyletic Eudermaptera. However, subsequent cladistic studies by Haas (1995) and Haas and Kukalová-Peck (2001) based on morphological datasets strongly supported the monophyly of Spongiphoridae + Chelisochidae + Forficulidae, which share several potentially apomorphic character states. Some earlier molecular studies also supported this view (Colgan et al. 2003; Kamimura 2004).

In subsequent molecular and morphological analysis, Jarvis et al. (2005) estimated that *Nesogaster aculeatus* de Bormans, 1900 (along with *Labia* sp.) of the "Spongiphoridae" forms a monophyletic clade with three Anisolabididae species, supported by a moderate bootstrap value of 76%. Four other "spongiphorids" were grouped in a clade with four Chelisochidae, eight Forficulidae, and *Hemimerus* sp. (Hemimeridae), with 95% support. This finding suggested the polyphyly of Spongiphoridae, recalling the possible affinity between Spongiphoridae and Anisolabididae proposed by Günther and Herter (1974) and Popham (1985, 2000). These molecular data were also included in analyses by Kočárek et al. (2013) and Naegle et al. (2016), yielding similar topologies. Subsequently, Wipfler et al. (2020) and Kočárek et al. (2024) included other species of genus *Nesogaster* Verhoeff, 1902 (Nesogastrinae Verhoeff, 1902), specifically *Nesogaster amoenus* (Stål, 1855) and *Nesogaster halli* Hincks, 1949, in their molecular phylogenetic analyses. *Nesogaster aculeatus* appears to be closely related to these two species, particularly *N. amoenus*, as they share similar female forceps (Hincks 1951b; Steinmann 1990; Sakai 1991). These additional *Nesogaster* species were placed deeper within Eudermaptera, suggesting that several samples used in Jarvis et al. (2005) may have been misidentified. When "*Nesogaster aculeatus*" and specimens identified only to the genus or family level are removed from the trees of Jarvis et al. (2005), Kočárek et al. (2013), and Naegle et al. (2016), the polyphyly of Spongiphoridae is resolved (Fig. 5).

Nevertheless, further evidence suggests the polyphyly or paraphyly of Spongiphoridae within Eudermaptera. Biliński et al. (2014) reported that distinctly different ovarian structures are exhibited by two spongiphorids: *Irdex chapmani* Brindle, 1980 (Spongiphorinae Verhoeff, 1902) and *Chaetospania borneensis* (Dubrony, 1879) (Sparattinae Verhoeff, 1902). *Irdex chapmani* features large germaria, eight-cell germline cysts, and long ovarioles attached to short lateral oviducts, resembling structures found in the Anisolabididae and Labiduridae. In contrast, the latter species has small germaria, two-cell germline cysts, and short ovarioles attached to markedly elongated lateral oviducts, similar to those in the Chelisochidae, Forficulidae, Arixeniidae, and Hemimeridae (Heymons 1912; Hagan 1951; Tworzydło et al., 2010, 2013a; Biliński et al. 2017). Notably, in a molecular and morphological analysis by Jarvis et al. (2005), two unidentified *Irdex* species clustered with two *Auchenomus* Karsch, 1886 (Sparattinae Verhoeff, 1902) species in the most basal clade of Eudermaptera. In a molecular phylogenetic study by Wipfler et al. (2020), two spongiphorids, *Ne. amoenus* and *Labia minor* (Labiinae), were placed separately but still within the monophyletic Eudermaptera, which also included Chelisochidae, Forficulidae, and specimens of Hemimeridae. In conclusion, although the transition of male genitalia from bifurcated (in Protodermaptera + Mesodermaptera) to non-bifurcated forms (in Eudermaptera) likely occurred only once in the evolution of the Neodermaptera (Fig. 5), Spongiphoridae could be a polyphyletic or paraphyletic taxon within the monophyletic Eudermaptera. Despite the surprising species richness of this family (approximately 500 valid species described across 12 subfamilies: Hopkins et al. 2023) (Table 3), very few species have been included in phylogenetic studies to date. Future studies should represent a much broader diversity of specimens.

4.10. Exploring the root of Neodermaptera

Ideally, a classification system for a group of organisms should reflect their evolutionary history, avoiding the formation of polyphyletic or paraphyletic taxa. Although it is well established that Dermaptera is a member of the monophyletic Polyneoptera, which includes nine other insect orders (e.g., Ishiwata et al. 2011; Yoshizawa 2011; Wipfler et al. 2019), determining the root of the neodermapteran groups by identifying the oldest offshoots remains challenging, and the conclusions are debated. In cladistic analyses based on morphological datasets, (sub)families such as the Karschiellinae, Haplodiplatyidae, and/or Diplatyidae, all of which are characterized by segmented cerci in the nymphal stages along with a blattoid neck type, have been estimated to be the oldest offshoots (Haas 1995; Haas and Kukalová-Peck 2001; Haas and Klass 2003). Among these estimations, Pygidicranidae is often considered paraphyletic. Subsequent studies that incorporated molecular data suggested that the root of the Neodermaptera is located within the paraphyletic Pygidicranidae (Jarvis et al. 2005; Kočárek et al. 2013; Naegle et al. 2016), although no specimens of the Karschiellinae, Haplodiplatyidae, and/or Diplatyidae were included in these analyses. These studies indicated that the polyneopteran orders closest to Dermaptera may include the Plecoptera Burmeister, 1839 (stoneflies), Zoraptera Silvestri, 1913 (angel insects), or Grylloblattodae Walker, 1914 (ice crawlers).

However, one of the most recent studies based on a larger molecular dataset indicated that Apachyidae is the most basal offshoot of Neodermaptera (Wipfler et al., 2020). Upon adopting the new definitions of the Protodermaptera and Epidermaptera proposed in the present study, Apachyidae was placed in the former; however, it also exhibits several traits that suggest an affinity to the Epidermaptera. These traits include the relatively large posterior ventral cervical sclerite (Fig. 2C), the shape of the anojugal fulcalare of the hindwings (Haas and Kukalová-Peck 2001), and the relatively low number of nymphal instars in Protodermaptera (Shimizu and Machida 2024). Shimizu and Machida (2011a) reported that female *Apachyus chartaceus* does not exhibit egg care behavior, which is usual among extant earwig species. However, their further observations (Shimizu and Machida 2024) revealed that the females of this species attach eggs to a substrate and care for them until hatching. Consequently, we cannot identify any single morphological or behavioral trait that could be considered plesiomorphic in Dermaptera to support the notion that Apachyidae is the oldest offshoot of extant Dermaptera.

When the questionable samples ("*Nesogaster aculeatus*" and those identified only to genus or family levels; see "4.9. Possible polyphyly and paraphyly of Spongiphoridae") were removed from the phylogenetic trees, it became evident that the analyses by Kočárek (2013) and Naegle et al. (2016) revealed ingroup relationships almost identical to those found in studies by Haas and Kukalová-Peck (2001, based on morphological traits), Wipfler et al. (2020, molecular data), and Kočárek et al. (2024, molecular data) (Fig. 5). Furthermore, differences in phylogenetic relationships among these various studies are primarily attributable to variation in estimated root positions, which depend on the outgroup placement.

Interestingly, Wipfler et al. (2020) estimated that Zoraptera, an order known for their dramatically accelerated substitution rates for both mitochondrial and nuclear genes (Yoshizawa and Johnson 2005; Ma et al. 2014), was a sister clade to Dermaptera among the outgroups simultaneously analyzed (see also Wipfler et al. 2019). Although they included 22 species from nine polyneopteran orders as outgroup taxa, Zoraptera was represented by only a single species, whereas two to four species were sampled from eight other orders. Given that the Apachyidae are also rare and typically represented by a single species, long-branch attraction may be a contributing factor in this case. Long-branch attraction refers to methodological artifacts in phylogenetic reconstructions, where two or more long branches are erroneously attracted to form sister groups, sometimes with high statistical support (Bergsten 2005). As noted in Bergsten's review (2005), outgroup taxa are often sampled less than ingroup taxa, which may result in longer branches. The inclusion of outgroups with high evolutionary rates can lead to incorrect placement of the root in the ingroup tree or even alter the topology of the ingroup tree. Consequently, Bergsten (2005) recommended estimating the phylogenetic relationships of the focal ingroup taxon both with and without the outgroup(s). Figure 5B suggests that ingroup relationships were not affected by the inclusion of a zorapteran sample in Wipfler et al. (2020). However, future studies should both present the tree with the highest likelihood and also quantify the relative likelihood of the root position along the branches of ingroup trees (e.g., Kamimura 2004), incorporating outgroup taxa with and without Zoraptera.

Following the revised definition of Protodermaptera, it is highly plausible that the root of Neodermaptera is located within Protodermaptera (Fig. 5), from which monophyletic Epidermaptera has been derived. Thus, the proposed system offers a more stable framework for the further refinement of the classification of dermapteran families based on their phylogenetic relationships.

Finally, it is important to discuss the newly proposed term "basal piece" in relation to Zoraptera and Plecoptera. The male genital structure that supports one or two penis lobes (along with a pair of parameres) in earwigs has lacked a widely accepted term (Hincks and Popham 1970). Several earlier studies referred to this part as a "central parameral plate" (e.g., Steinmann 1986) or "proparameres" (e.g., Srivastava 1988). However, according to Ramamurthi (1959), who studied the post-embryonic development of male genitalia in *Euborellia annulipes* (Lucas, 1847) (Anisolabididae), the basal piece is not formed by the fusion of two precursors; rather, the posterior incision gradually increases in length during the nymphal period. Therefore, names that include "parameres", which means "lateral bodies", could be misleading, particularly for eudermapteran species that do not exhibit a median incision.

In several representatives of both Plecoptera and Zoraptera, a similar plate that supports male structures for transferring sperm has been reported. Those structures are termed the "basal plate" in Zoraptera (Delamere-Deboutteville 1970; Matsumura et al. 2020) or "subanal plate" in Plecoptera (Brinck 1956, 1970). As the homologies of these structures remain unknown at present, the term "basal piece" is proposed in the present study to avoid unnecessary confusion with similar structures in related polyneopteran insect orders. Notably, the term "basal piece" is also used to refer to a similar-looking part in some coleopteran species (Lindroth and Palmén 1970; Girón and Short 2021).

4.11. Conclusions and future directions

(1) The dichotomy between Protodermaptera and Epidermaptera based on the relative sizes of the anterior and posterior ventral cervical sclerites is problematic. Instead, the condition of the posterior end of the posterior lateral cervical sclerites, which is either acutely bent inward and thus V-shaped in Protodermaptera (broadly including Allostethidae and Apachyidae) or only gently curved in Epidermaptera, can provide a more stable classification system correlated with other diagnostic traits.

(2) In the Neodermaptera (with the exception of the Apachyidae, Gonolabinidae, and Hemimeridae), the epiproct consists of two sclerites: the dorsal telson sclerite and the pygidium. The presence of further division in the dorsal telson sclerite cannot be used as a diagnostic trait for the Protodermaptera.

(3) There are two distinct groups of the Neodermaptera that exhibit two penises pointing in opposite directions when at rest. In the Apachyidae and Allostethidae (and possibly the Gonolabinidae), both penises bend anteriorly prior to the first copulation, similar to members of the Haplodiplatyidae, Diplatyidae, and Pygidicranidae. In contrast, in males of the Anisolabididae and Labiduridae, from which Allostethinae has been removed, both penises point posteriorly, as in the eudermapteran families. However, one of the penises changes direction within a few days after imaginal eclosion. These two families (or superfamilies, Anisolabidoidea and Labiduroidea) are challenging to differentiate and collectively form the Mesodermaptera.

(4) Although it is challenging to observe the conditions of dermapteran penises immediately after imaginal eclosion, whether they point posteriorly or anteriorly, this trait can provide a useful boundary between Protodermaptera and Epidermaptera, alongside the dichotomous variation in cervical structures.

(5) Although still under debate, the root of Neodermaptera is likely situated within Protodermaptera, which appears to be paraphyletic. The ingroup relationships of Neodermaptera have been largely established and are comparatively stable, with robust evidence supporting monophyly in both Epidermaptera and Eudermaptera. Mesodermaptera and Spongiphoridae (within Eudermaptera) may also be paraphyletic, necessitating further studies on more subfamilies of Anisolabididae and Spongiphoridae.

(6) Following Bergsten's (2005) suggestions, the estimation of phylogenetic relationships among earwigs should be conducted both with and without outgroup taxa.

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