Larval head microsculpture in Palaearctic Notodontidae (Noctuoidea) and its significance for the systematics of the family

Irina V. Dolinskaya

Schmalhausen Institute of Zoology, National Academy of Sciences of Ukraine, B. Chmielnicki St.15, Kiev, 01601 Ukraine; dd8v@mail.ru

Abstract. The larval head microsculpture of each instar of 66 species belonging to 35 genera of Palaeartic notodontids from Ukraine and Far East of Russia (Primorskii krai) was examined with the use of a scanning electron microscope. A comparison with representatives from Lasiocampoidea (Lasiocampidae) and Noctuoidea (Erebidae: Lymantriinae, Arctiinae; Noctuidae) is conducted. Differences in head microsculpture and the transformation during development of different larval instars are discussed. Apomorphic and plesiomorphic states of these characters are also discussed. The results of this study are discussed with reference to recently published classifications of Notodontidae.

Introduction

First studies of head microsculpture in notodontid larvae date back to the last century (Bell 1935, Gardner 1943). A more detailed study of the cranial surface of notodontid larvae was undertaken by Miller (1991). He studied 48 species of notodontid caterpillars that occur in the Palaearctic and the Americas and also examined 13 species from other groups (Doidae; Erebidae: Arctiinae and Lymantriinae; Noctuidae; and Oenosandridae). Miller (1996, 2009a, 2009b) later described the head surface of the Neotropical notodontid caterpillars in the subfamily Dioptinae. Unfortunately, these studies only looked at the final larval instar, making it impossible to draw any conclusions regarding the microsculpture of the larval head as it changes among the different instars.

Materials and Methods

This research is based on material collected in Ukraine and Far East of Russia (Primorskii krai). Eggs were obtained from females captured at light. Hatched larvae were reared to pupae. The epicrania left by caterpillars after moulting, as well as fresh material preserved in alcohol, were studied. The epicranium was examined with a scanning electron microscope (SEM) and a binocular light microscope (MBS 9). The microsculpture of the head of 1st through 5th larval instars belonging to 66 notodontid species from the following genera were studied: *Euhampsonia* Dyar, *Cerura* Schrank, *Furcula* Lamarck, *Uropyia* Staudinger, *Dicranura* Reichenbach, *Harpyia* Ochsenheimer, *Stauropus* Germar, *Cnethodonta* Staudinger, *Fentonia* Butler, *Neopheosia* Matsumura, *Drymonia* Hübner, *Notodonta* Ochsenheimer, *Peridea* Stephens, *Nerice* Walker, *Pheosia*

Hübner, *Leucodonta* Staudinger, *Lophocosma* Staudinger, *Ellida* Grote, *Pheosiopsis* Bryk, *Shaka* Matsumura, *Pterostoma* Germar, *Ptilodon* Hübner, *Lophontosia* Staudinger, *Hagapteryx* Matsumura, *Togepteryx* Matsumura, *Semidonta* Staudinger, *Allodonta* Staudinger, *Epodonta* Matsumura, *Phalera* Hübner, *Spatalia* Hübner, *Gluphisia* Boisduval, *Gonoclostera* Butler, *Pygaera* Ochsenheimer, *Clostera* Samouelle, and *Micromelalopha* Nagano. The taxonomic arrangement of these genera follows Schintlmeister (2008).

In order to clarify the character states and polarity within Notodontidae, representatives of related families belonging to Lasiocampoidea, as well as other members of Noctuoidea (Minet 1994; Kuznetzov & Stekolnikov 2001), were used as outgroup taxa. The following species were studied: *Euthrix potatoria* Linnaeus, *Gastropacha quercifolia* Linnaeus (Lasiocampidae), *Teia dubia* Tauscher, *Arctornis l-nigrum* Müller (Erebidae: Lymantriinae), *Rhyparioides amurensis* Bremer, *Chionarctia nivea* Mėnėtriės (Erebidae: Arctiinae), *Calocasia coryli* Linnaeus, and *Egira conspicillaris* Linnaeus (Noctuidae).

It should be noted that the degree to which microsculpture can be examined and described depends on the microscopic magnification. In this study the term "smooth microsculpture" is used only when microsculpture is not visible with magnifications under 2000x.

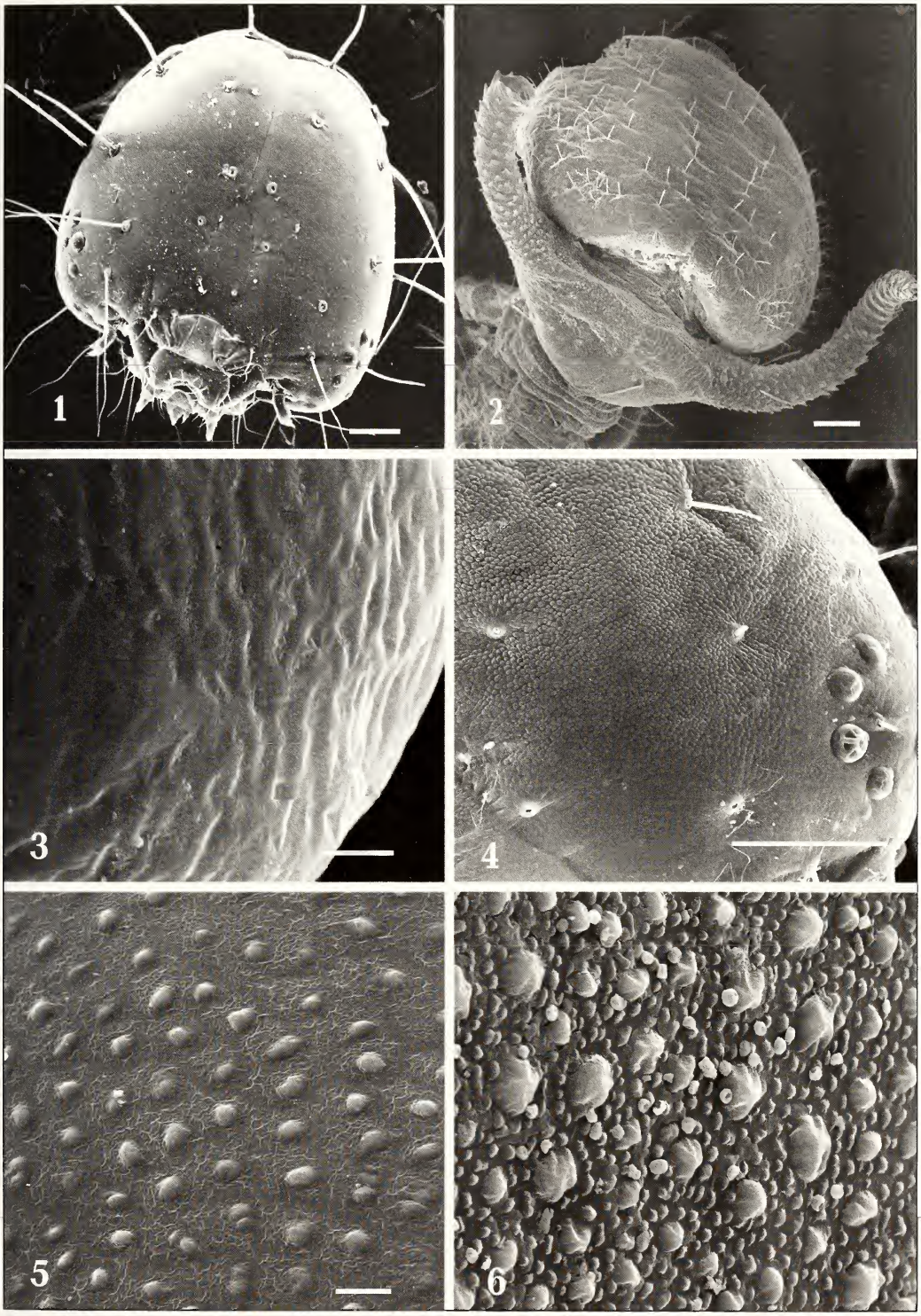
Results

Comparative Morphology of Larval Head Microsculpture

The taxa and characters examined are listed in Table 1. The microsculpture varies from instar to instar. First instar larvae are mostly without distinct microsculpture, with the head surface being smooth (*Ptilodon*, *Pterostoma*, *Spatalia* and others; Fig. 1) or slightly wrinkled (*Harpyia*, *Cnethodonta*; Fig. 2). In some genera, microsculpture is visible in the apical part of the head and partly laterally where it is expressed as slight wrinkles (*Gonoclostera*, *Fentonia*; Fig. 3) or pits (*Gluphisia*). In contrast, in *Pygaera*, *Cerura*, and *Furcula*, the surface bears homogeneous, small, densely situated tubercles. In *Pygaera* these structures are almost indistinct, smooth, and oval. In *Cerura* and *Furcula* these tubercles are very distinct and visible even with a light microscope (Fig. 4).

In 2nd instar, the microsculpture of many genera is still smooth (*Ptilodon*, *Allodonta*). However, sometimes the surface has small, homogeneous, and occasional tubercles arranged on a background of implicated fibrae (*Epodonta*, *Euhampsonia*, *Pheosia*; Fig. 5). In some genera (*Cerura*, *Furcula*, *Uropyia*, *Harpyia*, *Fentonia*) the head shows a background of heterogeneous small tubercles with occasional large tubercles distinguished by plicated edges. The latter are either scattered among smaller ones (Fig. 6) or arranged as more or less distinct groups (Fig. 7).

In 3rd instar some genera have a microsculpture identical to that of preceding instars. It is either smooth (*Phalera*; Fig. 8), slightly wrinkled with almost indistinct



Figs 1–6. Larval head surface of Notodontidae **1.** 1st instar *Ptilodon saturate hoegei*. **2.** 1st instar *Harpyia umbrosa*. **3.** 1st instar *Gonoclostera timoniorum*. **4.** 1st instar *Furcula bicuspis*. **5.** 2nd instar *Epodonta lineata*. **6.** 2nd instar *Fentonia ocypete*. Scale bar 1–4 (100 μ); 5, 6 (10 μ).

Table 1. Character states of the larval head surface of Palaearctic Notodontidae. FH: microsculpture of heterogeneous tubercles sparsely situated on a background of densely implicated fibrae; FO: microsculpture of tubercles sparsely situated on a background of densely implicated fibrae; H: heterogeneously tubercled microsculpture; M: microsculpture with microtrichiae; O: homogeneous microsculpture; P: pitted microsculpture; PO: microsculpture with tubercles in crateriform depressions; S: smooth microsculpture; SH: microsculpture with heterogeneous tubercles sparsely situated on smooth background; SO: microsculpture with homogeneous tubercles sparsely situated on a smooth background; SP: pits developed only on part of head; SW: head surface weakly wrinkled. WO: wrinkled microsculpture with homogeneous tubercles. Abbreviations: cone-shaped protuberances (co); corrugated microsculpture (cor); large tubercles concentrated in distinct groups (g).

	instar 1	instar 2	instar 3	instars 4–5
Notodontidae				
Euhampsonia cristata (Butler)	S	O	H, g	H, g
Euhampsonia splendida (Oberthür)	S	O	H, g	H, g
Cerura erminea (Esper)	O cor	H, cor	H, cor	H, cor,WO[1]
Furcula furcula (Clerck)	O cor	H, cor	H, cor	H, cor
Furcula bicuspis (Borkhausen)	O cor	H, cor	H, cor	H, cor
Furcula bifida (Brahm)	O	H, cor	H,g,cor	H, cor
Uropyia meticulodina (Oberthür)	S	H, g, co	H,g, co	H,g, co
Dicranura ulmi (Denis & Schiffermüller)	S	O	O	O
Harpyia milhauseri (Fabricius)	S	H, co	H, co	H, co
Harpyia umbrosa (Staudinger)	S	H, co	H, co	H, co
Stauropus fagi (Linnaeus)	S	O	O	H, co
Stauropus basalis Moore	S	S	–	–
Cnethodonta grisescens Staudinger	S	O	H, cor	H, cor
Fentonia ocypete (Bremer)	S	H, cor	H,g,cor	H, g, cor
Neopheosia mandschurica (Oberthür)	S	–	–	–
Drymonia dodonaea (Denis & Schiffermüller)	S	O	H	H
Notodonta torva (Hübner)	S	O	H, g	H, g
Notodonta dromedarius (Linnaeus)	S	O	H, g	H, g
Notodonta dembowskii Oberthür	S	O	H, g	H, g
Notodonta tritophus phoebe (Siebert)	S	O	H, g	H, g
Notodonta ziczac (Linnaeus)	S	O	H, g	H, g
Peridea anceps (Goeze)	S	O	H	H
Peridea lativitta (Wileman)	S	O	H	H
Peridea elzet Kiriakoff	S	O	H	H
Peridea graeseri (Staudinger)	S	O	H, co	H, co
Peridea gigantea (Butler)	S	O	H	H
Peridea oberthueri (Staudinger)	S	O	H	H
Peridea moltrechti (Oberthür)	S	O	H	H
Nerice leechi Staudinger	S	O	H, g	H, g
Nerice davidi Oberthür	S	O	H, g	H, g
Pheosia tremula (Clerck)	S	O	O	H
Pheosia grummi (Christoph)	S	–	–	–
Pheosia gnoma (Fabricius)	S	O	O	H
Pheosia rimosa Packard	S	O	O	H
Leucodonta bicoloria (Denis & Schiffermüller)	S	S	SW	SW
Lophocosma atriplaga Staudinger	S	O	H	H
Ellida branickii (Oberthür)	S	–	–	–
Pheosiopsis cinerea (Butler)	S	O	H, g	H, g
Shaka atrovittatus (Bremer)	S	O	H, g	H, g
Pterostoma palpina (Clerck)	S	O	H	H, g
Pterostoma sinica Moore	S	S	O	H, g
Pterostoma griseum (Bremer)	S	S	O	H, g
Ptilodon capucina (Linnaeus)	S	S	O	SO
Ptilodon saturate hoegei (Graeser)	S	S	O	SO

Table 1. Continuation.

	instar 1	instar 2	instar 3	instars 4–5
Notodontidae				
Ptilodon cucullina (Denis & Schiffermüller)	S	S	O	FO
Ptilodon ladislai (Oberthür)	S	S	O	SO, g
Lophontosia cuculus (Staudinger)	S	–	FH	FH, g
Hagapteryx admirabilis (Staudinger)	S	O	H, g	H, g
Togepteryx velutina (Oberthür)	–	–	–	H, g
Semidonta biloba (Oberthür)	S	S	SH	H
Allodonta plebeja (Oberthür)	S	S	O	H
Allodonta leucodera (Staudinger)	S	S	O	H
Epodonta lineata (Oberthür)	S	FO	FO	H, g
Phalera bucephala (Linnaeus)	S	S	S	S
Spatalia argentina (Denis & Schiffermüller)	S	S	H	H
Spatalia doerriesi Graeser	S	O	H	H
Spatalia plusiotis Oberthür	S	–	–	–
Spatalia dives Oberthür	S	S	H	H
Gluphisia crenata (Esper)	S, SP	SP	P	P
Gonoclostera timoniorum (Bremer)	SW	SW	O	PO
Pygaera timon (Hübner)	O	O	O	O
Clostera albosigma curtuloides (Erschoff)	S	S	SW	SW
Clostera pigra (Hufnagel)	S	S	SW	SW
Clostera anachoreta (Denis & Schiffermüller)	S	S	SW	SW
Clostera anastomosis (Linnaeus)	S	S	SW	SW
Micromelalopha troglodyta (Graeser)	S	S	SW	SW
Lasiocampidae				
Euthrix potatoria (Linnaeus)	S	M	M	M
Gastropacha quercifolia (Linnaeus)	S	M	M	M
Erebidae: Lymantrinae				
Teia dubia (Tauscher)	S	S	S	S
Arctornis l-nigrum (Müller)	S	S	–	M
Erebidae: Arctiinae				
Rhyparioides amurensis (Bremer)	S	S	–	S
Chionarctia nivea (Mėnėtriės)	S	S	S	SW
Noctuidae				
Egira conspicillaris (Linnaeus)	S	S	S	SW, O (partly)[2]
Calocasia coryli (Linnaeus)	S	S	S	SW

cells (*Micromelalopha*, *Clostera*, *Leucodonta*; Figs 9–11), pitted (*Gluphisia*; Figs 12, 13), or homogeneously tubercled (*Pheosia*, *Lophontosia*; Fig. 14). Most species have a consistent microsculpture similar to that of the last instar, but less distinct. In *Gonoclostera* the surface shows clearly visible small tubercles on a background of densely interlaced fibrae (Fig. 15). In *Ptilodon* species more or less distinctive tubercles can be observed on a smooth or interlaced fibrae background (Fig. 16). In most genera, the microsculpture becomes heterogeneously tubercled with large tubercles on a background of small homogeneous tubercles. It must be noted that the latter are arranged either randomly among more small tubercles (*Lophocosma*, *Pheosia*, *Spatalia*; Fig. 17) or are concentrated as separate groups (*Notodonta*, *Euhampsonia*, *Epodonta*;

[1] *Cerura erminea*: 'H, cor' refers to head sculpture of 4th instar and 'WO' to that of 5th instar.

[2] in 4th instar head microsculpture is smooth.

Fig. 18) that are more or less distinct. In some genera (*Furcula*, *Fentonia*, *Notodonta*, *Spatalia)* the microsculpture is more complex. In these groups sparsely distributed, large tubercles are found on a background of small tubercles. Sometimes the large tubercles are situated as separate groups (Fig. 19). Sometimes the tubercles are modified to form conical protrusions (*Harpyia*, *Stauropus*, *Peridea graeseri*). In *Harpyia*, conical protrusions become larger towards the apical and lateral sides of the head (Fig. 20).

In 4th and 5th instars the microsculpture is usually the same as in the preceding instar, but is expressed much more distinctly. In some genera the microsculpture changes from homogeneously tubercled to heterogeneously tubercled (*Pheosia*, *Lophontosia*, *Allodonta*, *Pterostoma sinica*, *P. griseum*). In *Gonoclostera* the microsculpture changes in 4th instar. In the background, which is the same as in 3rd instar (Fig. 15), there are large tubercles located in crateriform depressions (Fig. 21). Sometimes in 5th instar a simplification of the microsculpture takes place. For example, the head surface of *Cerura* in 1st instar is homogeneously knobby, in 2nd to 4th instars it changes to heterogeneously knobby. In 5th instar it becomes deeply wrinkled in the area of the epicranial suture, whereas towards the lateral surface it appears as homogeneously oval tubercles concentrated in somewhat separated groups.

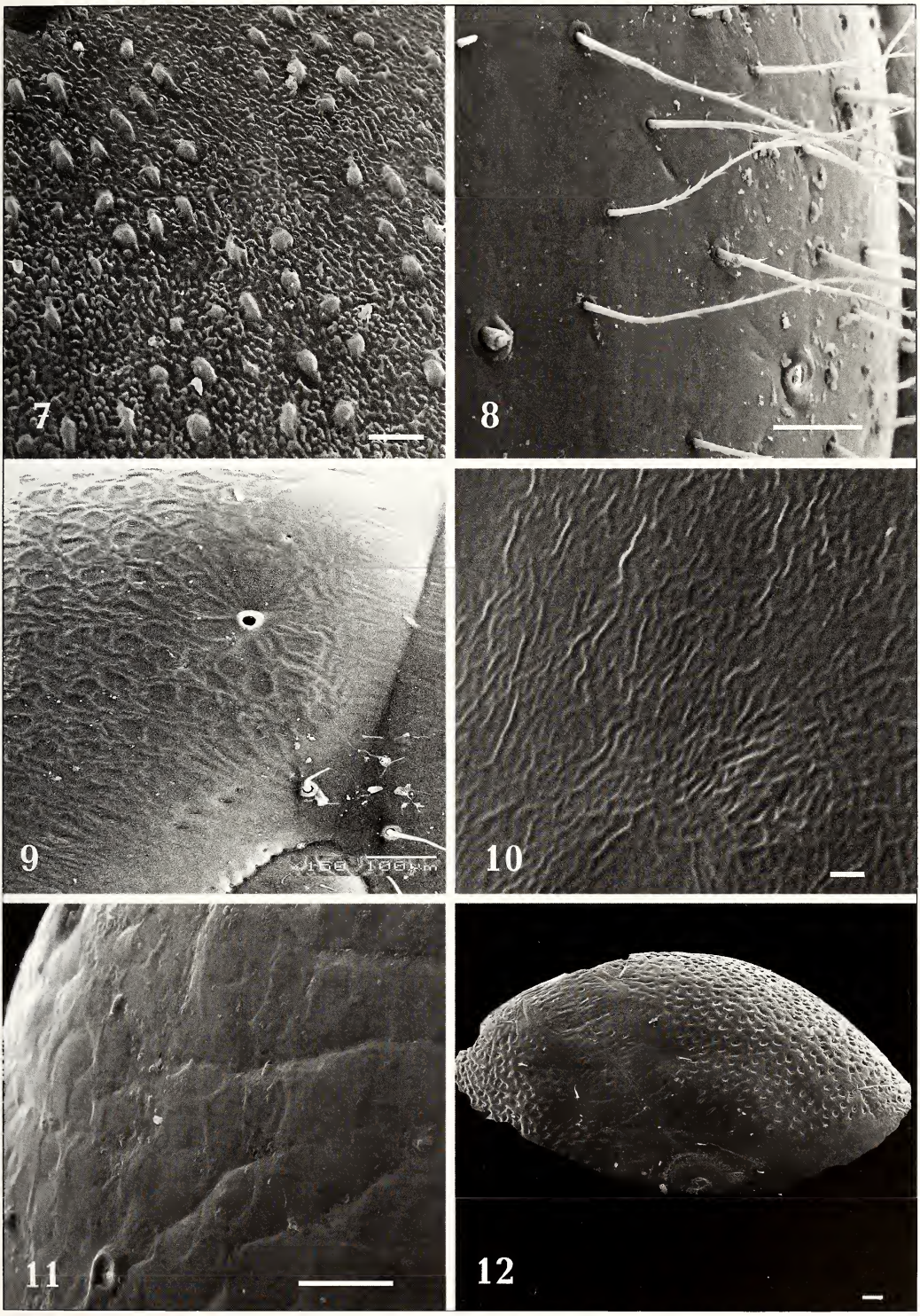
In general, the larval head microsculpture in Notodontidae may be more or less distinct. In the majority of genera it is clearly visible (*Notodonta*, *Pheosia*, *Pheosiopsis*). In *Harpyia*, *Uropyia*, and *Furcula* it is most prominent. In other notodontids (Pygaerinae) it is less prominent. Overall the most prominent microsculpture appears in 4th and 5th instars, while in 1st to 3rd instars it is usually poorly developed.

The head microsculpture is not completely homogeneous on the surface of the head capsule. In most cases it is smoother in the frontal area and around the epicranial suture (Fig. 22). In the vicinity of the stemmata and genae the microsculpture is finer, consisting of homogeneous, densely arranged tubercles (Fig. 23) and it may be more (*Stauropus*) or less expressed than elsewhere. Usually the microsculpture in 3rd to 5th instars consists of the microsculpture characteristic for the stemmatal and genal areas on which larger tubercles appear (Fig. 24).

Main Transformation Types of Head Microsculpture During Larval Development

There are 12 types of head microsculpture that occur in different instars of notodontids:

1. Head surface smooth, unmodified in all instars (*Phalera*).
2. Head surface smooth in 1st and 2nd instars, becoming weakly wrinkled with weakly developed cells in 3rd to 5th instars (*Clostera*, *Micromelalopha*).
3. Head surface smooth in 1st and 2nd instars, developing weak cells in 3rd to 5th instars (*Leucodonta*).
4. Main head surface smooth, but with pits in the apical part of the head and along the sides in 1st and 2nd instars, becoming pitted in 3rd to 5th instars (*Gluphisia*).
5. Head surface mostly smooth but wrinkled in the apical area and laterally in 1st and 2nd instars, developing somewhat expressed tubercles on a background of densely interlaced fibrae in 3rd instar, producing tubercles in crateriform depressions on a background of dense fibrae in 4th and 5th instars (*Gonoclostera*).



Figs 7–12. Larval head surface of Notodontidae. 7. 2nd instar *Furcula bifida*. 8. 3rd instar *Phalera bucephala*. 9. 3rd instar *Micromelalopha troglodyta*. 10. 3rd instar *Clostera anachoreta*. 11. 3rd instar *Leucodonta bicoloria*. 12. 3rd instar *Gluphisia crenata*. Scale bar 9, 11, 12 (100 μ); 7, 8, 10 (10 μ).

6a. Head surface smooth in 1st and 2nd instars, with large tubercles expressed only along the head margins and sparsely distributed on a smooth background in 3rd to 5th instars (*Ptilodon*).

6b. Head surface smooth in 1st and 2nd instars, with large tubercles expressed only along the head margins and sparsely distributed on a background of small tubercles in 3rd to 5th instars (*Allodonta*).

6c. Head surface smooth in 1st and 2nd instars, with large tubercles sparsely distributed on a background of densely implicated fibrae in 3rd to 5th instars (*Lophontosia*).

7. Head surface smooth in 1st and 2nd instars, with homogeneous microsculpture of small tubercles in 3rd instar, and larger tubercles on a homogeneous background of small tubercles in 4th and 5th instars (*Pterostoma sinica*, *P. griseum*). In *P. palpina* knobby microsculpture appears in 2nd instar.

8. Head surface smooth in 1st instar, with homogeneous microsculpture of small tubercles in 2nd instar, and larger tubercles on a background of homogeneous small tubercles in 3rd to 5th instars (*Euhampsonia*, *Drymonia*, *Notodonta*, *Peridea*, *Nerice*, *Lophocosma*, *Pheosiopsis*, *Shaka*, *Lophontosia*, *Hagapteryx*, *Epodonta*, *Cnethodonta*, *Stauropus*, *Pheosia*). There are some variations on this pattern. In *Pheosia* and *Stauropus* 3rd instar microsculpture is homogeneously tubercled, becoming heterogeneously tubercled only in 4th instar.

9a. Head surface smooth in 1st instar, with larger tubercles on a background of homogeneous small tubercles in 2nd to 5th instars (*Uropyia*, *Harpyia*, *Fentonia*).

9b. Head surface smooth in 1st and 2nd instars, with larger tubercles on a background of homogeneous small tubercles in 3rd to 5th instars (*Semidonta*, *Spatalia*). In *Semidonta* 3rd instar the microsculpture is only weakly expressed, becoming more distinctly visible only in 4th and 5th instars. In *Spatalia* the microsculpture appears only in 3rd instar in two species, *S. argentina* and *S. dives*, while in *S. doerriesi* it is homogeneously tubercled in 2nd instar and becomes heterogeneously tubercled in 3rd instar.

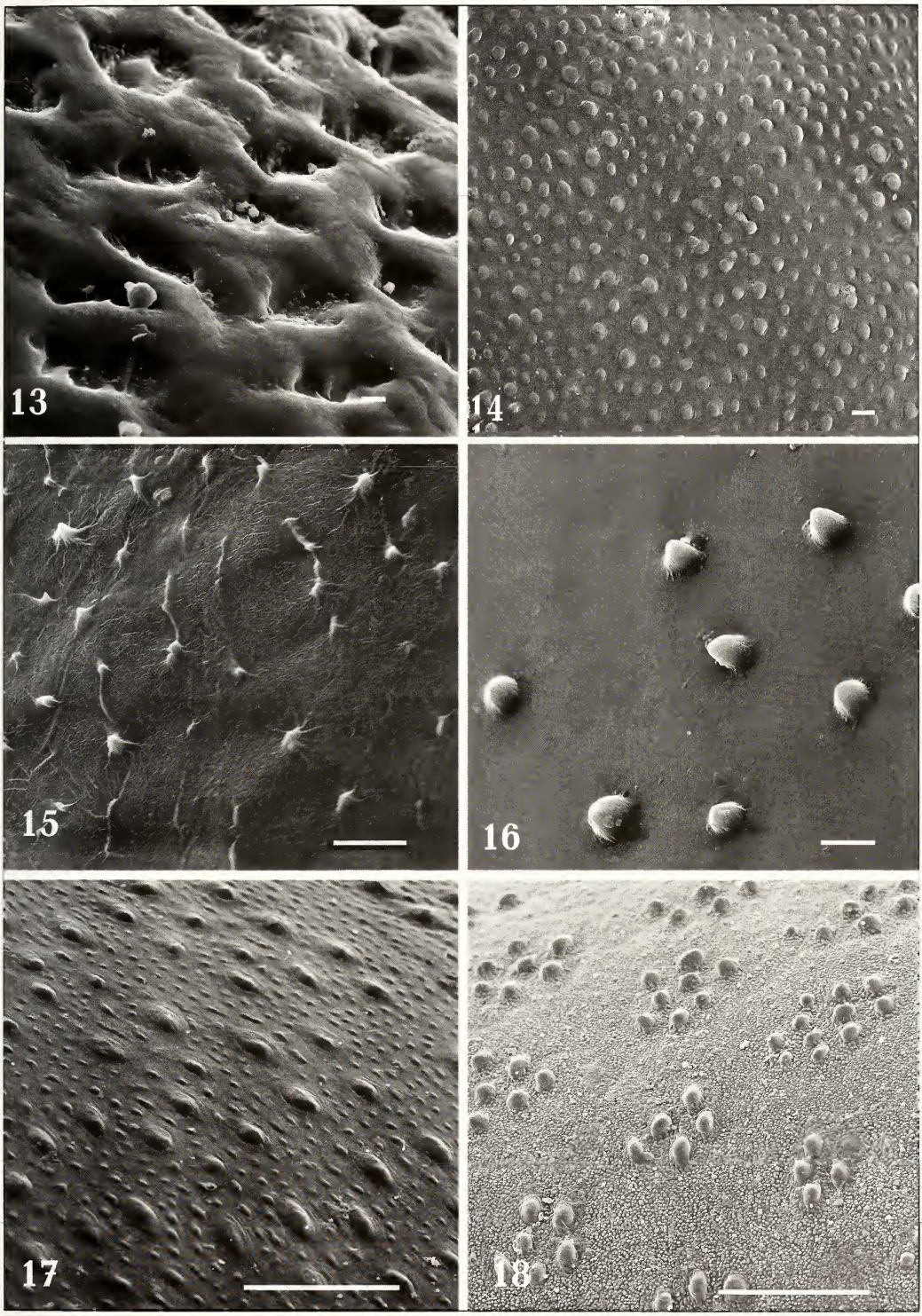
10. Head surface smooth in 1st instar, with very small, weakly expressed, homogeneously dispersed tubercles in 2nd to 5th instars (*Dicranura*).

11. Weakly expressed homogeneous microsculpture of small tubercles without transformation in all instars (*Pygaera*).

12. Distinctly expressed homogeneous microsculpture of small tubercles in 1st instar, with larger tubercles on a background of homogeneous small tubercles in 2nd to 5th instars (*Cerura*, *Furcula*).

Comparative Morphology of Larval Head Microsculpture in Other Families

It should be noted that head microsculpture is also variable in the studied outgroups, as is the case in Notodontidae. It is also modified depending on the instar. In Lasiocampidae that were examined, the head is smooth in 1st instar (*Euthrix potatoria*, *Gastropacha quercifolia*) while later (2nd to 5th instars) it develops microtrichiae (Fig. 25). One species of Lymantriinae has a smooth head in all instars (*Teia dubia*) while another (*Arctornis l-nigrum*) has microtrichia in 4th and 5th instars as in Lasiocampidae.



Figs 13–18. Larval head surface of 3rd instar Notodontidae. 13. *Gluphisia crenata*. 14. *Pheosia gnoma*. 15. *Gonoclostera timoniorum*. 16. *Ptilodon saturate hoegei*. 17. *Lophocosma atriplaga*. 18. *Notodonta dembowskii*. Scale bar 17, 18 (100 μ); 13–16 (10 μ).

In examined Arctiinae the microsculpture is either smooth in all instars (*Rhyparioides amurensis*) or slightly wrinkled in 4th and 5th instars (*Chionarctia nivea*). The head surface of the examined Noctuidae is smooth in 1st through 4th instars. In 5th instar it is weakly wrinkled in *Calocasia coryli* and *Egira conspicillaris*, with a few tubercles in *E. conspicillaris* (Fig. 26).

Discussion

Transformation of Head Microsculpture in Different Instars and Comparison with Representatives from Outgroups

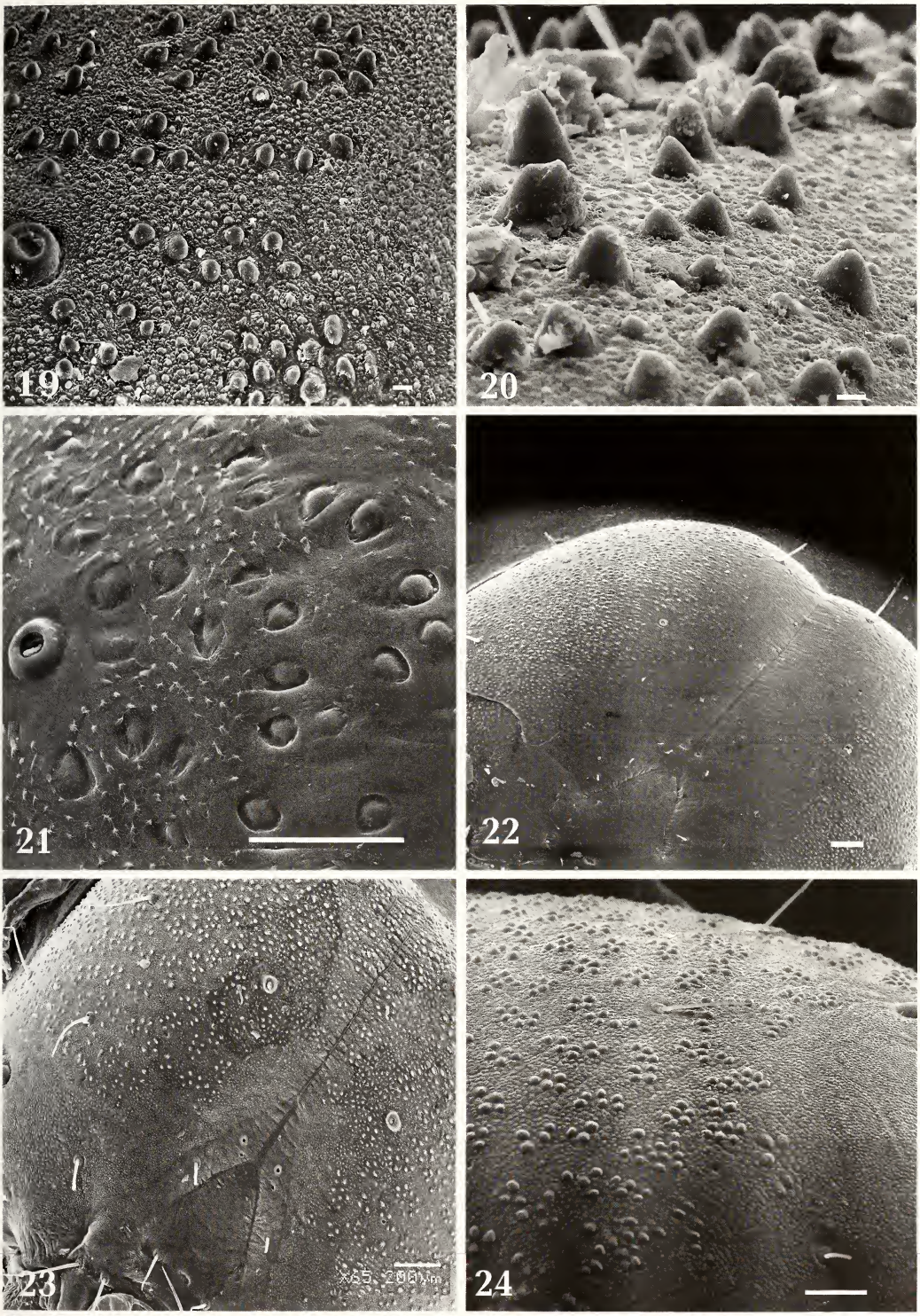
Miller (1991) defined six character states relating to the head surface in Notodontidae: "head surface mostly smooth, with fine creases" (0); "head surface rugose with rugosities in clusters" (1); "head surface covered with pits" (2); "rugosities extremely small" (3); "head surface smooth, glassy" (4); and "head surface spiculate" (5). Miller interpretated these characters as multistate nonadditive, where definite numbers (in brackets) were assigned to each state. He recognised (0) as plesiomorphic and (5) as autapomorphic for Notodontidae.

In many cases I have used the same character states as Miller, but sometimes it was necessary to redefine them. Thus, Miller's "head surface mostly smooth, with fine creases" is here described as weakly wrinkled sculpture, and "head surface rugose with rugosities in clusters" is divided into recognisable types of tuberculous microsculptures: large tubercles situated separately and randomly on a background of small tubercles, or concentrated into separate groups.

According to Miller's interpretation "head surface mostly smooth, with fine creases" is the plesiomorphic state for the family. Pitted sculpture is a derivation of the granulate head type. "Head surface smooth, glassy" in his rank of transformations precedes "head surface spiculate", which is the apomorphic state for the family. In his paper on Dioptinae, Miller (2009) noted that "a smooth, almost glassy head surface" is "a derived condition" compared with the sculpture of the so-called "pebblelike projections".

Following Miller (1991) I also consider that a spiculate sculpture is the apomorphic state for the family. However, I suggest that a weakly wrinkled microsculpture is intermediate between smooth, treated here as plesiomorphic, and tuberculous, which is secondary and more specialized in the morphological series of transformations. I also consider that a pitted sculpture is a derivation of the smooth head type. These notions are developed below.

Smooth head microsculpture in 1st instar was found in the majority of notodontid subfamilies that were examined. Since this character is also found in the examined outgroups (Erebidae: Lymantriinae and Arctiinae; Noctuidae; and Lasiocampidae), this state (smooth head) is considered plesiomorphic relative to other states. An exception is *Phalera*, which differs by having a smooth head microsculpture in each larval instar (Fig. 8), as is the case in some representatives of the outgroup (Lymantriinae,



Figs 19–24. Larval head surface of Notodontidae. **19.** 3rd instar *Furcula bifida*. **20.** 3rd instar *Harpyia milhauseri*. **21.** 4th–5th instars *Gonoclostera timoniorum*. **22.** 4th–5th instars *Spatalia argentina*. **23.** 4th–5th instars *Furcula bicuspis*. **24.** 4th–5th instars *Pterostoma griseum*. Scale bar 19, 21–24 (100 μ); 20 (10 μ).

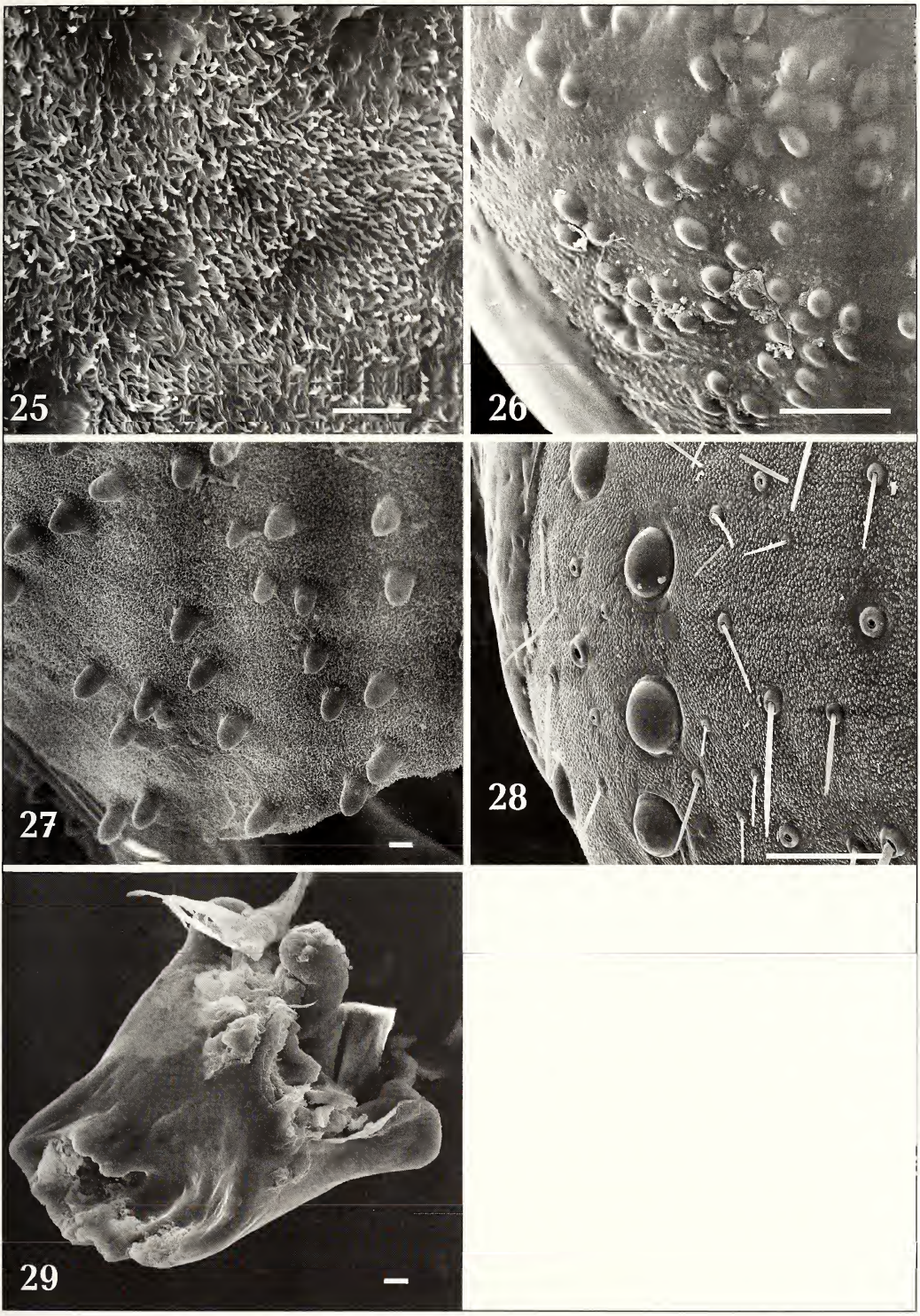
Arctiinae, Noctuidae) which have a smooth head from 1st to 3rd instar or sometimes until the last instar.

Weakly wrinkled head microsculpture in Notodontidae is present in larvae of four genera only. In *Clostera*, *Micromelalopha*, and *Leucodonta* such microsculpture appears in larvae of 3rd to 5th instars, while their larvae have a smooth head in 1st and 2nd instars. Since the representatives of the outgroups (Erebidae: Arctiinae; Noctuidae) have this kind of sculpture only in 4th and/or 5th instars, possessing smooth larval head in 1st to 3rd or 4th instars, the wrinkled microsculpture is considered a derived state (apomorphic). In *Gonoclostera* this type of microsculpture is present only in 1st and 2nd instars (Fig. 3) and is displaced by tubercles in 3rd to 5th instars. Wrinkled microsculpture is considered plesiomorphic relative to tuberculous microsculpture.

Tuberculous head microsculpture was found in the majority of the examined notodontid genera in 2nd to 5th instars, with them having a smooth head in 1st instar. In *Pygaera* such microsculpture is present in all instars. Tuberculous microsculpture is found in the examined outgroups only in 5th instar in *Egira conspicillaris* (Noctuidae), where it is present only in the apical part of the head, whereas in 1st to 4th instars the microsculpture is smooth. Since the majority of notodontid genera have this kind of microsculpture in 2nd to 5th instars, possessing smooth larval head in 1st instar, and since this character is absent in the outgroups (except for *Egira conspicillaris*), the tuberculous microsculpture is considered a derived state. There are several kinds of tuberculous head microsculptures in the studied larvae. The microsculpture with almost indistinct, very small, homogeneous tubercles (*Pygaera*, *Dicranura*; Fig. 28) is considered plesiomorphic. The microsculpture with large, uniform tubercles on a smooth or fibrous surface (*Ptilodon*; Fig. 16) either with tubercles situated randomly on a background of small tubercles (*Spatalia*, *Lophocosma*; Fig. 17), or concentrated in separate groups (*Notodonta*, *Euhampsonia*, *Epodonta*, and some others; Fig. 18) is presumably derived. A further derived state would be a microsculpture with conical projections in groups (*Harpyia*, *Uropyia*, *Stauropus*; Fig. 20).

Pitted head microsculpture in 1st instar is found only in *Gluphisia*. It is also present in 2nd instar and is found in the apical part of the head only, while the rest of the head capsule remains smooth. In later instars the pitted microsculpture extends across the remaining head surface (Figs 12, 13). Based on these observations it appears that such sculpture is secondary relative to the smooth one, and, probably, derived from the latter. The pitted microsculpture has not been observed in any other notodontids or outgroups. However, according to Miller (1991) such sculpture is characteristic for *Datana ministra* (Drury) of the American genus *Datana* Walker, Therefore, pitted microsculpture in *Gluphisia*, on the basis of this study, can be considered as a synapomorphy for these two genera.

Summarizing, the smooth head microsculpture in larvae of different noctuoid families could be treated as a plesiomorphic state. According to a comparative morphological study, the general tendency in its evolutionary transformation within Notodontidae (same as in other families of Noctuoidea) is changing towards a sculptured surface, at first with small-sized and finally large-sized sculptural elements.



Figs 25–29. Larval head surface. **25.** 4th–5th instars *Euthrix potatoria*. **26.** 5th instar *Egira conspicillaris*. **27.** 4th–5th instars *Uropyia meticulodina*. **28.** *Dicranura ulmi*. **29.** Oral surface of left mandible of 2nd instar *Leucodonta bicoloria*. Scale bar 26 (100 µ); 25, 27–29 (10 µ).

Phylogenetic Implications Within Genera

Head microsculpture can be also used for resolving phylogenetic relationships within genera. This is important as there has been insufficient work on this problem in Notodontidae. In *Peridea* the most complex microsculpture is recorded in *P. graeseri*, where tubercles are modified into conical projections. *In P. anceps*, *P. lativitta*, *P. elzet*, *P. gigantea*, *P. oberthueri*, and *P. moltrechti* the microsculpture appears as clearly visible oval tubercles. Based on these results it appears that *P. graeseri* possesses the most derived state of this character. The peculiarities of the head pattern (Dolinskaya 2009) corroborate this hypothesis.

In *Pterostoma*, in addition to the morphological similarity of the various species, the transformation of the microsculpture changes from a simple to a complex one. Thus, in 2nd instars of *P. palpina* the microsculpture is already homogeneously tubercled, whereas in *P. griseum* and *P. sinicum* it is smooth. In 3rd instar, the microsculpture of *P. palpina* becomes heterogeneously tubercled and distinct. In *P. griseum* and *P. sinicum* the microsculpture changes only to homogeneously tubercled. In *P. griseum* the sculpture is very well expressed and distinctive while in *P. sinicum* it is poorly expressed. In 4th and 5th instars the microsculpture of *P. palpina* and *P. griseum* becomes similar: large tubercles concentrated in distinct groups on a background of small ones, while in *P. sinicum* these groups are poorly expressed. Based on these results it appears that *P. palpina* possesses the more derived states of these characters, while *P. sinicum* has the less derived ones. *P. griseum* has an intermediate position between these two species. It should be noted that the morphological characters of the pupa support this hypothesis. The sculpture of the cremaster in *P. griseum* and *P. palpina* is very similar, and it is different in *P. sinicum* (Dolinskaya 1984, 1989).

In *Ptilodon* in addition to the morphological similarity of some species, a transformation of the microsculpture from simple to conical takes place. In *P. capucina* and *P. saturate hoegei* weakly expressed tubercles are randomly located on a smooth surface, while in *P. cucullina* these tubercles are placed on a background of densely implicated fibrae. In *P. ladislai* the latter are concentrated in weakly expressed groups. Based on these observations it appears that *P. ladislai* possesses a more derived states of this character, and *P. capucina* and *P. saturate hoegei* the less derived one, while *P. cucullina* appears to be intermediate.

In *Spatalia,* a transformation of microsculpture from simple to complex takes place. In 2nd instar of *S. doerriesi* the microsculpture appears weakly expressed and homogeneously tubercled while in *S. argentina* and *S. dives* it remains smooth. In 3rd to 5th instars the microsculpture of *S. argentina* appears as small and large oval tubercles arranged on a smooth background. In *S. dives* and *S. doerriesi* the microsculpture is more complex: on a background of small tubercles there are randomly located medium-sized and large tubercles, the latter with plicated edges and sometimes concentrated in poorly defined groups. Based on these observations, *S. doerriesi* appears to possess a more derived state of this character than *S. argentina*, with *S. dives* being intermediate.

The Importance of Larval Head Microsculpture for the Classification of Notodontidae

At present the classification of Notodontidae is in need of improvement. In the systems proposed by different authors the number of subfamilies within the family, as well as the number and generic composition of subfamilies remains uncertain. The most recent classifications are those of Tikhomirov (1981), Miller (1991), and Schintlmeister (2008). Below I discuss the implications of the results presented herein for the classification of the family.

Slightly visible head microsculpture in each larval instar is present in only eight genera. It is either smooth (*Phalera*), weakly wrinkled, looking like weakly expressed cells (*Clostera*, *Micromelalopha*, *Leucodonta*), very small, densely located homogeneous tubercles (*Dicranura*, *Pygaera*), tubercles placed in crateriform depressions (*Gonoclostera*) or pitted (*Gluphisia*). Concerning the genera *Clostera*, *Micromelalopha*, *Gonoclostera*, and *Pygaera* these data coincide with the classifications of the three above-mentioned authors, placing them into the subfamily Pygaerinae. This hypothesis is also supported by an examination of the larval mandible (Dolinskaya 2008).

In Pygaerinae a gradual development of the microsculpture takes place from weakly wrinkled to small-tubercled. In *Micromelalopha* and *Clostera* the head microsculpture remains weakly formed. In 1st and 2nd instars it is smooth, while in 3rd to 5th instars it is already weakly wrinkled or appears as indistinct homogeneous cells (Figs 9, 10). In *Gonoclostera* in 1st and 2nd instars the microsculpture is also smooth; however, apically and also partly laterally it becomes wrinkled (Fig. 3). In 3rd instar the surface appears as small, densely implicated fibrae on a background of weakly expressed, very small tubercles (Fig. 15). In 4th and 5th instars large tubercles are formed, arranged in crateriform depressions on a background of smaller tubercles (Fig. 21). This is likely a transitional state from wrinkled to tubercled microsculpture. In *Pygaera* the microsculpture appears as very small, weakly expressed, densely situated homogeneous tubercles in all instars. This character is considered apomorphic relative to the above-mentioned representatives of subfamily Pygaerinae. Based on these results, as well as an examination of the outgroups, it would appear that the most primitive microsculpture is found in *Clostera* and *Micromelalopha*. Head microsculpture of *Pygaera* and *Gonoclostera* is more derived.

In *Dicranura* in 1st instar the head microsculpture is smooth, and in 2nd to 5th instars it appears as very small, weakly expressed, densely situated homogeneous tubercles as in *Pygaera* (Fig. 28). This character along with mandibular structure (Dolinskaya 2008) supports the close affinity of *Dicranura* to Pygaerinae. Schintlmeister (2008) placed *Dicranura* in Dicranurinae together with *Stauropus*, *Cnethodonta*, and *Harpyia*. However, later in a personal communication he agreed with the conclusions published by Dolinskaya (2008) and acknowledged the need to clarify the taxonomic status of *Dicranura*.

Leucodonta needs additional examination. Tikhomirov (1981) and Schintlmeister (2008) placed it within Notodontinae. The results of this study show that the head

microsculpture of *Leucodonta* is similar to that of *Clostera* and *Micromelalopha*. It shares the same character states as the above genera, namely having smooth microsculpture in 1st and 2nd instars, while in 3rd to 5th instars it appears as almost indistinct cells (Fig. 11). These observations support the placement of *Leucodonta* in Pygaerinae. This hypothesis is augmented by the peculiarities of mandibular structures. A detailed examination of the mandibles using SEM showed the presence of a denticulated mandibular edge and a large retinaculum in 2nd instar (Fig. 29) as is found in *Clostera*, *Gonoclostera*, and *Micromelalopha* (Dolinskaya 2008).

The position of the genus *Gluphisia* within Notodontidae is anomalous. Tikhomirov (1981) placed it within Notodontinae. Miller (1991) also included *Gluphisia* within this subfamily, placing it in Notodontini along with *Cerura* and *Furcula*. Schintlmeister (2008) assigned *Gluphisia* to Pygaerinae. The peculiarities of the pupa and larval mandibles (Dolinskaya 1986, 1989, 2008) corroborate the opinion of Schintlmeister (2008). However, the characters of the larval head surface are not concordant with this hypothesis. Head microsculpture in *Gluphisia* is represented as distinct pits (Figs 12, 13). Such microsculpture is not found in either the ingroup or the examined outgroups. According to Miller (1991), pitted head microsculpture is characteristic for *Datana* (Phalerinae). Therefore it is necessary to carry out a more detailed examination of other taxa to clarify the systematic position of this genus.

The uncertainty of the systematic position of *Phalera* remains. Tikhomirov (1981) included this genus in Notodontinae. Miller (1991) placed *Phalera* in Phalerinae along with *Datana*, *Peridea*, and *Euhampsonia*. Schintlmeister (2008) also included this genus in Phalerinae together with *Phalerodonta*. Unfortunately I was not able to study the larval head microsculpture of *Phalerodonta*. The results of my studies show that in *Phalera* the head microsculpture is smooth in each instar (Fig. 8). The same type of microsculpture in 4th and 5th instars is absent in the rest of the notodontids examined. On the other hand, Miller (1991) noted the presence of 'extremely smooth, almost glassy, head surface' in some *Josia* Hübner and *Cyanotricha* Prout (Dioptinae), and *Didugua* Druce (Nystaleinae). At a later time Miller (2009) noted that this head surface of the final instar is unique for Josiini (Dioptinae). In addition to that Miller (1991), following Gardner (1943), noted that *Phalera* larvae have a pitted surface. However, my results do not support this hypothesis and hence the taxonomic position of this genus should be investigated further.

The majority of the genera in the family have a clearly visible and mainly heterogenously tubercled head microsculpture. Such microsculpture is present in 26 genera, namely *Euhampsonia*, *Cerura*, *Furcula*, *Uropyia*, *Harpyia*, *Stauropus*, *Cnethodonta*, *Fentonia*, *Neopheosia*, *Drymonia*, *Notodonta*, *Peridea*, *Nerice*, *Pheosia*, *Lophocosma*, *Pheosiopsis*, *Shaka*, *Pterostoma*, *Ptilodon*, *Lophontosia*, *Allodonta*, *Hagapteryx*, *Togepteryx*, *Semidonta*, *Epodonta*, and *Spatalia*. *Ptilodon* and *Allodonta* differ from these genera by having the most smoothened microsculpture. The head capsule is smooth medially, with microsculpture expressed only along the head margins. These data partially support the hypothesis of Schintlmeister (2008), who placed *Ptilodon* and *Allodonta* within Ptilodontinae together with *Pterostoma*, *Semidonta*, *Lophontosia*, and *Epodonta*. In these genera there is a tendency towards smooth head microsculpture (Table 1).

In *Cerura* and *Furcula* the head microsculpture is distinctive, being tubercled in 1st instar (Fig. 4). I treat this character state as apomorphic because most representatives of the ingroup as well as all of the examined outgroups have smooth microsculpture in 1st instar. These findings coincide with the systems of Tikhomirov (1981) and Schintlmeister (2008), who separated these genera into the subfamily Cerurinae. Miller (1991) included these genera within Notodontinae together with *Gluphisia*, *Pheosia*, and *Notodonta*. This arrangement is not supported by the results of this study.

In *Cerura*, *Furcula*, *Uropyia*, *Harpyia*, and *Fentonia* the head microsculpture is heterogeneously granulated in 2nd instar, with large tubercles on a background of small tubercles (Figs 6, 27). These findings partly coincide with the point of view of Schintlmeister (2008) in including *Uropyia*, *Harpyia*, and *Fentonia* within Dicranurinae.

Conclusions

Larval head microsculpture can provide useful phylogenetic information within and between genera. Similar types of larval head surface structures support monophyly of a number of groups of genera. Comparative morphological examinations of the larval head microsculpture can be used to determine the direction of morphological transformations. More derived taxa have a more complex microsculpture. For more generalized groups smooth or similar types of the larval head capsule surface are characteristic. Among these characters I have identified notodontid apomorphies (tubercled head microsculpture), as well as apomorphies that are characteristic for various other taxa in the family: 1) presence of tubercled microsculpture in 1st instar (*Cerura*, *Furcula*, *Pygaera*); 2) presence of heterogeneous microsculpture in 2nd instar (*Cerura*, *Furcula*, *Uropyia*, *Harpyia*, and *Fentonia*); and 3) development of conical projections on the head (*Harpyia*, *Uropyia*, *Stauropus*).

It is worth noting that it is possible to determine the larval instar according to head microsculpture. This additional diagnostic character can be used for genera and species together with such characters as the width of the head capsule and the larval head pattern (Dolinskaya 2009). On the basis of peculiarities of the head microsculpture it is also possible to estimate the degree of morphological similarity of species within the polytypic genera.

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