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An identification guide to the genera of aquatic larval Chironomidae (Diptera) of south-east Asia

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Abstract

We provide illustrated dichotomous keys for the identification of final (4th) instar larvae of south-east Asian genera of Chironomidae (Diptera), predominantly from aquatic (freshwater and maritime) habitats. The region considered comprises oriental China, Burma, Thailand, Malaysia (west and east), Brunei, Singapore and Indonesia. Eight subfamilies are represented and phylogenetically validated tribes are keyed. Terminal taxa, listed in the sequence used in this guide, comprise 28 genera of Tanypodinae, 71 of Chironominae, 2 of Podonominae, 1 of Buchonomyiinae, 8 of Diamesinae, 2 of Protanypodinae, 5 of Prodiamesinae, 2 of Telmatogetoninae and 61 of Orthocladiinae. The morphology terminology is standard for larval Chironomidae to which users are referred. Illustrations of selected features are provided as photographs with important details labelled. Short summaries of ecology and concise details of selected species and regional / global distribution are provided in brackets under each entry. Some suspect new synonymy is alluded to, but will be addressed formally in more detail elsewhere.

Key words: Keys, larvae, new records, south-east Asia, oriental China, photographic illustrations, morphology

Introduction

Benthic freshwater aquatic surveys reveal many larval Chironomidae (Diptera), and often the brief but well-identifiable pupal stage. Adults are short-lived with the male usually displaying morphological features that allow species identification. Historically this easily-collected life history stage has been used in descriptive taxonomy leaving the immature stages relatively neglected. The longer-lived larva integrates and therefore better reflects site-specific aquatic environmental conditions. Hence demand remains for a guidance to larval identification for biomonitoring of water bodies. This is true even as demand grows for valid vouchering of taxa revealed by barcoding and will be more so with building of reliable libraries for interpretation of eDNA sampling (Mrozińska & Obolewski 2024).

Since the earliest studies in south-east Asia, some regional Chironomidae have been identified to species including from individual rearing and with descriptions of early stages. Material from the 'Thienemann Limnological Sunda-Expedition' to current day Indonesia resulted in publications concerning adults (Johannsen 1931, 1932a, b) and selected larvae and pupae (Zavřel 1933, Lenz 1937). The approach was contemporary with continental European recognition of the importance of immature stages in chironomid research. These studies were continued by Masaaki Tokunaga of Kyoto Prefectural University, Japan. Aware of the European growing development of integrated taxonomy, he corresponded with the German scientists of the 'Thienemann group', and also with the British dipterist F.W. Edwards. Tokunaga's published research has stood the test of time, particularly in his astute observations of the diverse maritime Chironomidae. Tokunaga's thorough approach often combined full life-history information and became key to understanding the regional (with extension to a global) fauna. Unfortunately, the model was not adopted as a modus operandi by subsequent regional contemporary gurus (certain Japanese and Chinese) scientists of Chironomidae. Manabu Sasa came to chironomids as a retirement project from a career in mosquitoes and mites

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(Cranston 1996) apparently believing the field was open, ahistorical and with poor understanding or guidance from previous workers or from overseas. Massively productive with a team of collaborators working mainly with adult males, but described and illustrated from woeful slides, Sasa's name is associated with prolific synonymy (e.g. Kobayashi & Endo 2008, Niitsuma *et al*. 2011, Yamamoto & Yamamoto 2014) that has required already half century of ongoing remediation.

In China, assessment of biodiversity of aquatic midges based mainly on male stages was adopted by Xinhua Wang and his associates. This has resulted in 'cleaning up' of much of Sasa's prolific output, but has rarely advanced knowledge of the immature stages. Incorporation of drift nets to intercept drifting pupal exuviae (cast skins) with a by-product of pharate adults or occasionally even larval associations as used by the authors of this guide and their collaborators provide valuable life history data for the regional Chironomidae (e.g. Tang & Cranston 2017, 2019, Tang *et al*. 2022b). Additional life histories can derive from Japanese studies of shared taxa. Never-the-less, much diversity remains represented only by adult males and thus we incorporate key characteristics notably from the larval volume of 'Holarctic keys' (Andersen *et al*. 2013). Some images are from sources outside the region, but where possible our illustrations portray southeast Asian exemplars.

In the key, below the genus entry bracketed information (in [ ]) summarises the current species diversity, named if fewer than 3–4 described taxa, with authorship provided but with no further reference to the original description. Broader summary publications are referenced. Distribution data is summarized, minimally with country but in oriental China province(s) is specified, and the Malaysian states of Borneo are identified. Symbols and abbreviations used: ♂—male adult, < fewer than, > more than, ANIC—Australian National Insect Collection, c.—circa, about, e—east, EJNU—Department of Ecology, Jinan University, exc.—excluding, Fig.—figure, gp—group, inc.—including, L—larva, m.—metres (elevation, above sea level), mt—Mount(ain), n.—north, nr—near, N.Z.—New Zealand, P(e)—pupa (exuviae), s—south, se—southeast, s.g.—subgenus, sp. or spp.—species, s.s.—sensu strict, syn—synonym (junior), w—west, ZSM—Zoologische Staatssammlung, München, Germany.

The last entry summarises wider distribution, by biogeographic region, namely Holarctic (present in both Nearctic and Palaearctic), Palaearctic (e & w, if restricted), Afrotropical, Neotropical and Australia (includes New Zealand (N.Z.)) and Oceanian). Principal sources for wider (extralimital) distributions are for the Holarctic (Andersen *et al*. 2013), Afrotropical (Freeman & Cranston 1980), Neotropical (Silva *et al*. 2018), Australian and New Zealand (Cranston 2019). 'Global' is used for taxa occurring on all the major landmasses excepting Antarctica to avoid repetition of 'excepting Antarctica'.

Inclusion of taxa is based primarily on published records within the region under consideration. Ongoing studies by the second author has revealed many taxa newly observed in oriental China, and both authors continue to add taxa from Thailand, east Malaysia (Sabah, Sarawak) and Brunei from both contemporary and historic collections. Some entries are based on verified pupa or male adult for which an associated larva derives from elsewhere than south-east Asia. Predominantly these derive from the eastern Palaearctic, especially from Japan including its' islands e.g., the Ryukyus (Okinawa), and some also derive from Australia.

We use photographs of selected diagnostic larval morphological features. For users familiar with line drawings, examples include Andersen *et al*. (2013) for the Holarctic, Silva *et al*. (2018) for the Neotropics, Cranston (2019) for Australasia and Cranston (2004) for Malaysia, that can be consulted including for more detailed labelled morphology. Some of our images derive from extra-limital specimens that illustrate as-yet unreared Asian congeners. Many derive from a large gallery of global images for an interactive Lucid key to Chironomidae larvae (https://keys.lucidcentral.org/keys/v3/Chironomidae/). The majority of images photographed were stacked using an Automontage™ system attached to a Leica DMR™ microscope with oil immersion (×1000) and Nomarski Interference optics (producing blue background). The complete system is now defunct. Images were manipulated subsequently using Abode Photoshop™. Lettering colour (black or white) and location of labels are selected to not obscure specimen detail and to be visible against background.

The geographical area covered by this guide encompasses 'south-east Asia' constrained by the existence of modern published studies of Chironomidae (Fig. 1). Contemporary studies of the chironomid faunas of oriental China (Zhang *et al*. 2019), Thailand (Cranston 2007) and Malaysia (Sabah and Sarawak) are available. Records from Burma, notably by Brundin (1966), Brundin & Sæther (1978) and Reiss (ZSM), and the Indonesian Sunda islands of Sumatra and Java (Johannsen 1931, 1932a, b; Lenz 1937) provide early data for some regional chironomids. However, records from these large countries (e.g. Sumatra, Kikuchi & Sasa 1990, Sulawesi, Ashe 1990) rarely provide sole evidence for including uncommon taxa. Thai collections include those held in ZSM identified by F. Reiss and M.

Spies, nation-wide surveys (including post-tsunami, Cranston 2007), a wet rice field fauna investigation (Hashimoto *et al*. 1981) and a very competent study of the Phong River in Khon Kaen Province to genus-level (Sriariyanuwath *et al.* 2015). Distributions concerning taxa in Thailand derive from these and also include unpublished personal records. We note taxa in India, Nepal, Japan and Korea only relative to the keyed core south-east Asian fauna.

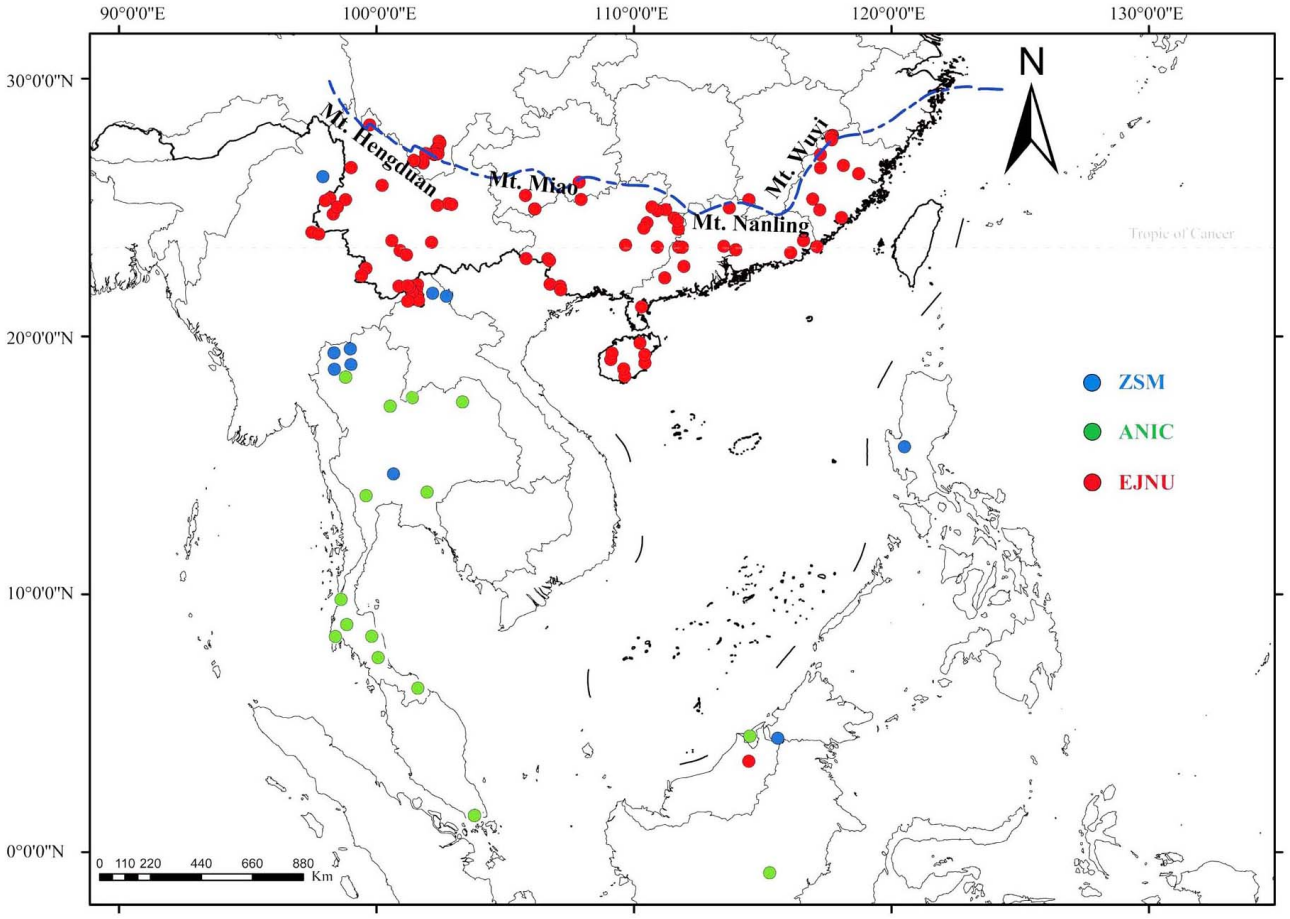

FIGURE 1. Collecting locations used in the guide (blue: ZSM; green: ANIC; red, EJNU, for institution abbreviations see the text. The boundary between palaearctic and oriental region of mainland China follows Hoffmann (2001). For location details see supplement file 1 (Zenodo.xx)

KEYS

We have adopted traditional dichotomous keys here, choosing the best distinguishing character state, and preferring to use singular for paired structures. The prior statement originates a hierarchical sorting step by step until a closed terminal taxon. If the rank is a higher taxon (subfamily or tribe) the name is in plain font if it is terminal, in bold font if a subkey follows. Some morphologically similar genera, notably *Cricotopus* (including *Paratrichocladius*) and *Orthocladius*, lack unambiguous diagnostic larval characters to allow straightforward separation on morphology. Thus, some taxa key to more than one terminal. None are keyed explicitly to their subgenera that are rarely validated by phylogenetic analysis. Similar treatments are also applied into highly speciose genera, e.g., *Chironomus*, *Polypedilum* and *Tanytarsus*. Illustrative photographs are provided where available: some that concern fine details are unavailable, but other morphology may be shown at the end of the couplet.

Chironomidae: subfamily key

1 Antenna retractile within head (Fig. 2A). Hypopharynx with toothed ligula (Fig. 2B). Mentum weak. . . . . **Tanypodinae**
1' Antenna non-retractile. Hypopharynx lacking toothed ligula. Mentum is dominant toothed plate. 2

2(1) Ventral (median) mentum laterally expanded into ventromental plate, usually striate (Fig. 2C, D), never with beard beneath [Exceptionally ventromental plate lacks striae in *Xiaomyia*, *Shangomyia* (Fig. 2E) (tribe Xiaomyiini), *Harrisius*, *Stenochironomus* (tribe Chironomini) (Fig. 2F) . . . . . **Chironominae**
2' Ventromental plate, if developed, never striate, sometimes with beard beneath 3

3(2) Labrum without premandibles (Fig. 2H) 4
3' Labrum with distinct premandibles (Fig. 2J) 5

4(3) Procercus well developed (Fig. 2K). Antenna well-developed with 4 or 5 segments, 2nd and/or 3rd annulate (Fig. 2L) . . . . . **Podonominae**
4' Procercus absent (Fig. 2I). Antenna weak, 3rd segment smooth . . . . . Buchonomyiinae [lotic, commensal/ectoparasitic, *B. burmanica* Brundin & Sæther, adults from Myanmar (Burma), oriental China (Yunnan)]

5(3) Antennal segment 3 annulate (Fig. 2O). Ligula and paraligula (of prementum) forming 3 setal brushes (Fig. 2P) . **Diamesinae**
5' Antennal segment 3 smooth (Fig. 2M, N) 6

6 Head capsule densely setose (Fig. 13C, D). Anterior labrum with transverse row of overlapping serrate lamellae (Fig. 13E, F), Prementum medially deeply divided into lamellae (Fig. 13H) . . . . . **Protanypodinae**
6' Head rarely with more than basic cephalic setae. Labrum without row of lamellae, or restricted to paired labral lamellae close to S1 setae. Prementum distinctive only in Telmatogetoninae. 7

7(6) Ventromental plate with setal beard beneath (Fig. 2G). Antenna long, 4-segmented (Fig. 2N) . . . . . **Prodiamesinae**
7' Ventromental plate, if developed, without setal beard beneath. Antenna, if 4-segmented, very short 8

8(7) Antenna squat, 4-segmented (Fig. 2M). Premandible with strong beard (Fig. 2J). Anal tubules absent, usually maritime . . . . . **Telmatogetoninae**
8' Antenna if short, rarely 4-segmented or indistinctly segmented. Premandible bare or with sparse beard. Anal tubules usually present in freshwater groups. . . . . **Orthocladiinae**

Tanypodinae: tribes and genera

This subfamily is the third most diverse, distributed widely excepting Antarctica, occupying many different microhabitats in major aquatic habitats, including phytotelmata and the hygropetric zone. Larvae are free-living and none make larval nests or pupal cases, pupa can directly utilize atmospheric oxygen through a specialized plastron plate at air-water interface. Typically, they are described as micro-predators, but some, notably in tribes Macropelopiini, Procladiini, and Tanypodini, perhaps many, feed on diatoms and detritus at least in early instars. The monophyly of the subfamily is well supported (Cranston *et al*. 2011; Silva & Ekrem 2016; Krosch *et al*. 2022), perhaps originating from the tropical region, with expectation of higher diversity in s.e. Asia. Seven of the 9 validated tribes of Tanypodinae occur in the region, lacking the Palaearctic Anatopyniini (for *Anatopynia* Johannsen) and the Australian Coelopyniini (for *Coelopynia* Freeman). Mature (4th instar) larvae can be identified but earlier instars rarely can. Delimitation of genera in the '*Thienemannimyia* group' may be aided by a developing thoracic horn in the mature fourth instar larvae. Cephalic setation, both dorsal and central, is valuable in generic identification in this subfamily.

1 Head elongate (Fig. 2A). Dorsomentum indistinct, teeth essentially absent (Fig. 2B). Body lacks complete fringe 2
1' Head round to oval (Fig. 3A). Dorsomental teeth on transverse plate or in longitudinal rows. Body with dense lateral setal fringe (Fig. 3B) 3

2(1) Body lacking organised lateral setal fringe on body . . . . . **Pentaneurini**
2' Body segments 4–10 with 4 larger setae located anterior-laterally (Fig. 3C) . . . . . Natarsiini [*Natarsia* Fittkau; *N. punctata* (Meigen) common, oriental China (Guangdong); 2 spp. as ♂♂ (Cheng & Wang 2006); Nearctic (inc. Mexico), Palaearctic, inc. Japan]

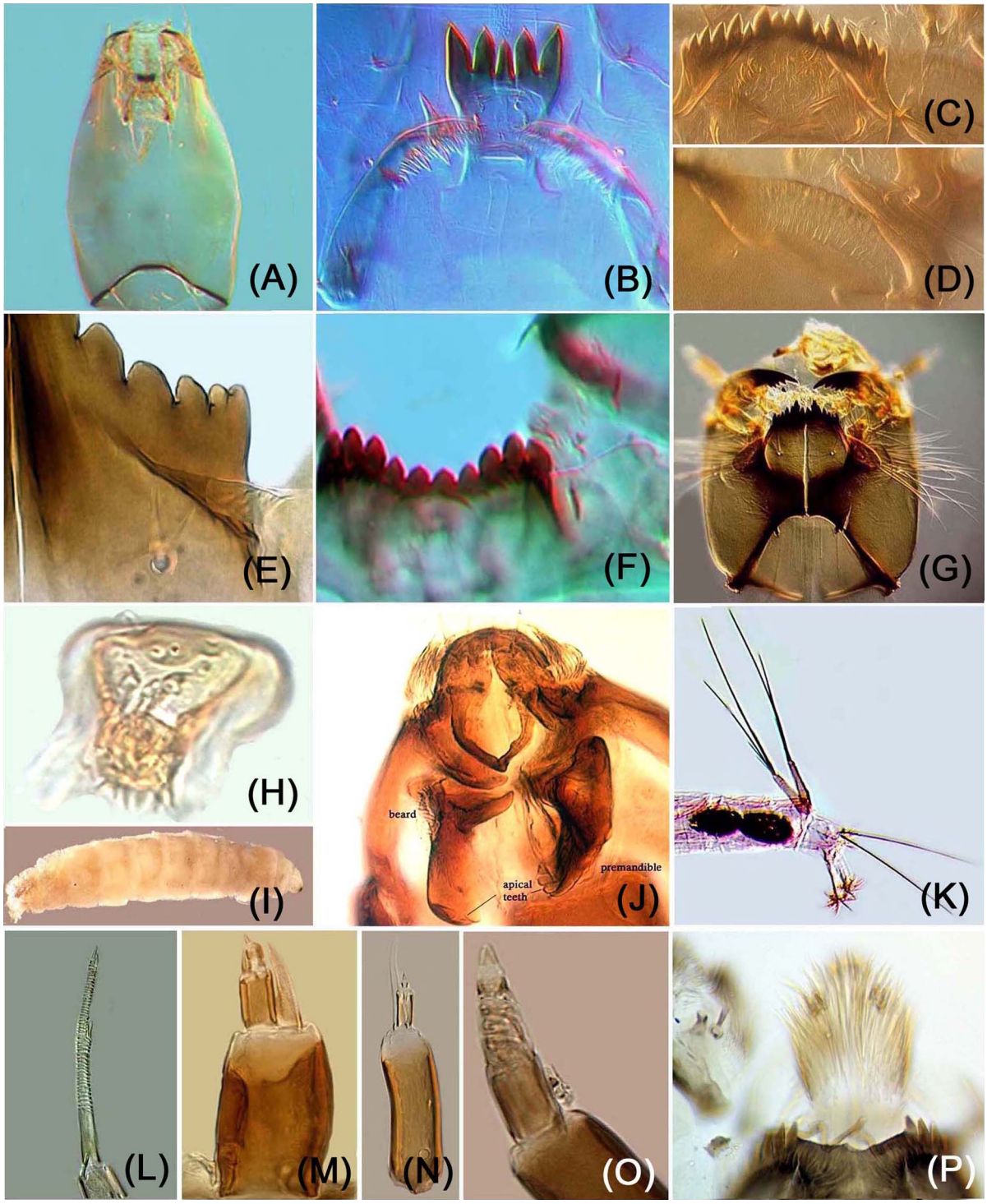

FIGURE 2. Subfamily key. Tanypodinae, *Ablabesmyia*, (A) ventral head, (B) ligula. Chironominae, *Conochironomus*, (C) mentum, (D) ventromental plate; *Shangomyia*, (E) mentum and ventromental plate; *Stenochironomus*, (F) mentum. Prodiamesinae, *Prodiamesa*, (G) ventral head. Buchonomyiinae, *Buchonomyia*, (H) labrum, (I) habitus. Telmatogetoninae, *Telmatogeton*, (J) anterior labrum. Podonominae, *Paraboreochlus*, (K) posterior body; *Boreochlus*, (L) antenna. Telmatogetoninae, *Telmatogeton*, (M) antenna. Prodiamesinae, *Prodiamesa*, (N) antenna. Diamesinae, *Diamesa*, (O) antenna, (P) mid-mentum, hypopharynx.

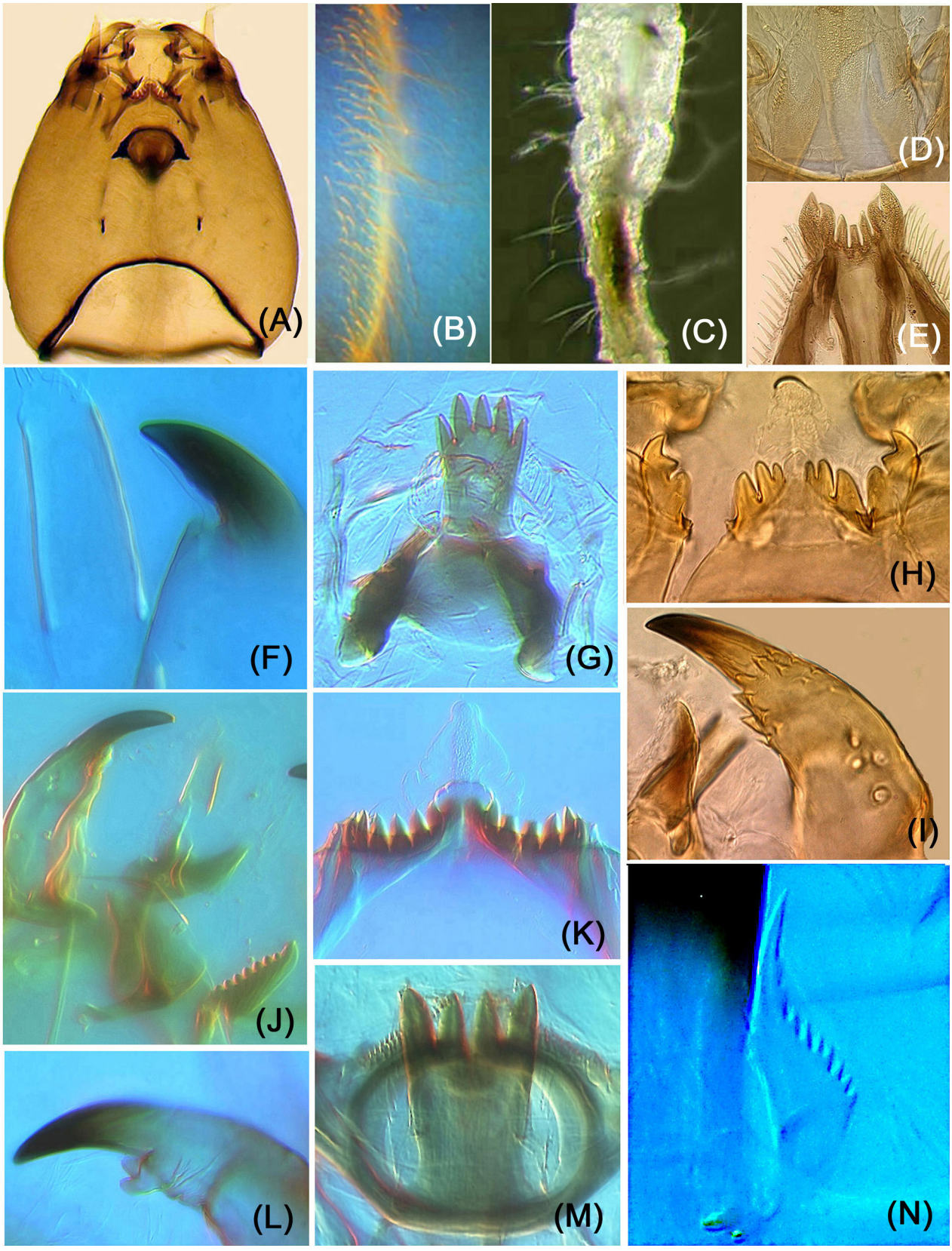

FIGURE 3. Tanypodinae, tribes. *Derotanypus*, (A) ventral head, (B) abdominal lateral fringe; *Natarsia*, (C) abdomen; *Clinotanypus*, (D) dorsomentum; *Coelotanypus*, (E) ligula; *Tanypus*, (F) mandible, (G) ligula; *Fittkauimyia*, (H) dorsomentum, radula, (I) mandible; *Procladius*, (J) mandible, dorsomentum; *Psectrotanypus*, (K) dorsomentum, radula; *Djalmabatista*, (L) mandible; *Psectrotanypus*, (M) ligula, paraligula; *Procladius*, (N) paraligula.

3(1) Dorsomental with teeth longitudinally aligned, not on distinct plate (Fig.3D). Ligula with 6–7 teeth (Fig. 3E) . . . . . Coelotanypodini
[sole regional genus *Clinotanypus* Kieffer; Indonesia (Sulawesi), Thailand, abundant, diverse esp. drying rivers. 5 spp oriental China (Cheng & Wang 2008), Holarctic, Neotropics, Australia]

3' Dorsomental teeth at margin of distinct plate (Fig. 3H). Ligula with 4 or 5 teeth (Fig. 3G) 4

4(3) Mandible with enlarged base and short apical tooth (Fig. 3F). Lacking pseudoradula and pecten hypopharyngis . . Tanypodini
[sole regional genus *Tanypus* Meigen is lentic, eurytolerant. Several spp. Singapore, Malaysia, Thailand; *T. punctipennis* Meigen, *T. chinensis* Wang, *T. formosanus* (Kieffer), oriental China; Holarctic, Neotropical, Australia]

4' Mandible with slender base and long apical tooth (Fig. 3I, J, L). Pseudoradula (Fig. 3K) and pecten hypopharyngis present 5

5(4) Dorsomentum with continuous toothed plate, concave-arched weakly subdivided into median and lateral sections (Fig. 3H). Mandible with several rows of additional small surface teeth (Fig. 3I). . . . . Fittkauimyiini
[sole regional genus *Fittkauimyia* Karunakaran, Singapore, Malaysia, Thailand, Indonesia (Sulawesi), China; all regional records may refer to acidophilic and pollution tolerant *F. disparipes* Karunakaran. Holarctic, Afrotropical, Neotropical, Australia]

5' Dorsomentum discontinuous plate, toothed in median and lateral sections (Fig. 3J, K). Mandible lacks extra teeth. 6

6(5) Mandible with weak basal tooth. Ligula with 5 dark or light teeth, paraligula bifid (rarely trifid) (Fig. 3M). . . **Macropelopiini**

6' Mandible with large basal tooth (Fig. 3L). Ligula with 4–5 dark teeth; paraligula pectinate (Fig. 3N) . . . . . **Procladiini**

Tanypodinae: Pentaneurini

The Pentaneurini is the most diverse tribe of Tanypodinae, regionally with at least 14 genera known as larvae, plus several informally recognised additional morphotypes (not keyed). Most genera are widely distributed including in oriental China and beyond in the Palaearctic and Australian regions. The '*Thienemannimyia* group' of genera is difficult to separate and may require pupal associations.

1 Palp basal segment with 2 or more sclerotized sections (Fig. 4A, B) 2

1' Palp with single sclerotised basal segment (Fig. 4C). 3

2(1) Palp with 2 unequal segments, base of divided 1st segment less than 0.5 length of apical part (Fig. 4A). Pseudoradula broadened posteriorly, granulation diffuse (Fig. 4D) . . . . . *Zavrelimyia* Fittkau (part)
[syn. *Paramerina* Fittkau, may be treated as s.g.; lotic, widespread regional; Japan; Holarctic, Neotropical, Australia]

2' Palp multisegmented; if only 2 segments then parts subequal or greater than 0.5 length of apical segment; in some spp. with > 2 segments, basal segment may be short (Fig. 4B). Pseudoradula not broad posteriorly, granulation often in longitudinal rows (Figs. 2B, 4E) . . . . . *Ablabesmyia* Johannsen
[lentic, lotic, abundant, speciose, s.g. Cranston & Epler, 2013; oriental region, Niitsuma (2013), Niitsuma & Tang (2019); global]

3(1) Ligula with median tooth longer than inner teeth, reaching or surpassing level of outer teeth (Fig. 4F). SSm strongly retracted posteriorly (Fig. 4G). Anal tubules longer than posterior parapods (Fig. 4H). . . . . *Nilotanypus* Kieffer
[psammophilic lotic, widespread regionally, *N. polycanthus* Cheng & Wang, *N. quadratus* Cheng & Wang, oriental China, Cranston *et al*. 2022; Holarctic, Neotropical, Afrotropical, Australia]

3' Ligula with median tooth subequal to or shorter than inner teeth (Fig. 4J). SSm not strongly retracted (Fig. 4L). Anal tubules not longer than posterior parapods 4

4(3) Apex of 2nd antennal segment with Lauterborn organs elongate, subequal in length to 3rd segment, giving bifid apex (Fig. 4I). 5

4' Lauterborn organs shorter or absent, apex thus not appearing bifid 7

5 (4) Ligula teeth in straight or weakly convex row (Fig. 4J). . . . . *Denopelopia* Roback & Rutter
[eutrophic wetlands, drain. Sulawesi, oriental China, Cheng & Wang 2005b (Pe, Ashe, 1990; Liu *et al*. 2017, as *Telmatopelopia*, both error)]

5' Ligula teeth in concave row (Fig. 4K, N). 6

6(5) Mid-section of ligula constricted; middle tooth smaller than inner tooth (Fig. 4K). Submentum (ventral star chart) with components trapezoid (Fig. 4L) . . . . . *Monopelopia* Fittkau
[inc. phytotelms, Indonesia (Sulawesi), oriental China (Hainan), Duan *et al.* 2021; Holarctic, New Zealand, monophyly and composition uncertain, Krosch *et al*. 2022]

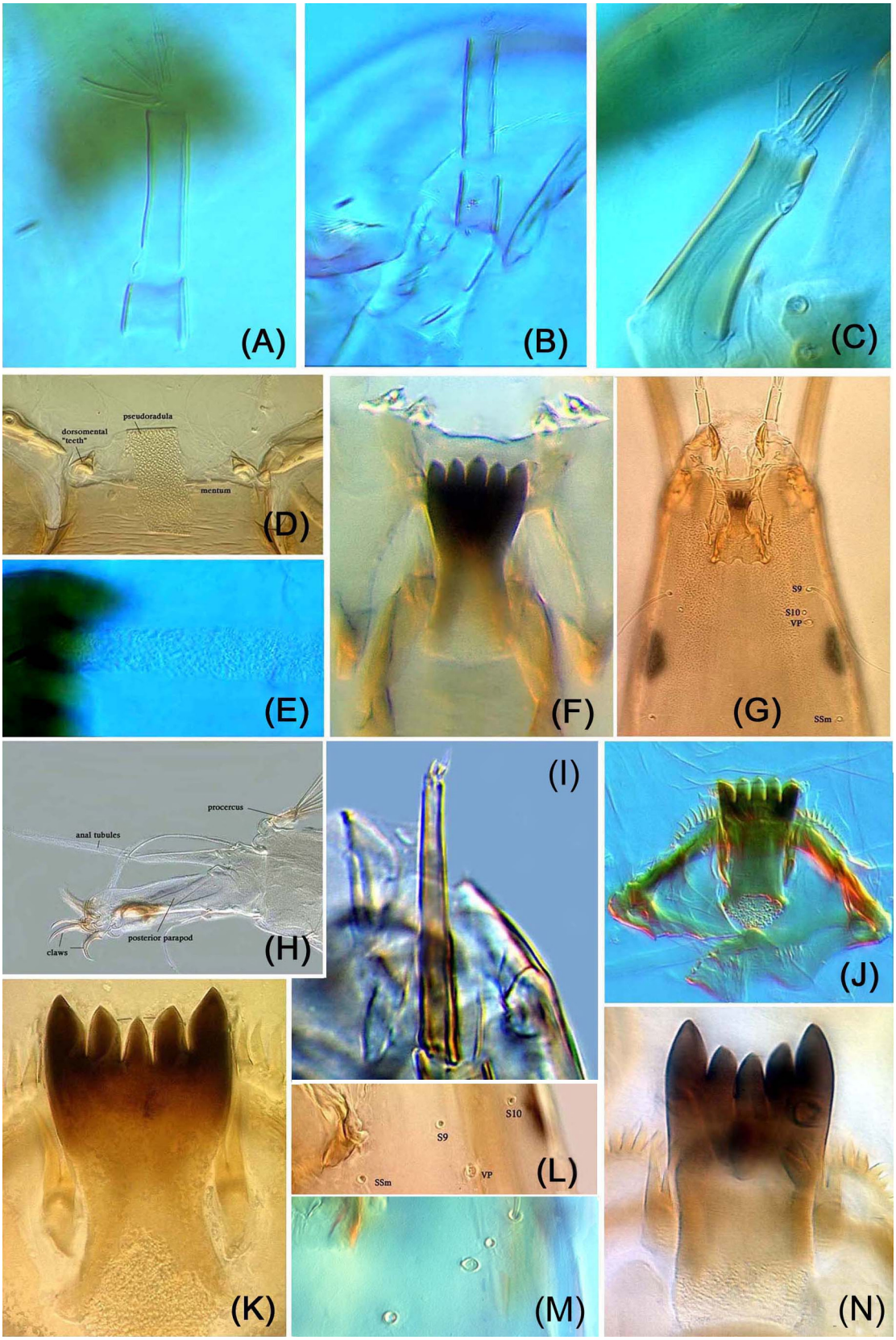

FIGURE 4. Tanypodinae, genera. *Zavrelimyia* (*Paramerina*), (A) palp; *Ablabesmyia*, (B) palp; *Natarsia*, (C) palp; *Zavrelimyia* (*Paramerina*), (D) radula; *Ablabesmyia*, (E) radula; *Nilotanypus*, (F) ligula, (G) submentum, (H) posterior abdomen; *Monopelopia*, (I) antenna; *Denopelopia* /*Telmatopelopia*, (J) ligula; *Monopelopia*, (K) ligula, (L) submentum; *Krenopelopia*, (M) submentum, (N) ligula.

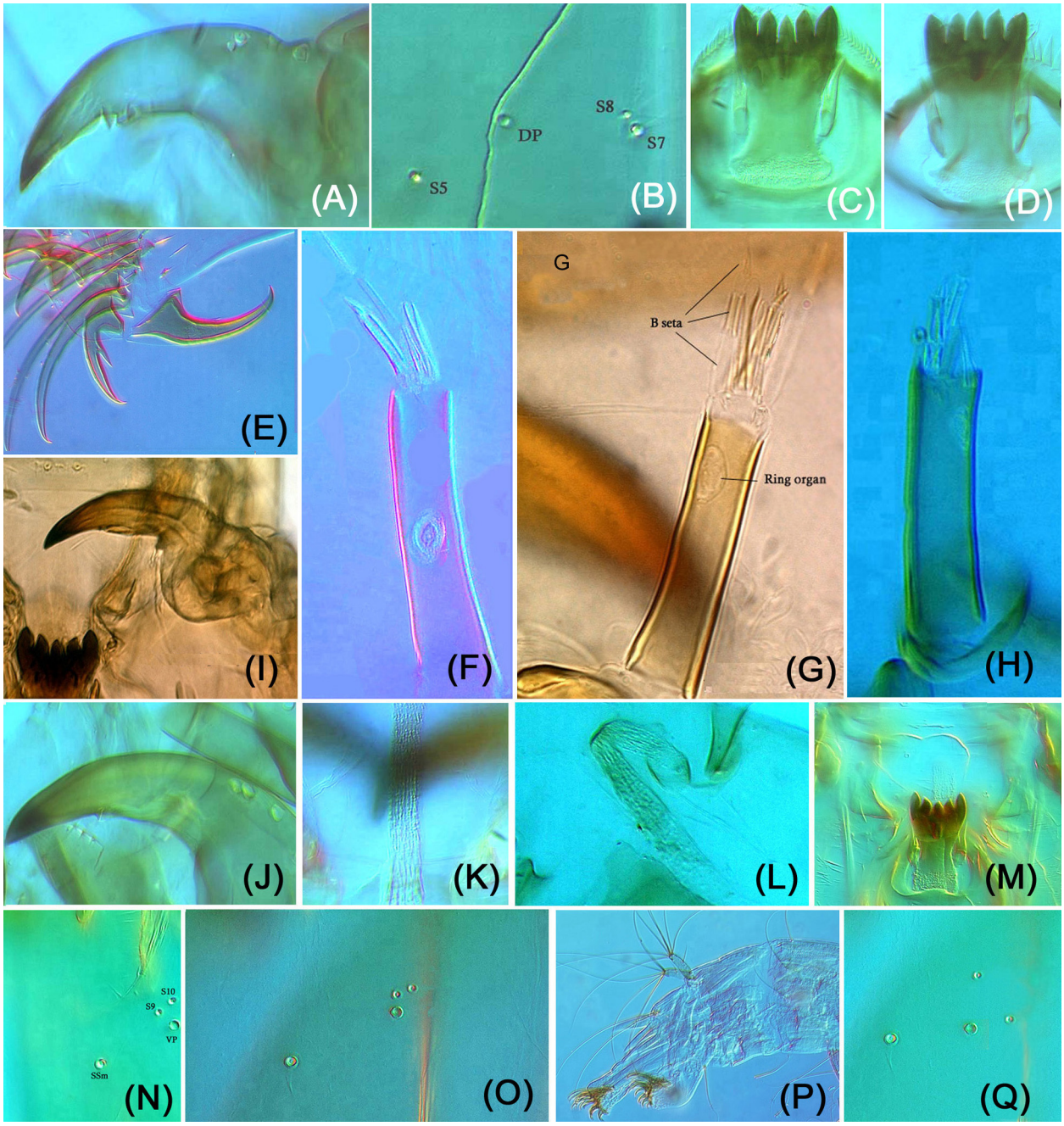

FIGURE 5. Tanypodinae genera. *Larsia*, (A) mandible, (B) dorsal cephalic setal pores/sockets ('star chart'), (C) ligula; *Zavrelimyia* (s.s.), (D) ligula, (E) posterior parapod claws; *Trissopelopia*, (F) palp; *Rheopelopia*, (G) palp; *Coffmania*, (H) palp; *Rheopelopia*, (I) mandible, ligula; *Coffmania*, (J) mandible; *Rheopelopia*, (K) pseudoradula, M-appendage; *Coffmania*, (L) pseudoradula; *Conchapelopia*, (M) ligula, pseudoradula, (N) ventral 'star chart'; *Thienemannimyia*, (O) ventral 'star chart', (P) posterior body; *Amnihayesomyia*, (Q) ventral 'star chart'.

6' Middle section of ligula not so constricted; middle tooth subequal to inner tooth (Fig. 4N). Submentum (ventral star chart) with components linear (Fig. 4M) . . . . . *Krenopelopia* Fittkau
[krenobiont, small lotic, Indonesia (Java), Singapore, Japan; Holarctic]

7 (4) Mandible with large molar tooth (Fig. 5A) 8
7' Mandible with mola tooth indistinct or absent (Fig. 5I). 9

8(7) Dorsal head with pore (DP) (Fig. 5B). Ligula with teeth directed anteriorly (Fig. 5C). Antennal ratio > 3.5. Small claws of posterior parapod without inner tooth . . . . . .*Larsia* Fittkau
[lotic, Indonesia (Sulawesi), *L. albiceps* (Johannsen) widespread Thailand, China, spp. on Pe; Holarctic, Neotropical, Afrotropical, Australia (Cranston & Krosch 2021)]

8' Dorsal pore absent. Ligula with apices of inner teeth directed slightly to strongly outward (Fig. 5D). Antennal ratio < 3.5. Small claw(s) of posterior parapod often with inner tooth (Fig. 5E) . . . . . *Zavrelimyia* Fittkau
[lotic, includes previous *Paramerina* spp. Regionally speciose and widespread, e.g. *Z. ignobilis*, *Z. dulosa*, *Z. facili*s, Z. *alterna* (all Johannsen) (Indonesia, inc. Sumatra, Bali, Java). Holarctic, Neotropical]

9(7) Palp with ring organ near middle of basal segment (Fig. 5F) . . . . . *Trissopelopia* Kieffer
[lotic, lentic, ♂. (perhaps only 1 common sp., *T. oyabetrispinosa* (Sasa, Kawai & Ueno), oriental China (Sichuan, Shaanxi), Cheng & Wang 2005a; Holarctic (inc. Japan), Nepal (Roback & Coffman 1987), Afrotropical, Neotropical]

9' Palp with ring organ subapical on basal segment (Fig. 5G, H) . . . . . *'Thienemannimyia* group'* 10

10(9) Palp with b sensillum 3-segmented (Fig. 5G) 11

10' Palp with b sensillum 2-segmented (Fig. 5H) 12

11(10) Mandible with teeth essentially absent (Fig. 5I). Pseudoradula tapers from base to apex, c. 20% of M-Appendage width at midpoint (Fig. 5K) . . . . . *Rheopelopia* Fittkau
[rheophilous; *R. joganflava* (Sasa & Okazawa), *R. tuberculata* (Chaudhuri & Debnath) in oriental China. Holarctic (c. 10 spp.)]

11' Mandible with accessory tooth visible at 400x (Fig. 5J). Pseudoradula narrow, ca. 10% of M-Appendage width with granulation in 5–8 rows (Fig. 5L) . . . . . *Coffmania* Hazra & Chaudhuri
[3–4 regional spp. (India), L in drains in Singapore; *C. insignis* Niitsuma, oriental China, Japan]

12(10) Pseudoradula narrow, ca.10% of width of M appendage; granulation in 5–8 closely adjacent, near parallel rows (Fig. 5M). Cephalic setae S9 and S10 adjacent, separated by width of VP (Fig. 5N) . . . . . .*Conchapelopia* Fittkau
[lotic, lentic, eurythermic. Indonesia (Sulawesi) *C. insolens* Murray; *C. brachiata* Niitsuma & Tang, oriental China; global exc. Australia]

12' Pseudoradula >20% of width of M appendage, tapered; granulation in at least 8 rows. Cephalic setae S9 and S10 more widely separated (Fig. 5Q) or approximated (Fig. 5O) 13

13(12) Cephalic setae S9 near S10, anterior to alignment of SSm and ventral pore (VP) (Fig. 5O). Posterior parapod with 5 small thick, dark claws, lacking an elongate long claw (Fig. 5P) . . . . . .*Thienemannimyia* Fittkau
[lotic, lentic, Indonesia (Sulawesi), Thailand, regionally speciose, abundant, 5 spp. oriental China (Cheng & Wang 2009); includes *Hayesomyia* Murray & Fittkau; global]

13' Cephalic setae S9 distant from S10, posterior / laterally aligned SSm and VP (Fig. 5Q) . . . . . .*Amnihayesomyia* Niitsuma
[lotic, *A. vittata* Tang & Niitsuma, oriental China (Guangdong, Yunnan), 2110 m. 7 spp. from elevation in Nepal and adjacent palaearctic China, Tang & Niitsuma 2020a. Holarctic, inc. Japan]

Tanypodinae: Procladiini

The tribe Procladiini, together with members of the Tanypodini, is usually treated as typical tolerant indicators in regional lentic waterbodies. The Procladiini is represented regionally by widespread *Procladius*, more restricted *Djalmabatista* and the narrowly distributed *Saetheromyia.*

1 Antennal blade extended well beyond flagellum (Fig. 6A). Ligula largely black, with 4 or 5 teeth, inner teeth curved inward (Fig. 6B). Anterior parapods connected ventrally by spinose area (Fig. 6C). . . . . *Djalmabatista* Fittkau
[lentic or slow lotic, *D. sinica* Liu & Tang, *D. reidi* (Freeman), Liu & Tang 2017. Indonesia (Sulawesi), Malaysia, Thailand, transition oriental China / Palaearctic; Holarctic, Neotropical, Australia]

1' Antennal blade not extending beyond apex of flagellum (Fig. 6E). Ligula brown, with 4–5 teeth, inner teeth directed anteriorly or curved outward (Fig. 6D). Anterior parapods separated ventrally by spine-free area 2

2(1) Ligula with inner teeth points directed forward (Fig. 6D). Ring organ of palp in mid-segment (Fig. 3J) . . . . *Procladius* Skuse
[lentic, many spp. taxonomically difficult, cryptic taxa; global]

2' Ligula with inner teeth points directed outward. Ring organ of palp in basal 1/3 . . . . . *Saetheromyia* Niitsuma
[slow lotic; *S. tedoriprima* (Sasa), oriental China (Guangdong, Guangxi, Yunnan); Japan]

Tanypodinae: Macropelopiini

The tribe Macropelopiini is represented in the region by several rather similar looking genera, differentiated only with difficulty in the larval stage. Several occur only at boundaries of the oriental region at elevation (e.g. northern Thailand, Burma, and the transitional zone of oriental and palaearctic China (Tang & Niitsuma 2020b, Tang pers. obs.). Keys are based on extralimital larvae.

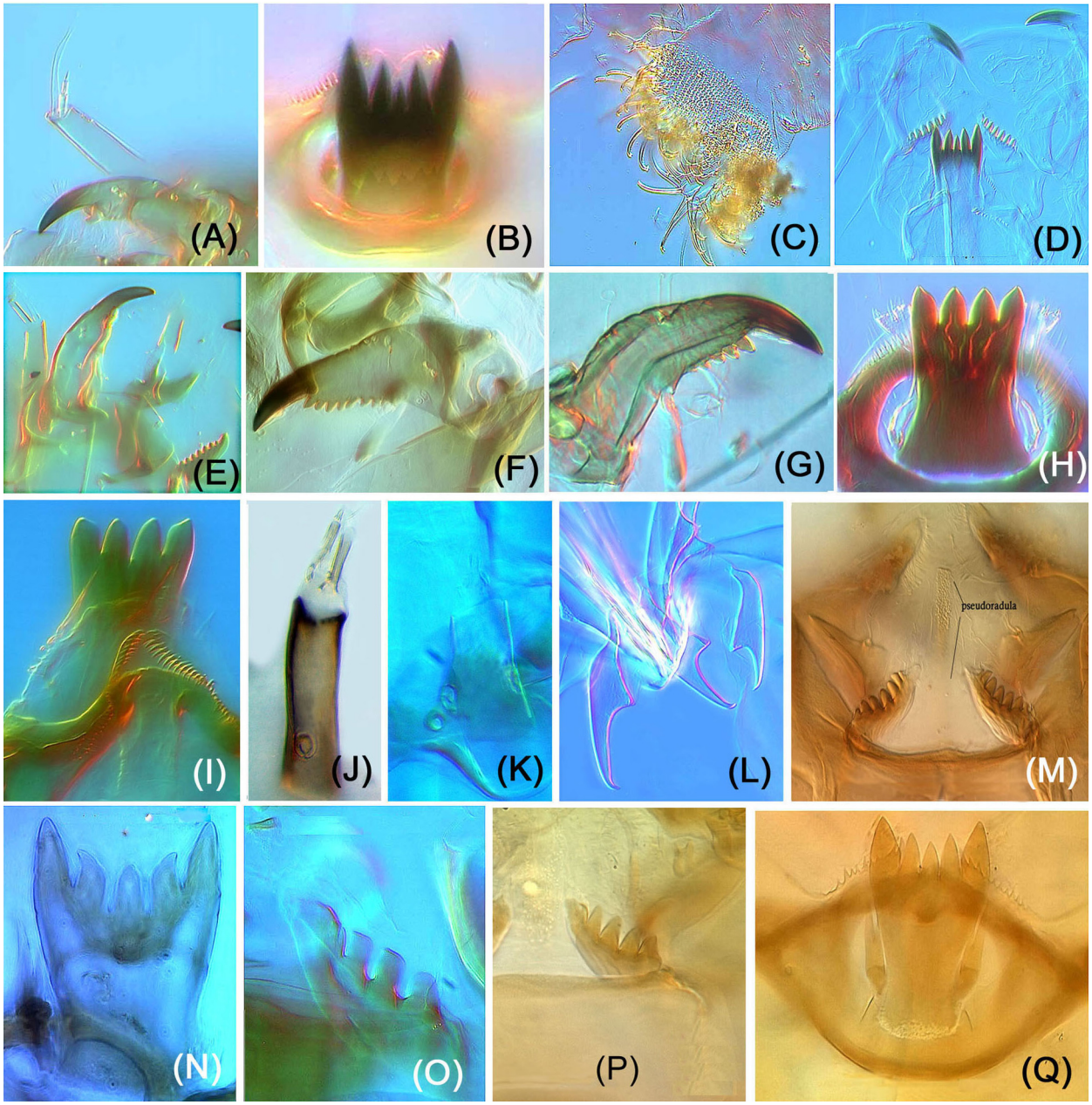

FIGURE 6. Tanypodinae genera. *Djalmabatista*, (A) antenna, (B) mentum, (C) anterior parapods; *Procladius*, (D) ligula, (E) anterior head; *Psectrotanypus*, (F) mandible; *Derotanypus*, (G) mandible; *Psectrotanypus*, (H) ligula; *Derotanypus*, (I) ligula, paraligula; *Bilyjomyia*, (J) palp; *Brundiniella*, (K) palp, (L) posterior parapod claws, (M) mentum, pseudoradula; *Apsectrotanypus*, (N) ligula, (O) mentum; *Radotanypus*, (P) mentum, (Q) ligula, paraligula and pecten hypopharyngis.

1 Mandible with several teeth in dorsal and ventral rows or on inner side of mandible (Fig. 6F, G) 2
1' Mandible with 1–2 small inner/accessory teeth and variably developed, tooth-like mola 3

2(1) Mandible lacks dorsal (surface) teeth (Fig. 6F). Ligula with all teeth tapering to anteriorly-directed point (Fig. 6H). Pecten hypopharyngis with c. 20 short teeth . . . . . *Psectrotanypus* Kieffer

[small lotic, lentic waterbodies, *P. lateralis* Cheng & Wang, *P. varius* (Fabricius), oriental China (inc. Guangdong, Fujian, Yunnan, Sichuan), Holarctic, Neotropical]

2' Mandible with dorsal (surface) teeth (Fig. 6G). Ligula with points of outer teeth directed outward (Fig. 6I). Pecten hypopharyngis with c. 30 long teeth . . . . . *Derotanypus* Roback [montane streams, L, Pe, oriental China (Yunnan, Sichuan), Tibet. Holarctic]

3(1) Palp with ring organ located basal (Fig. 6J) 4

3' Palp with ring organ located in middle or more apical (Fig. 6K). 5

4(3) Distinct labral sclerite anterior to labral rod. Cephalic S9 plumose. Several small posterior parapod claws with wide base . . . . . *Bilyjomyia* Niitsuma & Watson [springs, seeps, headwaters; *B. parallela* Niitsuma, oriental China (Guangdong), Japan; Holarctic. Niitsuma 2014]

4' Lacking labral sclerite. Cephalic S9 simple. No posterior parapod claw with wide base . . . . . *Macropelopia* Thienemann [slow, lotic; *M. kibunensis* (Tokunaga), oriental China (Guangdong), *M. pergrandis* Tang & Niitsuma, oriental China (Yunnan), + several spp, inc. unverified L. records (Yunnan, Hubei, Fujian), Thailand; Holarctic inc. Nepal; doubtful Neotropical, Australia. Inc. *Bethbilbeckia* Fittkau & Murray)]

5(3) Apex of dorsomental plate with bluntly pointed median extension (Fig. 6M). One to 4 small claws of posterior parapod with expanded base (Fig. 6L) . . . . . *Brundiniella* Roback [lotic, small streams, *B. galbina* (Wang, Cheng & Wang), oriental China (Yunnan), Thailand (Doi Inthanon, >1000 m.); Japan; Holarctic]

5' Apex of dorsomental plate not medially pointed. Small claws of posterior parapod lack dilate base 6

6(5) Points of inner teeth of ligula curved outward (Fig. 6N). Dorsomentum with 4 large teeth (Fig. 6O) . . . *Apsectrotanypus* Fittkau [small, cool, lotic; *A. yoshimurai* (Tokunaga), oriental China (Zhejiang). Holarctic inc. Nepal, India (as *Chaudhuriomyia* Paul & Mazumdar; Australia, N.Z. (as *Macropelopia*)]

6' Inner teeth of ligula directed anteriorly (Fig. 6Q). Dorsomentum with 5 large teeth (Fig. 6P) . . . *Radotanypus* Fittkau & Murray [slow lotic, bog drains; Thailand (Doi Inthanon, ZSM); oriental/palaearctic border China, at elevation > 2800 m.; Holarctic]

Chironominae: tribes and genera

This subfamily, the largest in the family, is almost exclusively aquatic although some immature stages can survive dry conditions by construction of larval or pupal cocoons or by desiccation tolerance, resuming development when rehydrated (Cranston 2014, Cornette *et al*. 2017). These exceptional taxa are not reported yet from south-east Asia. The tribal classification is not stable and can be inconsistent with emerging molecular data (e.g. Cranston *et al*. 2010, Cranston & Tang 2019). For example, the 'tribe' Pseudochironomini may be a grade. The Xiaomyiini for south-east Asian species is strongly supported, and the Tanytarsini appears to be monophyletic if the extralimital *Nandeva* Fittkau is included. Tribe Chironomini for the largest cluster of taxa is monophyletic, with distinctive included groupings of the '*Harnischia*-complex' and for genera related to *Chironomus* Meigen. Other emergent groupings may eventually be formalised but their validity and composition are not discussed here.

1 Ventromental plate lacks striae, with few weak distal hooks / lappets (Fig. 2E, F) 2

1' Ventromental plate striate, usually also with some distal hooks / lappets (Fig. 2C, D) 5

2(1) Head conventional, not flattened dorsoventrally or wedge-shaped (Fig. 7F). Mentum with median tooth protruding (Fig. 7A, B). Thoracic segments dilate only in pharate P. Abdomen cylindrical, not tapering, with well-developed procercus . . . . . tribe Xiaomyiini. 3

2' Head dorsoventrally flattened, tapered, wedge-shaped (Fig. 2E). Mentum strongly concave with characteristic arrangement of teeth (Figs. 2F, 7C, D). Thoracic segments swollen prior to pre-P. stage (Fig. 7E). Abdomen tapers, without or with reduced procercus. 4

3(2) Median tooth of mentum sagittate (like arrow head) (Fig. 7A) . . . . . *Shangomyia* Saether & Wang [*S. impectinata* Sæther & Wang, lotic, L. wood miner; regionally widespread, India to Borneo, oriental China, Cranston 2003; Tang & Cranston 2019]

3' Median tooth of mentum rounded, less protruding (Fig. 7B). . . . . *Xiaomyia* Saether & Wang [*X. aequipedes* Sæther & Wang, lotic. Regionally widespread, India, Thailand to oriental China. Tang & Cranston 2019]

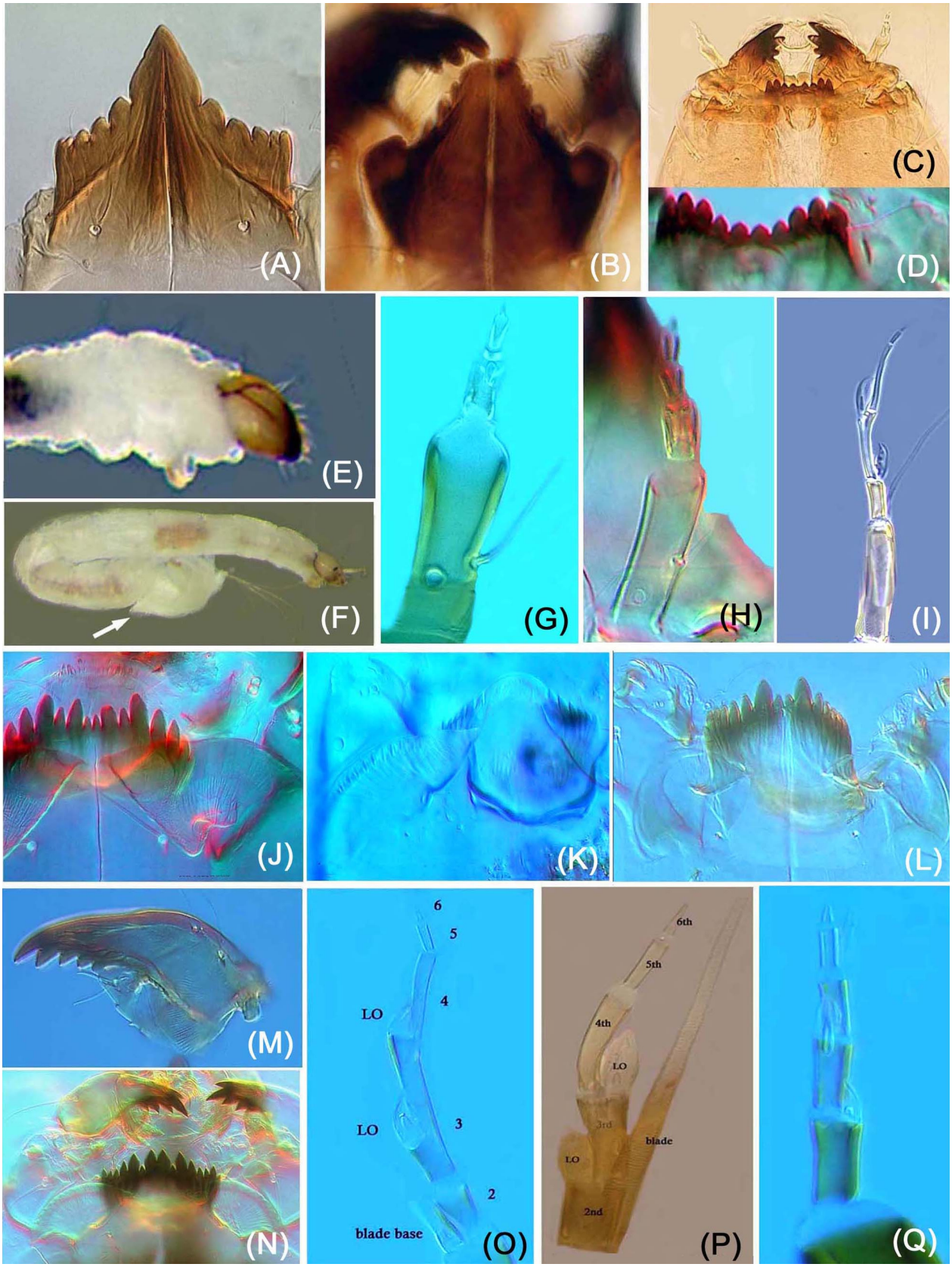

FIGURE 7. Larval Chironominae. *Shangomyia*, (A) mentum; *Xiaomyia*, (B) mentum; *Harrisius*, (C) mentum; *Stenochironomus*, (D) mentum; *Harrisius*, (E) anterior body; *Zavreliella*, (F) habitus; *Harrisius*, (G) antenna; *Stenochironomus*, (H) antenna; *Zavreliella*, (I) antenna, (J) mentum, ventromental plates; *Paralauterborniella*, (K) mentum, ventromental plates; *Xylochironomus*, (L) mentum, ventromental plates, (M) mandible; *Polypedilum nubifer*; (N) mentum, ventromental plates; *Skusella*, (O) antenna; *Conochirononomus*, (P) antenna; *Imparipecten*, (Q) antenna.

4(2) 3rd antennal segment short, subequal to 5th; 3rd & 5th each 1/2 length of 4th (Fig. 7G). . . . . *Harrisius* Freeman [tentative L, P, wood-mining, Thailand; Australia, N.Z.; Borkent 1984]

4' 3rd antennal segment shorter than 4th, both longer than 5th (Fig. 7H) . . . . . *Stenochironomus* Kieffer [abundant, L, wood- or leaf-miners; > 12 spp., inc. Thailand, Malaysia, oriental China; global, Borkent 1984]

5(1) Lauterborn organs large, alternate on segments 2 and 3 (Fig. 7I, O, P). Antenna 6-segmented (rarely 5 or 7). 6

5' Lauterborn organs absent to small, rarely large, opposite (Fig. 8E, F), rarely alternate. Antenna 5–9 segmented.. 18

6(5) Ventromental plate wedge-shaped (Fig. 7J). Body with dorsal hump on segment 11 (Fig. 7F), with long lateral tubules. L. in transportable case . . . . . *Zavreliella* Kieffer [*Z. marmorata* (v. d. Wulp), oriental China, *Z. cranstoni* Reiss, Sarawak (Malaysia), Reiss 1990; *Z. shidai* Cao & Tang, oriental China, Cao & Tang 2017; global]

6' Ventromental plate elongate, rarely wedge-shaped. Body without dorsal hump on segment 11, lacking lateral tubules. L. free-living, tubicolous or with fixed case (*Rheotanytarsus*) 7

7(6) Median tooth of mentum single, domed, pale (Fig. 7K) . . . . . .*Paralauterborniella* Lenz [widespread, *P. nigrohalteralis* (Malloch), Thailand, *P. ershanensis* Tang, oriental China, Tang 2016; Holarctic, Neotropical]

7' Median mentum with 2–4 pale teeth, or mentum all dark. 8

8(7) Mandibular and mental teeth all uniformly brown-black or yellow. 9

8' At least dorsal mandibular tooth pale. Median 3–4 teeth of mentum contrastingly pale. 16

9(8) Median mentum not clearly delimited as dorsomentum (Fig. 7L, N) 10

9' Median mentum delimited as dorsomentum by anteriorly-directed median ventromental plate, comprising 4 or 6 median mental teeth (Fig. 2C) 11

10(9) Median mentum with 2 recessed small teeth, ventromental plate semilunar (Fig. 7L). Mandible with basal striae (Fig. 7M). . . . . *Xylochironomus* Cranston [L. wood-mining, 1–2 undescribed spp., L, P. ♂, Thailand, oriental China; Australia; Cranston 2006]

10' Median mentum with 2 large teeth, ventromental plate fan-like (Fig. 7N). Mandible lacks striae . . . . . .*Polypedilum* Kieffer [part: *P. nubifer* Skuse, *P. tobaseptimum* Kikuchi & Sasa, widespread; *P. quasinubifer* Cranston, Singapore, Thailand; Australia. Cranston *et al.* 2016a]

11(9) Basal Lauterborn organ in mid-3rd segment, 2nd apical on 3rd (Fig. 7O) . . . . . *Skusella* Freeman [lotic, perhaps hyporheic, Singapore, Malaysia (inc. Brunei), Thailand, 3 spp., oriental China. Australia, Neotropics; Cranston & Tang 2018]

11' Lauterborn organs apical on 2nd and 3rd antennal segments (Fig. 7P, Q). 12

12(11) 4th antennal segment narrowed alongside apical Lauterborn organ, curved (Fig. 7P). 13

12' 4th antennal segment parallel-sided, straight (Fig. 7Q) 15

13(12) Ventromental plate elongate (Fig 2C, D). Antennal ring organ near middle . . . . . *Conochironomus* Freeman [lotic, lentic, modestly speciose, *C. tobaterdecimus* (Kikuchi & Sasa), Indonesia (Sumatra), Thailand, Malaysia; *C. nuengthai* Cranston, Thailand, oriental China; *C. sawngthai* Cranston, Thailand, *C. jat* Tang, oriental China (Hainan). Australia, Afrotropical; Cranston 2016, Pramual *et al*. 2016, Tang 2018]

13' Ventromental plate triangular. Antennal ring organ basal 14

14(13) Mentum pale, median flat, comprising similar-sized teeth across ventrementum . . . . . .*Kribiodosis* Kieffer [lotic or lentic, *K. cantonensis* Tang, oriental China (Guangdong) Han *et al*. 2021b; 1 sp. Malaysia (Sarawak); Brunei; Afrotropical]

14' Median mentum comprising paired dark central teeth protruding well beyond first laterals in 4 toothed ventrementum . . . . . *Yaeprimus* Sasa & Suzuki [oriental China, *Y. isigaabeus* Sasa & Suzuki, *Y. balteatus* Han & Tang; Japan, Afrotropical; Yamamoto & Yamamoto 2009, Han *et al*. 2020]

15(12) Mentum black, with 4 median ventromental teeth comprising small paired centrals flanked by larger teeth.1st lateral teeth of dorsomentum shorter than subequal remainder, diminishing to outermost (Fig. 8A) . . . . . *Imparipecten* Freeman [L, P. Thailand; Australia, Neotropics]

15' Mentum paler, not black, median ventromental teeth various, including *Chironomus*-like triple tooth (Fig. 8B); first lateral teeth of dorsomentum scarcely reduced relative to outer dorsomental teeth (Fig. 8C) . . . . . *Stictochironomus* Kieffer [*S. affinis* India, Australia, Indonesia, Singapore, Malaysia, oriental China (Cranston & Tang 2018), Thailand; *S. translucens* Johannsen, Indonesia, oriental China, plus *S. multannulatus* (Tokunaga), *S. simantomaculatus* (Sasa, Suzuki & Sakai), *S. quadrimaculatus* Song & Qi, *S. trifuscipes* Song & Qi (Song *et al.* 2024), oriental China, Japan; global]

16(8) Mentum with 3 median teeth (but may lack small central tooth) (Fig. 8G). . . . . *Microtendipes* Kieffer [*M. umbrosus* Freeman, regionally widespread, common (Tang & Niitsuma 2017); diverse (Song *et al*. 2023), Burma, Thailand to oriental China; global]

16' Mentum with even number of 4 or more median teeth (Fig. 8H) 17

17(16) Mandible with 2 inner teeth. Basal Lauterborn organ subapical on segment 2 (Fig. 8D, E). . . . . *Paratendipes* Kieffer [Lotic, widespread, Burma as ♂ (Reiss, ZSM); Pe common in lotic drift in Malaysia, Thailand; L in Malaysia, Indonesia; oriental China, 5 spp. as ♂♂; global]

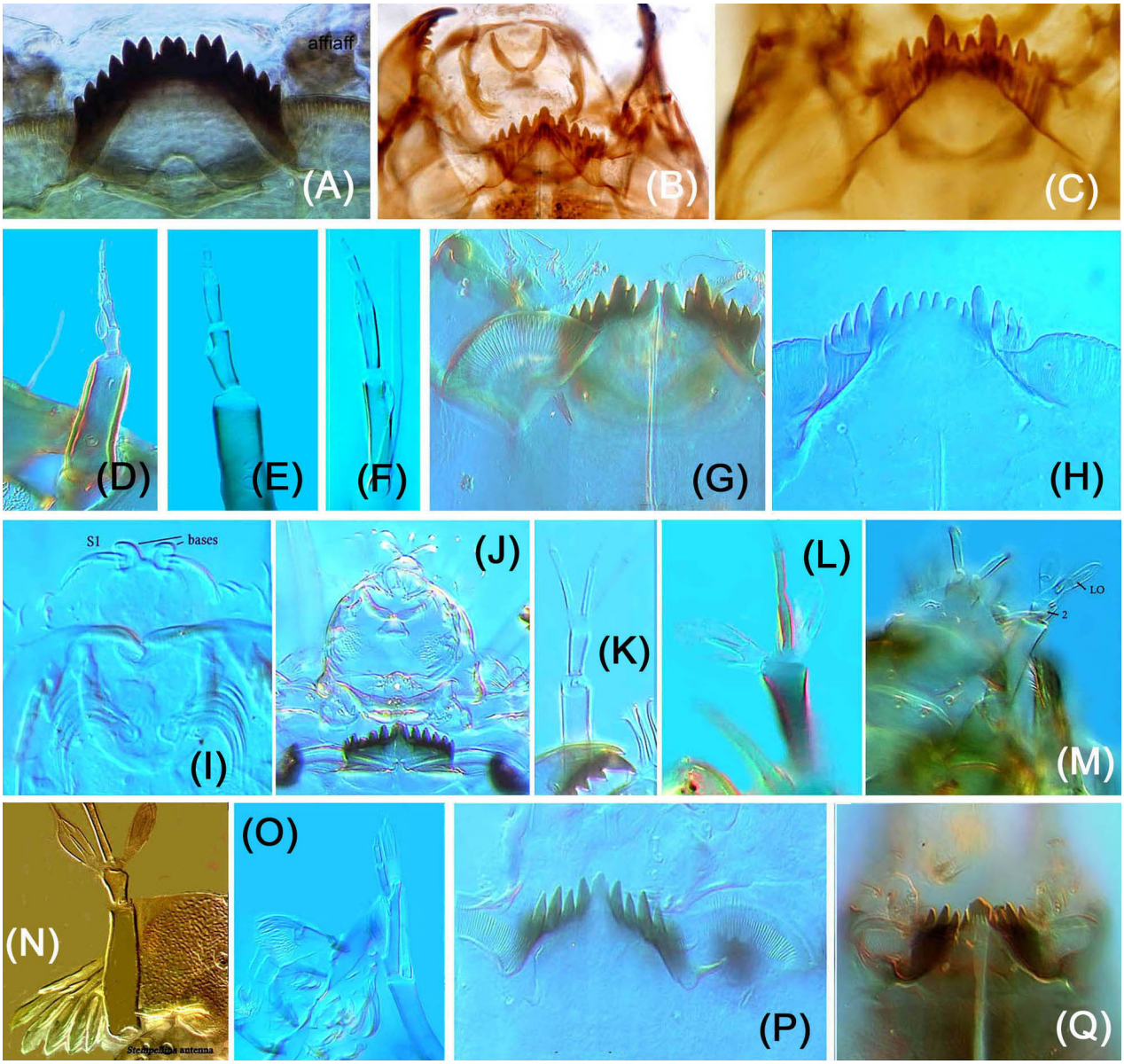

FIGURE 8. Larval Chironominae. *Imparipecten*, (A) mentum; *Stictochironomus affinis*, (B) mentum; *Stictochironomus* sp., (C) mentum; *Microtendipes*, (D) antenna; *Paratendipes nudisquama*, (E) antenna; *Paratendipes* sp., (F) antennal apex; *Microtendipes*, (G) mentum; *Paratendipes*, (H) mentum; *Rheotanytarsus*, (I) labrum-epipharynx; *Tanytarsus*, (J) labrum-epipharynx, (K) antenna; *Cladotanytarsus*, (L) antenna, (M) anterodorsal head; *Stempellina*, (N) anterodorsal head; *Stempellinella*, (O) antenna, labrum-epipharynx, (P) mentum, ventromental plates; *Yuasaiella*, (Q) mentum, ventromental plates.

17' Mandible with 3 inner teeth. Basal Lauterborn organ apical on segment 2. . . . . *Paraskusella* Cranston [ad, Borneo (Sarawak); L, Africa, Australia (Cranston 2018b).

18(5) S1 setal bases fused, SII on pedestals (Fig. 8I). Antenna 5 segmented with distinct Lauterborn organs (Fig. 8K, L, M) sometimes on pedestal. Ventromental plates approximated (Figs. 8J, 3B) or separated by up to 3 teeth width (Fig. 9B, L) . . . . . .tribe Tanytarsini 19

18’ S1 setal bases rarely fused, SII rarely on pedestal. Antenna 5–8 segmented, not on pedestals, Lauterborn organs prominent, opposite, rarely alternate or indistinct. Ventromental plates well separated medially (Fig. 10B, D, F) 33

19(18) Ventromental plates medially separated by > width of 3 median mental teeth (Fig. 8P, Q). 20
19’ Ventromental plates meet or separated only by width of median mental tooth (Figs. 8J, 9B) 25

20(19) Antennal pedestal with large multispined / palmate process (Fig. 8N) 21
20’ Antennal pedestal simple, without such palmate process 22

21(20) Antennal pedestal with spur and multispined process . . . . *Neostempellina* Reiss [lotic, Burma, Reiss, ZSM; *N. simantoneoa* (Sasa, Suzuki & Sakai), oriental China. Holarctic, Afrotropical]
21’ Antennal pedestal with only multispined process (Fig. 8N) . . . . . *Stempellina* Bause [L., Indonesia (Java) (Zavřel 1934; ♂ *S. clavata* Guo & Wang (Guo & Wang 2004), oriental China (Yunnan); spp. Thailand, Singapore; Burma, Reiss, ZSM; Holarctic, Neotropical, Australia]

22(20) Lauterborn organs alternate on 2nd antennal segment (Fig. 8O) 23
22’ Lauterborn organs opposite, apical on 2nd antennal segment (Figs. 8K, L; 9D–F). 24

23(22) Premandible with 4 teeth. Postoccipital plate well developed, continuous . . . . . *Zavrelia* Kieffer [Thailand, oriental China *Z. bragremia* Guo & Wang as ♂; Ekrem & Stur 2009; Neotropical]
23’ Premandible with 2–3 teeth; if 4 teeth, then postoccipital plate split . . . . . *Stempellinella* Brundin [Thailand, *S. tamaseptima* (Sasa) +2 spp. unreared ♂♂ oriental China; Japan, Holarctic, Neotropical]

24(22) Mentum with concave anterior margin. Clypeal seta S3 simple (seldom bifurcate) on small pedestal. . *Thienemanniola* Kieffer [lentic, oriental China; *T. motoharui* (Tokunaga); includes *Biwatendipes* Tokunaga, Japan]
24’ Mentum with straight or convex anterior margin (Fig. 8Q). Clypeal seta S3 simple (seldom bifurcate) on prominent pedestal . . . . . .*Yuasaiella* Tokunaga [*Y. kyotensis* Tokunaga, widespread N. China, Japan, e. Palaearctic, perhaps = *C. tokunagaia* Zorina; ? senior syn. of *Constempellina* Brundin]

25(19) Premandible with 3–5 main teeth 26
25’ Premandible with 2 main teeth (additional lateral spine or basal tooth may be present) 29

26(25) Mentum with 4 pairs of lateral teeth. Lauterborn organs small, sessile. Maritime 27
26’ Mentum with 5 pairs of lateral teeth. Lauterborn organs on pedestals (Fig. 9E, F). Freshwater 28

27(26) Posterior parapod claws numerous (c. 60). Abdominal segment VIII tapered. . . . . *Pontomyia* Edwards [coastal and open ocean; 3 regional spp., Huang *et al*. 2014; Pacific, Indian and Western Atlantic]
27’ Posterior parapod claws sparse (less than 20). Abdominal segment VIII conventional . . . . . *Yaetanyarsus* Sasa [coastal, North Pacific, Thailand (Andaman Sea), > 14 Pacific spp., Tang *et al*. 2022b]

28(26) Antennal segment 2 wedge-shaped, not longer than 3rd; Lauterborn organs large, on pedicels usually shorter than organs (Fig. 8L, M). Posterior parapod claws smooth or some with fine internal serrations. . . . . .*Cladotanytarsus* Kieffer [lotic, lentic, diverse, widespread; taxonomy uncertain; global]
28’ Antennal segment 2 cylindrical, longer than 3rd; Lauterborn organs small, on long pedicels (Fig. 8K). Posterior parapod claws simple, or some serrate / combs, or with pad or row of hooklets; none serrate . . . . . *Tanytarsus* v.d. Wulp [lotic, lectic, diverse, speciose, widespread: >24 spp. oriental China; *T. oscillans* Johannsen nuisance in Singapore reservoirs; global]

29(25) Antennal segment 2 subequal to 3rd. Premandible with lateral spine and 2 apical teeth . . . . . .*Neozavrelia* Goetghebuer [Burma (Reiss ZSM), Thailand, Pe; oriental China: 5 spp, ♂**,** only, Guo & Wang 2005; Holarctic, Neotropical, Australia]
29’ Antennal segment 2 usually longer than segment 3 (Fig. 9D, F). Premandible lacks lateral spine 30

30(29) Mandible with lateral hump (Fig. 9A). Mentum with 3 central teeth projecting well beyond more lateral teeth (Fig. 9B) . . . . . *Sublettea* Roback [*S. wilesi* Ashe & O’Connor, Sulawesi; 2+ undescribed regional spp., Pe common Borneo, oriental China; Nearctic, Neotropical]
30’ Mandible without lateral hump (apex may be constricted). Central mental teeth weakly projecting 31

31(30) Pedicels of Lauterborn organs short (Fig. 9D). Ventromental plate striae appear block-like (Fig. 9C). Pecten epipharyngis plate multitoothed comb or incompletely divided in three parts. . . . . *Rheotanytarsus* Bause [Rheophilic, widespread, > 20 described regional spp., few immature stages; Kyerematen *et al*. 2000; global]
31’ Lauterborn organs, sessile, placed on short or long pedicels (Fig. 9E, F). Ventromental plate striae fine. Pecten epipharyngis plate 3–5 distally rounded, pointed or serrated scales (Fig. 9G, H) 32

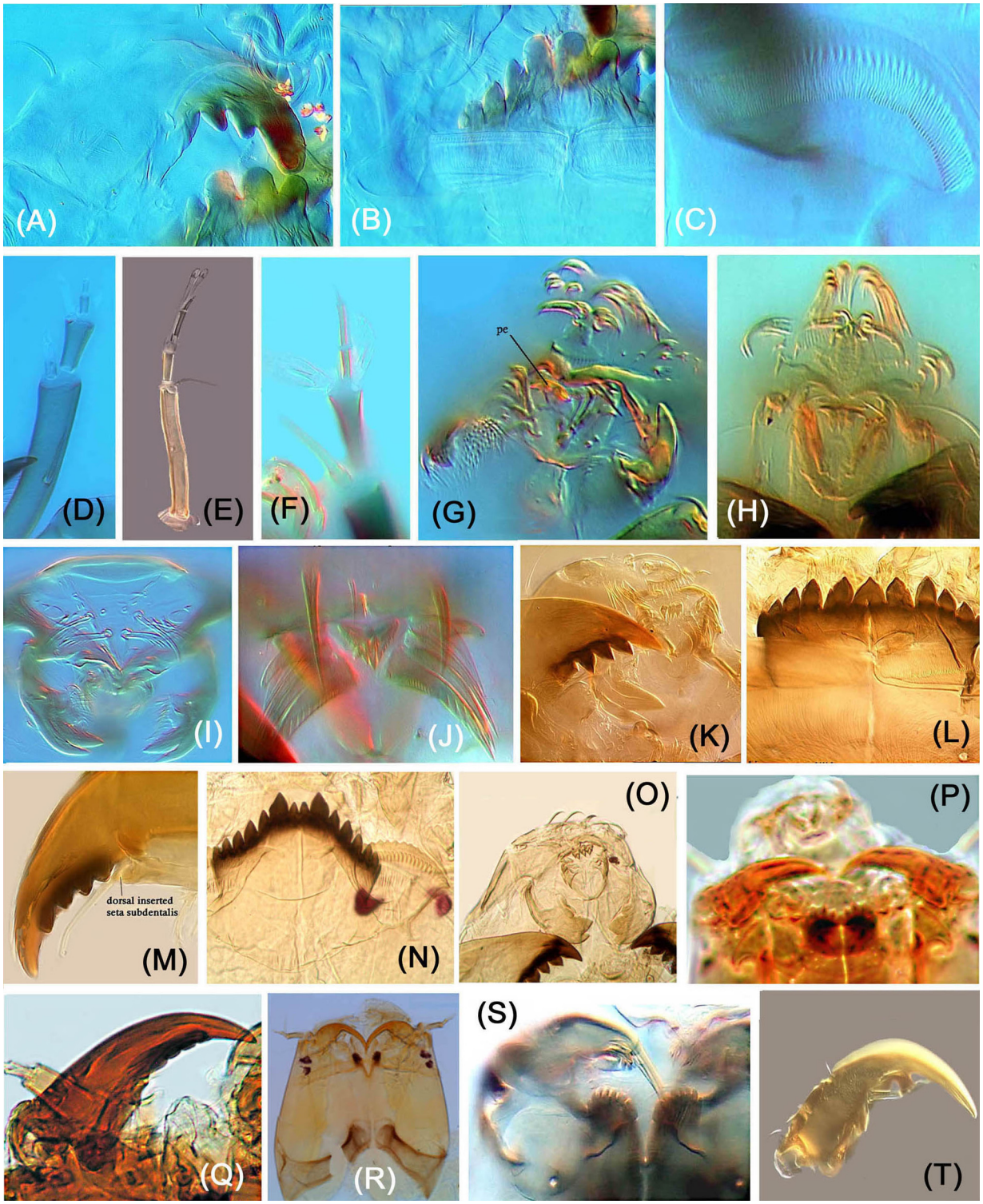

FIGURE 9. Larval Chironominae. *Sublettea*, (A) mandible, (B) mentum, ventromental plate; *Rheotanytarsus*, (C) ventromental plate, (D) antenna; *Tanytarsus*, (E) antenna; *Paratanytarsus*, (F) antenna, (G) labrum-epipharynx; *Micropsectra*, (H) labrum-epipharynx; *Dicrotendipes flexus*, (I) labrum–epipharynx; *Cryptochironomus*, (J) labrum-epipharynx; Pseudochironomini, (K) labrum-epipharynx, (L) mentum, (M) mandible; *Hyporhygma*, (N) mentum, (O) ventral head; *Kribiodorum*, (P) labrum-epipharynx, (Q) mandible; *Nilodosis*, (R) ventral head; *Kribiocosmus*, (S) mentum, ventromental plates, mandible, (T) mandible.

32(31) Lauterborn organs sessile or on pedicels no more than 2× longer than antennal segments 3–5 combined (Fig. 9F). Pecten epipharyngis 3–5 pointed or lobe-like scales (Fig. 9G), occasionally 3 serrate plates . . . . . *Paratanytarsus* Bause
[widespread, lotic and lentic, moderately speciose, 7+ from oriental China, 2 as P, no L; Li & Tang 2021; *P. grimmii* Schneider, parthenogenetic; global]

32' Lauterborn organs placed on pedicels always more than 2× longer than antennal segments 3–5 combined. Pecten epipharyngis always 3 apically serrate scales (Fig. 9H) . . . . . *Micropsectra* Kieffer
[lotic, lentic, immature stages difficult, regional status unclear, *M. atrofasciata* Kieffer, oriental China, sp. indet. N. Burma (Reiss, unpubl. ZSM; global exc. Australia]

33(18) Labrum with S I partially or fully plumose, S II never blade-like; labral lamella usually well-developed (Fig. 9I). Pecten epipharyngis plate wide, distally toothed (Fig. 9J) or divided into 3, usually toothed, rarely finger-like. Pecten mandibularis strong (Fig. 9K), rarely absent 34

33' Labrum with S I and S II simple, frequently bladelike, S I rarely divided into 3–5 slender lobes. Labral lamella usually absent. Pecten epipharyngis single scale, sometimes large, toothed, more commonly small, without distinct teeth though sometimes lobed or serrate. Pecten mandibularis absent or few lamellae . . . . . '*Harnischia* complex', tribe Chironomini 56

34(33) Ventromental plate bar-like, in near-contact medially (Fig. 9L). Insertion of seta subdentalis on same side (dorsal) of mandible as seta interna (Fig. 9M) . . . . . .'tribe Pseudochironomini'
[♂ *Manoa* Fittkau, *M. xianjuensis* Qi & Lin, oriental China (Zhejiang) Qi *et al*. 2017; ♂, Pe, oriental China (Guangdong, Yunnan); Pe, Thailand; Neotropical]

34' Ventromental plate very variable, not bar-like or rarely in near median contact. Seta subdentalis inserted opposite side (ventral) of mandible to seta interna 35

35(34) Median tooth or teeth of mentum recessed (Fig. 9P, R, S) 36

35' Median mentum not recessed (e.g., Fig. 10D, F) 39

36(35) Mentum shining black; 1st lateral tooth broad, slightly flanged; anterior margin of ventomental plate scalloped (Fig. 9N). Mandible with well-developed seta interna. Separate frons, clypeal and labral sclerites . . . . . ? *Hyporhygma* Reiss
[lotic, leaf-miner, oriental China: Pe nr genus, Wei & Tang 2019. Nearctic]

36' Mentum brown; 1st lateral tooth lower than 2nd, ventromental plate with smooth anterior margin (Fig. 9P, S). Mandible lacks seta interna (Fig. 9S, T). Dorsal head sclerites differ 37

37(36) Mentum with single median tooth in shallow recess; 1st lateral tooth lower than 2nd (Fig. 9P). Mandible with 4 inner teeth; seta subdentalis narrow and straight (Fig. 9Q). Pecten epipharyngis scales distally toothed. Clypeal and labral sclerites fused into single sclerite . . . . . *Kribiodorum* Kieffer
[syn. *Stelechomyia* Reiss. Wood-mining, *K. malicky* Cranston, Thailand, *K. belalong* Cranston, Brunei, Borneo; Cranston 2018a; Afrotropical, Nearctic, Neotropical]

37' Mentum deeply cleft without median teeth (Fig. 9S). Mandible with clumped 3 inner teeth; seta subdentalis broad, long, sinuous (Fig. 9S, T). Pecten epipharyngis scales simple. Clypeal sclerite fragmented, labral sclerite small, medial to SI seta. 38

38(37) Occipital margin with triangulum occipitale. Ventromental plate > 2× as long as high (Fig. 9R). Antenna blade extending well-beyond flagellum . . . . . *Nilodosis* Kieffer
[L, Indonesian Borneo: Kalimantan; Malaysia, Thailand, oriental China; Tang & Yamamoto 2012; *N. austrosinensis* Tang & Cranston 2017; previously confused with extralimital *Fissimentum* Cranston & Nolte]

38' Occipital margin conventional. Ventromental plate squat, seldom wider than high (Fig. 9S). Antenna blade ends short of flagellum. . . . . *Kribiocosmus* Kieffer
[L, Peninsular Malaysia, as *Fissimentum* sp. (Ahmad & Siti Hafizah 2017), undescribed ♂, China (Hainan, Yunnan), Japan (Okinawa) as *K. kanazawai* Yamamoto]

39(35) Mental and mandibular teeth pale (Fig. 10A, B). Mentum characteristic (Fig. 10B). Small, < 7 mm . . . . . *Nilothauma* Kieffer
[lotic, Thailand, 8 spp. oriental China, ♂♂, Yan *et al*. 2005a; Adam & Sæther 1999; global].

39' Mental and mandibular teeth dark (brown or black) in part at least. Mentum teeth different. Usually > 5 mm 40

40(39) Labrum with lamellar setal brush (Fig. 10C). Typical mentum (Fig. 10D) often worn flat. . . . . *Xenochironomus* Kieffer
[sponge-feeder (hence worn teeth); *X. xenolabis* (Kieffer), *X. canterburyensis* (Freeman), *X. glaber* Yu & Wang. oriental China (Yu & Wang 2010); L, Thailand; Holarctic, Australia, N.Z., Neotropics]

40' Labrum conventional, lacking lamellar brush. Mentum teeth otherwise arranged 40

41(40) Mandible with basal striae (Fig. 10E). Median mentum with tripartite central tooth (Fig. 10F). Premandible with 2 (Fig. 10G) or rarely 5–7 teeth (Fig. 10H). Typically,1–2 pairs of ventral tubules (Fig. 10I). . . . . .*Chironomus* Meigen
[speciose, morphological taxonomy difficult, 5, 6 or 7 pmd teeth in *C. javanus* Kieffer, *C. vitellinus* Freeman and *C. okinawanus* Hasegawa & Sasa. *Benthalia* Kieffer is included; molecular data Pramaul *et al*. 2016; global]

41' Mandible without basal striae. Ventral tubules absent or with 1 pair. Premandible variably toothed 42

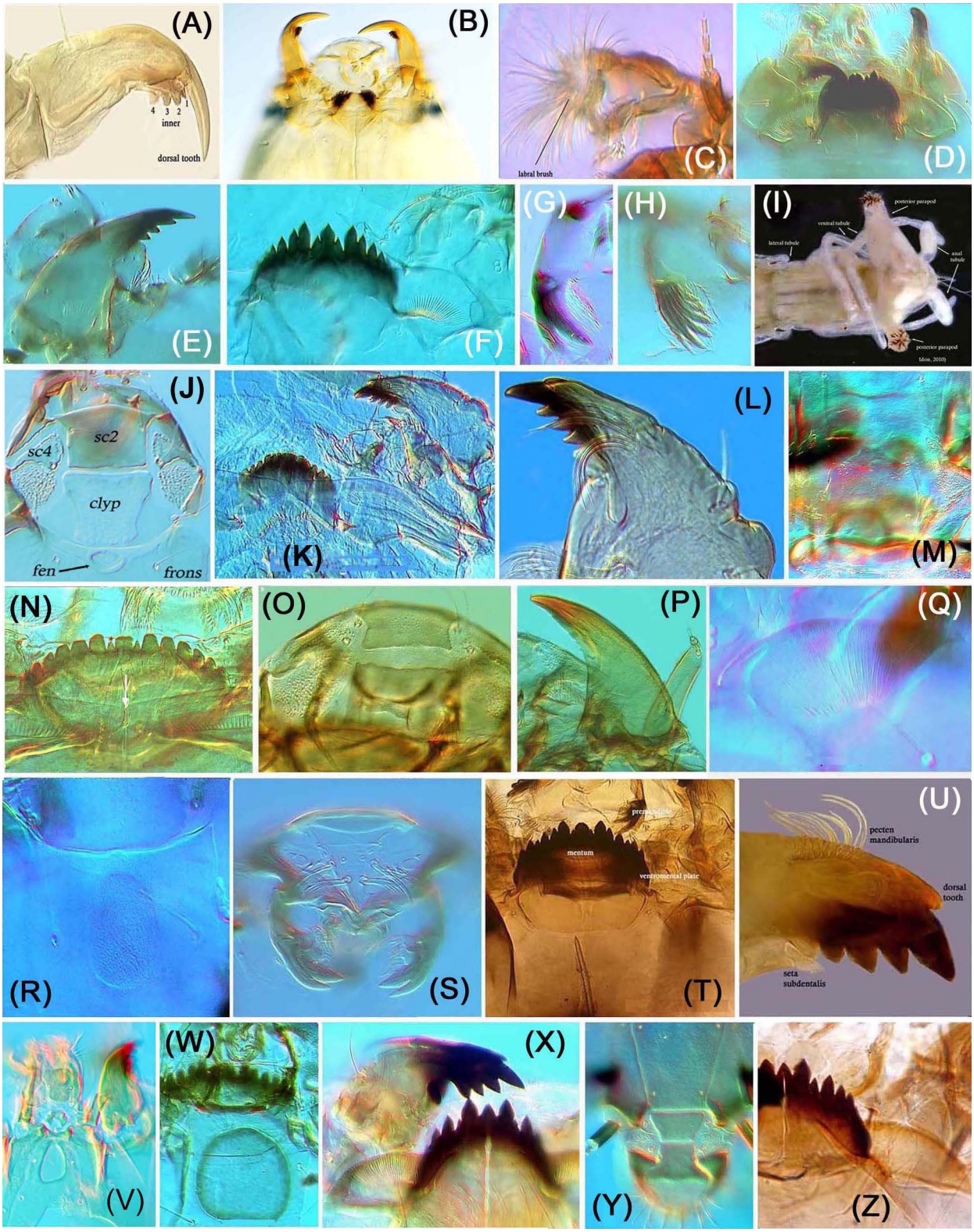

FIGURE 10. Larval Chironominae. *Nilothauma*, (A) mandible, (B) mentum; *Xenochironomus*, (C) labrum, (D) mentum; *Chironomus*, (E) mandible, (F) mentum, (G) premandible (usual), (H) premandible (*C. javanus*), (I) posterior abdomen (usual); *Dicrotendipes*, (J) dorsal head; *Lipiniella*, (K) mentum, ventromental plates, (L) mandible, (M) anterior dorsal head sclerites; *Axarus*, (N) mentum, ventromental plates, (O) dorsal head sclerites, (P) mandible; *Dicrotendipes*, (Q) ventromental plate, (R) fenestra (dorsal head), (S) labrum-epipharynx; *Kiefferulus*, (T) mentum, ventromental plates, (U) mandible; *Glyptotendipes* (*Heynotendipes*), (V) dorsal head sclerites; *Einfeldia*, (W) fenestra; *Endotribelos*, (X) mandible, mentum, (Y) dorsal head sclerites, (Z) mentum, ventromental plate.

42(41) Ventromental plate >1.5 x width of mentum, contiguous medially, narrowly drawn-out laterally (Fig. 10 K, N). Premandible teeth 2, or 5+ 43
42' Ventromental plate <1.5 × as wide as mentum, not narrowly drawn-out laterally and not contiguous medially (Fig. 10F, W, X, Z). Premandibles with no more than 3 teeth 45

43(42) Frons with +/- ovoid fenestra (fen, thinned cuticle) (Fig. 10J). Premandible with >5 teeth (Fig. 10T) . . . *Kiefferulus* Goetghebuer
[Lentic, widespread, 5–6 spp. oriental China, saline coastal-subcoastal *K. longilobus* (Kieffer) is potential nuisance; *K. nodulosus* Hashimoto (? = *K. trigonum* Song *et al*.) eutrophic inc. Thai rice-fields, oriental China (Hainan, Guangdong, Yunnan) (Hashimoto *et al*. 1981, Song *et al*. 2020); *Nilodorum* and *Carteronica* of regional auctt. are synonyms; L key for Thailand (Cranston 2007); Molecular data, Pramual *et al.* 2016; global]
43' Frons usually lacks fenestra (Fig. 10M, O, Y) 44

44(43) Frons fused with tuberculose clypeus (Fig. 10M). Mandible with pale dorsal tooth and 3 inner teeth, dorsally with hump; seta subdentalis simple (Fig. 10L) . . . . . *Lipiniella* Shilova
[L., ♂, oriental China (Yunnan, Guangdong); Holarctic inc. Japan]
44' Frons, clypeus and labral sclerites separate (Fig. 10O). Mandible with 4 flattened inner teeth, dorsal tooth absent (Fig. 10P). . . . . *Axarus* Roback
[L., Thailand, 1 sp., oriental China (Guangdong, Zhejiang). Holarctic, Neotropical]

45(42) Ventromental plate distinctly narrower than mentum width (Fig. 10Q). Pecten epipharyngis single, with < 13 broad, blunt apical teeth (Fig. 10S) . . . . . *Dicrotendipes* Kieffer
[*D. pelochloris (*Kieffer), widespread regionally, 7+ spp. oriental China; marine *D. inouei* Hashimoto, others lentic freshwater. L key Thailand (Cranston 2007); global]
45' Ventromental plate as wide or wider than mentum width (Fig. 10T). Pecten epipharyngis 3 separate scales, or if single, often with > 15 pointed, mostly slender teeth, also on surface (Fig. 10S) 46

46(45) Frons or frontoclypeus with fenestra of thinned cuticle (Fig. 10W) 47
46' Dorsal head smooth without fenestra (Fig. 10Y) 49

47(46) Premandible with >5 sharp teeth (Fig. 10T). Seta subdentalis broad, distally serrate (Fig. 10U). . . . . *Kiefferulus* (part)
[see couplet 39 for details]
47' Premandible with 2 pointed apical teeth. Seta subdentalis simple, slender 48

48(47) Separate clypeal sclerite present; frons smooth, anteriorly with oval fenestra or small distal-median depression or mark, with concave anterior margin (Fig. 10V) . . . . . *Glyptotendipes* Keiffer (s.g. *Heynotendipes*)
[*G.* (*Heytotendipes*) *cf. signatus* Kieffer, oriental China; Holarctic]
48' Frontoclypeus fused, with large cordate to subovate fenestra, sclerite granular in mid-section, with convex anterior margin (Fig. 10W) . . . . . *Einfeldia* (s.s.) Kieffer
[= *Einfeldia* 'group A'; minimally *E. pagana* (Meigen) in oriental China, Japan; Holarctic, Australia; Cranston *et al*. 2016b]

49(46) Mentum divided into median ventromentum; anteromedially-directed ends of ventromental plate links to base of teeth delimitating from more lateral dorsomental teeth (Fig. 10X, Z) 50
49' Inner (median) margins of ventromental plate not directed anteriorly, or if weakly indicated, then fused to mentum posterior to bases of mental teeth; median/central ventromentum indistinct 55

50(49) Mandible with deeply incised mola proximal to teeth (Fig. 10X). Mentum strongly arched (Fig. 10X, Z).. . . . . *Endotribelos* Grodhaus
[L, Thailand, Chiang Mai, L, Phrae; L/P, oriental China (*Endotribelos* of Qi *et al*. 2013 = *Endochironomus pekanus*), Li & Tang 2024]
50' Mandible with smooth rounded mola. Mentum less arched. 50

51(50) SI plumose on inner side only (Fig. 11A, B) 52
51' SI plumose on both sides 54

52(51) Premandible with 4 distinct teeth. Pecten epipharyngis only with apical teeth (Fig. 11C, D). . . *Ainuyusurika* Sasa & Shirasaka
[marine, 2 spp. oriental China; Japan, Korea (Russia: Sakhalin); Han & Tang 2019, inc. *Zhouomyia* Sæther & Wang]
52' Premandible with 2–3 teeth. Pecten epipharyngis with additional basal teeth (Fig. 11E) 53

53(52) Anterior margin of cardo tuberculate (Fig. 11F). Mandible with 3 inner teeth (Fig. 11G), seta premandibularis apically divided. . . . . *Endochironomus* Kieffer
[L, Thailand; in oriental China, *E. pekanus* (as *Endotribelos* of Qi *et al*. 2013) (Li & Tang 2024). Holarctic]
53' Anterior margin of cardo smooth or tuberculate. Mandible with 4 inner teeth (Fig. 11H), seta premandibularis apically divided, or mandible with 3 inner teeth and simple seta praemandibularis . . . . . *Synendotendipes* Grodhaus
[L, oriental China; Holarctic]

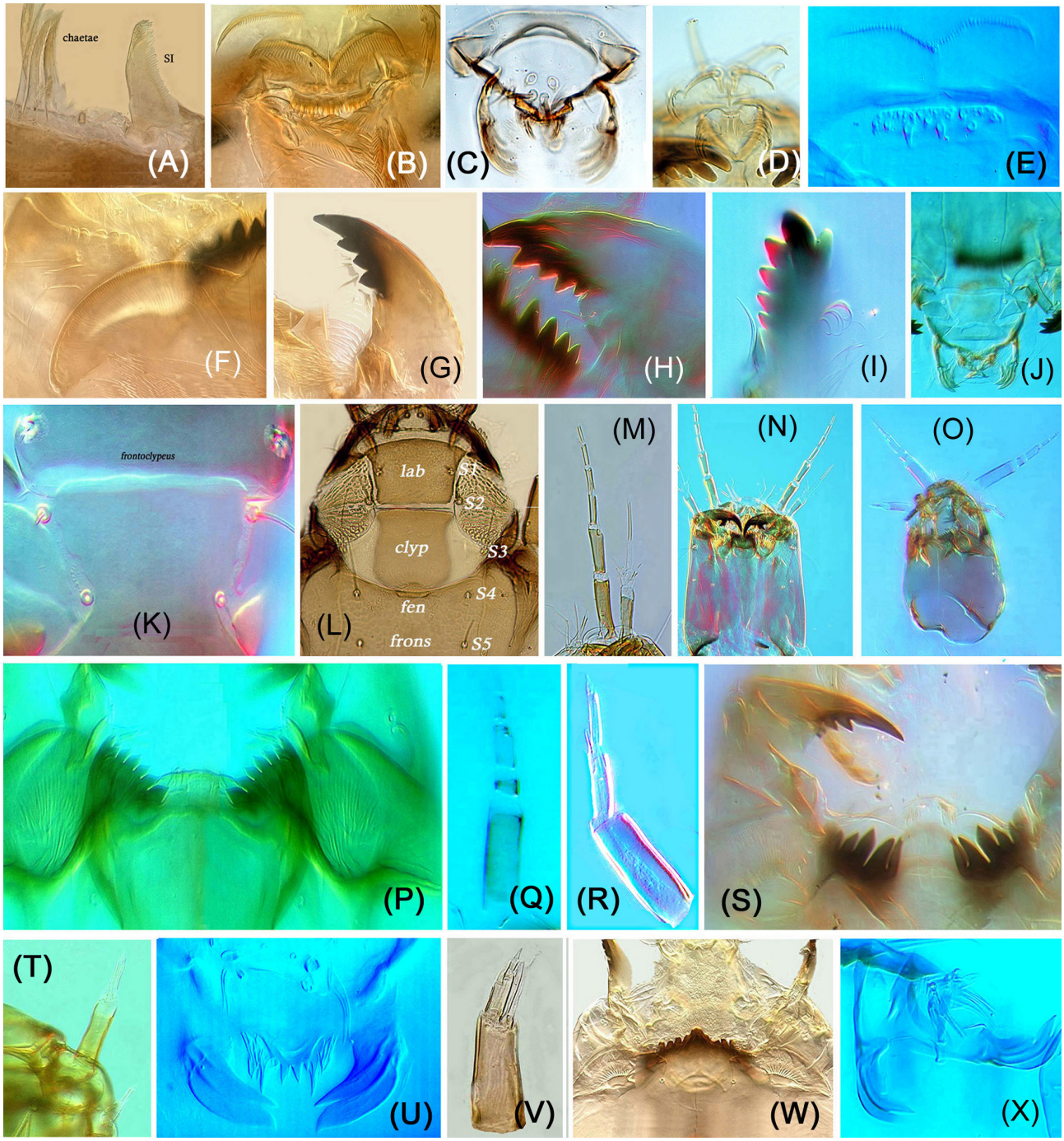

FIGURE 11. Larval Chironominae. *Endochironomus*, (A) S1 seta, (B) pecten epipharyngis, S1 setae; *Ainuyusurika*, (C) premandible, (D) pecten epipharyngis; *Synendotendipes*, (E) pecten epipharyngis; *Endochironomus*, (F) cardo, ventromental plate, (G) mandible; *Synendotendipes*, (H) mandible; *Sergentia*, (I) mandible; *Polypedilum* spp., (K) dorsal heads; *Glyptotendipes* (s.s.), (L) dorsal head; *Robackia*, (M) antenna, (N) ventral head; *Demicryptochironomus*, (O) ventral head, (P) mentum, ventromental plates, (Q) antenna; C*ryptochironomus*, (R) antenna, (S) mentum, ventromental plates; *Cyphomela*, (T) antenna; *Parachironomus*, (U) labrum; *Microchironomus*, (V) antenna, (W) mentum, ventromental plates, labrum; *Harnischia*, (X) labrum, premandible.

54(51) Mandible usually with 4 inner teeth (Fig. 11I) . . . . . *Sergentia* Kieffer
[*S. kizakiensis* (Tokunaga) oriental China, Zhejiang, Wang *et al*. 2019; Holarctic (*? inseparable from *Phaenopsectra*)]
54' Mandible with 3 inner teeth . . . . . *Phaenopsectra* Kieffer
[*P. flavipes* Meigen, oriental China; Holarctic]

55(49) Clypeus and frons fused as frontoclypeus, with straight anterior margin, broadened into lobes anterolaterally (Fig. 11J, K) . . . . . *Polypedilum* Kieffer
[very speciose, taxonomy based on ♂**,** keys Pe, L cannot reliably differentiate even to subgenus; Cranston *et al*. 2016; Tang *et al.* 2022a; global]
55' Clypeus and frons distinct, anterior margin concave (Fig. 11L) . . . . . *Glyptotendipes* Kieffer (s.s., part)
[Thailand; oriental China, inc. *G.* (s.s.) *tokunagai* Sasa & Kawai; Japan; widespread Holarctic]

56(33) Antenna > half head length, with 7–8 segments (Fig. 11M, N, O) 57
56' Antenna < half head length, with 5 or indistinctly 6 segments (Fig. 11Q, R) 58

57(56) Abdominal segments 1–7 subdivided. Antenna 8-segmented**.** Posterior parapods ventrally directed. Head long, narrow anteriorly. Mentum untoothed, ventromental plate weak . . . . . *Chernovskiia* Sæther
[Pe, oriental China (Yunnan); Holarctic; Japan]
57' Abdominal segments conventional. Antenna 7-segmented (Fig. 11M) (including hyaline 'bubble' at apex). Long thin posterior prolegs and procercus apical setae directed posteriorly. Mentum toothed, ventromental plate distinct (Fig. 12U). Head rectangular (Fig. 11N) . . . . . *Robackia* Sæther
[2–3 spp., Borneo, Malaysia, oriental China (Yunnan, Guangdong); Holarctic, Japan, Australia]

58(56) Mentum concave, with broad pale median tooth flanked by inward-directed, well sclerotized dark teeth (Fig. 11P, S). Ventromental plate > 3 × as wide as long (Fig. 11P) 59
58' Mentum convex (arched) or linear; if concave than mentum completely pale. Ventromental plate < 2× as wide as long 61

59(58) Antenna 7-segmented (Fig. 11Q). Mentum with 7 pairs of lateral teeth (Fig. 11P) . . . . . *Demicryptochironomus* Lenz
[7 spp., oriental China, in 2 subgenera, s.s., *Irmakia*, *D.* (*I.) bullum* (Song & Wang) (based on newly associated material), unidentified Pe, Malaysia (inc. Borneo); Holarctic, Japan, Australia]
59' Antenna 5-segmented (Fig. 11R) 60

60(59) Mentum with 4–6 pairs of lateral teeth (Fig. 11S). Ventromental plate conventional.. . . . . *Cryptochironomus* Kieffer
[widespread, abundant, 5+ spp. oriental China; global]
60 Mentum with 7 pairs of lateral teeth, Ventromental plate elongate, wrapped around ventral head . . . . . *Gillotia* Kieffer
[lotic, lentic, perhaps rare, ♂ C. *distractus* Johannsen, Indonesia (Java) likely belongs; distinctive Pe oriental China (Yunnan, Luosuo R); Holarctic, Afrotropical, India]

61(58) Antenna 5 segmented (Fig. 11T) 62
61' Antenna 6–7 segmented (Fig. 12R, T) 67

62(61) Pecten epipharyngis plate broad, multitoothed (Fig. 11U). Premandible with 2–4 teeth. . . . . *Parachironomus* Lenz
[lotic, lentic, Thailand, 4–5 spp. inc. widespread *P. atrophus* (Kieffer), *P. gracilior* (Kieffer) oriental China; Yan *et al*. 2015; Japan; global]
62' Pecten epipharyngis plate simple, rounded or weakly lobed; premandible bifid (Fig. 11X) or pecten epipharyngis plate triangular, shallowly trifid and premandible with several small inner teeth 63

63(62) Premandible apically bifid 64
63' Premandible with >2 teeth 66

64(63) Outline of mentum nearly linear, median tooth trifid (Fig. 11W); antennal blade extends to or beyond flagellum (Fig. 11V) . . . . . *Microchironomus* Kieffer
[lentic, some saline tolerance, 4+ spp., Thailand, Indonesia, Malaysia, Singapore, oriental China; inc. *M. lacteipennis* (Kieffer) Taiwan, widespread *M. tener* (Kieffer); Holarctic, Australia]
64' Outline of mentum convex (arched), with median tooth single (Fig. 12A, D) or notched laterally, appearing trifid, medially notched, or double; antennal blade shorter than flagellum 65

65(64) Median tooth of mentum broadly rounded or laterally notched to appear trifid, set well forward of lateral teeth so median mentum slopes sharply (Fig. 12A); basal segment of antenna about 2–2.5 × longer than wide and subequal to length of flagellum (Fig. 12B) . . . . . *Cryptotendipes* Lenz
[4–5 spp. Key to L., oriental China, Yan *et al*. 2005b, *C. nodus* Yan, Tang & Wang, ♂. oriental China, Hainan; Holarctic, Australia]
65' Median tooth of mentum usually double or notched medially, may be broadly rounded but not extending far forward of lateral teeth, so mentum less sloped (Fig. 12D); basal segment of antenna 2.8–4× > than flagellum (Fig. 12C) . . . *Cladopelma* Kieffer
[many regional synonyms, 2 spp. oriental China, widespread *C. edwardsi* (Kruseman); Japan, Holarctic, Australia]

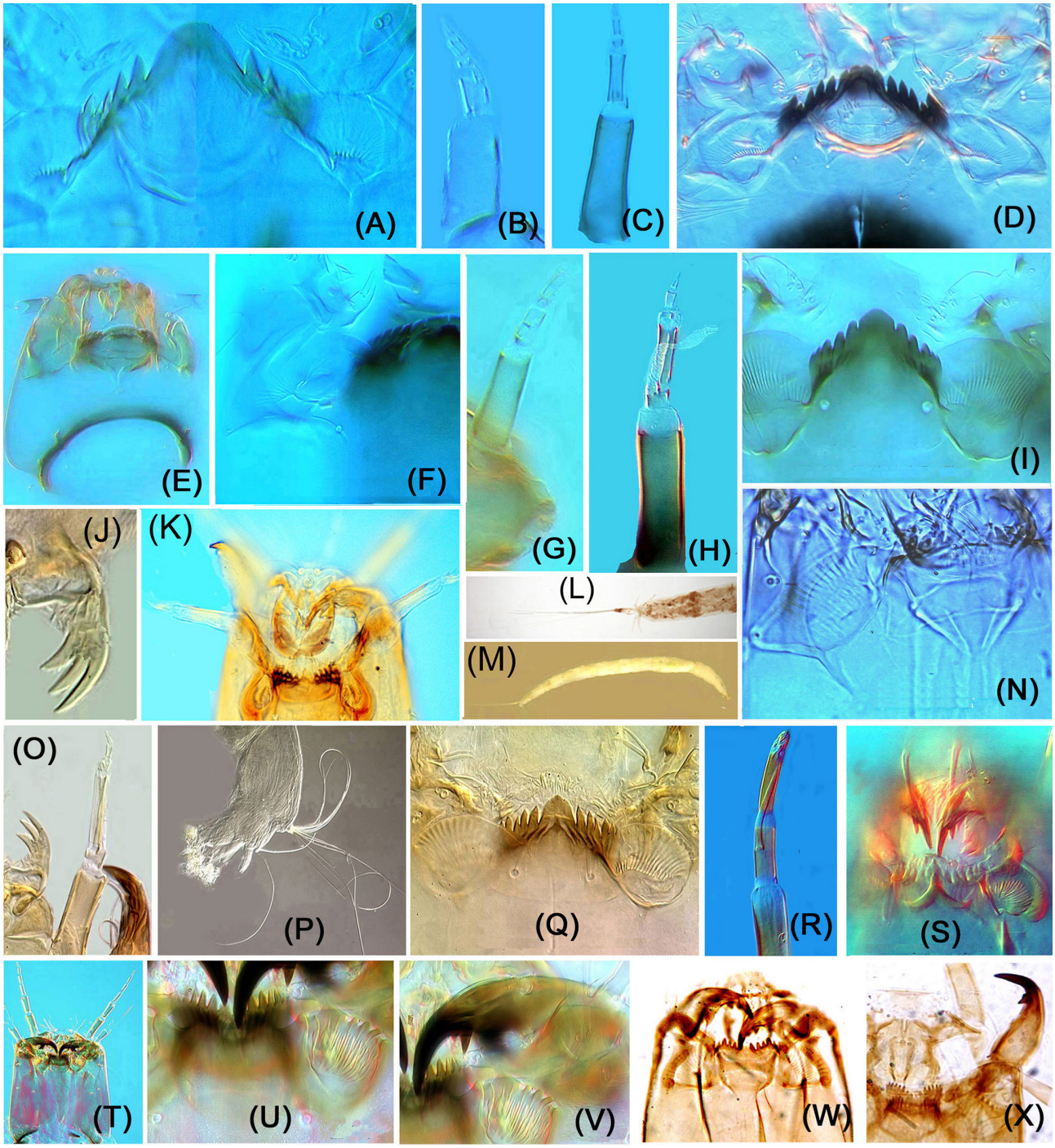

FIGURE 12. Larval Chironominae. *Cryptotendipes*, (A) mentum, ventromental plates, (B) antenna; *Cladopelma*, (C) antenna; (D) mentum, ventromental plates; *Harnischia*, E) ventral head capsule, (F) mentum, ventromental plates, (G) antenna; *Paracladopelma*, (H) antenna, (I) mentum, ventromental plates; *Hanochironomus*, (J) premandible; *Olecryptochironomus*, (K) labrum, premandible, mentum, (L) posterior body; *Anuncotendipes*, (M) whole body habitus, (N) mentum, ventromental plates; *Saetheria*, (O) antenna, premandible, (P) posterior body, (Q) mentum, ventromental plates; *Kloosia*, (R) antenna, (S) mentum, ventromental plates, mandible; *Robackia*, (T) ventral head, (U) mentum, ventromental plates, (V) mandible; *Beckdia*, (W) mentum, ventromental plates, (X) mandible.

66(63) Antennal segments 2 and 3 subequal (Fig. 12G); ventromental plate weakly striate (Fig.12E, F) . . . . . *Harnischia* Kieffer [Thailand; 4 spp. oriental China; Holarctic, Australia]

66’ Antennal segment 2 much longer than 3rd (Fig. 12H); ventromental plate coarsely striate (Fig. 12I) . . . . . *Paracladopelma* Harnisch [Thailand, Malaysia, 2 spp. oriental China; Holarctic]

67(61) Antenna 6-segmented (Fig. 12R); mandible with seta interna (Fig. 12O) 68

67’ Antenna 7-segmented (Fig. 12T); mandible without seta interna (Fig. 12V, X) 72

68(67) Mandible with dorsal tooth (Fig. 12K). 69

68’ Mandible lacks dorsal tooth (Fig. 12V, X) 70

69(68) Each anterior abdominal segment 1–7 subdivided, thus appearing 17 segmented. Posterior parapod elongate. Premandible with 2 broad teeth, at least 2 procercus setae > 50% body length (Fig. 12L) . . . . . .*Olecryptotendipes* Zorina [lotic, psammophilic, ♂ *O. exilis*, *O. melasmus*, both Yan, Wang & Bu, oriental China (Hainan, Fujian, Shaanxi), Yan *et al.* 2012; e. Palaearctic]

69’ Abdominal segmentation conventional, 10 segmented. Posterior parapod short. Premandible with 6 small teeth, procercus setae conventional (Fig. 12J). . . . . .*Hanochironomus* Ree [marine/seashore, *H. tumerestylus* Ree, Korea, Japan, oriental China]

70(68) Procercus anal setae > 50% body length (Fig. 12M). Mentum with 4 dark teeth flanking broad pale median tooth (Fig. 12N) . . . . . .*Anuncotendipes* Cranston [L, distinctive, lotic (burrows in clay banks), Thailand; Australia]

70’ Procercus anal setae conventional, <25% of body length (Fig. 12P). Mentum with 5 or more lateral teeth (Fig. 12Q, U) . . . 70

71(70) Most ventromental plate striae complete to anterior margin (Fig. 12Q) . . . . . .*Saetheria* Jackson [psammophilic, c. 4 spp, oriental China, *S. tylus* (Townes); Malaysia, Thailand. Japan. Holarctic, Australia, Neotropics]

71’ Ventromental plate striae not reaching anterior margin, separate row of short striae near anterior of plate (Fig. 12S). . . . . *Kloosia* Kluseman [lotic, *K. koreana* Reiss, Korea, oriental China; Japan. Holarctic, Afrotropical]

72(67) Mentum with even number of teeth (Fig. 12U); mandible with elongate apical tooth, innermost teeth enlarged (Fig. 12V). . . . . .*Robackia* Sæther [Lotic, lentic, psammophilic; *R. pilicauda* Sæther, *R. parallela* Yan & Wang, oriental China; Pe common Malaysia inc. Borneo, Thailand +; Holarctic, Australia]

72’ Mentum with odd number of teeth, median tooth trifid (Fig. 12W) but simple if worn; mandible conventional with modest-length apical tooth (Fig. 12X) . . . . . *Beckidia* Sæther [Lotic, psammophilic, Thailand, oriental China, L, Pe,? *B. tethys* Sæther. Holarctic, Afrotropical]

Podonominae: genera

The subfamily Podonominae is amphitropical, with highest representation in the austral south and temperate northern hemisphere. Two genera, each with one described sp., occur in oriental China: if tribes are warranted both would belong to Boreochlini.

1 Posterior body with 2 setae anterior to anal tubules; procercus with 8 anal setae (Fig. 13A) . . . . . *Paraboreochlus* Thienemann [lotic, *P. okinawanus* Kobayashi & Kuranishi, oriental China (Guangdong), Korea; Japan (Okinawa); Holarctic]

1’ No such setae anterior to anal tubules; procercus with 5 anal setae (Fig. 13B). . . . . .. *Boreochlus* Edwards [lotic, *B. burmanicus* Brundin, *B. malaisei* Brundin, Burma (Brundin 1966); *B. thienemanni*, oriental China (Guangdong); Japan, Holarctic].

Protanypodinae: genera

The subfamily Protanypodinae comprises two basically northern (boreal) genera. The concept was treated previously as a tribe of Diamesinae until raised by Semenchenko *et al*. (2024), based on molecular and morphological evidence. The key derives from Makarchenko & Endo (2009).

1 Head capsule with dense short simple setae; postoccipital margin on each side with long ventrolateral, posteriorly-directed projections (Fig. 13C). Mandible with 5 small inner teeth; seta interna absent (Fig. 13C). Broad central mentum without teeth, with 2 pairs of unusual-shaped lateral teeth (Fig. 13G) . . . . . *Protanypus* Kieffer [lentic, L (subfossil), oriental China (Yunnan, 3000–4000 m.). Holarctic, inc. China, Japan]

1' Head capsule with many pale, long, simple or terminally split setae; postoccipital margin without or with only short projections (Fig. 13D). Mandible with 4 subequal mid-length teeth (Fig. 13D), small seta interna present. Mentum with single wedge-shaped median tooth and 3 pairs of lateral teeth (Fig. 13H) . . . . . *Linevitshia* Makarchenko [lotic, *L. prima* Makarchenko, ♂, oriental China (Zhejiang); L, Shaanxi (Mt. Qinling), Sichuan, Yunnan (Mt. Laojun); Palaearctic, inc. China, Japan]

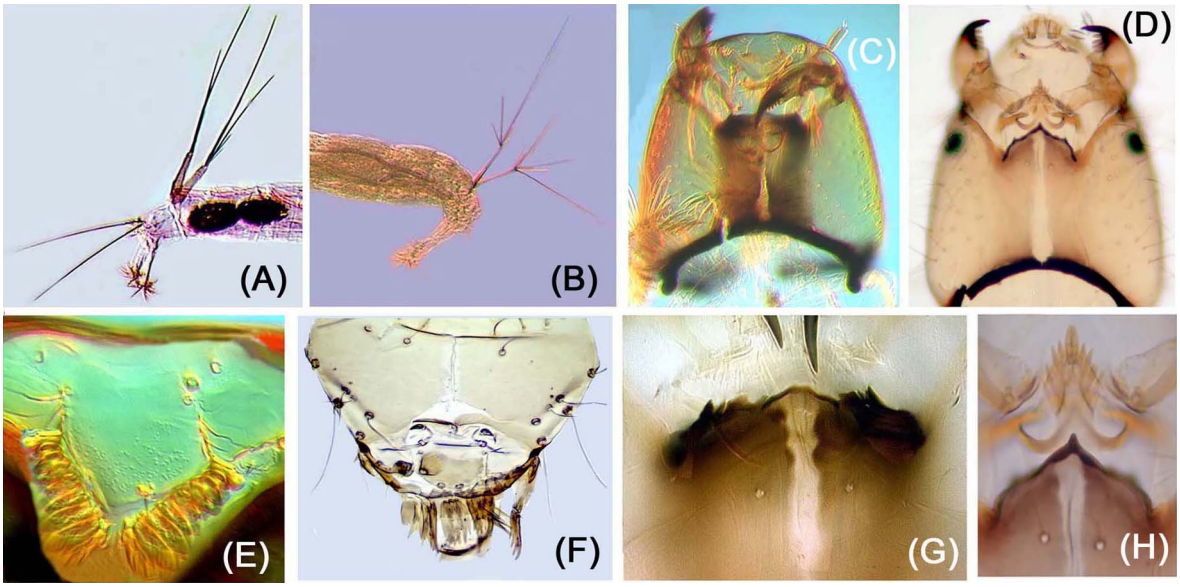

FIGURE 13. Larval Podonominae. Posterior abdomen of (A) *Paraboreochlus*, (B) *Boreochlus*. Larval Protanypodinae. Ventral head of (C) *Protanypus*, (D) *Linevitshia*; labrum-epipharynx of (E) *Protanypus*, (F) *Linevitshia*; mentum of (G) *Protanypus*, (H) *Linevitshia*.

Diamesinae: Tribes and genera

This subfamily comprises the austral tribes Heptagyiini, Lobodiamesini, South African Harrisonini, and the boreal Diamesini and Boreoheptagyiini (Semenchenko *et al*. 2024). Larvae are lotic, largely cool stenothermic. *Boreoheptagyia*, *Diamesa*, *Pagastia*, *Potthastia*, *Pseudodiamesa*, *Sasayusurika*, *Sympotthastia* and *Syndiamesa* all occur in oriental China (Sun *et al*. 2019) and may be expected at elevation in south-east Asia.

1 Dorsal head capsule tuberculose (Fig. 14A). Parapod claws arranged in circlet (Fig. 14B). Body with multipointed spines (Fig. 14C) . . . . . Tribe Boreoheptagyiini . . . . . *Boreoheptagyia* Brundin [L. in forest streams, seeps. *B. sasai* Makarchenko & Endo common oriental China (Fujian). *B. alulasetosa* Makarchenko, Wu & Wang, *B. kurobebrevis* (Sasa & Okazawa), *B. zhengi* Lin & Liu in sw China (Guizhou, Yunnan) (Makarchenko *et al*. 2008, Lin *et al*. 2021). *B.* cf. *ambigua* & *B. rotunda* Serra-Tosio near Sino-Burma border; Holarctic]

1' Head lacks tubercles. Body not spinose. Parapod claws irregular (Fig. 14D) . . . . . Tribe Diamesini. 2

2(1) Mentum toothless (Fig. 14E). Premandible with c.15 small, pointed teeth. Mandible lacks seta interna . . . . . *Potthastia longimanus* gp. [lotic *Potthastia* cf. *longimanus* (Kieffer) rare oriental China (Guangdong); Holarctic]

2' Mentum toothed (Fig. 14F). Premandible with 13 or fewer broader teeth. Mandible with or without seta interna 3

3(2) Median mentum with 3 subequal teeth separated from lateral teeth (Fig. 14F). . . . . *Pseudodiamesa* Goetghebuer [*P. nivosa* Goetghebuer from 3500 m. oriental China, n. Yunnan, e. Tibet, Hengduan Mt.; Holarctic)

3' Median mentum abutting to narrowly separated from first lateral tooth 4

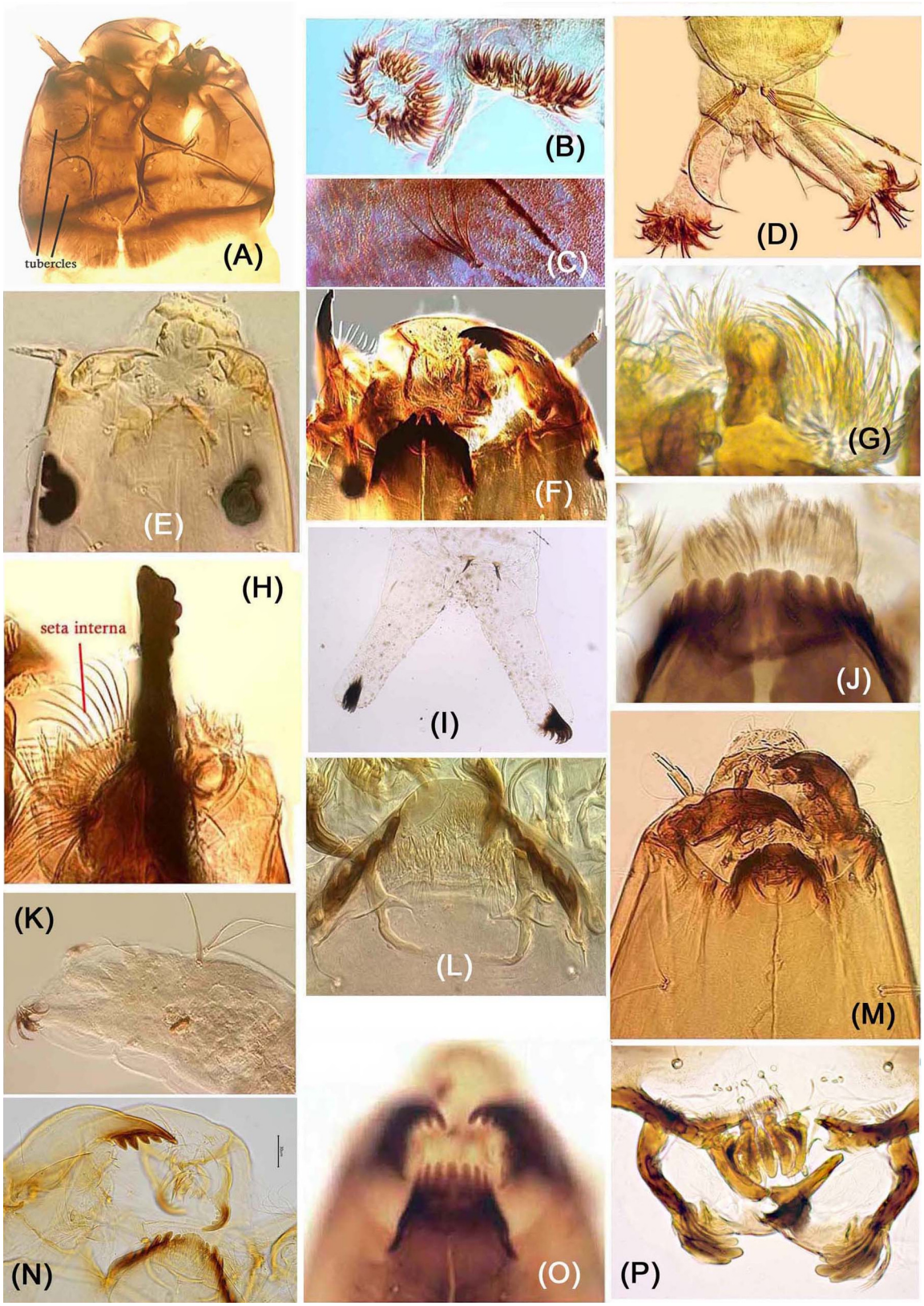

FIGURE 14. Larval Diamesinae. *Boreoheptagyia*, (A) dorsal head, (B) posterior parapods, (C) thoracic cuticle; *Potthastia*, (D) posterior abdomen, *Potthastia* cf. *longimana*, (E) ventral head; *Pseudodiamesa*, (F) ventral head; *Sasayusurika*, (G) palp; *Diamesa* (H) mandible, (I) posterior abdomen, (J) mentum, prementum; *Potthastia* cf. *gaedii*, (K) posterior abdomen, (L) mentum, ventromental plate; *Pagastia*, (M) ventral head; *Sympotthastia*, (N) labrum-epipharynx, premandible; *Syndiamesa*, (O) mentum, (P) labrum-epipharynx, premandibles.

4(3) Maxillary palp with setal fan each side (Fig. 14G). Mandible without seta interna. Premandible with 1 tooth . . . . . *Sasayusurika* Makarchenko [2 spp., *S. nigatana* (Tokunaga), ♂ Zhejiang Province (Sun *et al*. 2019): Pe oriental China (Fujian and Yunnan., inc. Gaoligong Mt.), e. Palaearctic]

4' Maxillary palp lacks setal fans. Mandible with seta interna (Fig. 14H). Premandible with 2 + teeth 5

5(4) Mentum evenly curved, with >16 subequal distinct teeth (Fig. 14J). Procercus small or absent; 4 anal setae arise from body wall; if procercus lacking, subapical seta arises anterior to anal setae (Fig. 14I) . . . . . *Diamesa* Meigen [*D. cranstoni* Willassen, e. Malaysia, Sabah, G. Kinabalu, 3200 m., 3 undescribed spp. in montane oriental China (Nanling Mt. and Wuyi Mt.) from 1000–1500 m., Holarctic, montane Afrotropics]

5' Mentum with fewer teeth (Fig. 14N) or teeth indistinct beneath ventromentum (Fig. 14M). Distinct procercus bears 5–7 anal and 2 subapical setae (Fig. 14K) 6

6(5) Mentum apically truncate with 4–6 ridge-like median projections (Fig. 14M). Setae submenti displaced posteriorly, nearer to postoccipital margin than mentum (Fig. 14M). . . . . *Pagastia* Oliver [*P. lanceolata* (Tokunaga), *P. tianmumontana* Makarchenko & Wang, oriental China (Guangdong), in montane subtropical streams at maximum elevation of 500 m., Pe from 1000–1500 m., oriental China (Yunnan, Fujian); Holarctic]

6' Mid-mentum rounded, not ridged (Fig. 14L, N). Setae submenti nearer mentum than postocciput 7

7(6) Mid-mentum broad, median tooth dome-shaped. 5–6× width of 1st lateral tooth (Fig. 14L) . . . . . *Potthastia gaedii* gp. [montane streams, *Potthastia* cf *gaedii*, *Potthastia montium* Edwards, oriental China; Holarctic]

7' Median tooth of mentum rounded or bi-lobed, < 3× width of 1st lateral tooth 8

8(7) Median mental teeth (sometimes also first laterals) paler than outers (Fig. 14N). Premandible with dominant apical tooth and 2–4 small inner teeth; labral lamellae comprising 2 rounded scales. . . . . *Sympotthastia* Pagast [*S. takatensis* (Tokunaga) Korea, *S. wuyiensis* Liu, Ferrington & Wang, Jiangxi, transitional oriental and palaearctic China (Liu *et al*. 2016); Holarctic]

8' Mental teeth unicoloured (Fig. 14O). Premandible apical tooth no stronger than 1st of 5 distinct inner teeth; labral lamellae comprising 5 well-developed scales (Fig. 14P) . . . . . *Syndiamesa* Kieffer [*S. montana* Tokunaga, *S. yosiii* Tokunaga, oriental China; Holarctic]

Prodiamesinae: genera

The small subfamily Prodiamesinae is cool temperate, largely northern hemisphere in distribution, and is represented in the region by all 5 known genera. Larvae of the subfamily are distinguished by a ventromental plate lacking striae (from Chironominae and Diamesinae), and from Orthocladiinae by fringed SI setae, presence of labral lamellae and the 4-segmented antenna. Inclusion of *Propsilocerus* Kieffer has been confirmed via molecular (Cranston *et al*. 2012) and morphological (Baranov 2021) analyses. A contemporary revision updates taxonomy for e. palaearctic and adjacent China fauna (Makarchenko & Semenchenko 2023).

1 Median mental tooth broad, convex, pale (Fig. 15A) . . . . . *Odontomesa* Pagast [1 sp., Thailand (ZSM); montane oriental China (Yunnan); Holarctic]

1' Median mentum either with 1 broad concave, or 2 or more small dark median teeth 2

2(1) Median mentum with many teeth. Ventromental plate large without setae beneath (Fig. 15B). . . . . *Propsilocerus* Kieffer [1 common sp., *P. akamusi* (Tokunaga) oriental China (Yunnan, Jiangxi); widespread inc. Korea, China; Japan. jun. syn. *Tokunagayusurika* Sasa; Baranov 2021. Holarctic]

2' Median mentum variable. Ventromental plate elongate with setae ('beard') beneath 3

3(2) Ventromental plate narrow, beard weak; 1 concave median mental tooth (Fig. 15C) . . . . . *Monodiamesa* Kieffer [*M. improvisa* Makarchenko (ZSM), montane oriental China (Hunan) (Han *et al*. 2021a); Holarctic, Neotropics]

3' Ventromental plate broad, beard strong; 2 recessed median mental teeth (Fig. 15D–F) 4

4(3) Ventromental plate with dense, long setae beneath (Fig. 15D, E). Premandible with 2 teeth. . . . . *Prodiamesa* Kieffer [Pe, 1500–2500 m., oriental China (Yunnan, Sichuan), Holarctic, Neotropics]

4' Ventromental plate with sparse, short setae beneath (Fig. 15F). Premandible with 1 tooth. . . . . *Compteromesa* Sæther [*C. haradensis* Niitsuma & Makarchenko, widespread, oriental China, Japan; *C. biramosa* Tang & Niitsuma, oriental China (Yunnan), Shi *et al.* 2021. Holarctic]

Telmatogetoninae: genera

Two genera, *Telmatogeton* and *Thalassomya*, in this subfamily are known from the region: larvae and pupae live in algal mats in the intertidal maritime zone. Although some *Telmatogeton* species have been found in torrential streams in Hawai'i (Wirth 1947), freshwater species are not reported in any regional off-shore islands.

1 Dorsal head anterior to frontal apotome with 2 distinct sclerites, cephalic seta S3 on strong tubercle; premandible with 3 blunt teeth (Fig. 15G, H) . . . . . *Telmatogeton* Schiner [marine coastal, *T. japonicus* Tokunaga, *T. pacificus* Tokunaga, n.w. Pacific, China, inc. Korea, Japan (Tang *et al*. 2022b); 24 spp.; global]

1' Dorsal head without distinct sclerites, seta S3 not on tubercle; premandible 1 toothed (Fig. 15I, J) . . . . . *Thalassomya* Schiner [maritime coastal, *T. japonica* Tokunaga & Etsuko, *T. maritima* Wirth, n.w. Pacific, inc. Japan, Tang *et al*. 2022b; 10 spp.; global]

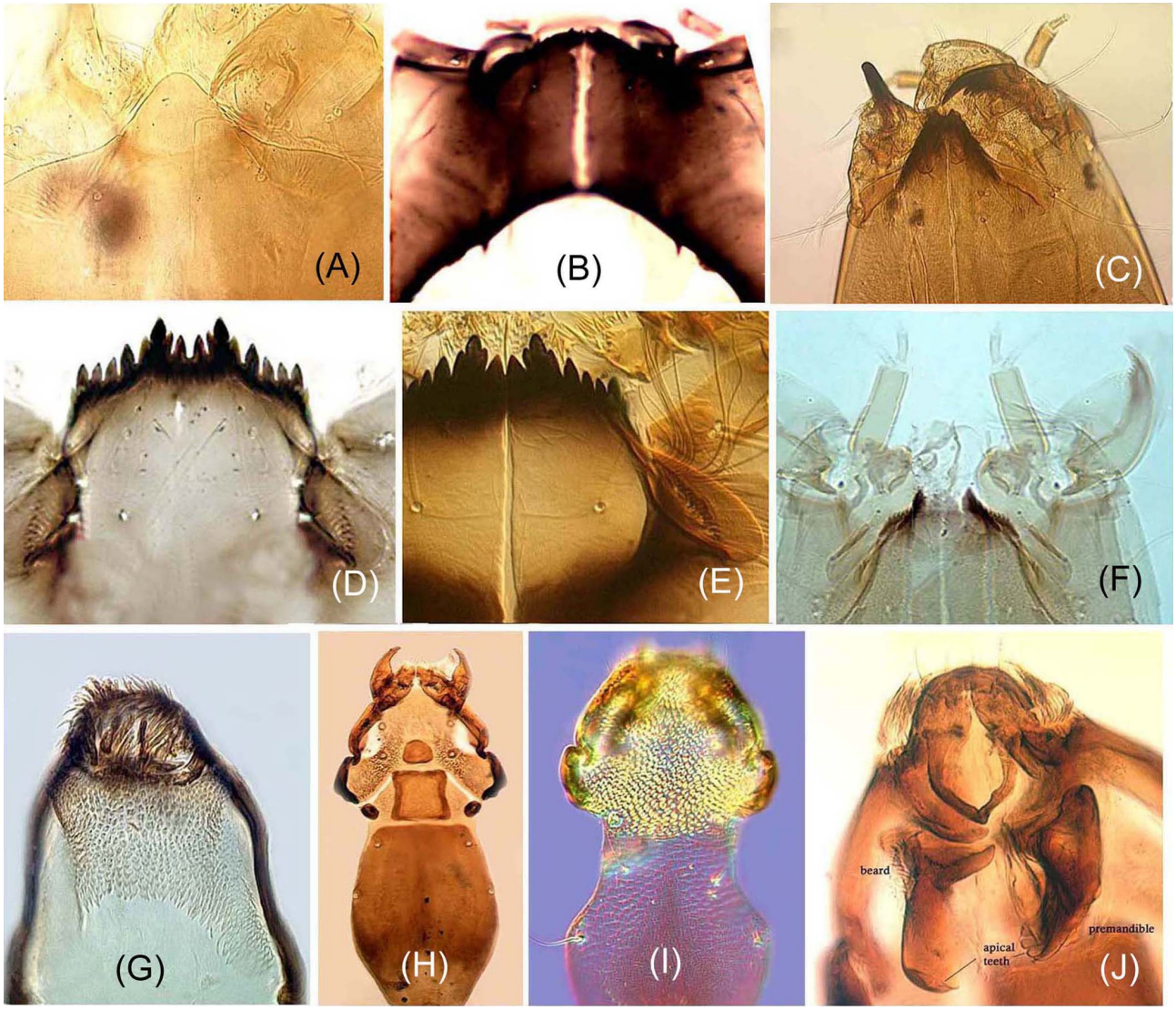

FIGURE 15. Larval Prodiamesinae. *Odontomesa*, (A) mentum; *Propsilocerus*, (B) mentum; *Monodiamesa*, (C) ventromental plate, mentum; *Prodiamesa* ?*rufovittata*, (D) mentum, ventromental plate; *Prodiamesa olivacea*, (E) mentum, ventromental plate; *Compteromesa*, (F) mentum, ventromental plate. Larval Telmatogetoninae. *Telmatogeton*, (G) hypopharynx, (H) dorsal head; *Thalassomya*, (I) dorsal head; *Telmatogeton*, (J) labrum-epipharynx.

Orthocladiinae: genera

This large subfamily, which is second only to Chironominae in diversity, clearly is less dominant in subtropical and tropical rainforests comparing to temperate zones. The Orthocladiinae includes taxa with larvae living in the marine / intertidal/ splash zone, including *Clunio*, *Thalassosmittia* and *Semiocladius* (Tang *et al*. 2022b). Selected terrestrial (or semi-terrestrial) larvae are included only if at least one sp. is suspected from aquatic habitat(s): these are not illustrated. Some genera, notably *Cricotopus* (including *Paratrichocladius*) and *Orthocladius* lack unambiguous diagnostic larval characters to separate unequivocally. These key in several places: none include their subgenera.

1 Anal end lacks procercus; if present, without distinct anal setae and posterior parapods; anal setae present or absent (Fig. 16A). Anterior parapods often partially fused 2

1' Procercus present, perhaps reduced; variable number of anal setae (Fig. 16T). Anterior parapods separated 15

2(1) Pecten epipharyngis scales each subdivided into 2–3 teeth, forming row of c. 8 teeth; S1 nearly palmate . . . *Antillocladius* Sæther [seeps, wet terrestrial moss. Thailand, *A. zhengi* Wang & Sæther (Hainan), *A. tokarameneus* (Sasa & Suzuki) Ryukyu, Japan, Korea; Nearctic, Neotropics; Mendes *et al*. 2004]

2' Pecten epipharyngis consisting of 3 scales. S I palmate only in *Parasmittia* and *Smittia* 3

3(2) Preanal and anal segments and posterior parapods bent ventrally at right angles to body axis (Fig. 16A). 4

3' Preanal and anal segments in same horizontal axis as body 5

4(3) Posterior parapods undivided. Anal tubules present. Usually lacking anal setae. . . . . *Bryophaenocladius* Thienemann [largely terrestrial, >8 spp. Oriental China, *B. fujidecimus* (Sasa), common; chaos in Asian spp. (M. Yamamoto, pers. comm. 2017), Kong *et al*. 2021, Lin *et al*. 2012. Japan, Korea, global]

4' Posterior parapods divided, anterior part with small claws, posterior bare. Anal tubules small or absent. Single anal seta. . . . . *Gymnometriocnemus* Edwards [semi-aquatic, terrestrial moss. Adults of several spp. inc. oriental China; global]

5(3) Anal tubules absent (Fig. 16D). Marine / maritime spp. 6

5' Anal tubules present (Fig. 16T). Not marine, few marine littoral *Pseudosmittia* 8

6(5) Basal antennal segment squat, much wider than high. Ventromental plate protruding, rounded, with second more posterolateral plate. Premandible with brush. S I bifid. . . . . *Semiocladius* Sublette & Wirth [marine coastal. *S. endocladiae* (Tokunaga), Korea, oriental China (Guangdong, Fujiang); Japan; Australia, western S. Pacific, Seychelles. Tang *et al*. 2022b].

6' Basal antennal segment not squat, higher than wide (Fig. 16C). Ventromental plate single. Premandible without brush (Fig. 16B). S I simple, pectinate or plumose. 7

7(6) Anal seta single. S I and S II broad, feathered. Seta submentum simple ... *Clunio* Haliday [marine, *C. tsushimensis* Tokunaga, *C. tuthilli* Tokunaga, *C. setoensis* Tokunaga, *C. pacificus* Edwards, e. coastal China, Japan, Tang *et al*. 2022b; global]

7' Anal setae 2 or 3, rarely 1 (Fig. 16D). S I simple, S II always simple. Seta submentum simple or plumose . . . . . *Thalassosmittia* Strenzke & Remmert [marine, shores *T. nemalione* (Tokunaga), oriental China; Japan, Tang *et al*. 2022b. Holarctic]

8(5) Commensal on Ephemeroptera (Fig. 16E). Mandible with spine-like teeth (Fig. 16F). Mentum with broad median depressed area (Fig.16G). . . . . *Symbiocladius* Keffer [*S. rhithrogenae* Zavřel, oriental China (Sichuan) Liu *et al*. 2023. Holarctic, Neotropical, Australia]

8' Rarely commensal/ectoparasitic. Mandibular teeth typical, rounded to subtriangular (Fig. 16I). Mentum medially toothed (Fig. 16J) or with narrower median untoothed part (Fig. 16N) 9

9(8) S I and S II bifid. 10

9' S II never bifid.. 13

10(9) Posterior parapods, procercus, anal setae and anal claws absent. Terminal antennal segment as long as preceding segment . . . . . *Camptocladius* v.d. Wulp [coprophagous, aquatic only in (cattle) faecal-contaminated water, *C. stercorarius* (De Geer), nr global]

10' Anal claws and posterior parapods present; if posterior parapods vestigial and without claws then terminal antennal segment about 3 x length of preceding segment 11

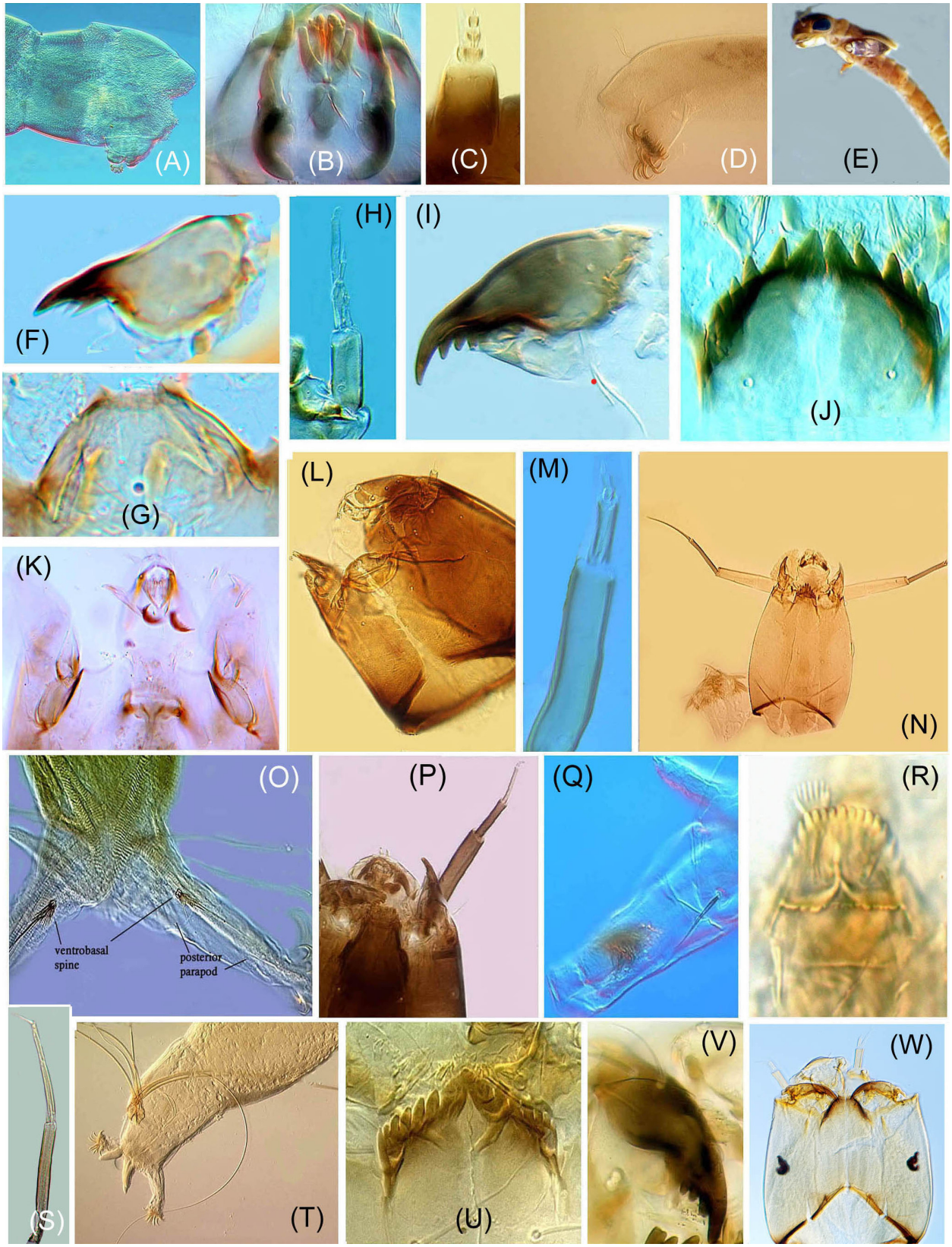

FIGURE 16. Larval Orthocladiinae. *Bryophaenocladius*, (A) posterior abdomen; *Clunio*, (B) labrum, epipharynx; *Thalassosmittia*, (C) antenna, (D) posterior abdomen; *Symbiocladius*, (E) larva on ephemeropteran host, (F) mandible, (G) mentum; *Heterotrissocladius*, (H) antenna, (I) mandible, (J) mentum; orthocladiine genus C (?"*Ninellia*"), (K) labrum, mentum; *Nanocladius*, (L) head capsule, (M) antenna; *Corynoneura*, (N) head capsule, (O) posterior abdomen; *Thienemanniella*, (P) head capsule, (Q) posterior abdomen; *Rheosmittia*, (R) mentum, hypopharynx, (S) antenna; *Krenosmittia*, (T) posterior abdomen, (U) mentum; *Pseudorthocladius*, (V) mandible, outer mentum; *Epoicocladius*, (W) ventral head and mentum.

11(10) Posterior parapod with 0–5 claws, 0–18 µm long. Mandible with 3 inner teeth. Antennal blade extending beyond flagellum 1 to 4 x as long as the width of basal segment . . . . *Pseudosmittia* Edwards
[speciose, few aquatic; *P. littoralis* (Tokunaga) marine coastal, Tang *et al.* 2022b; speciose, global]

11' Posterior parapod with 7–12 claws, 15–80 µm long. Mandible with 3 or 4 inner teeth. Antennal blade as long as width of basal segment, at most slightly extending beyond flagellum 12

12(11) Mandible with 4 inner teeth, lacking seta interna, mentum with 5 pairs of lateral teeth. If 3 inner mandibular teeth, then mentum with 4 pairs of lateral teeth, blade as long as flagellum and seta submenti bifid ... . *Allocladius* Kieffer
[*A. caspersi* Ferrington & Saether oriental China (Sichuan)., *A. aizaiensis* (Wang) (Hunan); Japan. Holarctic, Neotropical, Afrotropical]

12' Mandible with 3 inner teeth or when with 4 teeth, mentum with 4 pairs of lateral teeth. Seta interna occasionally present. Antennal blade extending beyond flagellum. Seta submenti simple . . . .*Hydrosmittia* Ferrington & Sæther
[aquatic *H. oxoniana* (Edwards) oriental China (Yunnan); *H. continalinea* & *H. sipinata* both Zhang *et al.* (Sichuan), Zhang *et al.* 2016; global]

13(9) Mandible without seta interna. S I simple . . . . *Mesosmittia* Brundin
L, some on wet surface of rainforest leaves (Australia, Brazil); *M. patrihortae* Sæther, oriental China 4 spp. (inc. Guangxi, Guizhou, Yunnan), seeming widespread. Holarctic, Neotropical, Afrotropical, Australia]

13' Mandible with seta interna. S I palmate or plumose. 14

14(13) Antenna very short, 4 segmented, distal segments indistinct, blade extending beyond antenna . . . . *Parasmittia* Strenzke
[terrestrial, 1–2 undescribed spp. oriental China; Holarctic; Japan]

14' Antenna even if reduced, with 4–5 distinct segments; blade less extended. . . . . *Smittia* Holmgren
[terrestrial, modest but largely unknown diversity; global]

15(1) Antenna at least 1/2 length of head (less blade) (Fig. 16N, P) 16

15' Antenna shorter than 1/2 length of head 20

16(15) Ventromental plate well developed. Mandible with globose base 17

16' Ventromental plate weak or indistinguishable. Mandible with normal base 18

17(16) Dorsomentum with numerous fine anterior and lateral teeth (Fig. 16K) . . . . nr. 'Orthocladiinae sp. C'. of Sæther
[lotic, undescr. L, P, oriental China (Hainan); (? = *Parakiefferiella* gp), Nearctic, Andersen *et al*. 2013]

17' Dorsomentum with few rudimentary median teeth (Fig. 16L, M) . . . .*Nanocladius* Kieffer (part)
[few spp. with long antenna key here, see couplet 32]

18(16) Antenna with 4 segments, longer than head (Fig. 16N). Head capsule sometimes with surface sculpturing. Seta at base of posterior parapod with accessory spinelets (Fig. 16O) . . . .*Corynoneura* Winnertz
[lentic, lotic. widespread regional, speciose, oriental China, Fu *et al*. 2019, 2022, global]

18' Antenna with 5 distinct segments or 5–6 indistinct segments, at most as long as head, usually shorter. Head capsule without surface sculpturing. Seta at base of posterior parapod simple 19

19(18) Antenna with 5 distinct segments, third segment frequently darkened (Fig.16P). Mentum without paired hypopharyngeal scales dorsal to it. Simple spine-like seta at base of posterior parapod (Fig. 16Q) . . . . *Thienemanniella* Kieffer
[lentic, lotic. widespread regional, speciose, oriental China, Fu *et al*. 2010a, 2013, 2020, global]

19' Antenna with second antennal segment unevenly sclerotised, with alternate Lauterborn organs (Fig. 16S). Multitoothed mentum with paired hypopharyngeal scales (Fig. 16R). No basiventral spine on posterior parapod . . . . *Rheosmittia* Brundin
[psammophilic, *R. yakytriangulata* (Sasa & Suzuki), oriental China (Guangdong); Japan, Holarctic]

20(15) One anal seta as long as 25% body length (Fig. 16T) 21

20' All anal setae shorter than 20% body length 23

21(20) Mentum with 6 pairs of narrow, sharply pointed lateral teeth and single median tooth with small median nipple (Fig. 16U). Premandible with 2 apical teeth. Maxillary palp long. Anal setae of procercus directed dorsally . . . . *Krenosmittia* Thiennemann & Krüger
[krenobiont, lotic, Thailand, Indonesia (Sulawesi), 3 spp. oriental China (Fujian, Guangdong, Yunnan); Holarctic, esp. e. Palaearctic, Japan]

21' Mentum with 4 pairs of lateral teeth, median tooth without median projection. Premandible with 1 apical tooth. Maxillary palp short. Preanal segment projects over anal segment, directing anal setae posteriorly. 22

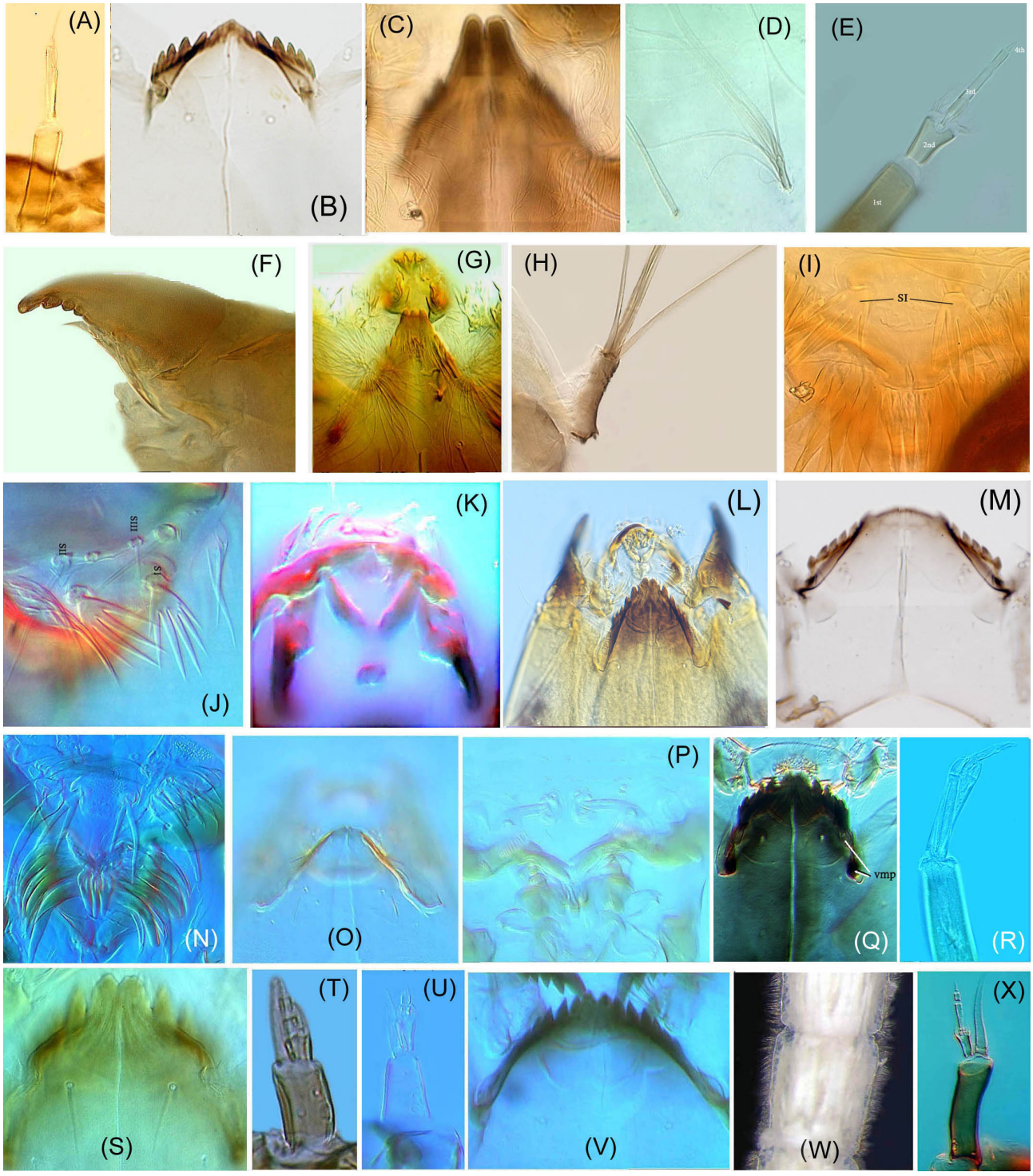

FIGURE 17. Larval Orthocladiinae. *Parakiefferiella*, (A) antenna, (B) mentum; *Synorthocladius*, (C) mentum, (D) abdominal setal tufts, (E) mandible; *Parorthocladius*, (F) mandible, (G) mentum; *Psectrocladius*, (H) procercus, (I) labrum-epipharynx, (J) anterior labrum, S setae indicated; *Rheocricotopus*, (K) labrum-epipharynx, (L) mentum, anterior head; *Paracladius*, (M) mentum, (N) labrum-epipharynx; *Nanocladius*, (O) mentum, (P) labrum (s.g. *Plecopteracoluthus*); *Parametriocnemus*, (Q) ventral head, ventromental plates; R) antenna, (S) mentum; *Paraphaenocladius*, (T) antenna; *Hydrobaenus*, (U) antenna, (V) mentum; *Xylotopus*, (W) abdomen seta, (X) antenna.

22(21) Mandible with 3 inner teeth (Fig. 16V) . . . . . *Pseudorthocladius* Goetghebuer [springs, hyporheic, mosses; speciose, 10+ spp. 3-4 as Pe, oriental China (Fujian, Guangdong, Guizhou, Hainan, Hunan, S. Shaanxi, Sichuan, Zhejiang) (Ren *et al*. 2014), errors/synonymy high in Asian spp. Japan, Holarctic, Afrotropical]

22' Mandible usually with only 1–2 inner teeth . . . . . .*Parachaetocladius* Wülker [lotic, krenobiont, 2Pe, oriental China (Guangdong), *P. akanoctavus* Sasa & Kamimura (Sichuan), *P. squamula* Liu & Cao (Zhejiang) Liu *et al.*, 2020. Japan, Holarctic]

23(20) Mentum with at least 16 teeth, strongly arched, giving impression of only 4–6 central teeth; lateral teeth visible only on compression of mentum (Fig. 16W). Phoretic / parasitic on ephemerid mayflies . . . . . .*Epoicocladius* Sulc & Zavřel [2 L / P spp. China/Japan, Hayashi & Kobayashi 2000. Holarctic, Neotropical]

23' Mentum with fewer than 15 teeth. Rarely phoretic / parasitic 24

24(23) Beard beneath (dorsal) to or closely laterally adjacent to ventromental plate (may be few setae, and require high magnification optics) (Fig. 17B) 25

24' Beard absent, although 1–4 vestigial setae may be present 30

25(24) 6th antennal segment hair-like, usually distinct (Fig. 17A). Mentum with single broad median tooth (Fig. 17B). . . . . .*Parakiefferiella* Thienemann (part.) [lotic, lentic, speciose in palaearctic, perhaps less so in s.e. Asia. Thailand, Indonesia (Sulawesi), *P. yakykelea* Sasa & Suzuki, oriental China (Guangdong), Japan; Holarctic, Neotropical, Afrotropical]

25' Antenna with 4 or 5 segments, never with 6th (Fig. 17E) 26

26(25) S I simple. Mentum with 2–3 median, equally sized, elongate teeth; beard well developed, radiating from a common area. Seta interna absent; seta subdentalis large 27

26' S I simple, bifid, coarsely pectinate, palmate or plumose. Mentum, beard and mandible not as above. Abdomen without alternating simple and plumose setae, but single pair of tufts may be present posterolaterally. 28

27(26) Mentum with 2 median teeth; beard with apically branched filaments (Fig. 17C). Mandible with inner spine. Abdominal segments with alternating simple and plumose setae (Fig. 17D) . . . . . .*Synorthocladius* Thienemann [*S. semivirens* (Kieffer) wide range inc. oriental China; *S. bifidus* Liu & Wang, oriental China (Guangdong, Yunnan) Liu & Wang 2005. Holarctic, Neotropical, Afrotropical]

27' Mentum with 3 median teeth; beard with simple filaments (Fig. 17G). Mandible without inner spine (Fig. 17F). Abdominal segments with simple and bifid or plumose setae, if plumose then only 1 on each posteroventral corner except for last abdominal segment. . . . . .*Parorthocladius* Thienemann [small waterbodies, *P. unicentrus* Liu & Wang, oriental China (Guangdong). Holarctic, inc. Korea, Japan; Afrotropical]

28(26) S I broadly trifid, palmate or with 4 long, narrow teeth, seldom bifid (Fig. 17I, J). Procercus with small to large spurs (Fig. 17H) . . . . . .*Psectrocladius* Kieffer (part.) [lentic, L. key to subgenera Andersen *et al*. 2013, sp. Thailand, uncertain in oriental China; global exc. Australia; Oceania]

28' S I simple, bifid, apically split, plumose or coarsely serrate. If procercus with spurs, S I bifid 29

29(28) Beard strong. Procercus with basal spurs. S I deeply bifid. (Fig. 17K, L). . . . . .*Rheocricotopus* Brundin [rheophilic, speciose, L keys to subgenera, s.s. & *Psilocricotopus* Sæther in Andersen *et al*. 2013; widespread, Thailand, Indonesia (Kalimantan, Sulawesi, Sumatra), Malaysia (Sabah), speciose in oriental China (e.g. 8 spp. Guangdong). Holarctic (c. 35 spp.), Neotropical. Afrotropical, Australia]

29' Beard weak. Procercus smooth, without spurs. SI simple, apically serrate (Fig. 17M, N) . . . . . .*Paracladius* Hirvenoja [*P. antennarius* Yan & Wang, *P. alpicola* (Zetterstedt) both oriental China (Sichuan), *P. ovatus* Fu *et al*. (Yunnan) Fu *et al.* 2010b; Japan, Holarctic]

30(24) Ventromental plate extending laterad of mentum (Fig. 17O) or broad, non-extended. 31

30' Ventromental plate small, not extending laterad of mentum, or plate very narrow 38

31(30) All S setae simple. Mentum with small paired median teeth often well separated from 0–6 pairs of lateral teeth which may be small, fused or closely adpressed (Fig. 17O); s.g *Plecopteracoluthus* Steffan with broad plate . . . . .*Nanocladius* Kieffer (part) [lotic, lentic, rheophilic, or phoretic or parasitic on range of aquatic insects (*N*. (*Plecopteracoluthus) asiaticus* Hayashi) Hayashi & Kobayashi 2000, *Nanocladius* s.s. nr. global, Andersen *et al.*, 2013]

31' S I never simple. Mentum not as above. Not phoretic 32

32(31) Antenna 7 segmented; 7th segment fine; 3rd minute, 1/3 length of 4th (Fig. 16H). 33

32' Antenna 5–6 segmented; 3rd not minute relative to 4th (Fig. 16M, P) 34

33(32) Mentum with 5 pairs of lateral teeth, ventromental plate wide. Premandible bifid . . . . . *Heterotrissocladius* Spärck [lotic, littoral, *H. marcidus* (Walker) China (o. & p.), Tibet, Holarctic. 3 spp (as nov.) oriental China (Zhejiang, Guizhou, Fujian, Guangxi); Tibet, Kong & Wang 2011. Holarctic, ?India).

33’ Mentum with 4 pairs of lateral teeth, ventromental plate modest. Premandible with apical tooth, 1 low accessory tooth . . . . . *Paratrissocladius* Zavřel [tubicolous in lotic sediment, *P. excerptus* (Walker) ssp. *pubis* Sæther & Wang Burma, sp. Thailand, oriental China (Henan, Fujian, Anhui) (Sæther & Wang 2000). L common, widespread, Japan; Holarctic, Afrotropical]

34(32) Ventromental plate appears double (Fig. 17Q). Seta submenti located anterior to posterior margin of plate (Fig. 17Q, S) . . . 35
34’ Ventromental plate simple. Seta submenti at posterior margin of ventromentum plate or more posteriad 36

35(34) Basal segment of antenna long. AR > 1.25. Blade shorter than flagellum (Fig. 17R) . . . . . *Parametriocnemus* Goetghebuer [lotic, lentic, *P. nigrescens* (Johannsen) Indonesia (Java), regionally abundant, 7 spp, widespread oriental China, Li *et al*. 2013; Japan, global]
35’ Basal segment of antenna short. AR <1.1. Bade equal to or longer than flagellum (Fig. 17U). . . *Paraphaenocladius* Thienemann [lotic, lentic, seeps, Indonesia (Java). *P. discretus* (Johannsen), *P. impensus* (Walker), *P. exagitans* (Johannsen), oriental China (Guangdong). Holarctic, Neotropical, Afrotropical. Sæther & Wang 1995]

36(34) Ventromental plate covers most or all of lateral teeth of mentum, median tooth broad and dome-shaped (Fig 17B). Antenna with 6 segments, sixth segment hair-like (Fig. 17A) . . . . . .*Parakiefferiella* Thienemann (part.) [comments, see couplet 26]
36’ Most lateral teeth of mentum outside ventromental plate, median tooth broad or narrow. Antenna 4–6 segmented 37

37(36) Antenna with 5 segments. Premandible with brush . . . . . *Chaetocladius* Kieffer (part.) [♂ only, oriental China (Zhejiang); Tibet; Holarctic, Afrotropical]

37’ Antenna with 6 segments, sixth segment vestigial (Fig. 17U). Premandible without brush . . . . . *Hydrobaenus* Fries [in lentic sediment, *H. kondoi* Sæther, oriental China (Jiangxi). Holarctic]

38(30) Antenna with 6–7 segments, terminal segment, hair-like. Ventromental plate wide . . . . . .*Parakiefferiella* Kieffer (part.) [see couplet 26]
38’ Antenna with 5 or fewer segments, last segment normal. Ventromental plate modest to vestigial 39

39(38) Abdomen with setal tufts in fringe, or 2 or 4 pairs per segment 40
39’ Abdomen without fringe or paired setal tufts, although individual setal tuft or long setae may be present 42

40(39) Abdominal segments with many setal tufts (Fig. 17W). Antenna with 5 segments, 2nd complete (Fig. 17X). . . .*Xylotopus* Oliver [lotic, wood-mining, *X. burmanensis* Oliver Burma, oriental China (Yunnan), *X. amamiapiatus* (Sasa) oriental China (Guangdong, Hainan), Liu *et al*. 2019, 2021b, Japan, Nearctic]
40 Abdominal segments each with 2 or 4 setal tufts. 2nd antennal segment divided into 2 parts 41

41(40) Antenna with 4 segments, Abdominal segments with 4 setal tufts . . . . . *Neobrillia* Kawai [lotic, wood-miner, *N. longistyla* Kawai (= *N. komorii* (Niitsuma) oriental China (Guangdong, Hainan); Japan]
41’ Antenna with 5 segments, Abdominal segments with 2 setal tufts . . . . . *Tokyobrillia* Kobayashi & Sasa [lotic, wood-miner, one common sp., *T. tamamegaseta* Kobayashi & Sasa, oriental China (Guangdong, Hainan, Yunnan); Japan]

42(39) Abdomen with long simple setae, some at least 1/2 as long as segment (Fig. 18D) 43
42’ Abdomen without long setae, or if present, arranged as pairs of single tufts, one posterolateral on each side on many body segments 47

43(42) S I simple or with indistinct apical dentations. Procercus short / stout, < 2× width 44
43’ S I bifid, with several apical teeth or plumose. Procercus long, usually > 2× width 46

44(43) Antennal blade longer than flagellum (Fig. 18A). Mandible with 4 inner teeth (Fig. 18B). Premandible with 2 apical teeth and brush (Fig. 18C). Abdominal setae about as long as the segment bearing them. . . . . *Paralimnophyes* Brundin [eutrophic pools, *P jii* Wang & Sæther oriental China (Hubei), undesc. spp., Wang & Sæther 2002; Holarctic, Australia]
44’ Antennal blade shorter than flagellum. Mandible with 3 inner teeth. Premandible simple, without brush. Abdominal setae about 1/2 length of segment bearing them 45

45(44) Inner margin / mola of mandible with several spines. Setae submenti adjacent to posterad mentum or slightly posterior from the mentum (Fig. 18G). Procercus without spurs (Fig. 18H). . . . . *Eukiefferiella* Thienemann (part.) [eurythermic, lotic, speciose, widespread, regional endemism low, Pe common, 8+ spp from oriental China (Guangdong) Japan - errors/synonymy high), spp. groups Andersen *et al*. 2013; global exc. Australia].

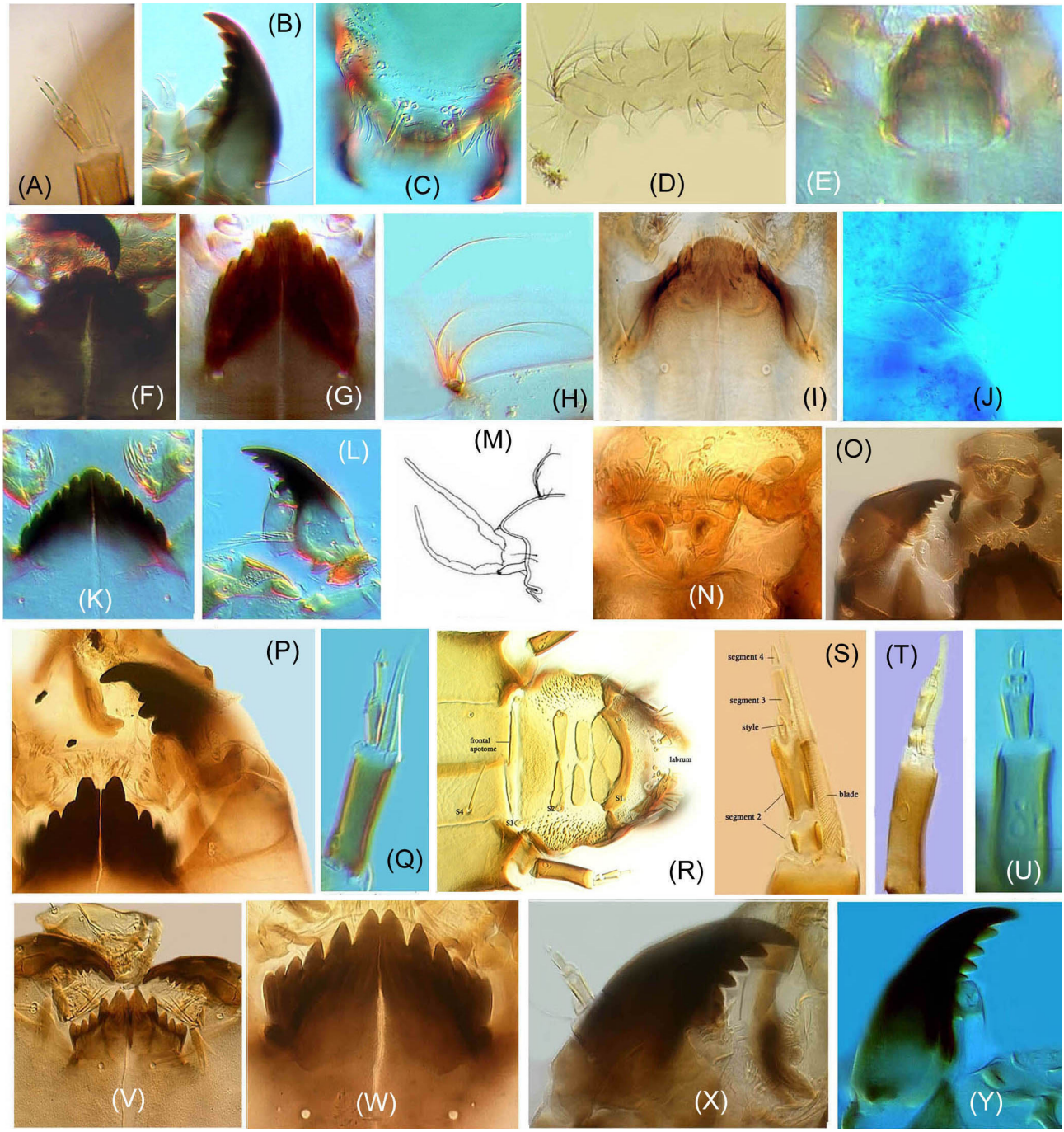

FIGURE 18. Larval Orthocladiinae. *Paralimnophyes*, (A) antenna, (B) ventral head, (C) labrum; *Tvetenia*, (D) body seta of posterior abdomen; *Onconeura*, (E) mentum; *Cardiocladius*, (F) mentum; *Eukiefferiella*, (G) mentum, (H) procercus; *Chaetocladius*, (I) mentum; *Cricotopus*, (J) abdominal setal tuft, (K) mentum, (L) mandible; *Doithrix*, (M) posterior abdomen; *Metriocnemus*, (N) labrum-epipharynx, (O) mentum, mandible; *Euryhapsis*, (P) anterior head, (Q) antenna; *Brillia*, (R) dorsal head, (S) antenna; *Heleniella*, (T) antenna, (V) mentum; *Limnophyes*, (U) antenna, (W) mentum, (X) mandible; *Compterosmittia*, (Y) mandible.

45’ Inner margin of mandible usually smooth. Insertion of seta submenti always clearly posterior from the mentum, gap about 1/2 length of mentum height. Procercus with spurs . . . . . .*Paracricotopus* Brundin [lotic, bogs, L/Pe, Indonesia (Sulawesi), Thailand, Singapore; *P. irregularis* Niitsuma, oriental China (Guangdong); Japan. Holarctic]

46(43) Mandible with 3 inner teeth and inner margin / mola with several spines. . . . . *Tvetenia* Kieffer [lotic, *T. calvescens* (Edwards), *T. tamaflava* (Sasa) (possibly synonymous) oriental China (Guangdong). Japan, Holarctic, Afrotropical]

46’ Mandible with 4 inner teeth and inner margin / mola smooth. (Fig. 18O). . . . . *Metriocnemus* v.d. Wulp (part.) [microaquatic habitats, esp. pitcher plants in tropical forest, speciose, ?12+ spp. oriental China Sæther 1995, Li & Wang 2014, inc. *M. tristellus* Edwards (Guangdong), *M. brusti* Sæther (Yunnan); Japan; global exc. Australia]

47(42) Mentum with 3 median teeth and 5 pairs of lateral teeth, first pair of lateral teeth closely adpressed to outer median teeth (Fig. 18E). Antenna 1/4–1/3 as long as head. S II strong, on tubercle . . . . . *Onconeura* Andersen & Sæther [*O. togamijika* (Sasa & Okazawa) Spies *et al*. 2022, Holarctic, Neotropical]

47’ Mentum with1–2 median teeth and 4–5 pairs of laterals. Antenna at most ¼ as long as head. S II not on tubercle 48

48(47) S I simple 49

48’ S I bifid, serrate, pectinate or plumose. 55

49(48) Antenna 4-segmented. Weak labral lamellae of 2 small, well separated, apically serrate lobes . . . . . *Eurycnemus* v.d. Wulp [lotic, possibly all inhabit caddis cases, *E.* cf. *nozakii* Kobayashi, oriental China (Fujian, Yunnan), Li & Tang 2017; Palaearctic, inc. Japan]

49’ Antenna 5-segmented. If labral lamellae absent, then 2 small separated lobes 49

50(49) Inner margin of mandible with spines (may be small). 51

50’ Inner margin of mandible usually smooth 53

51(50) Procercus reduced, with 2 setae thicker than others on each procercus. Seta interna of mandible with long stalk, branching apical. Mentum with 5 pairs of lateral teeth (Fig. 18F) . . . . . .*Cardiocladius* Kieffer [fast lotic, Indonesia (Sulawesi, Kalimantan), Thailand, oriental China, taxonomy problematic; global]

51’ Procercus conventional, at least as long as wide, setae about equally thick. Seta interna of mandible usually divided to near base, if divided near apex. Mentum with 4 pairs of lateral teeth. 52

52(51) Supraanal setae much longer than anal tubules. Abdomen with setae c. 1/2 as long as segment . . . .*Eukiefferiella* Thienemann (part)
[see comments under couplet #44]

52’ Supraanal setae shorter than anal tubules. Abdominal setae short. . . . . *Tokunagaia* Sæther[1] [lotic, in mosses, hygropetric, 5 spp oriental China (Yunnan, Sichuan, Guizhou) Liu & Wang 2006; speciose e. Palaearctic, inc. Japan, few Holarctic]

53(50) Body with posterolateral tufts (Fig. 18J). Mentum with single median tooth (Fig. 18K) . . . . . *Cricotopus* v.d. Wulp (part) [lotic, lentic, speciose, subgenera Anderson *et al.* 2013, includes some *Paratrichocladius* Santos Abreu; regionally widespread, e.g. 13 spp. oriental China (Guangdong); global] [Occasionally, a few *Orthocladius* (*Symposiocladius*) will key here]

53’ Body without posterolateral tufts. Mentum with bifid median tooth. 54

54(53) Premandible apically simple. Mentum with median teeth strongly projecting anteriorly; ventromental plate not rounded posterolaterally (Fig. 18I). . . . . *Chaetocladius* Kieffer (part) [semi-aquatic, spp. groups, Andersen *et al.* 2013; speciose, temperate. *C. oyabevenustus* Sasa, oriental China (Zhejiang, Guangdong). Holarctic, Afrotropical]

54’ Premandible apically bifid. Mentum with median teeth not strongly projecting anteriorly; with ventromental plate posterolaterally rounded (Fig. 18U, W, X). . . . . *Limnophyes* Eaton [semi-terrestrial, speciose, *L. minimus* (Meigen) widespread, 4+ spp. oriental China (Guangdong, Sichuan, Hubei), Liu *et al.* 2021a; global]

55(48) S I bifid. 56

55’ S I serrate, apically fringed, pectinate or plumose 57

56(55) Inner margin of mandible serrate (Fig. 18L). Some abdominal segments with posterolateral setal tuft . . . . . *Cricotopus* v.d. Wulp (part) [see couplet 52 for comments]

56’ Inner margin of mandible smooth. Without abdominal setal tufts . . . . . *Cricotopus* v.d. Wulp (part) [Includes some *Paratrichocladius* Santos Abreu. L, Pe inseparable, synonymised Cranston & Krosch 2015] [any *Orthocladius* larva will key here]

1 At least on immature stages doubtfully distinguished from *Eukiefferiella*, Tang *pers. obs.* 2024

57(55) Anal tubules twice or more as long as posterior parapods, with many constrictions. Procercus vestigial or consisting of 2 nearly contiguous, flat cones with basal, low plates, each with 2–3 hair-like setae (Fig. 18M). Labral lamellae simple, rounded, weakly sclerotised. Blade extending well beyond terminal antennal segment . . . . . *Doithrix* Sæther & Sublette [small streams, seeps, *D. emeiensis* Wang, oriental China (Sichuan), Japan, Holarctic, Afrotropical]

57' Anal tubules short or normal, without constrictions. Procercus weak to well developed, not vestigial. Labral lamellae well developed, vestigial or absent. Blade shorter or longer than flagellum 57

58(57) Labral lamellae well developed 59

58' Labral lamellae absent or vestigial 61

59(58) 2–4 subequal median mental teeth. Setae submenti located near base of mentum (Fig. 18O) . . . . . *Metriocnemus* (part.) [see comments couplet #45]

59' Mentum with 2 elongate median teeth, often small central tooth between median teeth (Fig. 18P). Setae submenti posterior from base of mentum 59

60(59) Second antennal segment complete (Fig. 18Q) . . . . . *Euryhapsis* Oliver [lotic, *E. fusciprope*s Sæther & Wang, Holarctic**)**

60' Second antennal segment with weakly sclerotised area near base (Fig. 18R, S) . . . . . *Brillia* Kieffer [lotic, lentic, springs, hygropetric, *B. japonica* Tokunaga, oriental China (Guangdong), Holarctic]

61(58) Mentum with 2 broad median teeth, separated medially by U- or wide V-shaped space (Fig. 18V). Second antennal segment weakly divided near base, antennal blade much longer than flagellum (Fig. 18T). Mandible with 3 inner teeth. (Fig. 18V) . . . . . *Heleniella* Gowin [*H. nebulosa* Andersen & Wang, Thailand, oriental China (Guangdong), sp. (Sichuan). Holarctic]

61' Median teeth of mentum not separated by such a U- or V- shaped gap (Fig. 18W). Second antennal segment not weakly divided near base (Fig. 18U). If blade longer than flagellum, then mandible with 4 inner teeth (Fig. 18Y) 62

62(61) Mandible with 3 inner teeth (Fig. 18X). Supraanal setae subequal to anal setae. . . . . *Limnophyes* (part.) [see comments #53]

62' Mandible with 4 inner teeth (Fig. 18Y). Supraanal setae c. 1/3 as long as anal setae . . . . . *Compterosmittia* Sæther [some spp. phytotelmic, speciose, 7+ spp. oriental China (Guangdong, Fujian); e. Palaearctic, Japan, Nearctic, Neotropical, Australia (inc., Oceania). Lin *et al*. 2013]

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Supplementary Materials. The following supporting information can be downloaded at the DOI landing page of this paper: s.e. Asia sampling sites.